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A STUDY OF THE PSEUDORTHOCERATIDAE (NAUTLOIDEA)

A dissertation submitted to the

Graduate School
of the University of Cincinnati

in partial fulfillment of the
requirements for the degree of

DOCTOR OF PHILOSOPHY

1939

by

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II

A. B. Cornell University, 1934

A. M. Cornell University, 1935

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PART I
MORPHOLOGY OF THE NAUTILOID SHELL WITH SPECIAL
REFERENCE TO THE PSEUDORTHOCERATIDAE

I GROSS FEATURES OF THE SHELL

The Wall of the Conch

The exterior of the shell wall of the Pseudorthoceratidae shows no unusual features. The surface markings are not different from those found in other cephalopods. Addition to the shell occurs very largely at the aperture, and for that reason the form of the aperture is retained on the surface in the form of lines of growth. This is frequently significant, for it reveals that in some instances the hyponomic sinus was present throughout life, while in other instances it was developed only in the late ephebic and gerontic stages.

Thin sections of various fossil Nautiloidea have thus far failed to show differentiation of shell layers in the wall of the conch, but this is doubtless due to alteration by replacement of the original shell material. Three layers are known in Nautilus. An outer porcellaneous layer is followed by a prismatic layer which is about three times as thick as the porcellaneous layer. The inner layer consists of a thin nacreous film. Judging from the amount of variation in recent molluscs in the texture and thickness of the shell layers it is safe to

assume that similar variation must have occurred in fossil Nautiloidea.

A constriction of the interior of the gerontic living chamber is an important feature of most orthoceracones. It is suspected that this constriction is produced by a thickening of the inner nacreous film, for that is the only shell layer known to be produced proximad of the tip of the mantle lobe. The location of the gerontic constriction and its form are important specific criteria in orthoceracones.

Other markings of the interior of the shell are concerned with the attachment of the soft parts. Nautilus possesses a pair of lateral shell muscles which produce crescent shaped ridges on the sides of the living chamber. Muscle scars have been noted in a few Paleozoic nautilicones, but have not yet been recognized in orthoceracones. In addition to the muscle scars, Nautilus possesses three aponeurotic bands,¹ one dorsal and two

1. Miller, A.K., Dunbar, C.O. and Condra, G.E., The nautiloid cephalopods of the Pennsylvanian system of the mid-continent region, Nebraska Geol. Surv., ser. 2, bull. 9, 1933, p. 32.

ventral. The dorsal bands are without a counterpart in fossil Nautiloidea, but the entire area subtended by the ventral bands is represented in fossil forms by a conchial

furrow, which is discussed below.

The Septa

The septa are the partitions which characterize most cephalopod shells and serve to distinguish the chambered portion, or phragmocone, from the adoral unchambered portion, the living chamber. It has been generally known that the septa are secreted by the posterior surface of the visceral mass. It has been suspected for some time from the lack of fossil or recent nautiloid shells showing incomplete septa that deposition was rapid, but only recently has this been confirmed by direct observation. Pruvot-Fol² noted that in Nautilus.

2. Pruvot-Fol, A., Remarques sur le Nautille, C.R. XII^e Congress International de Zoologie, Lisbonne, 1935, pp. 1652-1664, Lisboa, 1937.

forward progression in the shell is gradual, but that septation is sudden and discontinuous.

Three parts of the septum have been recognized by Teichert³, (Fig.1.). The free part of the septum divides

3. Teichert, C., Der Bau der ammonitoiden Cephalopoden, Paleontographica, Bd. 78, Abt. A, 1933, pp. 117-119, figs. 1-2.

the conch into camerae, and is properly that part of the septum which is not in contact with any other shell structure.

Secondarily, however, it may become incorporated in the siphuncle. The mural part of the septum extends orad of the free part of the septum with which it is continuous, to the next succeeding septum. (Fig. 1.) The point at which the siphon pierces the septum is referred to as the septal foramen, and at this point the septum extends apicad around the siphon for some distance. This portion of the septum has long been known as the septal neck. Upon its form depends the major divisions of the Nautiloidea proposed by Hyatt⁴.

4. Hyatt, A., Cephalopoda, in Zittel-Eastmann Textbook of Paleontology, 1st. ed., vol. 1, pp. 586-615, 1900.

LONGITUDINAL FURROWS OF THE INTERIOR OF THE SHELL

1. The Two Types of Furrows

The internal molds of many cephalopods bear longitudinal carinae which are the reflections of grooves on the interior of the shell. As carinae or ridges these have been described by various investigators⁵, and have

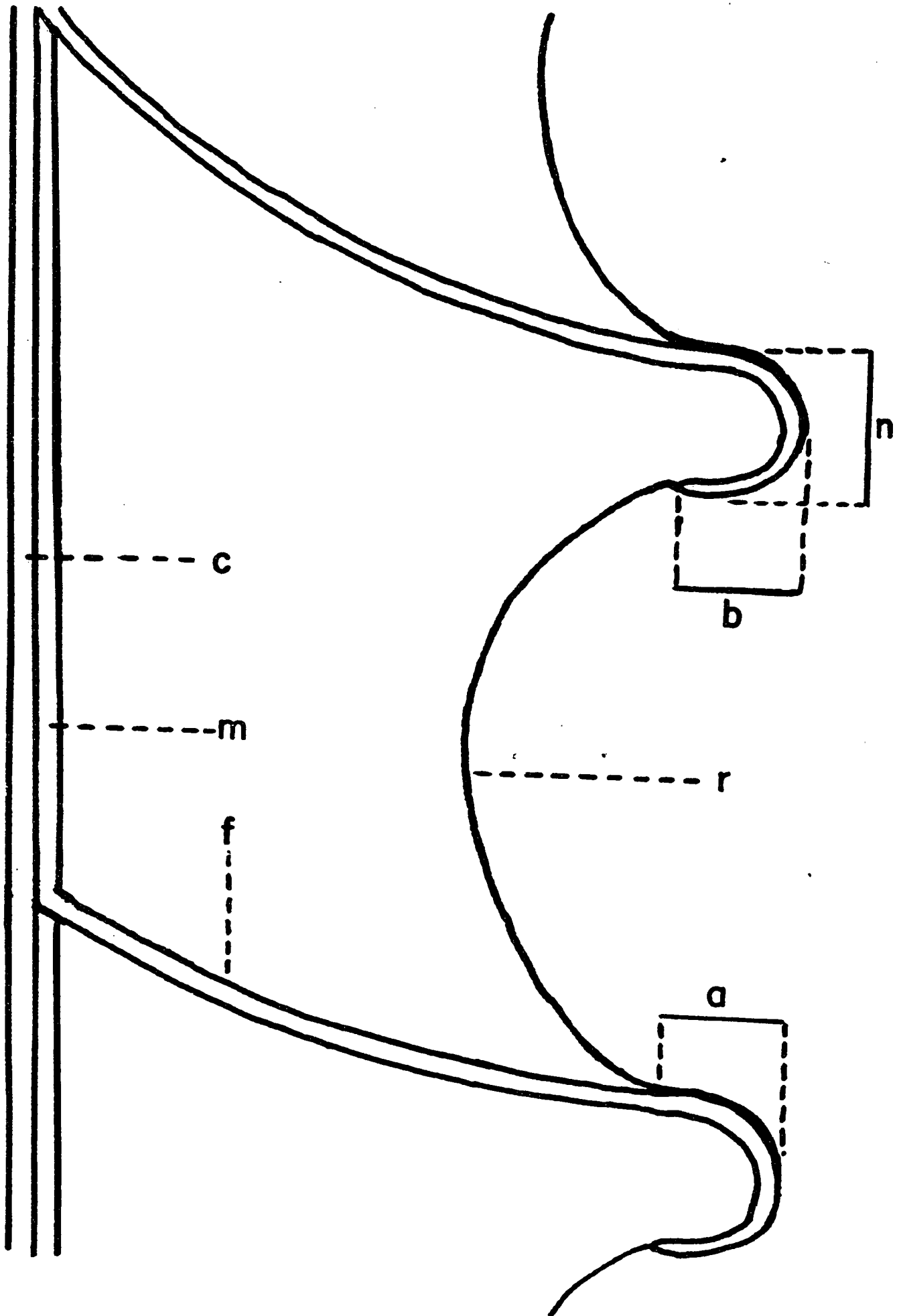
5. Hall, J., Paleontology of New York, vol. 5, pt. 2, 1879, pp. 240, 248, 250, 278, 287.

been variously interpreted. Flower⁶ pointed out that two

6. Flower, R.H., Cherry Valley cephalopods, Bull. Amer.

Fig. 1. Essential structural features of the
phragmocone

- c.- wall of conch
- m.- mural part of septum
- f.- free part of septum
- n.- septal neck
- b.- brim
- a.- area of adnation
- r.- connecting ring.



Paleont., vol. 22, 1936, p. 268.

distinct types of structure are involved, a continuous ventral "carina", which extends well into the living chamber, and a dorsal "carina" which is a metamerically repeated structure found on the mid-dorsal region of each camera. This is the "false siphuncle" at least in part of various authors. Miller, Dunbar and Condra⁷ stated

7. Miller, A.K., Dunbar, C.O. and Condra, G.E., The nautiloid cephalopods of the Pennsylvanian system of the mid-continent region, 1933, Nebraska Geol. Surv., ser. 2, bull. 9, p. 80.

that the structure appeared to be connected with the accumulation of globules of limonite in the upper side of the shell as it lay in the matrix, and considered it an inorganic phenomenon.

It is necessary to distinguish between the dorsal and ventral carinae. Failure to do so in the past has lead to some errors. Hall compared the dorsal furrow of Dolorthoceras tersum with the ventral furrow of Striacoceras typus (Saemann) (= Orthoceras marcellense Hall) and as a result described D. tersum upside down. Loomis⁸

8. Loomis, F.B., The dwarf fauna of the pyrite layer at the horizon of the Tully limestone in western New York. New York State Museum Bull. 69, 1903, p. 916, pl. 4, fig. 12-13.

8

mistook the dorsal furrow for a marginal siphuncle and as a result described a Michelinoceras as a Bactrites. The types were broken in such a way that the septum and the true siphuncle were not exposed. Additional material shows that the specimen figured by Loomis as Bactrites sp. mut. pygmaeus is probably not distinct from his Orthoceras subulatum Conrad mut. pygmaeum Loomis.

The ventral and dorsal furrows are very different in origin, structure and probably in function, and for that reason are best discussed separately. To prevent the possibility of confusing the very different structures it has seemed best to express the fundamental differences between the furrows by giving them rather distinct names. The continuous ventral furrow is called the conchial furrow. The name septal furrow is proposed for the dorsal structure.

In every instance in which a check has been possible it has been found that the conchial furrow is in line with the hyponomic sinus and is therefore mid-ventral in position. The septal furrow occurs on the opposite side on the mid-dorsal region. It may be noted further that the cameral deposits are concentrated ventrally, and I have found the three criteria of hyponomic sinus, shell furrows and the orientation of deposits to be reliable criteria for the orientation of the conch. It has been possible to demonstrate in numerous instances that neither the dorsal

nor the ventral furrows are connected with the orientation of the conch in the sediments. A circular orthoceracone with cameral deposits concentrated ventrally will normally come to lie with the venter below and the dorsum above. Such specimens alone would suggest an inorganic origin for the furrows. However, by noting in the field the position of the conch in the sediments it has been possible to demonstrate that the orientation of the conch in the sediments has no bearing on the position of the furrows. This discordance has been especially striking in the writer's experience while collecting the abundant orthoceracones which occur in a limestone at the top of the Pompey member of the Devonian (Hamilton group, Skanneateles formation,) of central New York. The discordance is further illustrated by Euloxoceras of the Pennsylvanian, which shows furrows on the dorsum and venter, although the strongly compressed shells of this genus are commonly found resting on a lateral surface.

2. The Conchial Furrow

The interior of the shell of many cephalopods bears a single mid-ventral conchial furrow. The structure is a widespread feature in the Nautiloidea, although it is rarely mentioned in descriptions. It is rarely seen as a furrow, but is frequently and readily observed as a ridge on the internal mold.

The conchial furrow is often best seen on the phragmocone but in several instances it has been possible to trace it nearly to the aperture of the living chamber. This shows that it is a feature of the inner surface of the wall of the conch, and not of the mural part of the septum. On the phragmocone the mural part of the septum appears to be of uniform thickness and to follow the slight emargination produced by the conchial furrow in the shell wall. Thus the conchial furrow may be preserved whether separation occurs between shell and matrix, or as sometimes happens, between the wall of the conch and the mural part of the septum.

It is probable that the conchial furrow is to be correlated with the entire area subtended by the pair of ventral aponeurotic bands of Nautilus.

Miller Dunbar and Condra⁹ noted that the aponeurotic

9. Miller, A.K., Dunbar, C.O. and Condra G.E., The Nautiloid cephalopods of the Pennsylvanian system of the mid-continent region, Nebraska Geol. Surv., ser. 2 Bull. 9, 1933, p. 32.

bands and the area of attachment between them had scarcely any relief, and that traces of the structures could be expected only in perfectly preserved specimens. In mature specimens of *Nautilus* it is often very difficult to determine the exact limits of the aponeurotic bands

which are often faint. Also, in some specimens there can be seen faint longitudinal markings which appear to be internal relics of longitudinal shell markings, and which have nothing to do with shell attachment. The presence of such markings makes the recognition of the aponeurotic bands almost impossible in some specimens. However there is indication that in immature specimens the aponeurotic bands are much clearer and more closely spaced than in the adults. In a specimen in which the whorl has a width of 87 mm. and a height from the impressed zone of 79 mm. the aponeurotic bands subtend a width of about 13 mm. but lie in a longitudinal polished band 25 mm. in width. In an immature individual where the whorl has a width of 45 mm. and a height of 34 mm., the bands are very clearly marked and encompass a width of only 1.5 mm. The increased clarity of the bands in the early stage may not be constant, as only a single immature individual was available for study. However it is significant that the bands are very close together in the earlier whorls of Nautilus, and present an appearance very similar to the conchial furrow of fossil forms.

The wide distribution of the conchial furrow in Nautiloidea, comprising a series of ellipchoanitic forms ranging from Ordovician to Tertiary, offers further substantiation for the correlation of that structure with the ventral aponeurotic bands of Nautilus. It occurs in

a wide variety of orthochoanitic genera, both straight and coiled, but appears to be absent in most cyrtchoanitic forms. Among the cyrtchoanites the Pseudorthoceratidae are a notable exception. It has been noted in Dolorthoceras, Adnatoceras, Pseudorthoceras and Mooreoceras. It is present in Euloxoceras, though it is difficult to distinguish there because of faint longitudinal ridges of the ornament which form as longitudinal ridges on the interior. In other genera it is either obscure by the ornament or not preserved on specimens known thus far owing to the coarse texture of the matrix. It is widely present in orthochoanitic orthoceracones, being well developed in Michelinoceras and Geisonoceras. Thus far I have been unable to detect any trace of the structure in orthochoanitic orthoceracones of the Chazy or Trenton limestones of the Ordovician, but the structure is not confined to forms occurring in the later part of the Paleozoic, for it is well developed on "Ooceras" perkinsi Ruedemann of the Chazy limestone, a cyrtchoanitic form of doubtful affinities but possibly related to the Stereoplasmodoceratidae.

Among coiled cephalopods it is of relatively common occurrence, though the genera on which it has thus far been observed make up a rather heterogeneous assemblage. It has been so far observed in Nephriticeras, Centroceras and Tetranodoceras of the Devonian, in Metacoceras, Titanoceras, Coelogasteroceras, Domatoceras and

Solenoccheilus of the Pennsylvanian, Cymatoceras and Eutrephoceras of the Cretaceous and Hercoglossa of the Eocene.

The genus Striacoceras Flower of the Devonian is unique as far as is known at present in possessing a pair of ventro-lateral furrows in addition to the usual mid-ventral furrow.

The conchial furrow is normally very shallow, and it is not uncommon to find it so obscurely preserved that it cannot be photographed from whitened specimens. It is rather variable within the species, as was shown in a large series of Striacoceras typus. The structure has not been observed on any specimens from coarse sandstones, and it appears that a limestone sufficiently fine grained that internal molds from it present a polished surface is the best medium for its preservation. The conchial furrow has been noted in Devonian and Pennsylvanian specimens preserved under such conditions, but under different conditions the same genera and often the same species may show no trace of the structure.

3. The Septal Furrow

The septal furrow occupies the mid-dorsal region of the conch. Unlike the conchial furrow it is not continuous, but is repeated on the mural part of each septum including the last. As a consequence, it can be seen on the base of the living chamber, but only on the extreme basal part

where the mural part of the last septum is developed. This is sufficient to indicate that the furrow is a structure of the mural part of the septum rather than of the wall of the conch.

The septal furrow is fairly constant in form. It is typically seen as a groove on the interior of the shell and a ridge on the internal mold. It is essentially linear. The adoral end extends nearly to the adoral suture, but is narrowly separated from it in well preserved specimens. The furrow typically extends apicad for the greater part of the length of the camera, always terminating, however, before the free part of the septum is attained. Occasionally it is short, extending barely apicad of the middle of the camera. This condition is typical of "Orthoceras" pelops Hall of the Schoharie grit of the Middle Devonian.

Three types of preservation have been found. The first, and commonest is that discussed above, in which a ridge on the internal mold fits into a groove on the interior of the shell. On such specimens the groove and ridge are regular and present smooth surfaces. A second type is one in which the condition is reversed, and a ridge on the interior of the shell fits into a groove of the internal mold. In such instances the crest of the ridge and the bottom of the groove are rough, suggesting that there was no original shell surface there to facilitate

a smooth separation.

A third type, one which has been observed only in pyritized specimens, is one in which the whole dorsal surface of both the interior of the shell and internal mold is smooth. The septal furrow is level with the rest of the surface. In most specimens it is outlined by a faint suture. In a few specimens, however, it appears only as a variation in color, evidently a phenomenon of weathering.

Thin cross sections of the conch have so far failed to show any trace of the structure, but its nature can be ascertained both by the preservation of the fossil forms and the existence of a similar structure in Nautilus, which has largely escaped notice.

In Nautilus it can be clearly seen that this area is one in which the mural part of the septum is not developed. In the first whorl the furrow occupies nearly the entire length of the dorsal wall of the camera, but it becomes shortened rapidly so that in the last half whorl of a mature individual the furrow is confined to the adoral third of the mural part of the septum. The function of this peculiar structure is not known. Obviously it has to do with the structure of the posterior mantle which secretes the septa, but further than that it is not possible to go at present. Probably an investigation of the structure in Nautilus in relation to the soft parts may yield a solution.

The mode of preservation of fossil forms shows that there, as in Nautilus, the structure represents a region in which the mural part of the septum is not developed. To demonstrate this it is necessary first to consider the different types of preservation individually. The so-called internal mold is not always a true internal mold in the Nautiloidea, because separation may occur not only between the shell and the matrix, but also between the mural part of the septum and the wall of the conch. This fact has not been generally recognized. Quite commonly an internal mold, particularly a limestone, will show two layers of separation along the phragmocone, with sutures visible at each level. In some specimens from the Cherry Valley limestone weathering was such that it was sometimes possible to separate the mural part of the septum from an apparent internal mold. Occasionally apparent internal molds, when sectioned, show traces of the mural part of the septum.

Typical specimens from the Schoharie grit of the Middle Devonian are true internal molds, all original shell material being dissolved away. In such specimens the matrix rises dorsally to form a well defined carina, showing conclusively that there was no shell material at the level of the inner surface of the mural part of the septum. Such a condition is shown in fig. 2B.

When the groove is on the internal mold and the carina is on the interior of the shell separation of two kinds

Fig. 2. Diagramatic sections through the dorsal wall of the conch, showing the septal furrow.

C.- wall of conch; s.- mural part of septum

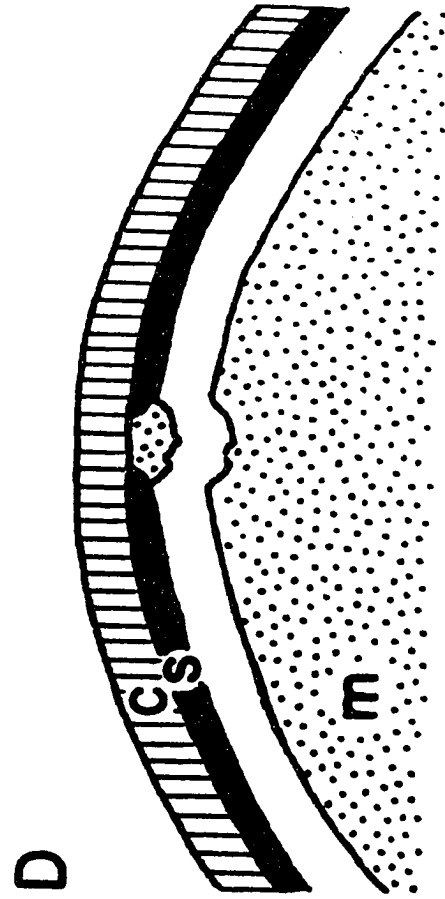
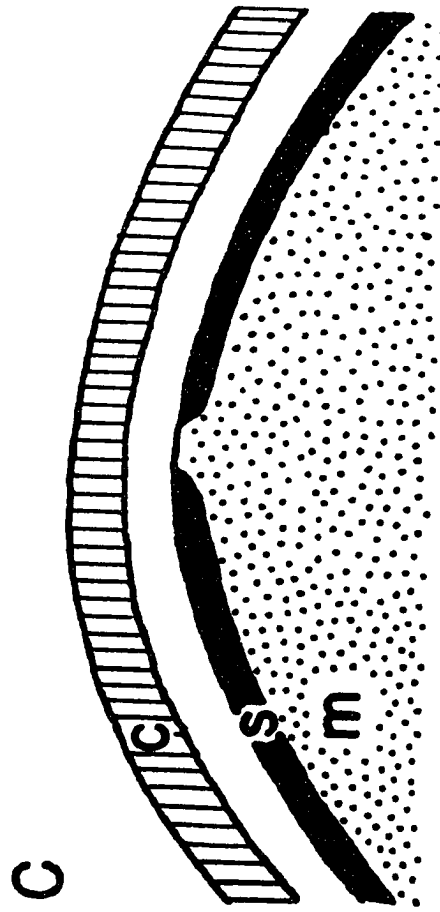
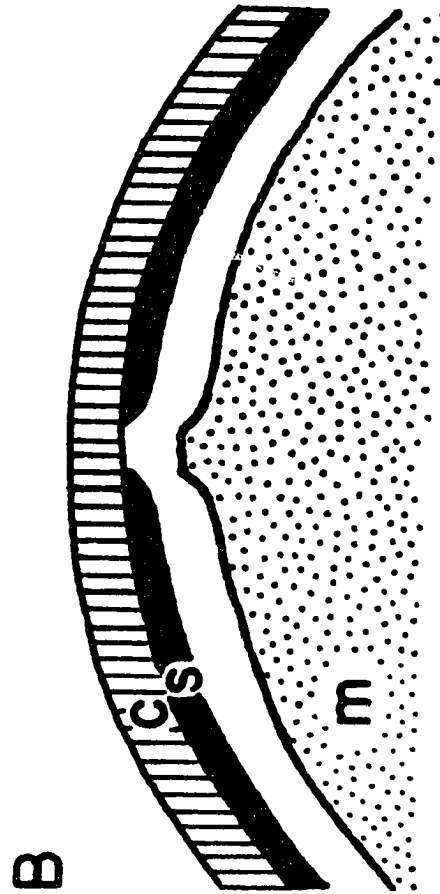
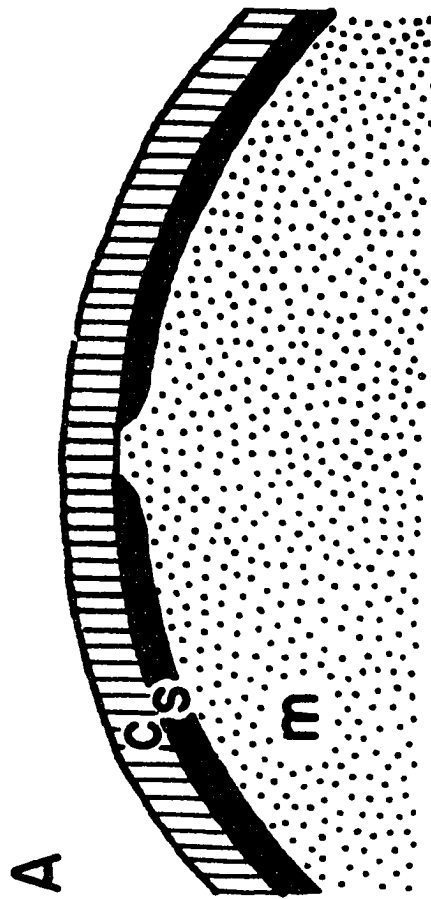
m.- matrix

A.- Normal condition, showing the shell before separation.

B. Separation of the matrix from the mural part of the septum results in a ridge on the internal mold and a groove on the interior of the shell.

C. Separation between the mural part of the septum and the wall of the conch produces a smooth surface, sometimes marked by a faint suture, and sometimes perfectly smooth, the septal furrow showing as variation in color due to differential weathering.

D. Separation is largely as in B, except that shearing has broken off the protruding portion of the matrix.



may be represented. Probably the commonest condition is that represented in fig. 2 D, in which separation, as before, occurs between the matrix and the mural part of the septum. Fracture has broken the matrix at, or centrad of, the level of the inside of the mural part of the septum, producing a roughened area. A similar phenomenon may occur with separation between the wall of the conch and the mural part of the septum, but with matrix adhering to the wall of the conch at its separation. This condition, however, has not been conclusively recognized.

In pyritized specimens, in which only one level is represented, separation takes place throughout at the contact of the wall of the conch and the mural part of the septum. The carina which may surround the septal furrow in such instances represents the true termination of the septum. (Fig. 2C.) Specimens in which the septal furrow appears only as a variation in color variation is due to differential weathering of the matrix.

The septal furrow is rather widespread among orthoceracones, but is known only sporadically in coiled forms. From the similarity of the structure found in orthoceracones to that of Nautilus, it is suspected that the structure is in reality widespread if not universal in Nautiloidea. Its apparent absence may be due in part to lack of study, in part to preservation, and in part to the inaccessibility of the dorsum in coiled cephalopods. It is present in all

smooth shelled Pseudorthoceratidae where the preservation is such that it can be reasonably expected. It is unknown in Cayutoceras and Bradfordoceras which are known only from specimens occurring in coarse grained sandstones and shales and in Sceptrites, which is known only from coarse grained limestones. It is widely present in orthochoanitic orthoceracones of the Silurian and Devonian. It is remarkably well developed in Cincinnati species of Ormoceras, but has thus far not been noted in other Actinoceroidea.

The septal furrow like the conchial furrow will serve as an accurate criterion of the orientation of specimens. Previously the only certain criterion in orthoceracones has been the hyponomic sinus, and too often that was absent. Troedsson¹⁰ figured and described a normal line in Orthoceras

10. Troedsson, G.T. Studies on Baltic fossil cephalopods, I. On the nautiloid genus Orthoceras, Lunds Univ. Arssk., N.F., Avd. 2, Bd. 27, Nr. 16, 1931, p. 20, pl. 3, fig. 2.

regulare Schlotheim, of the Orthoceras limestone of Sweden. Except that the region is very narrowly closed adorally if at all, this is identical with the septal furrow as seen in other orthoceracones. Troedsson regarded the structure as ventral in position. However, the strong similarity with the septal furrow and the apparent lack of any definite conflicting evidence, suggests that it is dorsal here also. It has often been assumed that the siphuncle when eccentric

lies ventrad of the center of the conch. That this is not always the case is shown by Euloxoceras. Both the septal furrow and the concentration of cameral deposits show that the siphuncle is dorsal.

THE SIPHUNCLE

Terminology

The siphuncle is a composite structure consisting of several distinct parts of different origin, and may best be defined as the tube which encases the siphon. Two divisions have been recognized, and ectosiphuncle and an endosiphuncle. The ectosiphuncle comprises the outer wall of the siphuncle, consisting of the septal necks and the connecting rings in ellipchoanitic cephalopods, and of the septal nicks alone in holochonanitic cephalopods. The endosiphuncle comprises all structures within, which take on different forms in different groups. The structures are often spoken of as endosiphuncular deposits. Since this suggests a counterpart "exosiphonal deposits", the term siphonal deposits is preferred here. The term has the further advantage of brevity; also it implies the origin of the structures from the siphon.

The term endosiphuncle was first used by Hyatt¹¹

11. Hyatt, A., Cephalopoda, in Zittel-Eastmann Textbook of Paleontology, vol. 1, 1st. ed., 1900, p. 596.

who said: "Organic deposits in the form of endocones,

and taper off at the center into a spire that is sometimes tubular and hollow, or again flattened and elliptical. This is the endosiphuncle." Later in the same work the term is used for the central canal of the Actinoceroidea^{11a}.

11a. Ibid., p. 608

The term was not more clearly defined until 1906 when Ruedemann¹² revised the morphological terminology as follows:

12. Ruedemann, R., Cephalopoda of the Champlain basin, New York State Museum, Bull. 90, 1906, p. 403.

"The ectosiphuncle is the external wall of the siphuncle; the endosiphuncle comprises all structures within the same." The tube which Hyatt apparently had in mind in wording his short definition is not a single structure, but is composed of the endosiphontube and the endosiphocoleon of Ruedemann. Further, as defined and used, the endosiphuncle of Hyatt is not a structure, but the cavity remaining within several calcareous structures. The term was employed by him for the central canal of the Actinoceroidea, as well as for the combined endosiphontube and endosiphocoleon of the Endoceroidea.

Foerste and Teichert,¹³ and later Teichert,¹⁴ have

13. Foerste, A.F., and Teichert, C., The actinoceroids of east-central North America. Denison Univ. Bull., Sci. Lab., Jour., vol. 25, 1930, pp. 201-296, pl. 27-58.

14. Teichert, C., Der bau der actinoceroïden Cephalopoden, *Paleontographica*, Bd. 78, Abt. A, 1933, pp. 111-230; pls 8-15.

used the terms endosiphuncle and endosiphuncular deposits for the calcareous structures within the siphuncles of Actinoceroïdea, which comply with Ruedemann's definition. Ruedemann's usage has been followed in many of the more important works on the structure of cephalopods in recent years and is followed here. The following of Hyatt's usage would lead to several difficulties. The endosiphuncle of the Endoceroïdea is a cavity with a definite wall which in part at least a structure distinct from the endocones, and involves the walls of the endosiphocoleon and the endosiphotube. The endosiphuncle of the Actinoceroïdea is the cavity within the siphuncle not occupied by annulosiphonate deposits, consisting of the cavity of the central canal in the apical portion, to which is added the cavity occupied by certain unknown but possibly parenchymal tissues in the adoral portion. It has no fixed wall.

Structure of the Ectosiphuncle

The ectosiphuncle in ellipchoanitic cephalopods is a composite structure, being made up of two distinct parts which are very different in structure and origin, the septal neck, and the connecting ring. The septal neck (Fig. 1 n) is essentially a part of the septum with which

it is continuous, and identical in structure.

It is largely upon the basis of the form of the septal neck that the major divisions of the Nautiloidea were based. Hyatt¹⁵ first divided the Nautiloidea into the Holochoanoidea

15. Hyatt, A., Genera of fossil cephalopods, Boston Soc. Nat. Hist., Proc., vol. 22, 1883, p. 260.

and the Ellipochoanoidea. In the Holochoanoidea the septal necks are long, extending at least the length of a camera, and connecting rings are absent. In the Ellipochoanoidea the necks are short and the greater part of the length of the siphuncular segment is made up of the connecting ring. Although these groups have been supplanted, the terms holochoanitic and ellipochoanitic are convenient for descriptive purposes and are often used. Hyatt¹⁶ later divided

16. Ibid., 1900.

the Nautiloidea into Holochoanites, Schistochoanites, Orthochoanites, Myxochoanites and Cyртоchoanites. The Holochoanites contain essentially the same forms as did the Holochoanoidea. The Schistochoanites are invalid structurally and need be given no attention here. The Orthochoanites are ellipochoanitic cephalopods characterized by straight septal necks. The Cyртоchoanites are ellipochoanitic forms with recurved septal necks and more or less expanded siphuncular segments. The Myxochoanites

constitute a small highly specialized group of forms which are orthochoanitic in the early stage and cyrtchoanitic in the later stage.

Foerste and Teichert¹⁷ have differentiated two regions

17. Foerste, A.F. and Teichert, C., The actinoceroids of east-central North America, Denison Univ. Bull., Sci. Lab., Jour., vol. 25, 1930, p. 222.

of the septal neck in cyrtchoanitic cephalopods. (Fig. 1) The apical extension of the septal neck is called the neck, (Fig. 1n) while the recurved portion is called the brim (Fig. 1b). Though these two regions often overlay, the relative development of neck and brim is characteristic of a genus and is a valuable character in all cyrtchoanitic cephalopods.

The connecting ring is very different from the septal neck in structure and in origin. It is composed of calcite spicules loosely arranged in stellate patterns in Nautilus. Thin sections through the connecting ring in Paleozoic Nautiloidea have thus far failed to show recognizable spicular elements. Replacement may account for this, and the discrepancy may be more apparent than real. In all Paleozoic forms studied the connecting ring appears spongy and porous under high magnification, with the openings clogged with fine organic matter which is at least in part identifiable with the matrix.

The connecting ring is the most fragile of the calcareous structures of the cephalopod shell, and is frequently entirely destroyed. It is not known for any of the Silurian species of Gigantoceras Hyatt¹⁸. Likewise it is consistently absent in Leurocycloceras Foerste¹⁹. It may

18. Hyatt, A., Cephalopoda, in Zittel-Eastmann Textbook of Paleontology, vol. 1, 1st. ed., 1900, p. 608. See also Foerste, A.F., Notes on cephalopod genera; chiefly coiled Silurian forms, Denison Univ. Bull., Sci. Lab. Jour., vol. 21, 1925, p. 37.

19. Foerste, A.F., A restudy of American orthoconic Silurian cephalopods, Denison Univ. Bull., Sci. Lab., Jour., vol. 23, 1928, p. 272.

be that in such forms no spicules were developed or that calcification was slight, and that the spicules were too few and too loosely arranged to be capable of preservation.

In some of the Pseudorthoceratidae the connecting ring is preserved only in the apical part of the phragmocone where it is strengthened by siphonal deposits. The apical preservation alone might suggest that the connecting ring was developed late in the history of the camera. However, a study of the conditions of preservation shows that there is a very real correlation between the destruction of the connecting ring and the invasion of the siphuncle by sediments. Further, the connecting ring is more often

destroyed when the invading matrix is coarse and sandy. Other factors, such as pressure by compaction of the sediments or the transportation and attendant damage of the shell prior to burial are doubtless contributory but are harder to estimate. Although the frequent destruction of the connecting ring in adoral camerae suggests a delayed development, the study of a considerable series of specimens shows that the extent of destruction is variable within a species and that it is frequently erratic. Further, in the best preserved specimens the connecting ring is retained in the last camera.

The form of the connecting ring is variable. It extends from the outside of the tip of one septal neck apical to the preceding neck, into which it disappears. In cyrtochoanitic cephalopods an area of adnation (Fig. 1a) is frequently developed, where the connecting ring lies in contact with the free part of the adipical septum. Frequently in Actinoceroidea and some other forms the brim of the septal neck is recumbent, that is, recurved so sharply that it lies in contact with the free part of the septum, the connecting ring may also lie in contact with the free part of the adoral septum. This feature is not developed in any of the Pseudorthoceratidae.

Early Siphuncular Stages

The condition of the siphuncle in the apical chamber and adjacent camerae has been figured and described by Miller Dunbar and Condra²⁰ and by Schindewolf.²¹ Miller

20. Miller, A.D., Dunbar, C.O. and Condra, G.E. The nautiloid cephalopods of the Pennsylvanian system in the mid-continent region, Nebraska Geol. Surv., ser. 2, bull. 9, 1933, p. 83, pl. 1, fig. 8-9.

21. Schindewolf, O.H., Bemerkungen zur Ontogenie der Actinoceren und Endoceren (Cephal., Nautil.). Neues Jahrb. für Mineralogie etc., Beil.-Bd. 74, Abt. B., 1935, p. 96, fig. 6.

Dunbar and Condra report the presence of a subspherical apical caecum which hangs freely within the chamber without touching the apical wall. The septal necks are described as slightly recurved throughout. Schindewolf figures a condition which might be considered on the border line between orthochoanitic and cyrtochoanitic, but fails to differentiate the septal necks and the connecting rings. The apical caecum is subspherical and very slightly broader than the succeeding siphuncular segments. The first segment of the siphuncle beyond the caecum is shown and appears cyrtochoanitic at a glance. Later segments show a progressive increase in length while the maximum and minimum diameters remain the same. The question arises as to whether the

condition of the early siphuncular segments is to be considered as cyrtchoanitic and pointing to a cyrtchoanitic ancestry, or whether the condition is only apparently cyrtchoanitic or coenogenetic. At first glance the earliest siphuncular segment appear to be distinctly convex in outline so as to suggest a cyrtchoanitic rather than an orthochoanitic stage. Close inspection shows that the difference is more apparent than real and that Schindewolf was correct in considering the form orthochoanitic.

The connecting ring is aligned with the outside but not the inside of the septal neck. Consequently there is a faint contraction of the interior of the siphuncle at the septal foramen. In later stages the difference is so slight in proportion to the diameter of the siphuncular segment that it is not apparent, (Fig. 3n) in the earlier camerae, however, the siphuncular segment is so small that the contraction is apparent and a cyrtchoanitic appearance results. (Fig. 3b) The length of the segment is also significant, as shown in Schindewolf's drawing. In the first three segments there is a marked increase in length, while the maximum and minimum diameters of the interior of the segment remain the same. The increase in length alone does much to reduce the apparent cyrtchoanitic effect.

The effect of size on the apparent cyrtchoanitic condition can be seen by comparing the difference between the small apical end of Pseudorthoceras with the larger

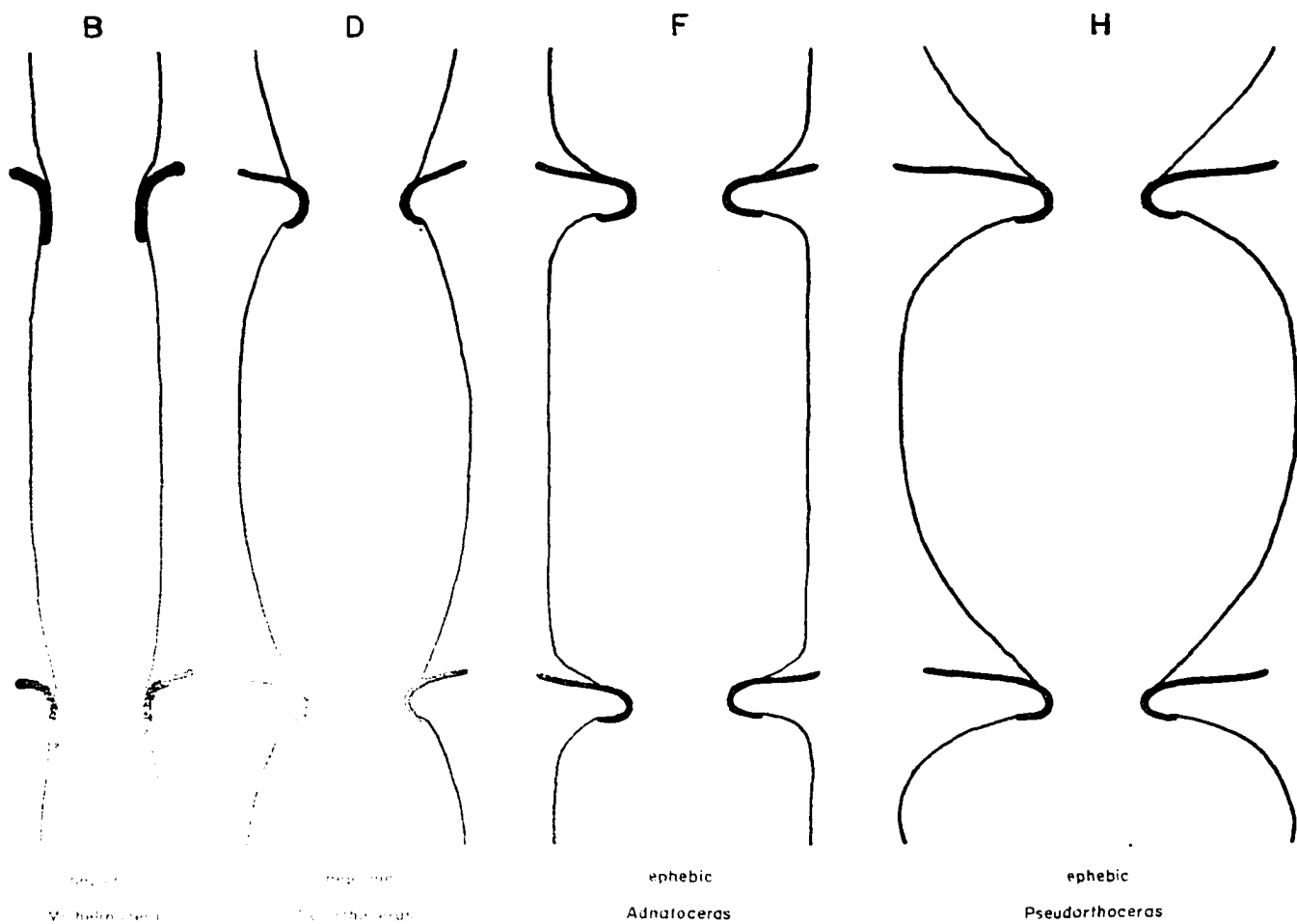
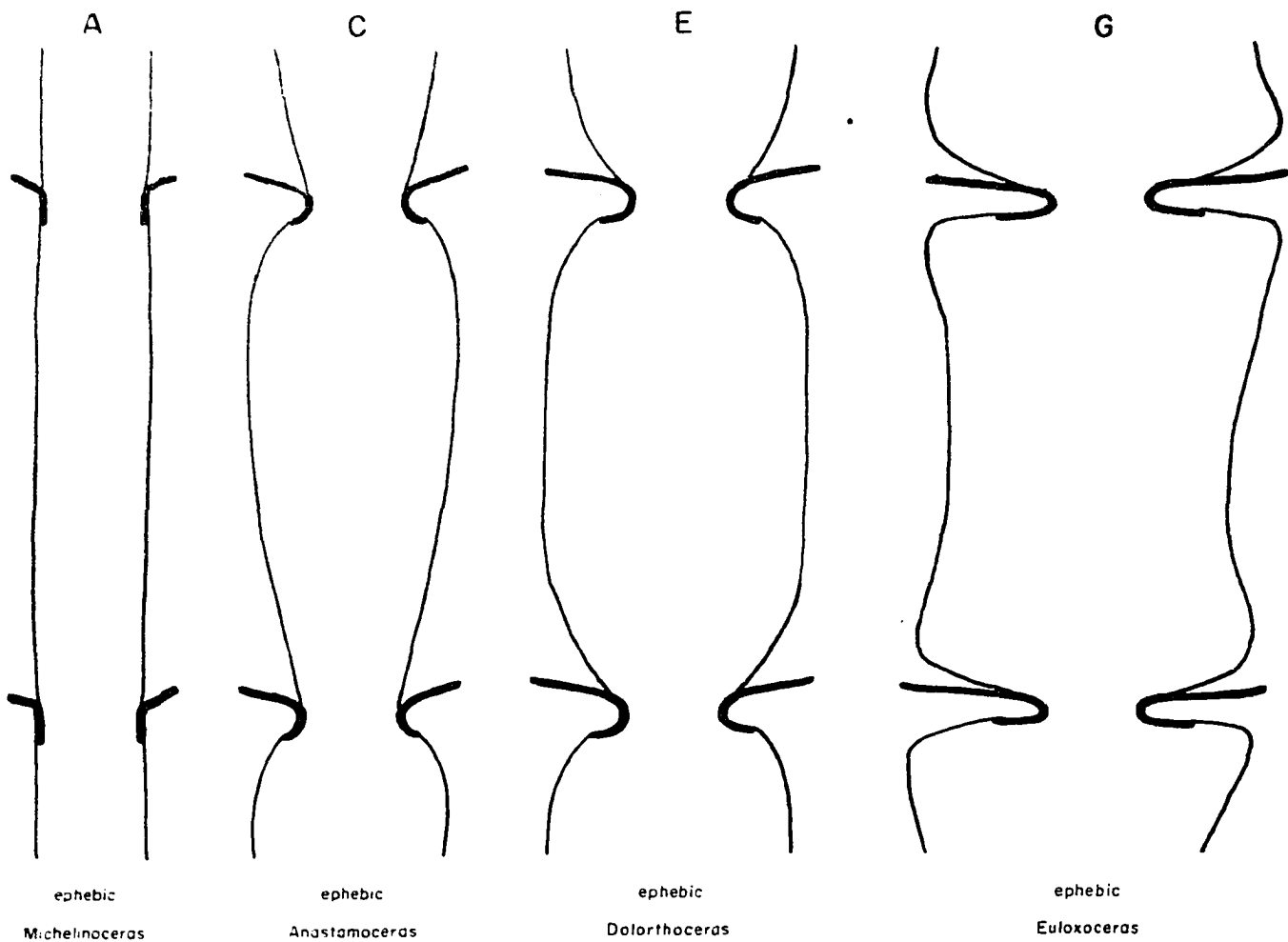
Fig. 3. Types of siphuncular outlines

- A. Michelinoceras type.- orthochoanitic condition with cylindrical outline.
- B. Nepionic Michelinoceras.- A false cyrtchoanitic condition of the interior results from the great difference in thickness of neck and connecting ring in proportion to the siphuncle segment.
- C. Anastamoceras.- A simple cyrtchoanitic condition, with the brim vestigial and no area of adnation.
- D. Nepionic Dolorthoceras.- The brim and area of adnation is one-half the neck; the connecting ring is slightly and nearly uniformly convex.
- E. Ephebic Dolorthoceras.- The brim increases and is subequal to the neck; the area of adnation remains one-half the neck. The siphuncle connecting ring tends to be less curved in the middle of the segment, but is still convex throughout.
- F. Adnatoceras.- The brim and area of adnation are subequal and slightly greater than the neck. The middle of the segment becomes straight, curvature being confined to the ends.
- G. Euloxoceras.- The brim and area of adnation increase further. The expansion is confined to the ends of the segments; the middle of each segment becomes faintly concave. Expansion is slightly greater on the venter,

Fig. 3 Con't.

showing on the left.

H. Pseudorthoceras. - The neck, brim and area of adnation are the same as in Dolorthoceras, but the segment becomes markedly convex, varying from pyriform to sub-globular.



apical end of *Trematoceras*²².

22. Schindewolf, Ibid., p. 91, fig. 3.

Here the early siphuncular segments are twice as wide as those of Pseudorthoceras and four times as long, with such dimensions the difference in thickness between the connecting ring and the septal neck become negligible and an unquestionably orthochoanitic outline is produced.

It may be further pointed out that the development of an orthochoanitic condition following apparently cyrtchoanitic segments in Pseudorthoceras would be difficult to explain; it would indicate a change from cyrtchoanitic to orthochoanitic, followed by a reversal of the condition in neanic segments. The development of the orthochoanitic condition seems to have no other explanation than the recapitulation of an ancestral condition. The early cyrtchoanitic effect is mechanical and is the direct result of the small size of the early portion of the conch.

Later Siphuncular Stages

The outline of the siphuncle undergoes a marked ontogenetic progression in the Pseudorthoceratidae, and the outline of the early stages of the more specialized genera recapitulates the ephebic outlines of earlier and simpler forms from the metanepionic stage onward. It has been found convenient to name the types from genera in which they occur as ephebic characters, and they are referred to as such in the descriptions in the systematic portion of

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this paper. Smooth shelled genera are selected as types for the various types of outlines, because such forms seem to represent the generalized stock in which siphuncular modification took place, while ornamented or otherwise specialized forms show scarcely any deviation from the types. The application of the names to other families in which the resemblance would be purely homeomorphic is not to be recommended. It is used here largely for brevity.

I. Michelinoceras type.- (Fig. 3a-b) This is not an ephebic feature in any of the Pseudorthoceratidae which are cyrtochoanitic by definition, but it is found in the early stages. The siphuncle is orthochoanitic, consisting of vertical septal necks and connecting rings which are either cylindrical or very faintly expanded within the camerae. The interior of the siphuncle may appear to be somewhat contracted at the region of the septal foramen, but this is attributed to the difference in the thickness of the septal necks and the connecting rings, which are aligned externally. The neck is vertical, which is the essential criterion of the orthochoanitic condition, and the outline of the exterior of the siphuncle is essentially cylindrical. The condition is typical of the ephebic segments of Michelinoceras Foerste, but is not found in the ephebic stage of the Pseudorthoceratidae. It has been noted in the early portions of Pseudorthoceras, Dolorthoceras and Spyroceras, the only genera for which sufficiently early portions of the

phragmocone are available at present.

2. Anastamoceras type.- (Fig. 3c) This is the first of the cyrtchoanitic types found in the ephebic stage of a member of the Pseudorthoceratidae. Siphuncular expansion is slight and is due more to the convexity of the connecting ring than to the septal neck. The neck is slightly recurved, but is without the development of a definite brim. There is no area of adnation. This type of structure is characteristic of the ephebic siphuncular segments of Anastamoceras Flower, n. gen., of the Lower Devonian. It has been noted in the early stages of Pseudorthoceras, Dolorthoceras, Spyroceras and Mooreoceras.

3. Neanic Dolorthoceras type.- (Fig. 3d) This is a shade more specialized than the preceding. The brim and area of adnation are developed, subequal, and are about one-half the neck. The outline of the free part of the connecting ring is faintly convex throughout. This is an ephebic feature in the earliest known species of Dolorthoceras, including D. parlenense (Williams) of the Oriskanian of Maine, and D. rudis (Hall) of the Onondaga limestone of New York. The separation of these species into a distinct genus has not seemed advisable in view of the gradation of the ephebic siphuncular outlines of these forms into the typical ephebic Dolorthoceras type of outline which characterizes Hamilton and younger species of Dolorthoceras. The neanic Dolorthoceras type appears to be an ephebic character in Diagoceras, although the condition of the area of adnation

is not known and the free part of the connecting ring seems to be slightly more convex than is typical. It is present in ephebic Sceptrites, and is persistent in Spyroceras extending farther orad in that genus than in Hamilton species of Dolorthoceras. It is found in the early stages of Hamilton and later Dolorthoceras, Petryoceras, Mooreoceras, Pseudorthoceras, and Cayutoceras.

4. Dolorthoceras type.- (Fig. 3c) The brim and neck are subequal and about twice the area of adnation, for while the brim increases beyond the neanic Dolorthoceras stage, the area of adnation remains static. The connecting ring is strongly curved at the ends but is only faintly convex in the middle. This type of structure appears in the ephebic siphuncular segments of Dolorthoceras, Petryoceras, Palmeroceras, Spyroceras, Geisonoceroides, Cayutoceras, Fusicoceras and Cryptothoceras. It is found in the early stages of Pseudorthoceras and Mooreoceras. Indeed, some species of Mooreoceras can hardly be said to pass beyond this stage, but may be distinguished by the form of siphonal deposits.

Adnatoceras type.- (Fig. 3f) The brim and area of adnation are subequal and are slightly greater than the neck. This form type can be readily distinguished by the form of the connecting ring which is straight over the middle portion and abruptly curved at the ends. It is known only in the ephebic siphuncular segments of

Adnatoceras. Palmeroceras is intermediate between Adnatoceras and Dolorthoceras in the form of the siphuncular segments.

Euloxoceras type.- (Fig. 3g) The brim and the transverse part of the connecting ring are easily three times the neck the area of adnation is nearly twice the neck. The siphuncular segments are contracted strongly at the ends, and are faintly concave in the middle. This type is found only in ephebic Euloxoceras, the ontogeny of which is unfortunately unknown.

Pseudorthoceras type.- (Fig. 3h) The brim and neck are subequal as in the Dolorthoceras type. The area of adnation is less than the brim and is occasionally vestigial. The free part of the connecting ring is more or less convex, forming siphuncular segments which may vary from pyriform to subglobular in form. This is found in the ephebic segments of Pseudorthoceras, Mooreoceras, Paraloxoceras, Bergoceras and Bradfordoceras. The development of this type of outline in Bradfordoceras is independant of that of the other genera which are closely related to each other.

The first four types follow each other in the order named whenever adequate early stages have been observed. (Fig. 9) Beyond the Dolorthoceras type expansion may occur in either of two ways. In Adnatoceras and Euloxoceras the segments remain slender in form, expanding at

the ends, but becoming first straight and then concave in the middle. The expanded condition is brought about by the increase in the brim and the transverse part of the connecting ring at one end, and the increase of the area of adnation and a free transverse part of the connecting ring on the other end of the segment. In the Pseudorthoceras type, on the other hand, the condition of brim, neck and area of adnation remains largely unchanged. The condition found is essentially that of Dolorthoceras, but expansion is brought about by the increased convexity of the free part of the connecting ring. (Fig. 4)

What may be gerontic reversion to an ancestral condition has been noted in Adnatoceras spissum, the earliest and simplest representative of the genus known. After the attainment of the Adnatoceras type of outline, the brim and area of adnation become gradually reduced, and the outline of the segments becomes much more uniformly curved, this producing in the gerontic stage fair replicas of the Dolorthoceras, neanic Dolorthoceras and Adnatoceras types. This reverse the ontogenetic progression and also the evolution. The appearance of similar phenomena in the Actinoceroidea suggests another solution than atavism. Here the earliest stages which are preceded by a small depressed protoconch are broadly expanded. There is no evidence of any relation between the group and any cephalopods with orthochoanitic siphuncles. Yet in a group of

Fig. 4.- Development of brim, neck and area of adnation in Pseudorthoceras and Adnatoceras,

N. length of septal neck

B. length of brom

A. length of area of adnation.

Generic stages repeated in the ontogeny are typically represented at the sections indicated by vertical lines.

1. Michelinoceras stage; orthochoanitic

2. Anastamoceras stage; cyrtchoanitic, brim vestigial, area of adnation wanting.

3. Nepionic Dolorthoceras.- Brim and area subequal and about one-half the neck.

4. Ephebic Dolorthoceras stage.- Brim and neck subequal, area one-half the neck.

5. Late ephebic condition found in Pseudorthoceras. The development of the Pseudorthoceras type of outline from the ephebic Dolorthoceras type results in no essential change in the relationship of neck, brim and area of adnation, but only in the increased convexity of the connecting ring. In late ephebic individuals the brim and area are apparently reduced; when measurements are considered the reduction can be seen to be only relative, as shows here.

6. Adnatoceras stage.- The brim and area are subequal and are greater than the neck.

Fig. 4 Con't.

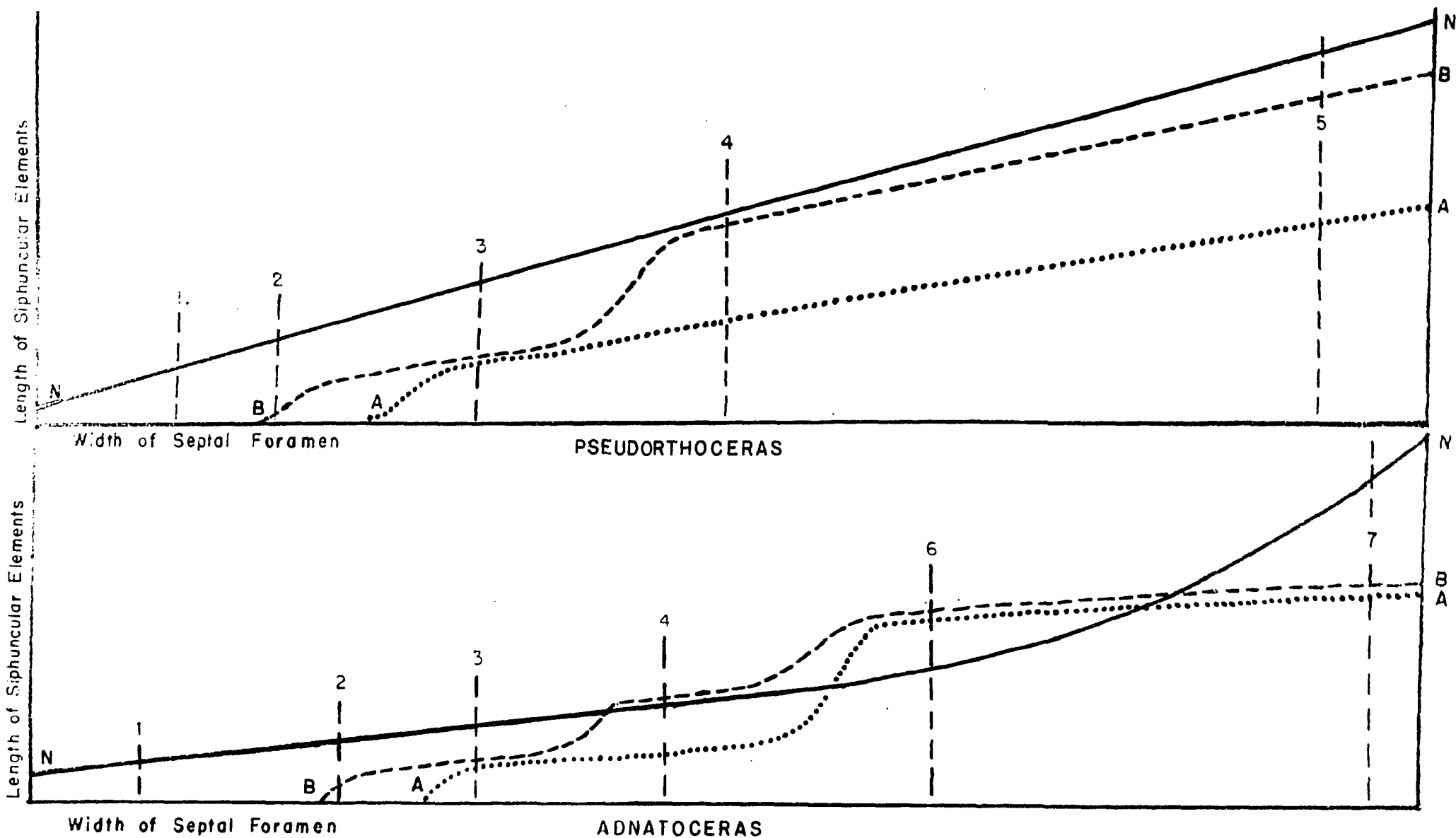
7. Gerontic Adnatoceras condition.- The brim and area of adnation become reduced in proportion to the septal neck. However, reduction is apparent rather than real, and is due to the rapid increase in the septal neck.

Pseudorthoceras is based on measurements of P. knoxense.

The first three stages of Adnatioceras are based upon

Dolorthoceras, sufficiently early stages of Adnatoceras

being unknown. Stages beyond 3 are known from A. spissum.



Cincinnatian species of Ormoceras,²³ successive segments

23. The exact generic reference is not beyond question in view of the marked changes in the siphuncular outlines. Doubtless species which have been placed in Deiroceras are congeneric, and it is possible that some species referred to Armenoceras may also be closely related.

pass through generic stages beginning with Armenoceras, through Ormoceras and Deiroceras, and finally attained in segments similar to those of Leurorthoceras a type of outline which is practically orthochoanitic. Here it is hardly possible to interpret the simplification of the siphuncular outline to a reversion to an ancestral condition, for such an ancestral condition cannot be demonstrated. Kobayashi²⁴ noted the similarity between the siphuncular

24. Kobayashi, T., On the Stereoplasmodermitidae, Japanese Jour. Geol. Geogr., vol. 13, no. 3-4, 1936 p. 234.

outlines of the Stereoplasmodermitidae and certain of the Sactoceratidae, and suggested a common origin of Sactoceras and Stereoplasmodermites in the genus Sactorthoceras Kobayashi. This is opposed not only by the ontogeny of the Actinoceroidea, but also by the fundamental differences in the organization of the siphonal deposits, and Kobayashi's position is hardly tenable.

The reduction of siphuncular expansion in Actinoceras

itself is well marked, but it is confined to the gerontic portion of the phragmocone, that part secreted during the slight apertural contraction which occurs in the gerontic stage. The simplification of the siphuncle in both the Actinoceroidea and in Adnatoceras seems to be a result of an increase in the rate of expansion of the septal foramen. This causes the minimum diameter of the siphuncle to increase more rapidly than the maximum diameter, causing a gradual reduction in the expansion of the siphuncular segment. Attendant modifications of the outline will naturally follow, but no radical changes are initiated; rather the complexities of the outline gradually disappear and the result is one of simplification rather than atavism.

SIPHONAL DEPOSITS

Morphology

Annulosiphonate deposits, the only type of siphonal deposits which is relevant to a discussion of the Pseudorthoceratidae, consist in their simplest state of small circumferentially complete rings formed within the septal foramen of nautiloid cephalopods. A section through a ring will show that it is made up of lamellae arranged about a center of deposition which is adjacent to the septal neck. Hypothetically the simplest ring is the annulus (Fig. 5A) which is attached by its outer surface or some part of it to the septal neck, while the remainder of the surface, which is free, is everywhere equidistant

from the center of deposition. This condition is normally found only in the earliest stage of growth of an annulosiphonate deposit.

Annulosiphonate deposits may vary greatly in form and may be divided into several categories. Teichert²⁵ proposed

25. Teichert, C., Der Bau der actinoceroiden Cephalopoden, Paleontographica, Bd. 78, Abt. A, 1933, p. 127.

to divide the deposits into two groups which he termed centripetal and centrifugal. While these groups are probably of fundamental importance, the terms which were proposed for them have been found to be somewhat confusing and not entirely descriptive. New terms are proposed here which it is hoped will be simpler and more descriptive.

Pendant deposits, which correspond to the centripetal deposits of Teichert, originate from the septal neck and develop markedly inward, constricting the endosiphuncular cavity, often to a remarkable degree. These deposits hang upon the septal necks at which they are formed, and are never in contact with the free part of the connecting ring, but are separated from it by the perispatium. (Fig. 5B)

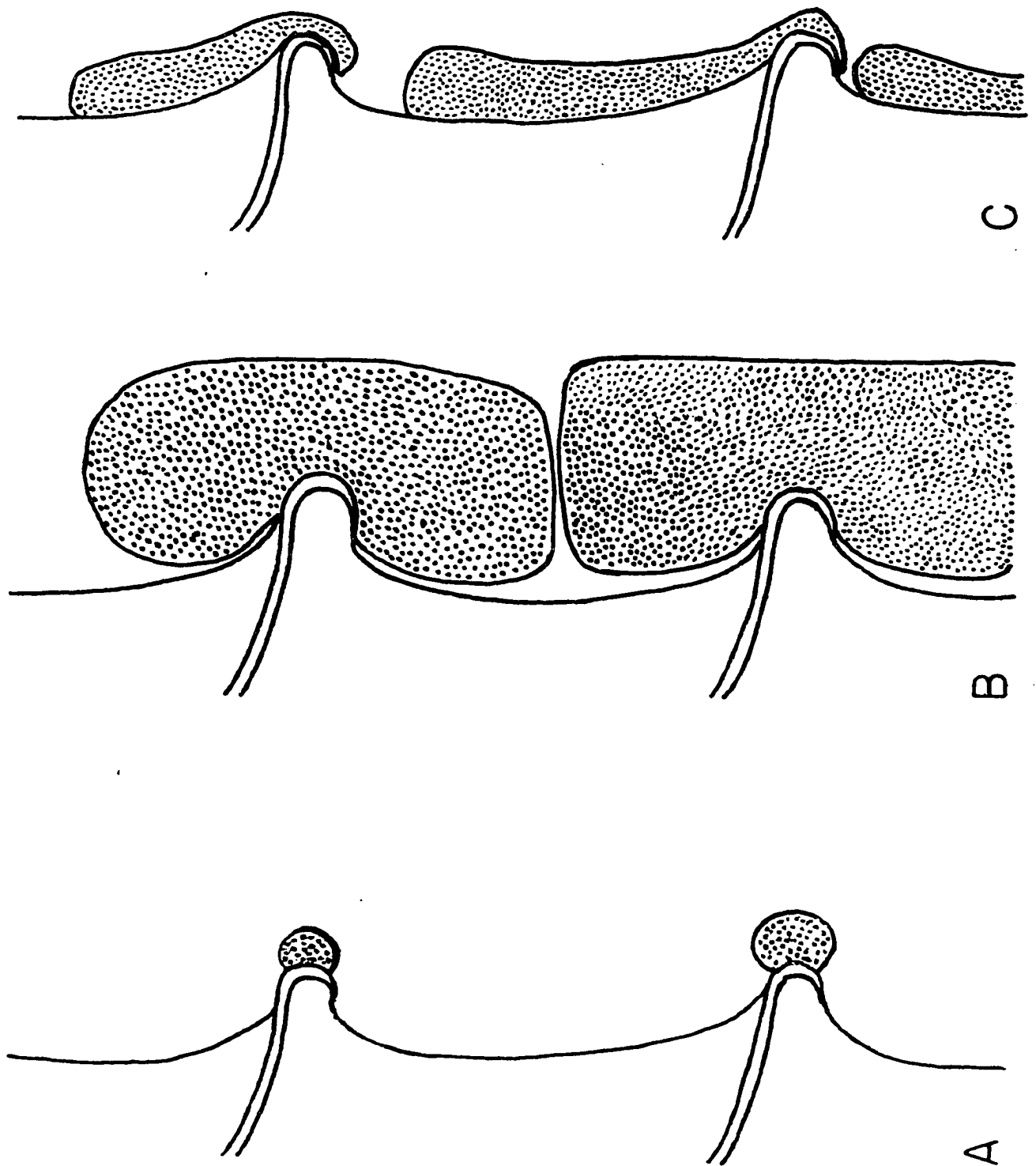
Parietal deposits, which correspond to the centrifugal deposits of Teichert, originate at the septal necks but never develop markedly inward. They grow mainly by the addition of material to the adoral or adapical ends of the deposit, and lie close against the connecting ring. No

Fig. 5. Types of annulosiphonate siphonal deposits.

A. The annulus.- Free surface regular in growth, equidistant from center of deposition. Developed only against septal neck.

B. Pendant deposit.- Deposit hangs free within the siphuncle, being attached only at the septal necks.

C. Parietal deposit.- Deposit extends along the wall of the siphuncle, Deposits may or may not fuse to form a continuous lining.



perispatium is developed. (Fig. 5c)

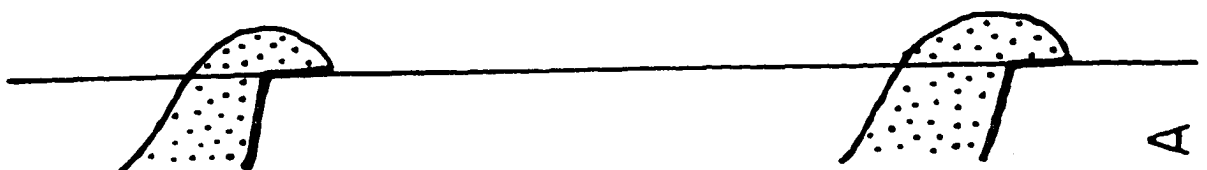
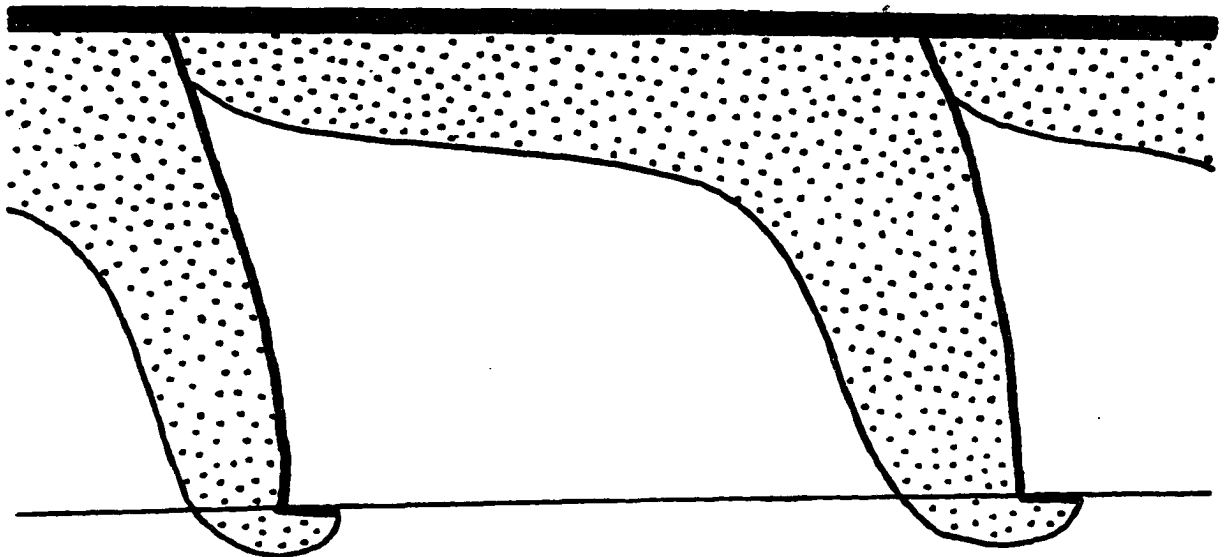
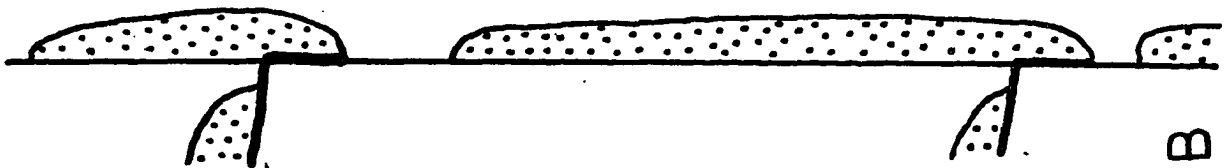
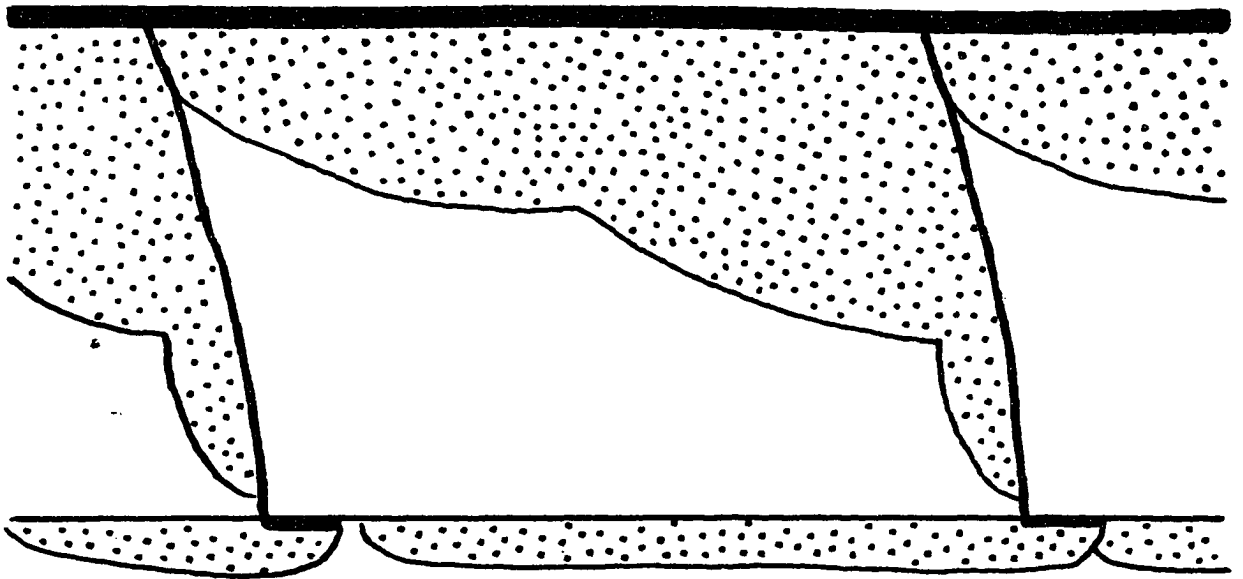
Two distinct types of parietal annulosiphonate deposits are recognized here. The first of these, the orthoceroid deposit (Fig. 6A) consists of small annulosiphonate rings which are extended considerably adorally from the septal foramen, but are scarcely produced adapically. The deposit rarely extends half the length of a camera. This is because the extent of the development along the inside of the connecting ring is limited by and commensurate with the development of cameral deposits outside of the ring.

The second type, the pseudorthoceroid deposit (Fig. 6B) differs from the orthoceroid deposit in appearance, for the adoral extension of the deposits has proceeded to such an extent that adjacent deposits fuse to form an apparently continuous lining within the siphuncle. The early stages of the pseudorthoceroid deposit resemble the orthoceroid deposits in form, and are probably derived from them. The fundamental change involved in the development of the pseudorthoceroid deposit is the ability of the siphonal deposit to extend along the connecting ring independent of cameral deposits.

Ontogeny

The development of the annulosiphonate deposits is very different from that of the ectosiphuncle already discussed above. In serially repeated parts ontogeny may work

Fig. 6. Diagramatic sections through phragmocones showing difference between (A) Orthoceroid deposits, in which cameral and siphonal deposits develop equally along the connecting ring, and (B) pseudorthoceroid deposits, in which the siphonal deposit develops along the connecting ring independent of cameral structures.



in two ways. First, there is the ontogeny of unalterable serial parts, parts which once secreted must remain unchanged. Here the oldest and earliest member of the series retains the earliest stage in the ontogeny, and in tracing the series from the oldest to the youngest member the ontogeny may be reviewed. This is exemplified in the sutures and siphuncular segments of cephalopods.

Second, there is the ontogeny of serial alterable parts which in one way or another may be modified by growth. Such modification is widespread. It may affect the exoskeletal parts by moulting as in the Arthropoda; it may affect endoskeletal parts which may be modified by resorption or addition of material; it may affect shell structures which may be modified by addition or resorption or by both. In such a series of parts the oldest part which has undergone the most modification shows not the earliest but the latest stage in ontogeny, while the last formed part may show the youngest ontogenetic stage. This is essentially Jackson's²⁶ principle of localized stages

26. Jackson, R.T., Localized stages of development in plants and animals, Boston Soc. Nat. Hist., Mem., vol. 5, 1899, p. 89-153, pl. 16-25.

of development.

The siphonal deposits exhibit only the normal series of the ontogenetic progression of alterable parts. The

youngest deposit, that nearest the aperture, shows the earliest ontogenetic stage, and as the series is traced apical older deposits are encountered which show more and more advanced stages. In the Pseudorthoceratidae three regions of the siphuncle can be recognized on the basis of the developmental stages of the deposits. There is an adoral portion of the siphuncle which has no deposits. This may vary from one to thirty camerae, and is constant within the growth stage of a species. The number of vacant camerae is not, however, the same for neanic, ephebic and gerontic individuals.

There follows a region in which deposits can be traced through their various stages of growth as they are traced apical in the conch from their inception. This is succeeded by a region in which the deposits have attained maturity and do not develop farther.

Annulosiphonate Deposits of the Pseudorthoceratidae

The Pseudorthoceratidae are characterized by the pseudorthoceroid type of siphonal deposit described above. However, within the family there is considerable variation of the development and structure of the deposits of the siphuncle. Some types hearken back to simpler and presumably ancestral annulosiphonate conditions; these are ontogenetic and presumably recapitulatory. Other deviations are clearly coenogenetic, and may affect all stages of growth. The following types seem significant enough to be given names:

Fig. 7. Types of siphonal deposits of the Pseudorthoceratidae. All sections are vertical, with the venter on the right.

A. The simple annulus, the earliest stage of annulo-siphonate deposits.

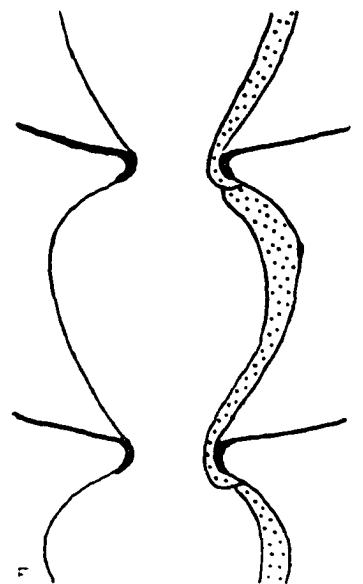
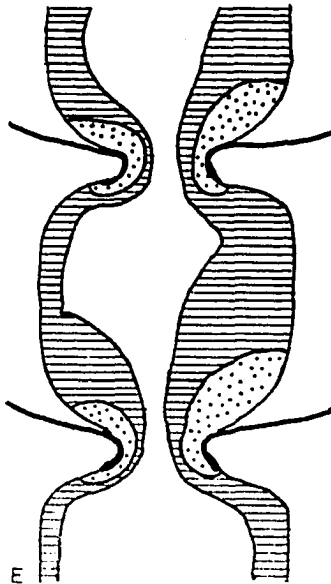
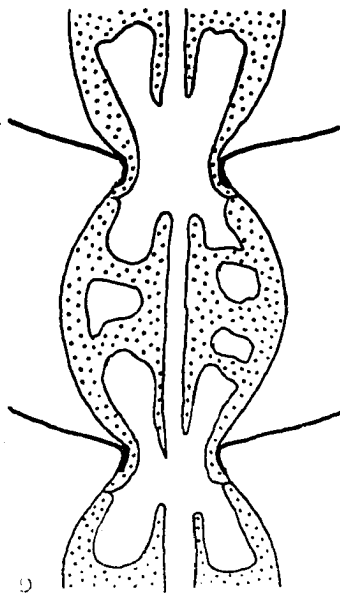
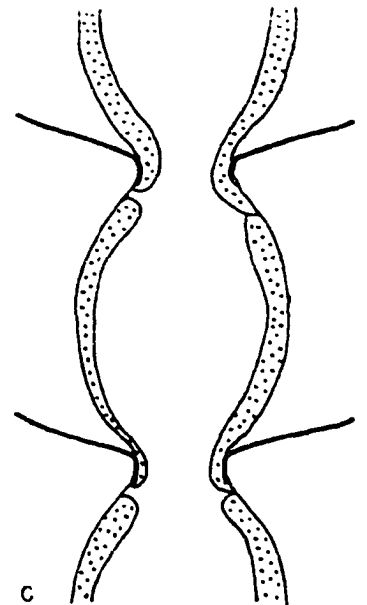
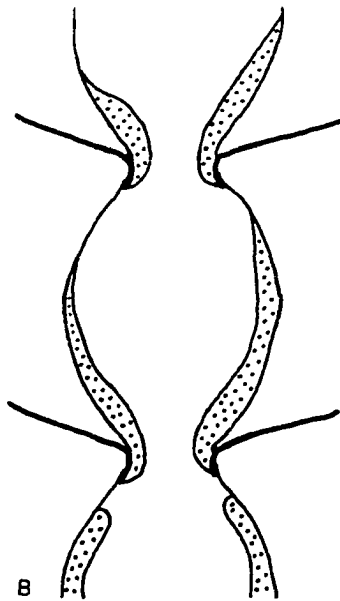
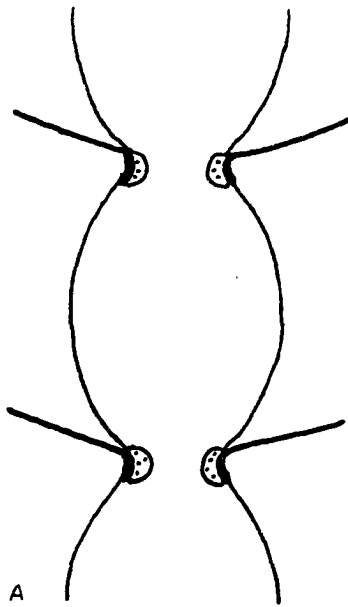
B. Michelinoceras type, the intermediate stage of siphonal deposits in the Pseudorthoceratidae. Deposits are extended orad but have not yet fused.

C. Dolorthoceras type, in which the deposits have extended farther orad until they have joined to make a continuous lining within the siphuncle. Characteristic of the ephebic stage in the Dolorthoceratinae.

D. Anastamoceras type, a gerontic deposit found only in the genus Anastamoceras. A central canal is connected to the Dolorthoceras type of deposit by irregular radial pillars.

E. Cayutoceras type, confined to the Cayutoceratinae. Discrete calcareous deposits are enclosed in carbonaceous fused segmental deposits.

F. Pseudorthoceras type, in which a continuous lining is formed on the venter before the deposit appears at all on the mid-dorsal region.



1. The simple Annulus.- (Fig. 7A) This, as already mentioned, consists of a simple ring attached by its exterior surface to the septal foramen. The inner surface of the ring is free, and is everywhere equidistant from the center of deposition, producing a semicircular appearance in section. This condition is found in the earliest stages of the siphonal deposits of all annulosiphonate nautiloids, and is suggestive of a common origin of all such forms. Included in the group are the annulosiphonate orthochoanites, the Pseudorthoceratidae and the Actinoceroidea. At the present time morphological and ontogenetic evidence seems to indicate that the Actinoceroidea may be very distinct from the other groups and that its annulosiphonate deposits may have been developed independantly of the others.

2. The Michelinoceras type.- (Fig. 7B) This is essentially the orthoceroid type of parietal deposit so far as the form of the deposit alone is concerned. The deposit is extended considerably orad of the septal neck, but is scarcely extended apically if at all. The interrelation between cameral and siphonal deposits in the orthochoanites fixes this as an ephebic feature there, but in the Pseudorthoceratidae the siphonal deposits develop over the connecting ring independant of cameral structures, and consequently the condition of discrete annulosiphonate rings is a neanic feature rather than an ephebic one. Its identity in form with the orthoceroid deposits as

developed in Michelinoceras and its allies in suggestive of the origin of the Pseudorthoceroid deposit in the orthoceroid deposit. Inasmuch as the orthoceroid type implies an interrelationship between cameral and siphonal deposits which ~~does~~ not exist here, the term Michelinoceras stage is found desirable.

The Michelinoceras type of deposit has been noted in the neanic deposits of all Pseudorthoceratidae for which the ontogeny is known. It is typically developed in the early stages of Anastamoceras, Dolorthoceras, Spyroceras, Fusicoceras and Adnatoceras, and is somewhat modified although still recognizable in Pseudorthoceras, Mooreoceras and Cayutoceras, which are specialized.

3. The Dolorthoceras type.- (Fig. 7C) The end of the adoral extension of the annulosiphonate deposits of the Michelinoceras type is attained when adjacent deposits meet, and a continuous lining of segmental origin is formed within the siphuncle. This is the Dolorthoceras type which is characteristic of the subfamily Dolorthoceratinae in the ephebic stage. Though deposits appear first on the venter and are thickest there, the adjacent rings do not fuse to form a continuous lining of the siphuncle on the venter before they appear on the dorsum. The deposit is simple and not differentiated into two distinct layers.

4. The Anastamoceras type.- (Fig. 7D) This type

is derived from the Dolorthoceras type which precedes it in development, by the formation of a central core in each segment, apparently about a central vascular tube. The core is connected with the Dolorthoceras type of deposit by irregular anastomosing radial processes. This is known only in the genus Anastamoceras of the Dolorthoceratinae, of which it is apparently a gerontic feature.

5. The Cayutoceras type.- (Fig. 7E) This type is another derivative from the more generalized Dolorthoceras type. Here the siphonal deposit has become differentiated into two layers. A primary layer is calcareous and consists of discrete deposits of the Michelinoceras type. This is covered by a carbonaceous outer layer which consists of fused-segmental elements essentially of the Dolorthoceras type. This type of structure is confined to Cayutoceratinae. and Bradfordoceras which make up the Cayutoceratinae. Transitional types connect the Cayutoceras type with the Dolorthoceras type. The structure is strongly reminiscent of Westonoceras of the Upper Ordovician, but the demonstrable relationship of Cayutoceras to Dolorthoceras shows that the resemblance to Westonoceras is merely isomorphic.

6. The Pseudorthoceras type.- (Fig. 7F) This differs from the Dolorthoceras type in the extreme dorso-ventral differentiation of the siphonal deposits. The annuli are incomplete, forming first on the venter. The deposit grows orad from the septal foramen rapidly, while lateral

growth is slow. The result is that a complete lining is formed on the venter before the rings are completed dorsally. Further growth of the deposit is brought about mainly by the addition of material to the lateral margins of the calcareous mass, and finally the two edges meet on the mid-dorsal line. This type of development is found in the Pseudorthoceratinae. The simple annulus and Michelinoceras stage can be recognized in development, but owing to the retardation of the secretion on the dorsum the pattern is distorted. Nevertheless the stages can be recognized, appearing first on the venter and only much later on the dorsum.

In the neanic segments of Pseudorthoceras a further modification appears. The deposit never becomes completed dorsally. It is suspected, although the evidence cannot be considered conclusive as yet, that this condition becomes an ephebic feature in Mooreoceras, at least in part. In Paraloxoceras and Bergoceras the siphonal deposits become greatly thickened and radial canals are developed in them.

CAMERAL DEPOSITS²⁹

29. These structures have been referred to as intracameral deposits by various authors. Intracameral implies that there are also intercameral or extracameral deposits which it is necessary to differentiate by the use of these prefixes. As there are no such deposits, the use of the prefix

seems unnecessary, and its elimination serves to shorten the term and, it is hoped, will tend to produce a less formidable nomenclature than that in general use.

Organic and Inorganic Cameral Deposits

The presence of various calcareous structures within the camerae of cephalopods has long been recognized, but until recently they have been given little attention. Barrande, Hyatt, Hall and Ruedemann recognized these structures as organic, and Hall³⁰ discussed them in some detail

30. Hall, J., *Paleontology of New York*, vol. 5, pt. 2, 1879, pp. 240, 245-9, 250, 256, 279-80.

and offered some speculations as to their origins. However the majority of paleontologists have preferred to tread on safer ground and to leave along structures which have no counterpart in any living form and which might after all turn out to be due to the deposition of infiltrated material after the death of the organism.

It remained for Teichert³¹ to point out some of the

31. Teichert, C., *Der Bau der actionceroiden Cephalopoden*, *Paleontographica*, Bd. 78, Abt. A, 1933, pp. 181-188.

differences between organic and inorganic structures. It is necessary to consider these and additional differences before proceeding to the structure and taxonomic value of

organic cameral deposits.

Inorganic deposits, of not only the camerae but also the siphuncles of cephalopods are often difficult to distinguish from organic structures, but it can be demonstrated that organic and inorganic deposits differ in their mode of occurrence. Organic deposits are formed in accordance with the symmetry and growth of the organism. Inorganic deposits bear no such relation to the shell; they are formed as geoidal fillings of cavities, either as complete fillings of hollow camerae, or as complemental fillings of incomplete internal molds.

Inorganic deposits within a closed cavity such as a camera which retains its walls and siphuncle intact infiltrated material is deposited evenly and uniformly over the inner surface. The first layers are normally thin and cryptocrystalline. Such layers often resemble the lamellae of growth of an organic deposit. Successive layers become gradually thicker and of coarser texture, and in the center of the cavity large crystals of calcite can be made out. In section this type of filling may occasionally resemble episeptal and hyposeptal deposits in an advanced stage of growth, but the condition can be recognized as inorganic by the uniform layers formed over the connecting ring. A false pseudoseptum³² may be

32. The term pseudoseptum, as shown below, refers to the line along which organic episeptal and hyposeptal deposits

of the camerae meet when well developed.

developed, running from the adoral outer corner of the camera to the central cavity occupied by coarse crystalline material, but not infrequently another similar line may be found running to the central adapical or adoral corner, or both, next to the siphuncle.

The shape of the camera seems to be a factor in the development of the false pseudoseptum.. It is best seen in very shallow camerae. The principles which govern the distribution of such a deposit are those governing the deposition of crystalline material in a hollow cavity. There is only one requirement for this type of structure: that the camera remain closed so that no material in suspension in water can enter. Deposition is chemical and follows saturation. Consequently this type of structure can occur in any closed camera, regardless of its proximity to the living chamber. Not infrequently camerae containing such organic deposits are found erratically spaced, alternating with camerae which have become filled with sediment.

The incomplete internal mold depends upon the invasion of sediments which fill the camerae only in part. Such sediments normally sink to the bottom of the camera, and the uppermost portion remains hollow, later to be filled in with calcite or other mineral substances after the burial of the conch. This calcite, which may often resemble organic deposits, is dependant not on the symmetry of the

conch, but upon gravity and the position of the conch in the sediments. The peculiar features of the incomplete internal mold are to be found not only in the camerae, but also in the siphuncle. The apparent deposit in the siphuncle of Adnatoceras napalense Flower n. sp., is of this type, (Pl. 3, fig. 2) the dark matrix occupying the lower part of the siphuncle as it lay in the sediments, while the upper part was originally left vacant and was later filled in by calcite.

The condition of the incomplete internal mold of the camerae may be somewhat different if the invading sediment was introduced through the siphuncle. In such instances the wall of the siphuncle, usually the connecting ring, is broken and is frequently entirely destroyed. If this occurs soon after the death of the organism the sediments may be washed into the camerae and arrange themselves on the lower side in the same manner as though the break had been in the wall of the conch. If, however, the sediments of the siphuncle have been partially consolidated, further pressure, possibly derived from the weight of overlying accumulating sediments may force the partially solidified material within the siphuncle to invade the camerae, breaking the connecting rings. This has been observed in a number of orthoceracones from the Richmond of Indiana and Ohio. Teichert³³ has illustrated and described a specimen of

33. Teichert, C., Einige actinoceroide Cephalopoden aus dänischen Diluvialgeschieben und aus dem Gotlandium Skandinaviens, Meddelelser fra Dansk Geologisk Forening, bd. 8, hft. 4, 1934, p. 374-380, pl. 8, fig. 1-2.

Armenoceras danicum Teichert in which the invasion of such material seems to have been stopped by some substance which has later been destroyed and which might, as Teichert suggests, indicate that the invading material was blocked by a tissue which later decayed, disappeared, and left a cavity which was finally filled in by infiltrated calcite. As it is evident that tissue must have been present in the camerae, it is quite possible that its presence at the time when invading sediments entered the conch might account for some of the peculiar phenomena of the relative distribution of sediment and matrix which cannot, or at least up to the present have not been explained in any other way.

Organic deposits.- The organic deposits can be distinguished from inorganic deposits by several characteristics which indicate that they were formed in accordance with laws governing the growth and bilateral symmetry of the organism as a whole, and are independent of breaks at either end of the shell. The number of camerae which contain no trace of deposits is constant for the growth stage within the species. Individuals in the same stage of growth will show a constant number of vacant camerae, but

individuals of a species representing different stages of growth are not necessarily comparable. It has been found, however, that in the greater number of orthoceraconic species examined there is no perceptible variation in this respect between neanic and ephebic individuals, and that gerontic variation is the exception rather than the rule. Tracing deposits apicad from their inception successive growth stages are found, and in the Pseudorthoceratidae there is a well defined region in which deposits are mature and growth has stopped. In other orthoceracones the mature region is less clearly defined, but a stage is reached in which there is no detectable difference in the amount of deposit in a considerable series of apical camerae which might not be due to variation in size of the camerae.

The inner surface of the cameral deposit shows a bilaterally symmetrical pattern, and usually there is a marked concentration of the deposits on the ventral side of the conch. The symmetry of the cameral deposits is in accordance with the symmetry of the conch as a whole, as is shown by correlation with the dorsal furrow, the conchial furrow and the aperture.

Furthermore, it has been possible to demonstrate by marking in the field the upper or lower side of the specimen as it lay in the matrix, that the dorso-ventral distribution of the deposit is independant of the position of the position of the conch in the sediments, and is therefore not affected by gravity as is the complemental

filling of the incomplete internal mold. Though the accumulation of the greater part of the mass of the cameral deposits on the venter often causes the conch to come to rest with the venter beneath, numerous examples are known in which the conch lay on a dorsal or lateral surface. Euloxoceras, because of its compressed form, is commonly found resting on a lateral surface, but the deposits are concentrated ventrally.

Striacoceras typus (Saemann) of the Cherry Valley limestone of the Middle Devonian has been an excellent species in which to study the independance of cameral deposits to the orientation of the conch in the matrix. It is possible to separate large slabs of the limestone along bedding planes, exposing the upper or lower surface, as the case may be, of a prolific cephalopod assemblage. In such slabs, one of which is on exhibition in the New York State Museum and has recently been figured by Miller,³⁴

34. Miller, A.K., Devonian ammonoids of America, Geol. Soc. Ameri., special paper, no. 14, 1938, pl. 1.

where numerous specimens are exposed and the position of the bedding plane is evident, determination of the matter is not difficult.

The complexity of the lobation when considered with its symmetry furnishes additional evidence of the organic nature of cameral deposits. The interior often bears a fine and elaborate pattern which is constant within the

species. More general features hold throughout generic or higher groups. In general the four regions of the cameral deposit noted above in Pseudorthoceras knoxense seem to hold fairly well throughout all stenosiphonate orthoceracones with mural deposits.

The similarity of the fine texture of the cameral deposits with that of the molluscan shell offers further evidence of the organic nature of the cameral deposits, although not conclusive by itself.

The independance of the cameral deposits from the character of the surrounding sediment shows that the structure is original in the shell and eliminates at least the possibility of geoidal filling. Remarkably clear impressions of such deposits are sometimes found on flattened internal molds from the Ithaca shale, in which the original shell material was completely dissolved. Again in the Oriskany sandstone, generally a medium unfavorable for the preservation of fine structural detail, well defined cameral deposits have been found. Striacoceras typus shows well developed deposits although differently preserved under different conditions. The species is found not only in the Cherry Valley limestone proper, but in an unnamed argillaceous lens in the limestone at Cherry Valley, and in the soft black shales which are the equivalent of the limestone in eastern New York.

Almost any specimen with deposits preserved will show that the deposits were present before sediments entered the

camerae. Specimens of Pseudorthoceras knoxense further show that not only did the deposits precede the breaking of the shell, but that they were a determining factor in the resistance to pressure during the consolidation of the sediments. The living chamber is not known for the species. Further, there has been as yet no record of adoral camerae which contain no deposits. The species is known then, entirely from apical portions of the phragmocone. Such specimens may be broken both adapically and adorally, but flattening is confined to the adoral end. If such a specimen is sectioned, it will be found that the flattening of the camerae decreases apicad in proportion to the increase in the mass of the cameral deposits. The unflattened condition of the apex is due to the added strength which these structures give to the shell.

Perhaps the best criterion of the organic nature of the deposits is that they are not common to all chambered shells but are confined to a relatively small though seemingly heterogeneous group of forms. Furthermore, the form of the deposit is constant within the species. The specific character of the deposits gives them taxonomic value. Cephalopods known to possess cameral deposits may be grouped as follows:

1. Orthoceracones of the Orthochoanites, Actinoceroidea, Pseudorthoceratidae and Stereiplasmoceratidae.
2. Crytoceracones derived from orthoceracones of the

above groups. This includes Troostoceras Foerste and Teichert of the Actinoceroidea, Sceptrittes Flower, n. gen., of the Pseudorthoceratidae and such species as "Ooceras" perkinsi Ruedemann which are evidently cyrtoconic Stereoplasmoceratidae and are possibly referable to Cyrtoonoceras Kobayashi.

3. Brevicones of several genera. Except for Poterioceras McCoy sensu strictu, which is probably not closely related to other brevicones, the deposits are vestigial and appear only in the gerontic stage. It is suspected that vestigial gerontic cameral deposits may be widespread among actinosiphonate brevicones, for while they have been thus far observed in only a very few genera, those genera are rather widely distributed and not closely related. Thus far deposits have been noted in Hexameroceras, Brevioceras, Herkimeroceras, Acleistoceras and Worthenoceras.

4. The only known occurrence in gyroceracones of any kind is confined to a peculiar Middle Devonian genus, not in process of description, of which Gomphoceras (?) cruciferum Hall of the Schoharie grit of the Middle Devonian is the only described representative.

Cameral deposits are not known in many early Paleozoic orthochoanitic orthoceracones. They appear to be uniformly absent in orthochoanitic longiconic cyrtoceracones, gyroceracones, and in all nautilicones and trochoceroids. They are not known in the camerae of Holochoanites. Organic

deposits were reported in Vaginoceras oppletum of the Chazy limestone by Ruedmann.³⁵ The uniform conditions of the de-

35. Ruedemann, R., Cephalopoda of the Champlain basin, New York State Museum, Bul. 90, 1906, p. 413-415, pl. 4, fig. 3; pl. 5, fig. 1-4; pl. 6, fig. 1; pl. 9, fig. 1-3.

posits on the interior of the camera and the obviously erratic development of several "false pseudosepta" in one camera suggest inorganic structures. At the present time the possibility of a connection between the camerae and the organism in *Holochoanites* seems remote.

It should be noted that aside from the original organic deposits and inorganic deposits mentioned above, there are frequently found irregular patches of calcite in the shell surrounded by sediment, for which neither explanation seems entirely satisfactory. Such patches appear to represent cameral tissue which was present at the time of burial of the conch and the filling of the camerae by sediments, but was later destroyed and the space which it formerly occupied became filled by inorganic material.

Morphology

Teichert³⁶ presented a classification and terminology

36. Teichert, C., Der Bau der actinoceroiden Cephalopoden, *Paleontographica*, Bd. 78, Abt. A, pp. 168-171.

for the cameral deposits, which is based entirely upon their

distribution in the camerae as seen in longitudinal section. Teichert's terminology is slightly modified and supplemented here. The following types can be recognized:

1. Episepal deposits.- (Fig. 8A,C) The episepal deposits, proposed by Teichert, form against the adapical septum of the camera, both against the free and mural parts, but do not attain the adoral septum.

2. Mural deposits.- (Fig. 8B) These are the circumferential deposits of Flower.³⁷ They are a specialized

37. Flower, R.H., Cherry Valley cephalopods, Bull. Amer. Paleont., vol. 22, 1936, p. 287.

type of episepal deposit developed in the absence of hyposeptal deposits. They form mainly against the mural part of the septum, and may encroach on the adoral wall as well as on the adapical free part of the septum.

3. Hyposeptal deposits.- (h, Fig. 8A, C) Deposits which form against the convex adoral wall of the camera.

4. The Circulus.- (Fig. 8D) This term is here proposed for the Stutzring of Teichert. It is a specialized hyposeptal deposit formed just outside the septal neck, and tends to strengthen it. The English equivalent of Stutzring is somewhat cumbersome. The term collar was previously proposed by me,³⁸ but it was found undesirable as the same

38. Flower, R.H., Cherry Valley cephalopods, Bull. Amer.

Fig. 8. Longitudinal sections of camerae illustrating various types of cameral deposits. A. Early stage in development of episeptal and hyposeptal deposits. B. Mural deposits, modified episeptal deposits in the absence of hyposeptal deposits. C. Advance stage of episeptal and hyposeptal deposits showing the pseudoseptum. D. The curculus, a specialization of the hyposeptal deposits.

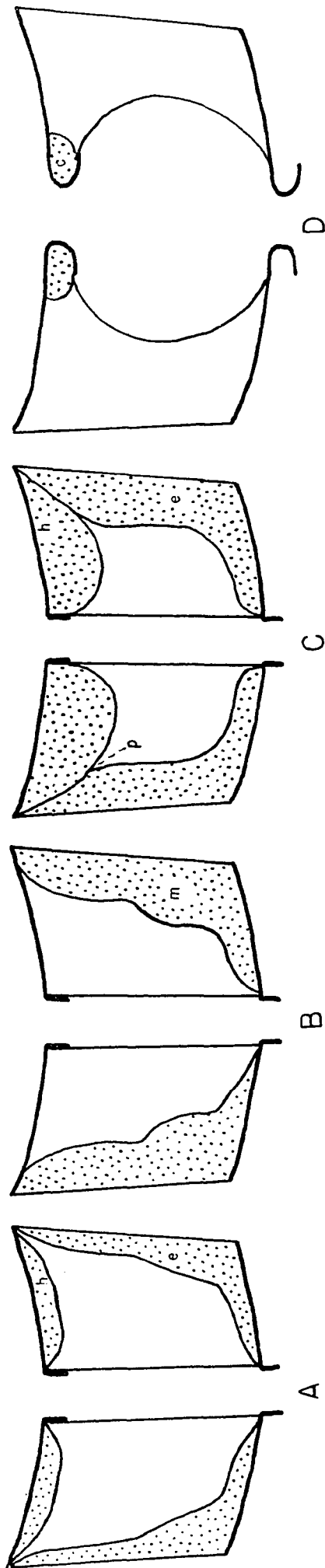
C.- curculus

e.- episeptal deposits

h.- hyposeptal deposits

m.- mural deposits

p.- pseudoseptum



Paleont., vol. 22, no. 76, 1936, p. 17.

term had been used for the prosiphonate Ammonoid necks.

The circulus is never developed in the Pseudorthoceratidae, and so far known only from the Actinoceroidea. Most of the Pseudorthoceratidae have mural deposits, but instances are known in which episeptal and hyposeptal deposits are developed. This occurs in Euloxoceras, Cayutoceras and in Adnatoceras ciscoense Miller Dunbar and Condra. Euloxoceras is derived from Adnatoceras in post-Devonian time, and A. ciscoense is closer to it stratigraphically than to any other known species of Adnatoceras. It is suspected that the similarity of the cameral deposits represents a genetic relationship in this instance. Cayutoceras is not related to the other two, and the appearance of hyposeptal deposits, in the presence of which mural deposits become episeptal, is entirely independant.

Numerous authors have referred to a pseudoseptum within the camerae of cephalopods. If the term is to be used at all it should be confined to the line running from the outer apical corner of the camera apicad and centrad, which marks the point of contact of episeptal and hyposeptal deposits when both are strongly developed. This line never attains the siphuncle, as the deposits are discrete in the central portion. The term pseudoseptum has been used improperly for a line along which inorganic deposits meet ,

as well as for limonitic bands which represent the margin of episeptal or mural deposits in the camerae. (Fig. 8C)

Teichert noted that deposits were normally heavier on the venter than on the dorsum. Cross sections of the camerae show this unequal distribution in all forms, but it is especially marked in orthochoanitic forms where the inner surface of the cameral deposits is complexly lobed. The best specimens on which to study this lobation are those which by weathering, exfoliation or dolomitization have lost the shell and the cameral deposits, and which retain the molds of the deposits. Such specimens show a characteristic pattern of lobes, striae and bosses on the internal mold. The details of the sculpture are of specific value, though more general features may be characteristic of higher groups, and a general pattern can be postulated which will hold for most stenosphonate cephalopods with mural deposits. The pattern exhibited by Striacoceras typsu (Saemann) of the Cherry Valley limestone has already been described and illustrated.³⁹

39. Flower, R.H., Cherry Valley Cephalopods, Bull. Amer. Paleonto., vol. 22, 1936, p. 310, pl. 24, fig. 3; pl. 25, fig. 3-5, 7.

Hall⁴⁰ has figured numerous specimens representing

40. Hall, J., Paleontology of New York, vol. 5, pt. 2, 1879, pl. 35, fig. 5-6; pl. 81, fig. 122; pl. 112, fig. 11-15

various species from the Schoharie grit of the Middle Devonian of New York, which show similar but not identical phenomena, and among Barrande's illustrations in his *Système Silurien du Centre de la Bohême* there are examples too numerous to cite.

A similar though somewhat more generalized pattern may be seen in orthoceraones of the Richmond which are referable to the genus Ormoceras.

The mural lobation shows several persistent features which may be summarized as follows:

1. A persistent ventral sinus which will appear as a ridge on exfoliated specimens. (Fig. 8, V.)

2. Ventro-lateral masses.— These are massive and variously lobed, and flank the ventral sinus. In exfoliated specimens these regions are often quite complexly lobed or pitted on the surface. (Fig. 9, vl.)

3. Dorso-lateral bands.— These are relatively thin bands of deposit in comparison to the ventro-lateral masses, and normally present a transversely banded surface in exfoliated specimens. The transition between the dorso-lateral bands and the ventro-lateral masses is usually abrupt, especially in the early stages of the development of the mural deposit, but it is occasionally poorly defined, and in Ormoceras the two regions are not well differentiated. (Fig. 9, dl)

4. The dorsal hiatus.— This is a small area on the

Fig. 9. Cross sections through the cameras of
Pseudarthoceras, showing the radial distribution of
deposits. A. Immature deposits. B. Mature deposits.

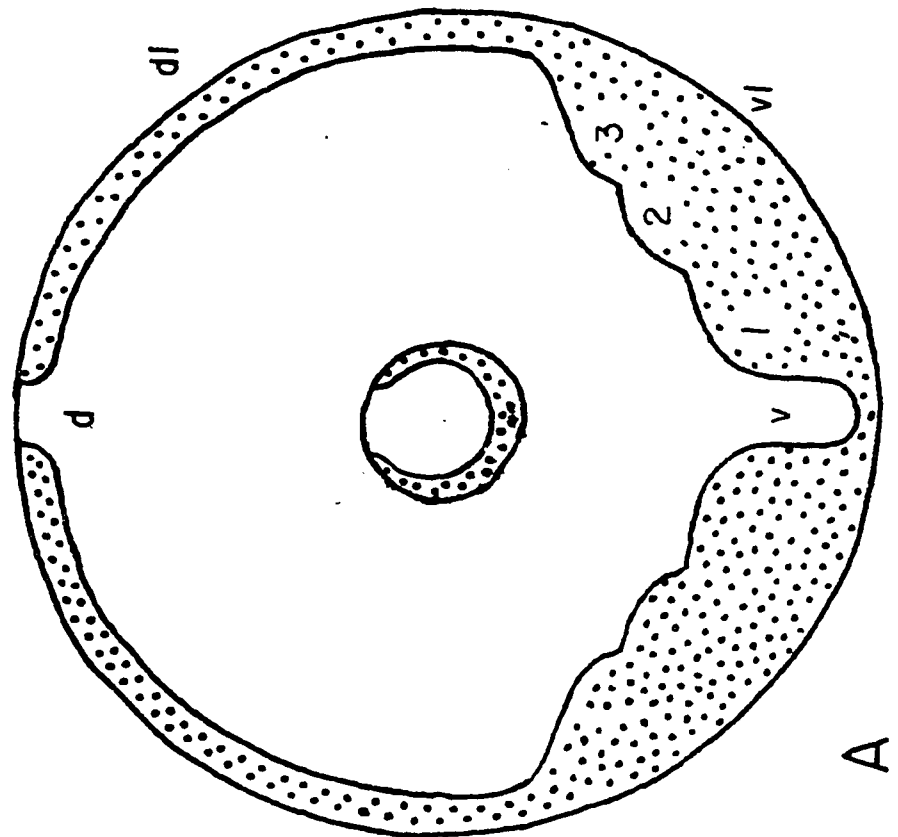
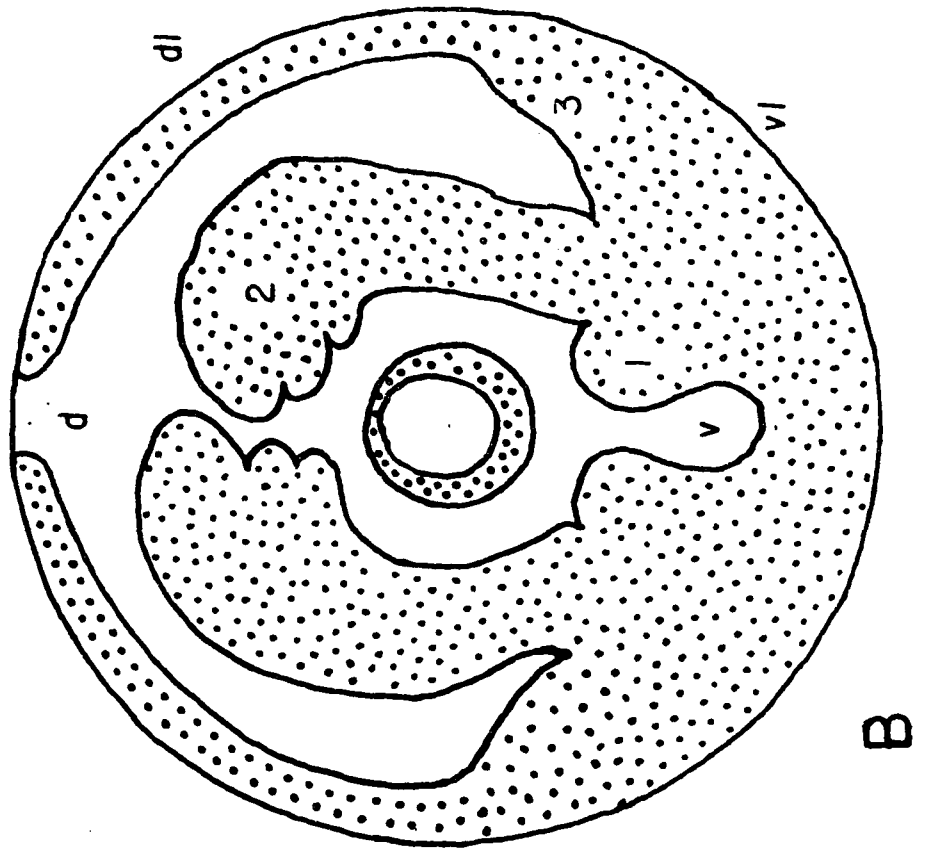
d.- dorsal hiatus

dl.- dorso-lateral bands

vl.- ventro-lateral masses

v.- ventral sinus.

1,2, and 3, indicate the first, second and third pair of
lobes of the ventro-lateral masses.



mid-dorsal region, not always extending the length of the mural part of the septum, in which no deposits are laid down. It is, when localized, confined to the adoral portion of the mid-dorsal region of the camera. In position it agrees precisely with the septal furrow, but is a structure of the cameral deposits rather than of the septum. (Fig. 9, d)

In Pseudorthoceras knoxense the ventr-lateral masses are obscurely trilobed in the early stages of development. In the later stages the two outer lobes become obscured, and the inner pair of lobes become greatly produced and nearly surrounds the siphuncle. (Fig. 9 A-B)

It has not been possible to make a detailed study of the lobation of the deposits in any of the Pseudorthoceratidae except Pseudorthoceras knoxense, owing to the limited amount of material available. Dorso-ventral differentiation of the deposits is shown on exfoliated specimens of Dolorthoceras, Adnatoceras, and Sceptrites, and complex sculpture is indicated throughout. In sectioning D. palmerae (Flower and Caster) it was evident that the lobes derived from the ventro-lateral masses nearly surround the siphuncle, as in Pseudorthoceras. Exfoliated specimens of Pennsylvanian species of Mooreoceras have shown the four main regions noted above. The condition of the lobation of the deposits of Euloxoceras, Adnatoceras ciscoense and Cayutoceras is unfortunately unknown, so it is not certain whether the

same radial pattern is retained when hyposeptal deposits appear in the Pseudorthoceratidae.

Investigation of the radial distribution of cameral deposits in other groups of cephalopods is still very incomplete. There is indication of a considerable diversity of structure, but data are at present inadequate for evaluation of the genetic significance of the characters supplied. Quite a distinctive pattern may appear when hyposeptal deposits appear, the main feature of which is a massive mid-ventral deposit. This occurs in *Elrodoceras*, where episeptal and hyposeptal deposits join on the mid-ventral region at a very early stage. In *Leurocycloeras* a similar though more elaborate pattern is developed. *Michelinoceras* (?) *ludlowense* (Miller and Faber) of the Trenton of Kentucky, develops mid-ventral hemispherical bosses on the mural part of the septum, and concentric striae surround the protuberances. These will be described and illustrated in detail at another time.

Ontogeny

The deposits of the camerae, like those of the siphuncle are serially arranged structures and follow the principle of localized stages of development in thier growth. All undergo a similar development at a nearly uniform rate until a mature condition is attained. Thus in any species in which deposits are developed the phragmocone may be divided into three regions:

1. A region of empty camerae near the living chamber.
2. A region in which deposits are exhibited in successive stages of growth as they are traced apicad.
3. An adapical region, which is increased as the shell grows, in which deposits are mature and undergo no further change. A similar series has been shown for the siphonal deposits. Two main features hold throughout the deposits and are believed to be of fundamental importance:

1. The first trace of cameral deposit is found some distance from the base of the living chamber, and the number of septa between the first trace of deposit and the living chamber is constant for the growth stage within the species. Often this is constant within the species except for the very earliest stages of growth. Certainly it holds for all moderately developed individuals in a considerable number of species.

2. The dorso-ventral differentiation of the cameral deposits varies directly with the distance of the siphuncle from the venter. In species with markedly ventral siphuncles the amount of material secreted against the dorsal and ventral walls may vary only slightly. In species with central siphuncles the dorso-ventral differentiation is more marked, but it reaches its climax in such forms as Euloxoceras, in which the siphuncle lies dorsal of the center of the conch. In Actinoceroids an additional factor is to be seen, for

the dorso-ventral differentiation of the cameral deposit varies inversely with the size of the siphuncle.

Microscopic Structure of Cameral Deposits.

In general the aragonitic portions of the molluscan shell show in section in thin section two kinds of markings, lines of growth which represent successive secreting surfaces, and lines oblique, or perpendicular in some sections, which represent the rows of aragonite prisms. Such structures are known in the shell of Nautilus pompilius, Aigoceras planicosta, and in the guard of Belemnites.⁴¹

41. Cayeux, M.Y., Introduction a l'étude petrographique des roches sedimentaires, Memoires pour suivre & l'explication de la carte geologique detailee de la France, Paris, 1931, p. 490-493; pl. 54, fig. 3-6.

The organic deposits of the siphuncle and camerae of Pseudorthoceras knoxense retain similar markings under favorable conditions of preservation. Both types of markings have been retained on specimens from the Hazleton Bridge member⁴² of the Upper Pennsylvanian of Indiana. (Pl. 1, fig. 6)

42. Mallot, C.A., in manuscript.

Normally only the lines of growth are preserved, but they may be very clearly shown on silicified specimens.

The fine structure is not in itself diagnostic of the organic nature of the cameral deposits, which is established

on other grounds. Such marking in an organic structure are apparently original and indicate that the cameral and siphonal deposits were formed by mantle secretion as are the wall of the conch and the septa.

PART II
SECRETION OF THE SHELL ELEMENTS

TYPES OF SHELL SECRETION

An attack from a physiological point of view may serve to clarify the problems relating to the calcareous deposits of nautiloids under discussion. In all Nautiloidea calcareous material is secreted in three regions:

1. The secretion of the wall of the conch at the tip of the mantle forming the two outer layers of the shell, and supplemented by the secretion of the thin nacreous layer in a slightly posterior region.

2. The secretion of the septa at the posterior end of the visceral mass.

3. The secretion of the connecting ring by tissues of the siphon.

In orthoceracones two other types of deposit appear:

4. The deposits of the siphuncle, secreted by siphonal tissues.

5. The deposits of the camerae, secreted by cameral tissues.

On the basis of composition, the shell elements may be divided into two categories, mantle deposits and connecting ring deposits.

The connecting ring differs from all other structures of the Nautiloid shell in being composed of loosely

arranged spicules of calcite. Its origin in *Nautilus* seems to have been given no attention. However, a survey of other spicular structures in the animal kingdom shows a mesodermal origin throughout. The silicious spicules of the Porifera are the product of cells in the jelly-like layer; the spicules of the Alcyonaria are formed in the mesoogloea. The spicular elements of the skeleton of the Echinodermata are mesodermal, as are the primitive elements of the chordate skeleton. This analogy, one which holds throughout the animal kingdom wherever a study of the soft parts has been made, indicates that the connecting ring of the Nautiloidea may be of mesodermal origin. Further, this is consistent with what can be reconstructed of the tissues of the phragmocone on the basis of a study of calcareous structures and propitiously preserved carbonaceous remnants of tissue. Whether the connecting ring of *Nautilus* is still actually formed within tissue or not, is hardly a determining factor. Nautilus is the last survivor of a long line which has had no need of cameral tissue since the close of the Paleozoic, and possibly not since the close of the Ordovician.

Yet in this long interval cameral tissues have not been entirely lost, although they have apparently come to be somewhat modified. Teichert⁴² mentions the occurrence

42. Teichert, C., Der Bau der actinoceroiden Cephalopoden, Paleontographica, 1933, bd. 78, Abt. A, pp. 186-188.

of tissue on the adoral side of the camera. Traces of such tissue can be seen in any recently sectioned Nautilus, and traces of dendritic structures which appear to have been blood tubes can be made out in the. Unfortunately the origin and physiology of the tissue in Nautilus have not been studied, and the very existence of such tissue is but rarely mentioned. Indeed, there appears to have developed among zoologists a widespread conception of the connecting ring as a structure formed around the siphon, with apparently no tissue outside of it. Parker and Haswell are⁴³

43. Parker, T.J. and Haswell, W.A., A text-book of zoology, vol. 1, 1910, p. 776, Macmillan, London.

among the few who have not fallen into this error. Though the connecting ring is not mentioned as such, they state that the siphuncle, here used synonymously with the siphon, has its wall supported by scattered spicules of lime.

Aturia is a significant reminder of the specialization which have come to pass in the Nautilidae, which are far from being a static group. Miller⁴⁴ has recently shown

44. Miller, A.K., Beiträge sur Kenntniss tropischamerikanischer Tertiärmollusken. VI. Some Tertiary nautiloids from Venezuela and Trinidad. Ecologiae geologicae Helvetiae, vol. 30, no. 1, 1937, p. 65-67, text fig. 3, pl. 9, fig. 5.

that in Aturia there has been a remarkable elongation of both the septal neck and the connecting ring, with the result that for some distance the connecting ring lies close between two septal necks. It appears impossible under such conditions that there could have been any living cameral tissues. Further, the connecting ring is so closely appressed between the two septal necks that its original condition, that is, secretion within a tissue which encloses it, would have been patently impossible.

Nautilus furnishes some evidence which is reassuring, such as the presence of cameral tissues and the enclosure of the connecting ring in tissue, but it is hardly a reliable guide in explaining the structures of fossil forms. This is only in part because of the meagre knowledge of Nautilus as an organism, the lack of study of features of the conch with special reference to their function, origin and relation to the soft parts, and the contradictory nature of the observations so far recorded. It is very largely because it is by no means as certain as we would like to believe that what holds true for Nautilus should hold true for its Paleozoic forbears. For example, the

peculiar localization of the retractile fold of the tentacles of Nautilus is doubtless a specialization as was suggested by Dean,⁴⁵ and is hardly a valid basis for the

45. Dean, B., Notes on living Nautilus, American Naturalist, vol. 35, 1901, pp. 819-837.

homologization of the tentacles of Nautilus with the sucking discs of the Dibranchiata. Nautilus is the last survivor of a long line of coiled cephalopods which by reason of their form and mode of life have probably never had need of cameral deposits. Indeed, as will be discussed later, there is some reason to doubt whether such forms are directly descend from orthoceracones with cameral deposits.

In direct contrast to the connecting ring which is endoskeletal and serves to support the siphonal strand within the camerae, are the mantle secretions. These are aragonitic, showing in thin section lammellae of growth and growth and vertical, or occasionally oblique markings, indicative of rows of aragonite prisms perpendicular to the surface of secretion. Such structures are formed outside the membranes from which they originate, membranes which we propose to designate as mantles, appropriating a term which has originally a considerably broader connotation. In this category fall all of the shell structures except the connecting ring.

The molluscan mantle originates from the ectodermal

epithelium of the larva. Morphologically it is the dorsal covering of the primitive mollusc. It is differentiated from the remainder of the ectodermal epithelium mainly by its ability to secrete a shell. This is not constant, for not only are there numerous examples in which the mantle fails to secrete a shell, but there are also numerous instances in which shell material is secreted by the foot, as in the case of the gastropod operculum. Probably ap-tychi and anaptychi of cephalopods are similarly formed.

The present discussion is concerned mainly with the physiological aspects of the mantle and its various regions and modes of secretion. It is convenient to designate several significant regions which may be summarized as follows:

1. The terminal mantle which is responsible for the secretion of the wall of the conch.
2. The posterior mantle which is responsible for the secretion of the septa.
3. The siphonal mantle which is responsible for the secretion of annulosiphonate deposits within the siphuncle.
4. The cameral mantle which is responsible for the secretion of cameral deposits.

Only the cameral and siphonal deposits have a direct bearing on the interpretation of the calcareous deposits formed within the phragmocone. As no such material is secreted within Nautilus or any other nautilicone for that

matter, all that is known of these mantle surfaces is derived from the calcareous deposits in other groups and whatever analogies can be found with the terminal and posterior mantles.

THE TERMINAL MANTLE

The name terminal mantle is proposed for the portion of the mantle which is responsible for the secretion of the shell wall. It constitutes the margin of the true mantle, and is responsible for the addition of shell material at the aperture. A brief discussion of its rather variable properties may serve as a basis for a knowledge of the secretion of calcareous structures elsewhere in the phragmocone.

The molluscan periostracum is commonly secreted in a terminal groove of the mantle. The main part of the shell, the prismatic layer or layers as the case may be, is commonly secreted by the region of the mantle directly proximal of the terminal groove. The thin nacreous film is secreted over a wider area. In Nautilus this layer is very thin. In orthoceracones it is probably this layer which is thickened to form the gerontic constriction of the internal mold, although no orthoceracones sufficiently well preserved to permit a study of the shell wall at this point by means of thin sections have yet been found, and it is therefore not possible to test this suggestion.

The secretion of the shell wall may be continuous, or

it may be more or less intermittent. In forms with fine regular growth lines and smooth shells it appears that the terminal mantle was active constantly, and at a constant rate throughout the life of the organism.

Periodic alternating stages of rest and secretion are found in Geisonoceras, sensu strictu. Here prominent bands ending apically in slightly elevated areas and containing on their surfaces fine lines of growth, obviously represent the product of a period of secretion.

The acme of periodicity is to be found in coiled forms of the Devonian represented by such forms as Cophinoceras Hyatt, Rhyticeras Hyatt and Tetranodoceras Flower. Here the aperture is produced at the end of each period of secretion into patterns of frills and spines. During the resting stage the terminal mantle is withdrawn or resorbed, and the next cycle of secretion begins with the addition of material within the tip of the last aperture. Almost identical phenomena are common in the gastropoda.

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Ruedemann has shown that in Orthoceras cf. trans-

46. Ruedemann, R., Observations on the mode of life of primitive cephalopods, Bull. Geol. Soc. Amer., vol. 32, 1921, p. 319-320.

versum S.A. Miller, a species which probably falls in the genus Geisonocerina Foerste, there is a crowding of growth lines at regular intervals which corresponds to the distances

between the septa. The writer has noted the same phenomenon in an undescribed Geisonocerina from the Onondaga limestone of New York. In the same publication Ruedemann called attention to the synchronization between septa and internal annulations in Orygoceras, and between septa and annulations in Protocycloceras, and suggested that annulations may have originated on the inside of the shell by absorption. He suggested that this may have been due to the necessity of gaining more room in the living chamber for the voluminous sexual products. The main objection to this hypothesis is that the annulations, even those of Orygoceras, are apparently formed at the aperture. Certainly they are found on living chambers of the genus near the aperture and too far forward to have been caused by resorption at the posterior end of the living chamber where the sexual organs are located in Nautilus.

The correlation between septa and growth lines of Geisonocerina is analagous to the development of annuli in some annulated forms. Where in some instances a correlation is possible between septa and annuli. In many instances however, no such correlation is possible. Annulations are developed independantly many times in the Nautiloidea. They are one of the devices which are particularly characteristic of shelled forms which must have lead an essentially pelagic existence, though they are not confined to thin-shelled forms.

(1)

Annulations in most cephalopods are clearly modifications of ornament and shell forms, resulting in a corrugation which adds greatly to the strength of the shell without increasing its weight materially. Annulations appear many times in the development of the Nautiloidea alone, and it is not impossible that different physiological and ecological factors may have produced similar results in different lines of descent. The development of annulations in Spyroceras is essentially ecological, for Spyroceras, sensu strictu was almost certainly pelagic or planctonic, as is shown by its reduced deposits of camerae and siphuncle, and also by its prevalence in strata in which the associated fauna is made up entirely of pelagic forms. The large Dawsonoceras of the Silurian is harder to visualize as an active swimmer, but its exceptionally wide range, without any geographic localization of variations is suggestive of a nectonic rather than a benthonic organism.

THE POSTERIOR MANTLE

The posterior mantle is the surface which is responsible for the formation of the septa. As its name implies, it occupies the posterior surface of the visceral mass as oriented in the typical orthoceracone. Yet the posterior mantle and the septa which it secretes are really dorsal in position with reference to the orientation of the

primitive cephalopod. The enteron of the cephalopod forms a U-shaped canal which is indicative of the drawing together of the oral and anal extremities. This has been accompanied by the reduction of the true foot, the homologue of the gastropod foot, to a semi-internal organ, while the original dorsal surface is greatly increased. The vital organs are still dorsal, and correspond in position to the visceral hump of the gastropod. In the gastropod, as secretion of the terminal mantle increases the shell, there is an increase in the length of the visceral mass. In the cephalopod, however, the visceral mass does not increase, but moves forward in the conch, or ventrad, if the primitive orientation is to be retained, while septa are secreted at rhythmic intervals. Only the siphuncle increases materially in length as the shell grows.

It has been suggested that the large siphuncular cavity of certain early Paleozoic cephalopods, particularly the Endoceroids and Piloceroids, may have served as receptacles for glandular or sexual organs. The main vital organs of the gastropod are confined to the body whorl, while the liver and gonads occupy the spire. Perhaps a comparison between the gastropod spire and the siphuncle of certain early cephalopods is rash, but it is at least very suggestive and tends to support this proposal.

From the complete absence of thin or incomplete

septa at the base of the living chamber. in nautiloid shells, it would appear that the septum was secreted rapidly, and that short periods of secretion alternate with long periods of inactivity of the posterior mantle. This has recently been corroborated by a study of Nautilus.⁴⁷

47. Pruvot-Fol, A., Remarques sur le Nautil, C.R. XII^e Congrès International de Zoologie, Lisbonne, 1935, pp. 1652-1663, Lisboa, 1937.

In general there is a definite rhythmic pattern in the formation of the septa. The ratio of the diameter of the conch to the spacing of the camerae has become an important and extremely useful specific criterion in nautiloids. Usually the septa are slightly farther apart in the neanic stage in proportion to the diameter than in the ephebic stage, while the gerontic stage is marked by very closely spaced septa, usually more or less irregular in arrangement. This is suggestive of a rapid rate of growth of the shell in the neanic stage, and a gradual retardation in the ephebic stage, followed by very marked and often abrupt retardation in the gerontic stage. Such a statement can only be made, however, on the basis of an assumption that the septa are secreted at regular rhythmic time intervals throughout the life of the organism. While there is no direct evidence that this is so, it is consistent with what can be learned of the rate of secretion by the

spacing of the growth lines.

Though the spacing of the septa has come to be a useful criterion for specific determination, it is not always a reliable one. Minor and erratic variations are not uncommonly met with, but can usually be recognized as such. The study of a large series of specimens of Striacoceras typus (Saemann) of the Cherry Valley limestone has shown that practically all the long-used specific criteria, such as the spacing of the septa, the rate of expansion, and the position of the gerontic features of the conch, may vary markedly within a single species. To what extent this may apply to cephalopods of other horizons and regions is uncertain, and can only be determined by the study of a large series of specimens in each instance, a task which is often impossible owing to practical difficulties in the accumulation of suitable material.

The rhythmic nature of septation has been recognized but no adequate explanation has been offered. The voiding of sexual elements should be periodic and might affect the secretion of the septa; but here we might further expect to find a widespread sexual difference owing to the differences has been found in the Nautiloidea with a very few possible exceptions. In the early stages of the Actinoceroidea there may be found such differences which might be attributed to sexual dimorphism as was suggested by Kobayashi.⁴⁸ According to his hypothesis forms now

48. Kobayashi, T., Contributions to the study of the apical end of the Ordovician nautiloid, Japanese Jour. Geol., Geogr., vol. 14, no. 1-2, 1937, p. 1-21, pl. 1-2.

regarded as specifically distinct may represent sexes of the same species. Practical difficulties arise in the inability thus far to correlate "species" into pairs, and also the complete absence of one sex, and that presumably the female, in the Cape Calhoun series of Northern Greenland. Further, in possible sexual forms of brevicones there is some difference in the depth of the camerae, but this is involved with so many other variations in form that it is hardly significant in itself. Variation of this sort appears to be the exception rather than the rule, and it appears that the explanation of the rhythmic nature of septation must be sought elsewhere.

THE CAMERAL MANTLE

Evidence of Cameral Mantle

Once it is demonstrated that the deposits within the camerae are organic in origin, the problem of the mode of their secretion arises. They are formed in closed camerae, often far from the living chamber; they agree with the nautiloid shell in microscopic structure; they are complexly lobed, the general pattern of the lobation

is bilaterally symmetrical and its finer details furnish characters of specific value.

Chemical deposition can be safely eliminated, and will be discussed below in the section dealing with shell morphology. There is no inherent property of the interior of the camera which can explain the specific lobation, nor can it be accounted for on the basis of any property of a hypothetical cameral fluid. The only remaining possibility, the one which is the simplest and the most obvious, particularly in the light of the microscopic structure, is that the deposits must have been formed by a living tissue capable of secreting calcareous material, probably in the form of aragonite. For this tissue, which there will be some occasion to discuss, the term cameral mantle is proposed.

Evidence of the tissue itself is only rarely to be met with in nautiloids. ⁴⁹Teichert has figured and discussed

49. Teichert, C., Einige actinoceroide Cephalopoden aus Dänischen Diluvialgeschieben und aus dem Gotlandium Skandinaviens, Meddelelser fra Dansk Geologisk Forening, Bd. 8, hefte 4, 1934, p. 374 ff., pl. 8, fig. 1-2.

a specimen of Armenoceras danicum Teichert in which invading matrix has broken the connecting rings and has forced its way into the camerae. Its progress was stopped before the camera was completely filled, apparently by some substance

which was later destroyed, for the remainder of the space is occupied by infiltrated calcite. As Teichert suggests, this obstruction must have been caused by a tissue which was still preserved when the conch was buried, but which later decayed, leaving a cavity which was finally filled in by inorganic infiltration. I have observed almost identical phenomena in various specimens and species of Ormoceras in the Richmond.

An even more striking example of the obstruction of invading matrix by cameral tissues is shown in an undescribed species of *Rayonnoceras* from the Chester of Indiana. The conch rested on the ventral or siphonal side. The connecting rings have been destroyed, and sediments from the siphuncle have invaded the camerae. Further, the wall of the conch is broken on the dorsal side, so that sediments have entered one of the camerae from above. Gravity would cause the sediment entering from above to mingle with that entering through the siphuncle, but the two are separated by an area of calcite which must, as in Teichert's specimen, indicate the presence of a tissue which was present at the time when the conch was buried and filled with matrix, but which has later been destroyed. This specimen will be described elsewhere in detail.

Further evidence of the cameral mantle may be found in unbroken camerae. An undescribed species of *Geisonoceras* from the Onondaga limestone of New York which has been

figured by Teichert,⁵⁰ retains perfect camerae in the

50. Teichert, C., Der Bau der actinoceroiden Cephalopoden, Paleontographica, Bd. 78, Abt. A, 1933, p. 182, fig. 33, pl. 13, fig. 44, 46.

adapical end. Episeptal and hyposeptal deposits are present, and are represented by white calcite. The cavity within the camerae is occluded by light calcite, but there is a layer adjacent to the organic cameral deposits which is highly carbonaceous. The carbonaceous material is undoubtedly derived from a tissue, and must represent a structure present within the conch before burial and infiltration occurred. It may or may not be significant that the carbonaceous band occupies the position postulated below for the cameral mantle or physiological and morphological grounds.

Form of Cameral Mantle

It is very doubtful whether any of the calcite-filled areas representing the position of the cameral mantle at the time of burial of the conch preserve either its original form or position. Some time doubtless elapsed between the death of the organism and the burial of the shell. Decay had removed the visceral mass and the siphon. The camerae were open either through the broken connecting ring, the broken wall of the conch or both, and doubtless

decay had affected the cameral mantle, separating it from its deposits and altering its original form. There is little in such specimens to indicate regularity of form or position. Only in camerae which remained closed and in which the probable course of the mantle is indicated by carbonaceous material is there any reason to suppose that either the original form or position have been retained.

Certain inferences can be drawn concerning the original form of the mantle from the nature of the deposits of the camerae. Gas must have been present in the camerae, or the orthoceracone could hardly have lived as nection or plancton, as some of them are known to have done. If gas was present in a camera, it must have lain either in a vacuolate inner layer or in a cavity surrounded by the cameral mantle. Vacuolate tissues are generally primitive, as is the vacuolate pseudocoelom of the Nemathelminthes, and are not to be expected in such highly organized forms as the cephalopods. The cameral mantle must have lain against the concave adapical wall of the camera, both against the free and mural parts of the septum, for episeptal and mural deposits were formed in those regions. It must have lain against the convex adapical wall, at least in those species possessing hyposeptal deposits. Lastly, it must have lain against the outside of the connecting ring in order that an exchange of metabolic materials could take place with the siphon.

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The cameral mantle was a secreting tissue, and as such was active metabolically. It required ingredients for its deposits. Such ingredients are unconsolidated; the materials which would constitute a mature deposit such as that of Pseudorthoceras knoxense would require a space larger than the camera. Further, were such ingredients present in the cameral mantle, the calcareous materials should so strengthen it that it would be frequently preserved. As has been seen, it is infrequently preserved, and then only poorly. Further, the mantle itself would have required food for nourishment, since it was highly active metabolically, and all of the waste materials could not have been eliminated in the form of calcareous deposits or as gas within the camera; certain substances must have been eliminated through the usual excretory channels. Obviously the mantle must have been connected with the rest of the organism. The only possible connection is through the connecting ring with the tissues of the siphon which join directly to the visceral mass. That such a connection existed is shown by the relationship which obtains between cameral and siphonal deposits, and by the vascular system of the Actinoceroidea, which admits of no other interpretation. The presence of an apparently rather solid connecting ring has seemed a serious obstacle to the acceptance of such a belief. An exchange of materials might take place by osmosis through a permeable connecting ring. However, it may be that there

is a much more direct and simpler connection. The connecting ring of Nautilus is composed of loosely placed spicules of calcite, arranged in stellate patterns and held together by organic matter. All thin sections of connecting rings of fossil forms which I have examined show a spongy texture, and often the cavities of the connecting ring are clogged with fine invading sediments. It seems probable that the pores of the connecting ring were large enough to permit capillaries to pass directly through the ring into the cameral mantle. The vascular system of the siphon in its primitive condition was made up of numerous fine tubes in a parenchymous tissue. There are no radial tubes in any of the Pseudorthoceratidae except Paraloxoceras which were large enough to be preserved embedded in calcareous deposits. The Actinoceroidea alone have a complex system of radial canals, and this group is admittedly highly specialized. Most orthochoanitic forms show no vascular structure. Only in one small group of forms is there even a trace of a central canal. The capillary vessels which passed through the connecting ring doubtless continued without modification into the cameral mantle.

Origin Of The Cameral Mantle

Another problem which must rest to some extent upon conjecture is the origin of the cameral mantle. There are two possibilities: an origin by lateral proliferation from the siphonal strand, and an origin from the posterior mantle at the time when the animal moves forward in the conch. The evidence seems to favor the latter possibility. Though cameral deposits generally appear some distance from the living chamber, a few instances are known in which well defined deposits are present, though small, in the last camera, next to the base of the living chamber. It seems improbable, though it is not impossible since nothing is known of the time required for the formation of new camerae in fossil nautiloids, that a functional mantle could have been produced so readily from the siphon. Nor does a hypothesis of an origin of the mantle from the siphon explain why episeptal deposits normally precede hyposeptal deposits in their appearance. Further evidence of the origin of the cameral mantle from the posterior mantle is found in the striking similarity between the septal furrow and the dorsal hiatus. Two distinct calcareous deposits are characterized by small mid-dorsal areas where secretion does not take place; further, these areas lie adjacent to one another. This suggests more strongly that any other bit of evidence that the tissue which secreted the cameral deposits and that which secreted the

septa were one and the same, and that the cameral mantle is developed from the septal mantle which is separated from the visceral mass and left behind when it moves forward in the conch, the new septum being secreted by a fresh layer of cells.

As the visceral mass moves forward, a new segment of the siphon is formed. The tissue which is to develop into the cameral mantle is in direct contact with it, and the two were doubtless supplied by the same blood vessels. (Fig. 10A).

A question arises as to whether the part of the cameral mantle lying against the connecting ring is an outgrowth of the sloughed off posterior mantle or whether it is derived from the siphonal strand. One fact seems significant, though it has been consistently overlooked. The connecting ring is spicular, thereby differing from all other shell structures. Spicular deposits elsewhere in the animal kingdom are mesodermal with exception, save when they appear in the mesogloea or the jelly-layer which preceeds the mesogloea in primitive forms. There is no information available concerning the formation of the connecting ring in either recent or fossil cephalopods, but by analogy it should also be of mesodermal origin. It is recognized that reasoning by analogy may lead to erroneous conclusions; but in this instance there is little else to serve as guidance, and an analogy is employed which has been found to hold not in one instance, but in all

Fig. 10. Growth stages of the cameral mantle.

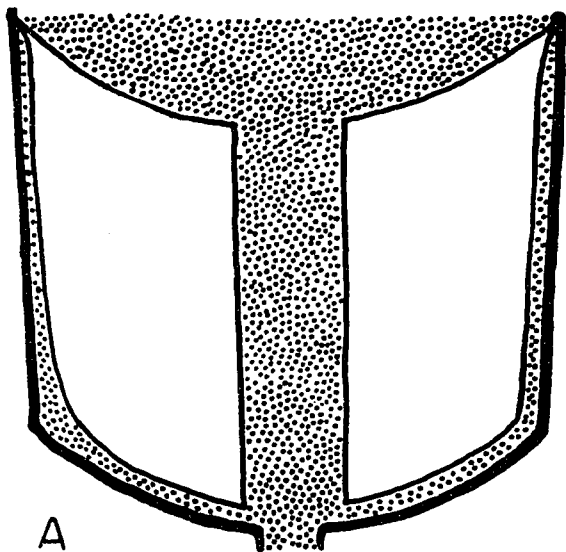
Tissues indicated by stippling; mantle secretions by black; connecting ring by dotted line.

A. The visceral mass has moved forward in the conch previous to the formation of a new septum, leaving behind the sloughed off posterior mantle, and a large siphonal strand.

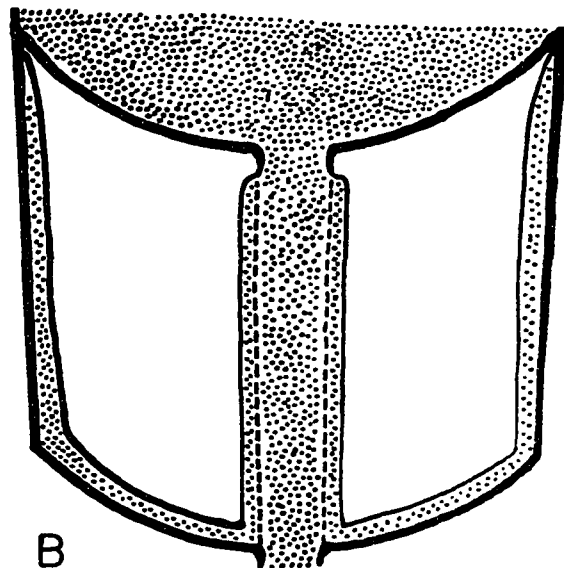
B. The new septum is secreted by the new secreting surface. The connecting ring is formed within the siphonal strand.

C. The mantle tissue of the siphonal strand extends adorally, coming into position for the secretion of hyposeptal deposits.

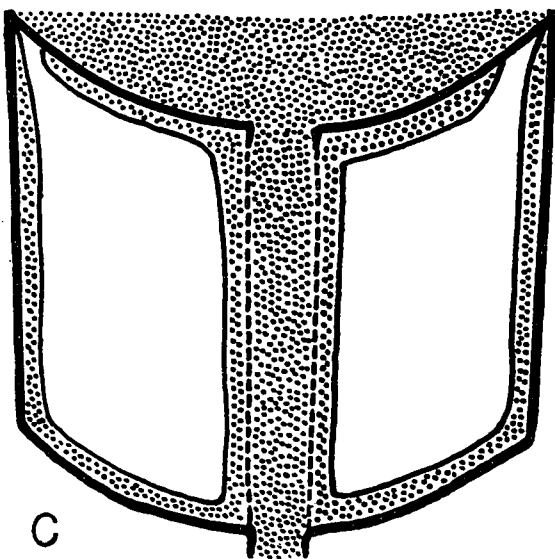
D. The growth of the mantle is completed, forming a complete lining for the camera. Episeptal deposits are being secreted.



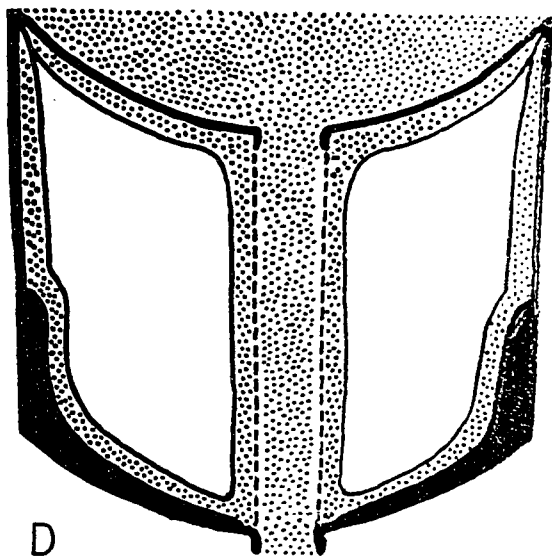
A



B



C



D

instances in which it can be applied and checked by a study of the soft parts of recent forms.

If the connecting ring was secreted inside the tissue, the strand of siphonal tissue passing orad from the bud of the cameral mantle may have formed a part of the cameral mantle, and would not have been entirely incorporated in the siphon. The spicules of calcite were placed about the fine blood vessels which had preceded them in development. (Fig. 10B).

The cameral mantle is already in position for the secretion of episeptal deposits and for communication with the rest of the organism through the connecting ring. It remains for the mantle to extend anteriorly from about the siphuncle, over the convex side of the newly formed septum, thereby coming into position for the secretion of the hyposeptal deposits. (Fig. 10C-D). This is doubtless the explanation of the fact noted by Teichert that the hyposeptal deposit normally follows the episeptal deposit in its appearance in a camera. A large number of species never develop the hyposeptal deposits at all. This fact leads to the question as to whether in such forms the cameral mantle actually extends over the adoral surface of the camera. In the Pseudorthoceratidae hyposeptal deposits are developed in Adnatoceras ciscoense (Miller Dunbar and Condra) in Euloxoceras, and in Cayutoceras. Cayutoceras is only distantly related to the other two,

while there is reason to believe that Euloxoceras must have sprung from Adnatoceras in post-Devonian, and possibly Pennsylvanian time. We have, then, in the family Pseud-orthoceratidae hyposeptal deposits appearing in two isolated instances. Were the absence of hyposeptal deposits connected with the failure of the adoral part of the cameral mantle to develop, it would be necessary to conclude that the break thus formed had been closed twice independantly. More examples of the isolated loss and reappearance of the hyposeptal deposit can be found in the Actinoceroidea, and the distribution is somewhat erratic in the orthochoanites, where as yet we have no clear guide to the phylogeny except the cameral and siphonal deposits. The evidence seems to indicate that the hyposeptal portion of the cameral mantle was present throughtout, but that it was not always active as a secreting surface.

Growth Of The Cameral Mantle

Once the cameral mantle has been formed, the further tracing of its development rests upon safer ground. It is essentially that of any other tissue. It has just been traced through a period of regional growth without any apparent differentiation of tissues other than the elements of the circulatory system which must have been present from the beginning. After the mantle is so developed as to completely line the camera, the cells in various regions

begin to undergo functional modifications. The secreting surfaces begin to develop; doubtless also the secretion of gas is a function of the inner surface of the mantle. Growth of the tissue does not cease when secretion begins; rather it continues very much as before. The surface of the mantle becomes greater, while by reason of the deposits, the areal extent of the camera is typically lessened. This is compensated for by a folding of the mantle, accompanied by regional differentiation in the rate of secretion. In this way the characteristic lobes and "ornamentation" of the interior of the deposit is developed. At length differentiation in the rate of secretion has become so great that secretion is going on only in a few isolated areas, on the crest of a few lobes of the deposit, as on the middle pair of ventro-lateral lobes of Pseudorthoceras, while it has ceased in other areas.

The final cessation of deposition appears to be the logical conclusion of a retardation of growth which at first is apparent only in certain areas, as upon the dorso-lateral bands or the ventral sinus. The apparent acceleration in other areas is probably only relative. In the Actinoceroidea and the Orthochoanites the retardation is apparently functional, as is the cessation of deposition. The siphonal and cameral tissues are not separated, and the cessation of deposition can only be explained on the basis of a physiological change in the cameral mantle.

The continuous lining of the siphuncle of the Pseudorthoceratidae, Stereoplasmoderatidae and Troedssonoceratidae presents another problem. Does this lining serve to sever the connection between the siphonal and cameral tissues and thereby control the amount of calcareous material secreted within a given camera? Or is it the deposition of material around the siphon in regions in which no exchange of metabolic materials is taking place? The fact that cessation of deposition in other groups is apparently to be attributed to physiological causes⁵¹ would

51. It has not been possible to demonstrate beyond all possible doubt that the cameral deposits in such forms completely cease to develop. Growth is reduced to a negligible quantity in the apical camerae, apparently because of the axial gradient, as is shown below in connection with the discussion of the relation of cameral and siphonal deposits.

favor the latter possibility, but it is by no means conclusive. Fortunately for the solution of the problem there is some direct evidence. In the apical segments of Pseudorthoceras there is typically a region in which the siphonal deposit is incomplete; that is, it is not closed on the dorsum, and a connection between the cameral and siphonal tissues is never completely broken. In more anteriorly located cameral mantle is cut off from the remainder

of the organism. A comparison of the two regions shows that the cameral deposits are markedly heavier where the siphonal deposit is incomplete; indeed, they practically fill the camerae, leaving only small interstices among the various lobes, and present a sharp contrast to the relatively slight development in slightly more adoral segments, which is too marked to be accounted for by the normal ontogenetic progression which is to be found in camerae with immature deposits. Further, the closure of the dorsal wall of the siphonal deposit is indicative of a mature condition. This indicates that in the Pseudorthoceratidae the closure of the siphonal wall is the controlling factor in determining the amount of stereoplasm which is secreted within the camera. From this it is concluded that the physiological relationship between the siphonal and cameral deposits is different in the Pseudorthoceratidae from that in the Actinoceroidea or "Orthoceratidae". What condition obtains in the Stereoplasmoceratidae and Troedssonoceratidae is as yet uncertain, but can doubtless be ascertained by further study of the groups.

THE SIPHONAL MANTLE

The annulosiphonate⁵² siphonal deposits were secreted

52. The present discussion is concerned only with annulosiphonate deposits. It is not certain whether actinosiphonate deposits are formed within or outside of the siphonal tissues. The deposits of the endoceroids and ellesmeroceroids, are not considered, for while they are probably mantle secretions also, they are very different in structure and were probably derived independantly.

by the surface of the siphon, which is here called the siphonal mantle. Teichert⁵³ suggested that the annulo-

53. Teichert, C., Structures and phylogeny of actinoceroid cephalopods, Amer. Jour. Sci., ser. 5, vol. 29, 1935 p. 11.

siphonate deposits of the Actinoceroidea may represent the gradual calcification of siphonal tissues. This conclusion is opposed by the form of the deposits, their microscopic structure and evidence of a mantle surface. Annulosiphonate deposits make their appearance at the septal neck, the only point at which the surface of the composite tissues of the phragmocone lies within the siphuncle. Elsewhere the connecting ring is formed within the wall of the siphonal strand, so that part of the original strand lies within the camera rather than in the siphuncle. The fine structure of the siphonal deposits of Pseudorthoceras knoxense shows

that they were similar to the aragonitic shells known to be secreted by the surface of a membrane. No siphonal deposits in actinoceroidea have been found which show more internal structure than fine growth lines, but all available specimens are pseudomorphs of calcite or other material, and recrystallization has usually proceeded to such an extent that the retention of the original fine structure cannot be expected. The same loss of structure can be seen in many specimens of Pseudorthoceras, and it is only rarely that traces of the rows of aragonite prisms are preserved.

On the basis of the form of the siphonal deposits it might appear that the Actinoceroidea and other annulo-siphonate orthoceracones represent a genetic line. The deposits of the Actinoceroidea are pendant; those of orthochoanites and their derivatives are parietal. Differentiation occurs upon the modification of a simple type, the annulus, which is common to the earliest ontogenetic stages of both types of deposit. A phylogenetic relation is suggested. Yet the ontogeny of the Actinoceroidea is such as to suggest that a relationship with other annulo-siphonate cephalopods may be more apparent than real, and that Teichert's suggestion of a relationship with the Endoceroidea, made originally upon the basis of ephebic characters, appears to offer the most nearly adequate for the placing of these singular forms in a plausible relationship with other cephalopods.

But even without a demonstrable relationship, it seems highly improbable that such strikingly similar structures as annulosiphonate deposits of the Actinoceroidea and those of the stenosiphonate cephalopods could have evolved from the structures of totally different origin. Occasionally exceptional specimens of the Actinoceroidea may show evidence of a siphonal mantle. Teichert⁵⁴ has

54. Teichert, C., Der Bau der actinoceroiden Cephalopoden, Paleontographica, Bd. 78, Abt. A, 1933, pl. 12, fig. 39.

figured a section through several radial canals of Crytonybyoceras barrandei Teichert, which shows two carbonaceous layers separated by calcite which may be organic or inorganic. The inner layer I take to represent the wall of the vascular tube, probably slightly calcified during the life of the organism. The outer layer, which is separated from the inner one by calcite, lies at the margin of the annulosiphonate deposits. It is suggestive of a mantle surface, originally continuous, which has come to be complexly lobes and folded until it comes to form a sheath for the vascular system. The outer carbonaceous layer should not appear if only the gradual calcification of siphonal tissues produced the deposit.

The siphonal and cameral mantles behave very similarly and as will be shown presently, the two are doubtless closely related, both structurally and functionally. In

both secretion begins at a definite stage in development and this can be estimated in relation to the growth of the conch by the distance from the base of the living chamber to the first trace of deposits. Both cameral and siphonal deposits appear at a definite distance from the base of the living chamber, but are usually thinner when completely formed. It is not certain whether adoral extension of deposits in the gerontic stage is widespread or whether it is confined to the Actinoceroidea. In both siphonal and cameral deposits deposition is gradual, extending over a considerable period of time, so that the developmental stages of the deposits extend over a considerable length of the phragmocone.

The growth stages of the siphonal mantle are very similar to those already discussed for the cameral mantle which have been discussed above:

1. Regional growth of the mantle from its rudiments.
2. Development of a generalized secreting surface.
3. Local variation in the rate of secretion accompanied by folding and growth of the mantle.
4. Final attainment of a mature condition and cessation of secretion.

The first stage, that of regional growth, is accomplished when the siphonal strand is developed, which must occur previous to the formation of a new camera. Deposition begins at localized areas, at the septal neck. This

is the only point at which the surface of the tissue lies within the siphuncle as was pointed out above. The deposit grows, and the secreting surface is increased. As a necessary result of the formation of annulosiphonate deposits, the endosiphuncular cavity is reduced. Reduction may be relatively slight as in most orthochoanites, or it may be great as in the Actinoceroidea. In either case the surface of the siphonal mantle is increased, and invagination occurs to a more or less marked extent. This must be accompanied by a reduction in the mass of the siphonal tissue, probably by resorption. The blood vessels remain, which are represented by the endosiphuncular vascular system of the Actinoceroidea. Other tissue is reduced, and in the Actinoceroidea is almost completely eliminated. What this tissue could have been can hardly be determined. It was certainly parenchymous and generalized; it is just possible that it may have been glandular and that the large siphuncles of the Actinoceroidea may have served for the storage of food.

The end of siphonal deposition is rarely abrupt, but may be brought about in various ways. In most Actinoceroidea deposition continues until further resorption of tissue is impossible. In most Orthochoanites there can be seen the same gradual decrease in rate of growth that can be found in the cameral deposits. In the Pseudorthoceratidae a definite mature condition is attained which

is not as easily explained; apparently the siphonal deposits attain maturity without the same gradual decrease in rate of deposition which is found in the Orthochoanites, and which suggests the axial gradient as a possible physiological explanation. All that can be said with certainty is that the appearance of a definite mature condition is reached when the deposits effectively isolate the camerae.

RELATION OF CAMERAL AND SIPHONAL MANTLES

Types of secretion patterns

Among the known annulosiphonate and related nautiloids several groups can be distinguished on the basis of the relations which obtain between the cameral and siphonal deposits if considered in terms of the surfaces of the deposits and the variations in the development of secreting surfaces within the phragmocone. It is evident that some of these groups are genetic, for they form compact units of restricted range. It is too early as yet to say that others are genetic, but they at least serve to clarify the relationships which hold between the tissues and deposits of the phragmocone.

1. Group of Geisonoceras, sensu stricto

First to be considered is a group in which the development of cameral and siphonal deposits is such that there is a single active secreting surface in the phragmocone which is continuous from one camera to the next. (Fig. 11) In all other groups the secreting surface, and therefore the outline of the deposits, is discontinuous, in one way or another. The development of episeptal and hyposeptal deposits against the outside of the connecting ring and the development of the Michelinoceras type of deposit against the inside of the connecting ring are structurally commensurate, so that the surface of the growing deposit, which is the surface of active secretion within the phragmocone, is continuous from its beginning in relatively adoral camerae, to its termination in the apical part of the phragmocone if not in the apical part of the shell. The beginning of deposition in any given camera is dependant upon the development of the secreting surface of the cameral mantle as outlined above. The cause of the cessation of deposition is more obscure. There is apparently no definite region in which deposition ceases entirely as in the Pseudorthoceratidae, or if there is one it has not been possible to detect it. In the Pseudorthoceratidae there are three well delimited areas, one of no secretion, one of developing secretion, and one of mature secretion, and the boundaries of these areas move forward in the phrag-

Fig. 11. Form of deposits of the phragmocone, relation of secreting surfaces, and supposed genetic relationship of the main types. Geisonoceras.- Continuous secreting surface.

Dawsonoceras.- Hyposeptal deposits lost.

O. brucense.- Siphonal deposits lost

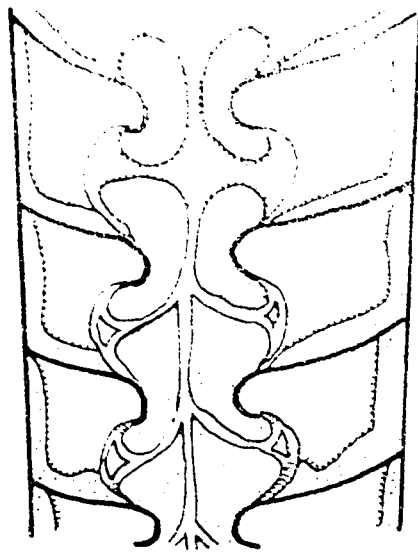
Striacoceras.- Siphonal and hyposeptal deposits lost

Virgoceras, a Pseudorthoceroid,- Hyposeptal deposits absent; siphonal deposits delayed in appearance, developed rapidly.

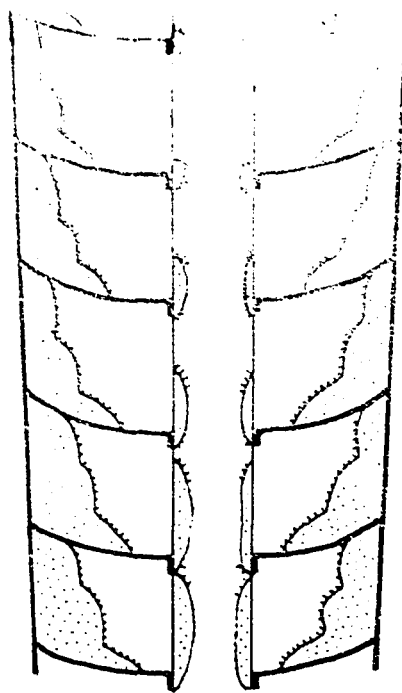
Harrisoceras.- Siphonal deposits appear early, lying in contact with ectosiphoncle only at septal neck. Central canal developed gerontically, showing in apical end.

Episeptal deposits appear after siphonal deposits, hyposeptal deposits appear still later or may be absent.

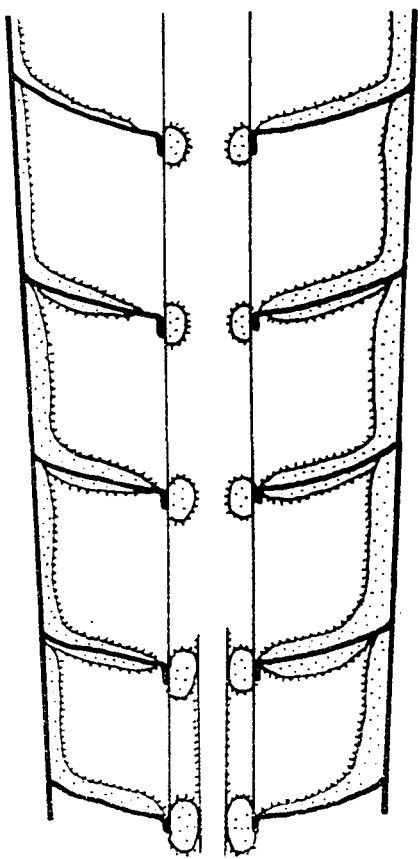
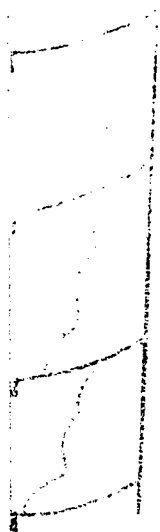
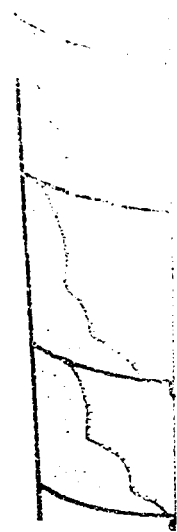
Actinoceras.- Time relationship of appearance of deposits as in Harrisoceras. Deposits pendant, practically filling siphuncle except for radial canal system. The apical siphuncular segment shows the perispatial deposit.



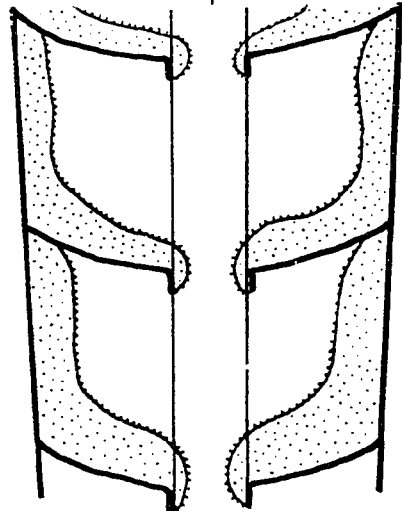
Actinoceras
(isomorphic)



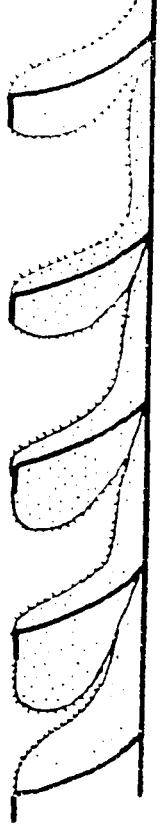
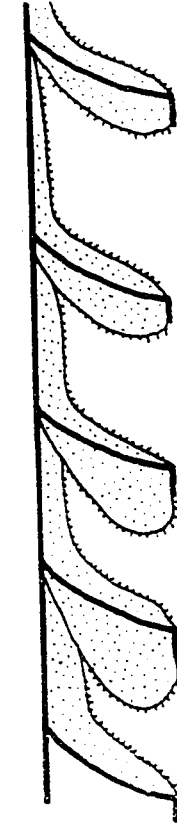
Virgoceras



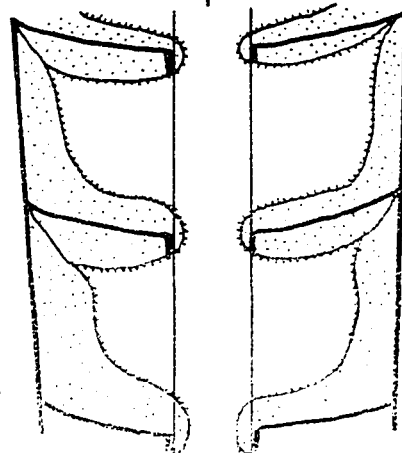
Harrisoceras



Dawsonoceras



W. brucei



Geisonoceras

mocone in an orderly procession as the shell grows at the aperture and more camerae are added at the base of the living chamber, so that the region of no secretion and the region of immature deposits are uniform, but not mathematically constant, throughout life of the organism, and the region of mature deposits is constantly being increased in extent. In the group under discussion, however, there appears to be no sharply defined boundary between regions of mature and immature deposits. In fact, it is questionable whether there is a region in which deposition has entirely ceased. It appears that deposition is rapid in the early stages, as is shown by the considerable advance in the volume of deposits in a series of adoral camerae. A marked contrast is afforded by the imperceptible difference in the volume of deposits in a series of adapical camerae, indicating that deposition there is very slow. Further, in tracing a series of camerae from the inception of cameral deposits apicad, the difference in volume of the deposits of adjacent camerae becomes progressively less as the apex is approached. Any control which may exist over deposition in the camerae is strictly physiological, and is not aided by any structural device. The gradual decrease in the rate of deposition as a series of camerae is traced apicad indicates that the controlling factor is the axial gradient. The tissues of the phragmocone which are nearest the metabolically active visceral mass are the ones which

Fig. 12. Diagrammatic representation of the essential relations between various secretions in the phragmocone, showing their relative appearance, rate of growth, and cessation of growth.

h. hyposeptal deposits

s. siphonal deposits

e. episeptal deposits

Geisonoceras.- All three deposits are uniform and form a single secreting surface. The relative time of appearance may be variable; siphonal deposits sometimes appearing slightly after the other two.

O. brucense.- Siphonal deposits are completely lost; hyposeptal deposits develop more rapidly than episeptal deposits.

Dawsonoceras.- Hyposeptal deposits are lost. Siphonal deposits normally follow episeptal deposits, which are here modified to mural deposits.

Striacoceras.- Only the episeptal deposit develops, which is here mural in form.

Pseudorthoceras.- Hyposeptal deposits are typically absent. Episeptal deposits appear and complete a considerable part of their growth before siphonal deposits appear. Completion of the siphonal deposits isolates the camera, and therefore stops the growth of the cameral deposits.

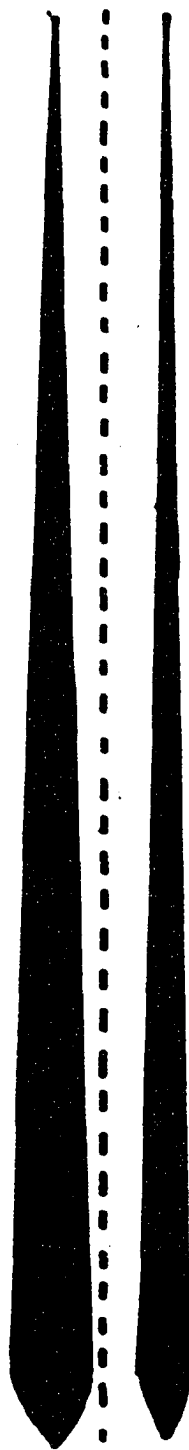
Fig. 12 Con't.

Harrisoceras.- Siphonal deposits appear first and are well developed before deposits in the camerae appear. Hyposeptal deposits normally follow episeptal deposits, but may be entirely wanting.



h s e

Geisonoceras



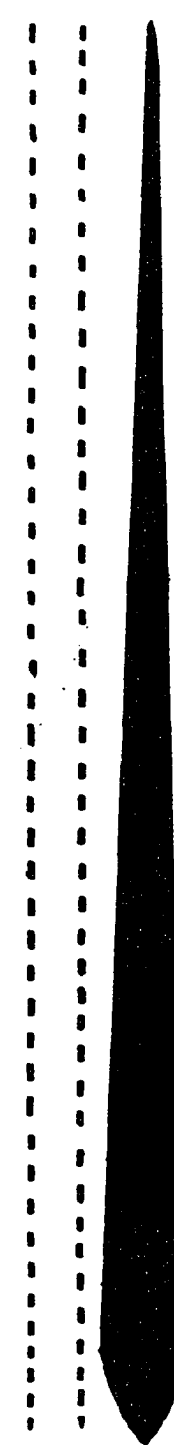
h s e

O. bruce



h s e

Dawsonoceras



h s e

Striacoceras



h s e

Pseudorthoceras



h s e

Harrisoceras

receive the most nourishment from the blood stream of the siphon, and the amount of nourishment and the speed of development in any camera varies inversely with the distance from the living chamber.

This type of structure is widespread in orthochoanitic orthoceracones, though it is far from including all forms. It occurs in the genotypes of Michelinoceras Foerste and Geisonoceras Hyatt; it is present in some but not all Protokionoceras. The type of structure is well developed in forms of Middle Silurian age and persists at least into the Middle Devonian. It is a generalized type of structure and a simple one, but it is apparently not primitive on purely stratigraphic grounds, for the structures have not been observed in Chazy or Trenton Orthochoanites, in spite of careful examination of numerous individuals and a considerable number of species with their particular features in mind.

It should be emphasized that this type of structure runs across genera as recognized on the basis of ornament, and does not include all species placed in those genera. But there is little variation in the structural pattern, and the group seems to be rather well limited stratigraphically, suggesting that it may represent a closely knit genetic group, and that the internal structures are more reliable guides to genetic relationship than the surface ornamentation.

The other types differ from the above in that the continuous secreting surface is interrupted in some way, and there are a number of different ways in which it has been done.

2. Group of "Orthoceras" brucense

In this group siphonal deposits are lost. (Fig. 11, 12.) Episeptal deposits are present but are relatively thin, while the greater part of the space within the camera is filled by the massive hyposeptal deposits. The forms thus far known to fall into this group are thus far relatively slender species, with deep camerae. The form of the interior of the cameral deposits is rather characteristic, being marked by many radial furrows and concentric lines of growth. This type of surface, which will be described and illustrated in detail at another time, seems sufficient to warrant the recognition of this group. Another singular feature is the characteristic absence of the connecting ring in all specimens so far studied. Its outline can be seen only where it is surrounded by cameral deposits, and the consistency of this type of preservation in various formations and types of sediments leads to the belief that the connecting ring must have been either entirely absent, or else that its spicular elements were so poorly integrated that it will not hold together after the destruction of the tissue which contain them.

The group is wide ranging, but not over common at any one horizon or locality. It is represented in the Laurel, Liston Creek, Racine and Guelph of the Middle Silurian. Species of this horizon are commonly more or less strongly banded or annulated, and in this group fall species which have been placed in *Cycloceras*, *Leurocycloceras* and *Geisonoceras* by Foerste. The presence of the group in the Helderbergian is doubtful, though *O. paucicameratum* Hall is likely suspect. It is well represented in the Schoharie grit of the Middle Devonian, and it appears again in the St. Louis limestone of the Mississippian of Indiana.

3. Group of Dawsonoceras

This group is derived from the group of Geisonoceras by the loss of the hyposeptal deposits, thereby forming a break in the continuity of the secreting surface in each camera. The episeptal deposits are modified into mural deposits in the absence of hyposeptal deposits, and generally precede the siphonal annulosiphonate deposits in appearance. This type of structure is well exemplified in the genus Dawsonoceras. It is present also in smooth-shelled orthoceracones.

4. Group of Striacoceras

In this group, as in the group of O. brucense the siphonal deposits have been lost, but hyposeptal deposits are absent also, and the episeptal deposits are modified into mural deposits and are generally massive. (Fig. 11,12) To what extent this is a genetic group is uncertain. It is possible that it may have originated from several lines of descent at different times. As a stage in the reduction and localization of the deposits of the phragmocone it might be derived from the group of O. brucense, from the group of Dawsonoceras, or independantly from the group of Geisonoceras. Members of this group differ from that of O. brucense, which is characterized by slender forms with deep camerae and no preserved connecting ring. It is more probably derived largely if not entirely from the group of Dawsonoceras. Some smooth orthoceracones formerly included in Michelinoceras and Geisonoceras fall here, as well as species of Kionoceras and Protokionoceras, and also Striacoceras, from which the group takes its name.

5. The Pseudorthoceroids

This group contains not only the Pseudorthoceratidae but also their orthochoanitic forbears which agree with them in the form of the siphonal and cameral deposits. Here the continuity of the secreting surface is broken, but the siphonal deposits are preserved and put in a late appearance (Fig. 12). The main modifications have to do with the time of appearance and speed of development of the various deposits. Cameral deposits appear first, and come to be fairly well developed before siphonal deposits appear. When the siphonal deposits are established, however, they grow with unusual rapidity, and in a series of from six to nine siphuncular segments the entire development from the youngest to the mature siphonal deposits can be traced. The type of structure has been discussed so extensively in the first section of this paper, that its repetition here is unnecessary. It will suffice to point out that originally discrete segments of the annulosiphonate deposit fuse to form a complete sheath about the siphon. The direct result of this is the isolation of the cameral tissue, and with the source of metabolic materials removed, the secretion of further calcareous material in the camerae becomes physically impossible. As has already been stated, the marked contrast of cameral deposits in the neanic region of Pseudorthoceras in which the

siphonal deposit is not completed dorsally and the adoral regions in which it is normally closed show that the siphonal deposits control the extent of cameral deposits, and that the completion of the siphonal deposits is not delayed until the cameral deposits attain a mature condition; rather they determine what shall constitute maturity in this particular instance.

This group is apparently monophyletic, and is represented in the Silurian by the orthochoanitic forbears of the Pseudorthoceratidae, from which the Pseudorthoceratidae are derived in the Devonian. It is derived from the Geisonoceras type by the general, though not universal loss of hyposeptal deposits, and by the specializations in the time of appearance and rate of growth of cameral and siphonal deposits, as well as by the development of siphonal deposits over the connecting ring independent of cameral structures.

Hyposeptal deposits reappear in several members of the group. They are found in Euloxoceras, in Adnatoceras ciscoense (Miller Dunbar and Condra) and in Cayutoceras.

Before leaving this group it should be noted that the development of siphonal deposits to control the deposition of cameral deposits is apparently an advantageous structure. It attained independently in the Stereoplasmoceratidae and Troedssonoceratidae of the Ordovician which are not annulosiphonate in origin and are not related

to the Pseudorthoceratidae. Further, it is a structure which is only gradually perfected in the Pseudorthoceratidae, as is shown by the progressive thinning which can be traced from Silurian orthochoanitic forms to Pennsylvanian species of Pseudorthoceras and Mooreoceras.

6. Group of Harrisoceras

Still another group is differentiated by an acceleration of the development of siphonal over cameral deposits. This is a small group for which the generic name Harrisoceras has been proposed.⁵⁵ (Fig. 11, 12)

55. Flower, R.H., Harrisoceras, a new structural type of orthochoanitic nautiloid, Journal of Paleontology, in press, (1939).

Annulosiphonate deposits are large and symmetrical or nearly so. Hyposeptal deposits are thin when present and greatly delayed in their appearance. A central canal develops gerontically. The significant feature of the group is the confinement of the siphonal deposits to the septal neck as in the Actinoceroidea. They never become massive enough to develop a recognizable perispatium, but their size and shape suggest the pendant deposits of the Actinoceroidea, though without ever departing far from the simple annulus in form. The group contains thus far only the genus Harrisoceras which is world wide in distribution in the

Middle Silurian, and is thus far known in America only from strata of Clinton age. Typical Harrisoceras is smooth externally. Identical internal structure has been found in species with cancellate ornament which would formerly have been placed in Protokinoceras.

7. The Actinoceroidea

The Actinoceroidea may be taken as representing another group closely similar to that of Harrisoceras, but representing an isomorphic rather than a genetic relationship. The siphonal deposits are massive and usually outstrip the cameral deposits in development. The relative appearance of the cameral and siphonal deposits is variable. In Cincinnati species of Ormoceras the appearance of siphonal deposits is greatly delayed, and such deposits are present only in the extreme apical end, while cameral deposits make their appearance at the usual distance of about twelve camerae from the base of the living chamber. In the Actinoceratidae and Armenoceratidae cameral and siphonal deposits may appear simultaneously, or siphonal deposits may precede cameral deposits in appearance. The growth relations in such instances are identical with those of Harrisoceras (Fig. 12.).

The essential characteristic of the Actinoceroidea have to do with the specialization of the siphonal vascular system and the attendant modification of the siphonal

deposits. The presence of a perispatium alone is diagnostic, and it is the presence of this empty space inside the connecting ring which is responsible for the pendant nature of the deposits. Although the deposits of Harrisoceras appear to be pendant, hanging within the siphuncle from the septal necks, they never develop far enough to show whether a true functional perispatium is developed in that genus. The nature of tissue in the perispatium remains in doubt. Teichert considered it a space in which blood could accumulate near to the connecting ring, a sort of haemocoel, so that osmotic exchange of materials could take place between the cameral and siphonal tissues. This does not appear to take into consideration the mesodermal nature of the connecting ring or the high degree of specialization which is represented by the siphonal vascular system of the Actinoceroidea.

The primitive condition of the siphon must have been one of generalized parenchymous tissue with numerous fine blood tubes in a rather irregular arrangement. The Actinoceroidea represent a specialization by reduction and simplification of the numerous fine tubes to an orderly and regular system of large tubes. Yet the cameral tissue is probably a primitive feature even though cameral deposits probably are not, and the blood vessels which nourish it must pass through the connecting ring as fine capillaries.

For this reason the reduction of the blood tubes of the

siphon must remain internal; perispherally the capillary condition must remain in order that the blood tubes may pass through the connecting ring into the cameral tissue. Doubtless the perispatium was originally occupied by a tissue in which rapid division of the blood tubes was taking place, as is suggested further by the observable divisions of the radial canals as they approach the perispatia in many forms. There are still complex problems involved in the interpretation of the siphonal vascular system, but it is not necessary to discuss them further at this time. It will suffice to point out here that central canals are known elsewhere only in the gerontic stages of two unrelated genera, Harrisoceras of the Orthochoanites, and Anastamoceras of the Pseudorthoceratidae.

The Pseudorthoceratidae owe their development to the ability of the siphonal tissues to sever their connection with cameral tissues, being cut off from them by deposits which act as a valve. It was thought that the development of such structures as radial canals should be impossible in the family, yet in Paraloxoceras, obviously a derivative of Mooreoceras, a simple series of radial canals is retained throughout life. No perispatium, however, is evident.

It might be possible to regard all annulosiphonate cephalopods as originating from a common type. The idea is intriguing, but closer study will show that some insurmountable obstacles are encountered. First of all,

it is impossible to correlate the Actinoceroidea with any other types on the basis of the siphonal structures. The siphuncular outline varies sufficiently within the group that it might be possible to accept such a hypothesis as that already proposed by Kobayashi⁵⁶ who regarded the

56. Kobayashi, T., On the Stereoplasmoderata, Japanese Jour. Geol., Geogr., vol. 13, 1936, p. 234.

Sactoceratidae as the ancestral radicle of the Actinoceroidea, deriving it from the orthochoanites through such a form as Sactorthoceras Kobayashi, and regarding it as a not distant relative of the Stereoplasmoderata. The other members of the Actinoceroidea might be derived from the Sactoceratidae. This is opposed not only by the evidence of the siphonal vascular system and the structure of the deposits, but by the evidence of the siphonal vascular system and the structure of the deposits, which were not considered at all in building up that hypothesis, but by the stratigraphic evidence which shows that the oldest Actinoceroidea are those which possess large and markedly cyrtochoanitic siphuncles. Further, many of the older species which have been referred to Ormoceras, Sactoceras or Deiroceras are not Actinoceroidea at all, but are cyrtochoanites of rather doubtful affinities which should possibly be referred to the Stereoplasmoderata.⁵⁷

57. The study of these forms will be dealt with elsewhere. I have in mind particularly species from the Chazyan of the Mingan Islands recently referred to Deiroceras, particularly Deiroceras diffidens (Billings) which is closely related to "Loxoceras" moniliforme Ruedemann and "Ooceras" perkinsi Ruedemann of the Chazyan of the Champlain basin.

The earliest stages of the Actinoceroidea as recently reported by Kobayashi⁵⁸ and the present author⁵⁹, agree

58. Kobayashi, T., Contributions to the study of the apical end of the Ordovician nautiloid, Japanese Jour. Geol., Geogr., vol. 14, no. 1-2; 1937, p. 1-21; pl. 1-2.

59. Flower, R. H. , Early stages of Actinoceras (Abstract), Geol. Soc. Amer., Bull. vol. , 1938, p.

(Abstracts of papers to be offered at the annual meeting of the Paleontological Society, p. 76, 1937.)

in the form of the protoconch and the condition of the beginning of the siphuncle, but the initial chamber itself is not very revealing. The possibilities for variation in form of an initial chamber are definitely limited.

Kobayashi saw a possible clew in the central position of the siphuncle, but the value of such an interpretation as a basis for major divisions of Nautiloidea into Ventralsiphonata and Centrosiphonata is questionable. Rather it

seems that a quite different division based on the presence or absence of an apical caecum is more significant, and such divisions will coincide exactly with the Steno-siphonata and Eury-siphonata proposed by Teichert on the basis of the septal necks.

General Classification of Orthoceracones

From the above evidence, which will be set forth in more detail elsewhere, it appears that the Actinoceroidea cannot be regarded as related to the annulosiphonate orthochoanites, though striking resemblances occur. It is not even possible to trace the forms back to a common annulosiphonate ancestor, but it is necessary to conclude that annulosiphonate structure has evolved independantly in these two instances. The orthochoanitic annulosiphonata however appear to represent a genetic group, of which the Pseudorthoceratidae form a part.

Further, it can be seen that the groups outlines above may serve as major taxonomic divisions for the orthochoanitic orthoceracones. Perhaps one group will have to be added for orthoceracones which lack cameral and siphonal deposits completely. The study of a considerable number of specimens representing various species of Trenton and Chazy orthochoanitic orthoceracones have lead to the conclusion that cameral and siphonal deposits must have been absennt

in such forms.

The present classification of orthochoanitic orthoceracones is that of Hyatt (1900) and is based upon the ornament. At that time it was not suspected that there were cyrtchoanitic orthoceracones similarly ornamented. At the present time it is possible to point to one or more cyrtchoanitic isomorphs of orthochoanitic genera with the exception of Dawsonoceras, as is shown by the table at the end of this chapter. In the past it was considered adequate to know the ornamentation of an orthoceracone to refer it to a genus. Now it is known that the ornament alone is not trustworthy, but that at least the outline of the siphuncle must be known as well. From this it naturally follows that all similarly ornamented orthoceracones are not necessarily members of the same genetic group, but at first there seemed no better criterion available. One is now furnished in the patterns of the deposits of the phragmocone. Its use will be complicated by the fact that it cannot be employed for the identification of fragments representing adoral portions of the phragmocone in which such deposits are normally absent, or for flattened specimens or living chambers. Practical difficulties will tend to restrict its use. The task of ascertaining the internal deposits of the type species of established and long used "ornament genera" is in

itself no small undertaking. There is already some indication that families and genera remodeled on such a basis will not only bring the classification into closer accord with the phylogeny, which is the constant aim of such revision, but that the restricted generic groups will become useful in unraveling the stratigraphic and paleogeographical problems of the Paleozoic. If as has been generally supposed, the cephalopods were more motile than most other shelled forms, they should be the first to invade new areas following the breaking down of land barriers.

DISTRIBUTION OF ORNAMENT TYPES
IN ORTHOCERACONES

I Transverse lirae and striae

A. Orthochoanitic

Harrisoceras
O. brucense
Geisonoceras
Leurocycloceras

B. Cyртоchoanitic

Pseudorthoceratidae
Dolorthoceras
Diagoceras
Actinoceroidea
Elrodoceras
Ormoceras (pars)

II Annulations and transverse ornament

A. Orthochoanitic

O. brucense
Brachycycloceras
"Cycloceras"

B. Cyртоchoanitic

Pseudorthoceratidae
Geisonoceroidea
?Neocycloceras
Stereoplasmoceratidae
Tofangoceras
Tofangocerina
Incertae sedis
Eskimoceras

III Annulations and longitudinal ornament

A. Orthochoanitic

Metaspyroceras
Ordovician and Silurian
species referred to
"Spyroceras"

B. Cyртоchoanitic

Pseudorthoceratidae
Spyroceras
Incertae sedis
Group of "Spyroceras"
clintoni

IV Longitudinal ridges

A. Orthochoanitic

Kionoceras
Geisonoceras
Harrisoceras
Virgoceras

B. Cyртоchoanitic

Troedssonoceratidae
Troedssonoceras
Pseudorthoceratidae
Euloxoceras
Mooreoceras (pars)
Actinoceroidea
Deiropoceras

V Cancellate "Protocycloceras" ornament

A. Orthochoanitic

Harrisoceras
Geisonoceras
Striacoceras
Virgoceras

B. Cyртоchoanitic

Pseudorthoceratidae
Palmeroceras
Actinoceroidea
Deiroceras

EXCRETORY ASPECT OF SHELL SECRETION

It is generally conceded that such secretions as fall under the general category of shells may have been originally excretory in function, serving to eliminate mineral wastes from the system of the organism. This has been applied by various investigators to the molluscan shell, the arthropod exoskeleton and to the tests of various of the Protozoa. In the arthropoda moulting and the secretion of a new exoskeleton are cyclic activities which recur at regular intervals. In the Crustacea, which have remained generalized in many respects, moulting continues throughout the life of the organism and serves to eliminate waste material to such an extent that the only true excretory organ is the small anteriorly situated green gland. The Insecta represent a specialized case, for moulting ceases when the wings are developed. Here the Malpighian tubules are present and serve as specialized excretory organs to meet a new need.

The secretion of septa at rhythmic intervals doubtless served the cephalopod just as the secretion of a new carapace served the crustacean. A problem of some interest and importance is found in the variations in the secretion of the septa, in the growth of the shell, or in both? The septa are normally rather widely spaced in the neanic portion, slightly more closely spaced in proportion to

the diameter in the ephebic portion, and very closely and sometimes rather irregularly spaced in the gerontic portion of the phragmocone. The wide spacing of neanic septa is probably indicative of a rapid growth of both the visceral mass and the shell wall. Relatively rapid growth is a common feature in organisms at this stage. In the ephebic portion the normal specific pattern is attained, which is held over the greater part of the phragmocone with astonishingly little variation. The approach of the gerontic condition is usually abrupt. This may indicate one of three things:

1. A more frequent secretion of septa in old age, due to more rapid accumulation of minerals in the organism. It is generally held, however, that such accumulations are a feature of a gerontic condition only because completed growth has caused the normal channels for the elimination of waste to be functionally closed.

2. A slowing up in the rate of secretion of the shell wall, accompanied by its thickening. If this were all, it would appear that the gerontic septa should be subject to the same thickening which affects the shell wall.

3. It seems more probable that the slowing up of growth is due to the cessation of the growth of the soft parts of the organism. Calcareous materials accumulate in the system as before, but with a retardation in the

rate of growth, there is less need than before of periodic forward migration in the conch. Consequently though septa are formed at the same rhythmic intervals as before, less material is added to the aperture and forward migrations in the conch become less extensive.

Brevicones present a rather special case. The contraction of the aperture inhibits further growth of the soft parts of the organism, and the form of the contracted aperture is essentially an ephebic rather than a gerontic feature. When the contraction of the aperture begins, the secretion of septa at a normal rate will necessarily result in a compression of the visceral mass which would have to have some sort of compensation as resorption would offer. However, proportions shows that if the length of the living chamber does not vary materially, the beginning of the contraction of the camerae and of the aperture occur at the same time. Further, the degree of contraction of the camerae can be correlated with that of the aperture. In forms with slightly contracted apertures such as Acleistoceras or Amphicyrtoceras, the ephebic contraction of the camerae is slight, while it is a prominent feature where the aperture is more completely and gradually closed, as in Hexameroceras.

In Brevicones the gerontic features may be summarized as follows:

- (1) Thichening of the shell wall interiorally be-

fore the aperture.

(2) Secretion of material by the posterior mantle. This forms the impressed zone of Hall. Unfortunately that term is better known in connection with coiled cephalopods through the works of Hyatt, so the term basal zone⁶⁰ has been proposed for the structure of brevicones.

60. Flower, R.H., Devonian brevicones of New York and adjacent areas, *Paleontographica Americana*, vol. 2, 1938, p. 171.

This is a gerontic feature. It consists in the thickening of the final septum, both in its mural and free portions. Often an "ornamented" radial pattern is formed. This has been little studied, but appears to be constant within a species and may be useful taxonomically when it has been given more attention.

(3) The deposits of the siphuncle. Foerste has noted upon several occasions that the occurrence of actinosiphonate structure is highly variable in several specimens of the same species. I have found such deposits confined to individuals showing some other trace of gerontic features, but not in immature or early ephebic individuals. This may well account for the variability within generic and higher groups, particularly since brevicones are so rare in many instances species are known from only a few individuals.

MODE OF LIFE AND ECOLOGICAL SIGNIFICANCE
OF SIPHONAL AND CAMERAL DEPOSITS

Problems of Gas in Camerae

The mode of life of fossil cephalopods, and particularly of orthoceracones, is still a matter of conjecture. However a consideration of the ecological significance of the cameral and siphonal deposits brings new evidence to bear upon the solution of the problem, and permits the checking and modification of previous hypotheses.

Probably the greatest obstacle to the understanding of the mode of life of Paleozoic cephalopods is uncertainty as to whether gas was present in the camerae of such forms. Gas has been assumed to be both present and absent by various authors. Dunbar⁶¹ assumed that gas must be absent

61. Dunbar, C.O., Phases of cephalopod adaptation, in Organic adaptation to environment, Yale Univ. Press, 1924, p. 191.

on the basis of the horizontal mode of life indicated by the color bands, yet postulated a nectonic existence. Teichert⁶² has assumed the presence of gas and has presented

62. Teichert, C., Der Bau der actinoceroiden Cephalopoden Paleontographica, bd. 78, Abt. A, 1933, pp. 186-200.

a very convincing hypothesis of the probable hydrostatic relations on a quantitative basis.

Although Nautilus is known to contain gas in its camerae it does not necessarily follow that gas was present in the camerae of primitive forms. Indeed, it has been postulated that the development of coiling was the result of the appearance of gas in an orthoconic shell and the attendant elevation of the apex. However, it is evident that the appearance of gas will not account for such a progressively coiled series as that illustrated by Schinderwolf⁶³ from Rhynchorthoceras through Ancistroceras

63. Schinderwolf, O.H., *Paleontologie, Entwicklungslehre und Genetik*, Berlin, 1936, p. 36-38.

and Lituites to Cyclolituites where coiling appears at the apex.

Although the origin of cameral gas is unknown, it is perfectly possible that even the earliest cephalopods may have secreted gas in the camerae. Among the earliest cephalopods there are numerous cyrtoconic forms which are rapidly expanding and breviconic rather than longiconic. The shortness of the shell and the wide aperture suggest crawling forms which carried the shell with the apex directed upward. This, as was shown above, is the primitive orientation. The camerae of such forms are exceedingly shallow, and gas would not have had a sufficiently buoyant

effect to interfere with a benthonic mode of life.

Further, the color bands, though not known for these particular cyrtoceracones, suggest that cyrtococonic shells were held in this position in life.

In the case of orthoceraconic forms, however, two possibilities exist; The shell may have been dragged along the bottom by benthonic organisms, or the shells may have been held more or less suspended either in crawling or swimming forms. If we assume a continued benthonic existence, the orthoceraconic form suggests a normally horizontal position of the conch. Among the Gastropoda many forms show a similar development, but the dragging along the sea bottom of a long heavy shell of such a form as Cerithium giganteum would considerably handicap movement. Shells dragged in this manner might, as Dunbar⁶⁴ suggested

64. Dunbar, C.O., Phases of cephalopod adaptation, in Organic adaptation to environment, Yale Univ. Press, 1924, p. 191.

for orthoceracones, should show signs of wear on the ventral side. And it is possible that lack of such evidence in orthoceracones may be due to poor preservation of the shell surface, as in Actinoceras. However granting that gas was present in the camerae, it is conceivable that the weight of the shell was so lessened that it was approximately equal to the weight of the water it displaced.

Under such conditions the shell would have ceased to be a handicap in movement and it would have become light enough to preclude wear of the shell as the animal crept over the sea floor.

Accompanying the increase in the length of the shell there is an increase in the depth of the camerae. This implies, though it does not require that the the buoyant effect of the phrogmocone was increased. One would here bear in mind that it is not altogether certain that the entire cavity of the camerae was occupied by gas; the available space in the camerae may have been only partially occupied by gas and variability of the extent of gas secretion is quite possible. Increased buoyancy would result in a shift of the center of gravity orad, and a shift to the center of buoyancy apicad. As a result the shell would tend to occupy a horizontal position, as Dunbar suggested. Dunbar argued that since the color bands of orthoceracones indicate a horizontal position, and since gas in the camerae would necessitate a vertical position, that gas must have been absent. However, the deposits of the phragmocone are developed only adapically, and would therefore tend to weigh down the apex of the shell. The addition of such deposits to an orthoceracone containing gas in the camerae would cause the center of gravity to move apicad until it lay near enough to the center of

the shell that a horizontal position is possible. Furthermore, in such an orthoceracone the buoyant effect of the gas would not be entirely counteracted by the weight of the deposits, but gas would still have enough lifting power to lessen the weight of the organism materially, and might even permit a pelagic or planctonic existence.

Furthermore, gas would be necessary to an orthoceracone which lived with its shell in a vertical position. Such a condition was suggested by Foerste⁶⁵ on the basis of

65. Foerste, A.F.. The color patterns of fossil cephalopods and brachiopods, with notes on gastropods and pelecypods. Michigan Univ., Mus. of Pal., Contrib., vol.3, 1930, p. 140.

color bands which encompass the shell in Orthoceras pellucidum Barrande. As is shown in the discussion of the color bands below, this condition may be more widespread than has generally been supposed.

Evidence of gas in the camerae

The deposits within the phragomcone are in themselves evidence of an active mode of life of orthoceracones which would hardly have been possible were the camerae not occupied by gas. They quite obviously serve two distinct functions.

Ventral concentration supplied a stabilizing device which tended to orient the conch with the venter beneath.

That this device is ecological in its significance is shown by its formation in several different ways in different genetic lines. In the Endoceroidea the stabilizing effect is produced by deposits in the form of endocones within the large ventral siphuncle. In the Actinoceratidae and most other Actinoceroidea the heavy annulosiphonate deposits practically fill the large ventral siphuncle, and cameral deposits, though doubtless contributory, were of minor importance. However, when the siphuncle becomes small, or when it is removed from the venter as in the Sactoceratidae of the Actinoceroidea, the cameral deposits become both heavier and more markedly concentrated on the venter. The cameral deposits of the Pseudorthoceratidae and the Orthochoanites are the essential stabilizing organs, and the small siphonal deposits may be reduced, highly modified for other than hydrostatic functions, or may be altogether wanting.

The second feature of the deposits of the phragmocone which is significant ecologically is their apical concentration. This serves a double function. First, it weighs down the apex, counteracting the buoyant effect of the gas in the camerae sufficiently to permit a horizontal mode of life. Second, the weighted apex is essential for the arrow-like flight of the organism in hyponomic swimming.

The ecological importance of the apical concentration of the deposits of the phragmocone is shown by the number

of ways in which it has been developed in different genetic lines. In the Endoceroidea the siphonal deposits of endocones alone serve to weigh down the apex. It is not generally recognized to what extent the development of endocones is confined to the apical part of the shell. The author has collected a specimen of Endoceras proteiforme Hall which attains a diameter of about seven inches at the base of the living chamber. The first trace of endocones is found more than three feet farther apicad. Assuming a constant rate of expansion, this would imply a maximum length of about two and a half feet of siphuncle filled with deposits in the form of endocones, while the adoral three feet, followed by a living chamber of unknown length, contains no accessory calcareous materials. Further, in many Endoceroidea the so-called nepionic bulb will add materially to the weight of the apex as soon as deposition begins within the siphuncle.

In the Actinoceroidea the siphuncle is also filled with calcareous deposits, but here the deposits are in the form of annulosiphonate rings rather than endocones. Cameral deposits are contributory, but come to be important only in the Sactoceratidae, where the siphuncle is too small to be very important hydrostatically.

In stenosiphonate orthoceracones the siphonal and cameral deposits may both serve to weigh the apex, but

usually the cameral deposits, being much more massive, are the more significant of the two as ballancing factors.

The apex is again weighted in the Dibranchiata, but in an entirely new way. The mantle has grown over the shell, and the addition of material to the outside of the shell forms an apical guard on the outside of the phragmocone.

Ecological Evidence

That at least some of the orthoceraconic cephalopods had sufficient gas in the camerae to make possible a planctonic existence is shown convincingly by the fact that orthoceracones appear as regular members of plancton faunas. They are in fact, the first cephalopods to appear in such associations. It is quite evident that a cephalopod with an external shell could not have made up a part of a plancton association had the camerae not been occupied by gas. That the cephalopods were an integral part of such faunules and were not carried into those environments as dead shells is shown by the absence of conspecific forms in contemporaneous benthonic facies. Air filled orthoceracones should be capable of transportation from planctonic to nono planctonic facies. Such shells might be carried until breakage or solution liberated the gas within the phragmocone. That no planctonic Naples species are known from the Ithaca suggests that any shell that may have

been thus transported were broken too badly to be recognizable.

Ruedemann,⁶⁶ has found orthoceracones in the Silurian

66. Ruedmann, R., Paleozoic plancton faunas of North America, Geol., Soc., Amer., Mem. 2, 1934, p. 34.

graptolite shales of the Prince of Wales Island. It is not surprising that the orthoceracones of such an association are characterized by types of ornament and shell corrugation which have long been considered diagnostic of the genera Spyroceras and Kionoceras. It is not surprising that these, the first cephalopods to occur in such an association, belong to a group, ecological rather than taxonomic, in which the shell wall has been so modified as to result in a structure of minimum weight and maximum strength. Smooth orthoceracones have since been found in Silurian graptolite shales of Belgium. The flattened condition of the specimens and the destruction of internal structure makes impossible a study of their genetic relationships.

In the Devonian of New York orthoceracones are abundant in plancton associations. Here again the shells are usually flattened and generic identification is largely impossible. Orthoceracones occur in the Union Springs member of the Marcellus, at the base of the Hamilton stage. Small thin-shelled species of Spyroceras,

such as S. idmon and S. lima are known largely if not entirely from highly carbonaceous shales of the Hamilton in which the other faunal elements are definitely known to be planctonic. In the Upper Devonian smooth orthoceracones, sometimes of considerable size, occur in the Genesee shale.⁶⁷ Small forms occur in the Genundewa limestone,

67. The author has collected flattened portions of phragmocones up to two inches in width from the Genesee as developed in the vicinity of Ithaca.

which owes its limy condition to the presence of myriad of Styliolina. In higher strata orthoceracones occur commonly in the Middlesex and Rhinestreet shales. Orthoceracones have not been generally recognized in these formations in the past, and have been apparently confused with Bactrites which occurs in the same horizons and associations. Bactrites can be distinguished by its more slender form, even in the flattened state.

Color Bands as Criteria of the Mode of Life

Color bands should serve as an excellent test for the position of the conch of the orthoceracone in life, and further, it should be possible to correlate the color bands of a species with its siphonal and cameral deposits and thereby check the ecological importance of the deposits of the phragmocone. In one instance, that of the Trenton

orthoceracones described by Ruedemann, it is known that color bands were confined to one side of the shell, indicating a horizontal mode of life, and that deposits are developed within the phragmocones of the several species concerned. In other instances, as is shown below, the color bands are much less reliable.

Color bands which were confined to one side of the shell were first reported by Ruedemann,⁶⁸ who pointed out

68. Ruedemann, R., Observations on the mode of life of primitive cephalopods. Bull. Geol. Soc. Amer., vol. 32, p. 315-317.

that this indicated that the shell was held in a horizontal position during life. He suggested a benthonic mode of life on the grounds that the long straight conch could hardly have been carried horizontally in swimming.

Dunbar⁶⁹ accepted the idea of the horizontal mode of

69. Dunbar, C.O., Phases of cephalopod adaptation, in Organic adaptation to environment, Yale Univ. Press, 1924, pp. 191, 197.

life on the basis of color bands but rejected the benthonic mode of life on the basis of the absence of wear on the ventral side of the shell. The argument is a legitimate one, but conditions of preservation may destroy such evidence. Ventral wear should be best developed on a shell

which has heavy deposits, such as an Actinoceras. An Actinoceras which retains much of the surface is exceptional. The shell wall is usually recrystalized, and it only rarely separated from the rock at the shell surface, and then only in small patches. Again, if gas is present in the camerae of even a form with heavy deposits, the weight would be greatly lessened, and friction would be reduced.

Foerste⁷⁰ studied the color bands of orthoceracones

70. Foerste, A.F., The color bands of fossil cephalopods and brachiopods, with notes on gastropods and pelecypods. Univ. of Michigan, Mus. of Geol., Contrib., vol. 3, no. 6, (pp. 109-150, 5 pls.) 1930; and The cephalopods of the Hølandet area, Skr. ut. av. Det. Norske Videnskaps-Akademie i Oslo I Mat.-Naturv. Klasse. 1932, no. 4, pp. 149-150.

and came to the conclusion that the color patterns of ellipchoanitic orthoceracones were ventral while those of holochonites were dorsal. From this he concluded that the ellipchoanitic cephalopods must have occupied a horizontal position with the venter upward. However a close examination will show that the evidence of the color bands which has been so widely accepted is not always reliable.

Form and orientation of color bands; Color bands may be divided into three great groups on the basis of their form: the diagonal zigzag bands typified by Orthoceras anguliferum D'Archiac and de Vernuil, the longitudinal bands found in Orthoceras trusitum Hall of the Trenton, and the transverse bands typified by O. dunbari Foerste of the Pennsylvanian. The diagonal zigzag pattern is bilaterally symmetrical and is doubtless oriented in regard to the symmetry of the conch. The specimens of Orthoceras anguliferum alpenense which Foerste figured show no trace of the aperture, the position of the siphuncle, cameral deposits or the furrows of the interior. There is no dorsal or ventral in position. A Hedstromoceras with color bands shows them only on the siphonal side which may be ventral. The only orthoceracone in which the color bands are indisputably ventral is a Mooreoceras collected and described by Mr. Richard Schweers,⁷¹ in which diagonal

71. Unfortunately still unpublished.

color bands are present on the ventral side as shown by the conchial furrow.

The longitudinal color bands reported by Ruedemann⁷²

72. Ruedemann, R., Paleontological contributions from the New York State Museum, 4. On color bands in Orthoceras, New York State Mus., Bull. 227-228, 1919, pp. 79-88.

in Trenton orthoceracones are unquestionably confined to one side of the shell. Ruedemann points out that the orthoceracone is not perfectly straight, but that the side bearing color bands is faintly convex. This would seem to support Foerste's proposal that the color bands are ventral, but it is not known whether the curvature is endogastric or exogastric. Thus far specimens retaining color bands have failed to show deposits within the phragmocone, and the furrows of the interior of the shell are either originally absent or not preserved. Consequently there is no sure criterion of orientation. Mural deposits are present in the camerae in the species concerned. Although the deposits are not definitely known to be concentrated on the venter, it is reasonably safe to assume that they are, for the ventral concentration has been found to be universal wherever orientation can be checked.

The transverse bands are known from only two species, O. dunbari Foerste of the Pennsylvanian, and "Orthoceras", sp. Flower and Caster of the Onewango of the Upper Devonian. In neither is there any means whereby it is possible to determine the relation of the color bands to the dorso-ventral plane. The transverse black bands in O. dunbari end laterally in densely black areas. The dorsal condition is not known. A thick black unmarked band has been noted in Geisonocerooides woodae, of the

Hamilton shales of New York where it is dorsal. The venter is too poorly preserved to show color markings. However there is a suggestive resemblance between the black band of this form and those of O. dunbari. It is possible that species the dorsum may have been uniformly dark and the venter transversely banded.

Preservation of color bands. Color bands are only rarely preserved on orthoceracones, and require special conditions for preservation. The Stafford limestone which contains orthoceracones showing faint traces of color bands, the Trenton limestone in which color bands are not uncommonly preserved and the Alpena limestone are similar in texture. Fracture and mode of preservation of the cephalopods.

In typical specimens the distribution of color bands depends upon the distribution of calcite in the shell. This was recognized for Trenton specimens by Ruedemann. Calcite is commonly present against the side of the shell which lay uppermost, and is the complemental filling of an incomplete internal mold. In the Trenton orthoceracones good color bands can be seen where the dorsum lay uppermost. Where a lateral surface is uppermost the gradual lateral disappearance of color bands can be seen. Such a specimen has been figured by Ruedemann.⁷³ Only

73. Ruedemann, R., Paleontological contributions from the New York State Museum, 4. On color bands in *Orthoceras* New York State Museum, Bull. 227-228, 1919, fig. 23.

rarely are specimens found in the Trenton in which the color bands are not confined to the side of the shell occupied by calcite. In such instances they are not actually preserved as color bands but are indicated by elevated and depressed bands on the surface of the shell due to differential weathering.

Ruedemann considered the inorganic factors in the orientation of color bands and was able to show in spite of them that the color bands were originally present on only one side of the shell. Other investigators have not taken the inorganic factors into account. The pattern of *Orthoceras anguliferum alpenense* Foerste is bilaterally symmetrical, but the center of symmetry of the pattern does not lie in the center of preserved part of the pattern. This shows that other factors besides the original distribution of the pattern determine the present alignment of the pattern on the shell. It is not surprising, therefore, to find that in the two specimens figured by Foerste the colorbands are present only on the side which contains calcite.

Calcite occurs on the ventral side of the *Mooreoceras*

cited above as having ventral color markings. From what has been said above it follows that the present orientation of the color bands on these specimens need not be the complete original pattern. It is quite possible that diagonal color bands may have extended originally completely around the shell of orthoceracones as they did in cyrtoceracones.

The longitudinal color bands of Trenton orthoceracones indicate a horizontal mode of life. This is also suggested by the transverse bands which give way to a dense black dorsal area, though here the matter is not beyond dispute. Diagonal color bands are not conclusive, but probably extended completely around the shell, suggesting a vertical rather than a horizontal mode of life. A vertical mode of life is further suggested by Orthoceras pleucidum var. contrahens Barrande, of the Silurian of Bohemia, which possesses longitudinal bands which pass entirely around the shell. This alone would suggest that the mode of life is not the same in all orthoceracones.

Most specimens which preserve color bands fail to show any of the internal features of the shell. For this reason it is often not possible to identify a specimen showing color bands with a species in a more typical condition of preservation. Consequently most forms which possess color bands are described as "species" of "Orthoceras." With the generic and specific identification uncertain

all that such specimens tell us is that some orthoceracones had color markings on one side of the shell, while in others the color bands may have extended around the shell. This is not very satisfactory.

Only in one instance has it been possible to establish a correlation between color bands and the deposits of the phragmocone. The orthoceracones of the Trenton limestone which show traces of color bands represent several allied species. Preservation of the interior is rare, but a few specimens are known which show the siphuncle is small, orthochoanitic and subcentral, showing that the species should be placed into genus Michelinoceras. Mural deposits are known to be present in the camerae. Both deposits and the color bands suggest a horizontal mode of life. The ventral concentration of the cameral deposits is not known here. It may be assumed however, from that fact that cameral deposits are not known which do not show ventral concentration. Likewise the dorsal position of the color bands is an assumption, but it is difficult to see how any other condition could have held.

In the specimen of Mooreoceras mentioned above, on the other hand, the diagonal color bands are known to be ventral. Deposits are known to be concentrated ventrally, making possible a horizontal mode of life with the venter down, but not with the venter up. It is therefore necessary to conclude that the present distribution of

the color bands represents only a part of the original pattern. The color bands may have passed entirely around the shell originally, and may have been preserved only against the side which lay uppermost and which was filled in by calcite. Such a color pattern would seem to imply a vertical position for the shell in life, and the deposits indicate a horizontal position with the venter down. Two possible explanations for the discrepancy suggest themselves. Nothing is known of the condition of the color bands on the dorsum which may have been much darker than those on the venter. Again, the original color pattern maybe preserved only as a negative. The calcite which represents the shell is normally white. The relatively insoluble melanin pigment which make up the color bands may have prevented the entry of discoloring minerals in originally dark areas, while originally light areas may be discolored and darkened by them. In this way the original relationship may be reversed. That something of that sort has happened in the Mooreoceras under discussion is suggested by the appearance of color bands on the inside of the shell.

The possibilities of error in the interpretation of color bands is so great that they can hardly be considered reliable indicators of the mode of life of orthoceracones. When the evidence of the color bands agrees with that of the deposits of the phragmocone in indicating a horizontal

mode of life, such a conclusion is safe, but too often there is either a grave discrepancy or complete inability to compare the two lines of evidence in a species. In cases of discrepancy, it appears that the deposits are the more reliable guides.

General conclusions and outlook

From the ecological and structural evidence it is fairly clear that gas must have been present in at least the majority of orthoceracones. This may have been a condition inherited from the earliest cyrtconic cephalopods. Changes of several sorts have come about in the history of the cephalopods in which the presence of gas and the hydrostatic relationship may have been significant. A crawling ancestral form with a short cyrtconic erect chambered shell has been postulated. In such forms the camerae are so shallow that the buoyant effect of the gas could hardly compensate for the weight of the camera walls. However, very shallow camerae are essentially an early Paleozoic feature. Elongation of the shell and elongation of the camerae may have gone hand in hand. This would result in increased buoyancy of the apex of the animal. However, cameral tissues are probably a primitive feature, even though deposition of cameral deposits is not. Quite probably the beginning of septation was marked by a split in the posterior mantle forming a cameral mantle connected

with the siphonal strand between the septal necks. This is suggested by the obvious retention of cameral tissues and the development of gerontic deposits in brevicones, where such features were not only characteristic of the gerontic stage, but were excretory in function, at a time when the normal elimination of calcareous material from the system by the normal processes of shell growth and septation was no longer possible.

The development of the contracted aperture of the brevicone is probably associated with a floating mode of life which followed the increase in buoyancy of the phragmocone. Such forms have light shells, often very thin in proportion to the size of the conch as a whole. Deposits formed within the phragmocone are gerontic features, and are never massive, as are the deposits of orthoceracones which are useful to the organism by virtue of their weight.

Orthoceracones may have developed at several different times in different ways, and the present indications of the wide gaps separating the Holochoanites, Actinoceroidea and stenosiphonate orthoceracones suggest something of the sort. Three possible modes of life must be considered for the orthoceracones. 1. The orthoceracone may have developed from the primitive cyrtoconic type by elongation of the shell, elongation of the camerae, increased buoyancy of the phragmocone

which was counteracted by the building of apical deposits in one of several possible ways which have been enumerated above. This produces a horizontal potentially nectonic form. 2. Again, it is possible that the elongation of the camerae may have been accompanied by a reduction in the amount of gas, and that some cephalopods may have lived benthonic lives with the shell held horizontally, with little or no gas in the camerae. 3. Again, some forms may have developed gas without compensating deposits, and may have lived with the shell in a vertical position, as is suggested by some color bands in the absence of deposits in some forms. If it can be demonstrated that color bands occur on all sides of an orthoceracones which lacks cameral and siphonal deposits, this condition would seem to be demonstrated; at present it is only a possibility.

To add to the complexity, it is possible that one or more of the three possible types of orthoceracones may have derived from either of the other two. This seems a hopelessly complicated picture, but in dealing with possibilities which are not yet capable of proof or dismissal, it must be considered.

It might be pointed out that flattened orthoceracones which were unquestionably benthonic and were probably derived from more active ancestors, have very shallow camerae. This is found in the Tripteroceratidae,

particularly Allumetoceras, and in the Gonioceratidae. It is difficult to explain why shallow camerae should develop in forms which by their flattened form were obviously crawlers, unless it was a return to the condition postulated as ancestral, in which the camerae were so shallow that buoyant effect of the gas within them did not compensate for the weight of the camerae walls.

The other great development of the Nautiloidea is coiling. It is now known that coiling may be initiated at the apex of the shell and spread anteriorly. It is still highly probable on the basis of ontogeny, that the gradual and uniform increase in shell curvature postulated by Hyatt may also have occurred. In the series of gradual increase in curvature it is possible that increased buoyancy of the apex may have played a part; in the other series it could not, and if a single explanation is to be postulated for coiling it need not be found in a response to environmental conditions.

It would probably be simplest to think of the orthoceracone the brevicone and the coiled cephalopod as three different responses to the development of buoyant phrangmocones, in only one of which did the tissues of the phragmocone develop into lime secreting organs to any considerable extent. However the ~~true~~ condition was doubtless much more complex, being complicated by possible

series of uncoiling, by return of nautilicones to benthos as trochoceroids, return of brevicones to benthos as trochoceroids, and by complex interrelations in the three possible ecological group of orthoceracones: gas-filled forms with apical deposits living horizontally, gas-filled forms living vertically, and horizontally living forms with little or no gas, and what gas there is localized anteriorly. However this is entering a field of conjecture which we are not as yet equipped to test thoroughly and in such fields it is well not to venture too far.

PART III

TAXONOMY

A REVIEW OF THE CYRTOCHOANITES

Hyatt⁷⁴ originally divided the Nautiloid cephalopods

74. Hyatt, A., Genera of fossil cephalopods, Proc. Boston Soc. Nat. Hist., vol. 22, 1884, p. 266.

into two orders, the Holochoanoidea and the Ellipochoanoidea. In the first group were included forms in which the wall of the siphuncle is formed by long septal necks, and in the second group were placed forms in which the necks are short and the greater part of the wall of the siphuncular segment is formed by the connecting ring. Later Hyatt⁷⁵ replaced the order Ellipochoanoidea by

75. Hyatt, A., Cephalopoda, in Zittel-Eastmann Textbook of Paleontology, 1st. ed., vol. 1, 1900, p. 514 ff., reprinted in later editions.

four orders: Orthochoanites, Cyrtochoanites, Schistochoanites and Myxochoanites, and changed the term Holochoanoidea to Holochoanites for the sake of uniformity.

The Schistochoanites comprises a small group of little understood early Paleozoic forms. The Myxochoanites likewise a small group, are aberrant forms.

Miller⁷⁶ has shown reason to believe that they are

76. Miller, A.K., The myxochoanitic cephalopods, Univ. of Iowa Studies, Studies in Natural History, vol. 14, no. 4, 1932.

derived from the Oncoceratidae of the Cyrtchoanites.

In the Orthochoanites were included forms in which the siphuncular segments were cylindrical or nearly so, consisting of straight septal necks and connecting rings. In the Cyrtchoanites, on the other hand, were placed forms in which the septal necks are recurved, and the segments of the siphuncle are more or less expanded in the camerae. It may be pointed out here that the validity of the Orthochoanites and Cyrtchoanites has not been substantiated by recent findings, for there are numerous gradations between the groups. Some species of Stereoplasmoceras Graoau⁷⁷ could be placed in either group,

77. See Kobayashi, T., On the Stereoplasmoceratidae, Japanese Jour. Geol., Geogr., vol. 13, no. 3-4, 1936, pp. 229-242, pl. 26.

though on the whole the group appears to be cyrtchoanitic rather than orthochoanitic. In the Actinoceroidea gerontic siphuncular segments of three genera, Ormoceras Stokes, Paractinoceras Hyatt and Leurorthoceras Foerste become slender and cannot be distinguished from

orthochoanitic forms. Many orthochoanitic forms possess slightly inflated siphuncular segments and may be considered as border line cases. The Pseudorthoceratidae, as is shown below is a cyrtochoanitic family of orthochoanitic origin, and is apparently unrelated to other cyrtochoanitic groups.

Hyatt⁷⁸ divided the Cyrtochoanites into two sub-

78. Hyatt, A., Cephalopoda, in Zittel-Eastmann Textbook of Paleontology, 1st ed., vol. 1, p. 527 ff. 1900.

orders on the basis of organic deposits within the siphuncle. The first of these groups, the Annulosiphonata, is characterized by deposits which form calcareous rings at each septal neck. The other group, the Actinosiphonata, comprises forms in which the calcareous deposits of the siphuncle consist of discrete vertical almellae arranged in a radial pattern so that the lamellae converge toward the center. Hyatt believed that the two types of structure were of independant origin, and he included in each group families and genera which were without any known siphonal deposits and which he regarded as primitive.

Three families were placed in the Annulosiphonata. The first of these, the Loxoceratidae, contained two genera, and was erected for forms with nummuloidal siphuncles which were either empty or contained an

"irregular deposit." Unfortunately the genotype of Loxoceras McCoy is so little known that no species can be referred to the genus with certainty. Hyatt's statement concerning the presence of irregular deposits appears to be an assumption. Neither the genus nor the family can be used until the structure of the genotype has been studied.

The second family, the Uranoceratidae of Hyatt, contains gyroceracones and nautilicones with empty nummuloidal siphuncles. The genera Uranoceras Hyatt and Gigantoceras Hyatt were originally referred to the family. These and related genera have been studied by Foerste⁷⁹

79. Foerste, A.F., Notes on cephalopod genera; chiefly coiled Silurian forms, Denison Univ. Bull., Sci. Lab., Jour., vol. 21, 1925, pp. 28ff.; pl. 1-24.

who showed that the siphuncle of Uranoceras is definitely cyrtochoanitic. The necks are recumbent; the free part of the connecting ring is essentially cylindrical, but there is a broad area of adnation. Foerste's figures do not clearly differentiate between the septal neck and the connecting ring, but the two together are recumbent, appearing as projections inside the siphuncle, and they are curved slightly apicad, so that when the free part of the connecting ring is destroyed, they resemble orthochoanitic

septal necks. This is precisely the condition which is found in all of the Silurian specimens and species referred by Foerste to Gigantoceras. Unfortunately no specimens of any of the species discussed by Foerste have been found which retain the connecting rings. Foerste did not see the possibility of a cyrtchoanitic condition of Gigantoceras, and suggested that the genus be placed in the Orthochoanites.

The third family, the Actinoceratidae of Hyatt, with some slight modification has become the superfamily Actinoceroidea Foerste and Teichert.⁸⁰ The group has

80. Foerste, A.F. and Teichert, C., The Actinoceroids of east-central North America, Denison Univ. Bull, Sci. Lab., Jour., vol. 25, 1930, pp. 201-296, pls. 27-59.

received careful study by Foerste and Teichert, and later by Teichert.⁸¹

81. Teichert, C., Der Bau der actinoceroiden Cephalopoden, Paleontographica, Bd. 78, Abt. A, 1933, p. 111-234, pl. 8-15, 50 text figs.

The superfamily Actinoceroidea contain numerous genera described since Hyatt's day, largely due to division of Hyatt's genera. Teichert⁸² has shown that the genus

82. Teichert, C., On the systematic position of the genus Discosorous Hall and related genera. Amer. Mus. Novitates, no. 512, 11 pp., 9 figs. 1931.

Discosorous Hall differs fundamentally from the Actinoceroidea in the structure of the siphonal deposits, and has set it apart with its allies Stokesoceras Foerste and Endodiscocourus Teichert in the family Discocouridae.

The Actinoceroidea remains the only group originally placed in the Annulosiphonata of the Cyrtchoanites which can still be confidently considered as included under that group.

Aside from the Actinoceroidea the Pseudorthoceratidae appears to be the only group of cephalopods which is cyrtchoanitic and annulosiphonate. On the other hand, annulosiphonate structure is prevalent in many orthochoanitic genera, particularly those of the Silurian. Whether annulosiphonate structure is sufficient to warrant the recognition of the Annulosiphonata as a taxonomic group is very doubtful, though in some instances at least the annulosiphonate deposits serve as a more reliable guide to phylogeny than does the outline of the siphuncle. The present study deals with the Pseudorthoceratidae, an annulosiphonate family of cyrtchoanitic aspect which appears to have an origin in orthochoanitic

annulosiphonate forms, the change in the siphuncular outline taking place between Middle Silurian and Lower Devonian time.

THE PSEUDORTHOCERATIDAE

The family Pseudorthoceratidae Flower and Caster⁸³

83. Flower, R.H. and Caster, K.E., The stratigraphy and paleontology of northwestern Pennsylvania, Pt. II, Paleontology, Sec. A: The cephalopod fauna of the Conewango series of the Upper Devonian in New York and Pennsylvania, Bull. American Paleontology, vol. 22, 1935, p. 225.

was referred to the Annulosiphonata of the Cyrtuchoanites largely as a receptacle to contain forms customarily assigned to the uncertain Loxoceratidae. The family Sactoceratidae was previously proposed by Troedsson⁸⁴

84. Troedsson, G.T., On the Middle and Upper Ordovician faunas of northern Greenland, I. Cephalopods. Jubilaeumseks-
peditionen Nord om Grønland 1920-23, Nr. 3, 1926, p. 79.
(Reprinted in Meddelelser om Grønland, Bd. 71, 1929.)

for the same purpose, but cannot be used in that way because Sactoceras is a true Actinoceroid, and the family was placed in the Actinoceroidea by Foerste and Teichert.⁸⁵

85. Ibid., p. 208.

In the Pseudorthoceratidae were included five late Paleozoic genera of cyrtochoanitic orthoceracones. The siphuncles were regarded as either empty or lined with a continuous lamellar deposit. The segments of the siphuncle are variously expanded, but never wider than long. The statement, in the original designation of the family, that the connecting rings do not attain the preceeding septa is both erroneous and misleading. The word septum was used here in reference to the free part of the septum as contrasted with the septal neck. Further, the adnate condition of the connecting ring in Adnatoceras ciscoense (Miller Dunbar and Condra)⁸⁶ was overlooked.

86. Miller, A.K., Dunbar, C.O. and Condra, G.E., The nautiloid cephalopods of the Pennsylvanian system of the mid-continent region. Nebraska Geol. Surv., ser. 2, bull. 9, 1933, p. 96, pl. 1, fig. 1.

At the time of the original description of the family the nature of the deposits of the siphuncle was not clearly understood, nor was it known whether the Pseudorthoceratidae were in any related to the Actinoceroidea. The study of Devonian orthoceracones has brought to light numerous forms belonging to the

Pseudorthoceratidae and representing both new and old genera. It is largely upon the basis of this material that a morphological and systematic revision of the family is based. The family is redescribed as follows:

The Pseudorthoceratidae contains largely orthocercones, with slightly exogastric cyrtconic apices, although two specialized genera attain a cyrtchoanitic form and one is breviconic. The earliest stages of the siphuncle are slender and orthochoanitic. Later segments are definitely expanded and cyrtchoanitic, though rarely wider than long. The necks are short, their length averaging less than one-seventh the length of the segment. The brims are variously developed, but are never recumbent. Siphonal deposits are annulosiphonate and parietal, consisting of rings formed at the septal foramina, extended adorally. When well developed the segmental deposits fuse to form a continuous lining with the siphuncle. Deposits of the camerae are mainly mural, although episepal and hyposepal occur in a few specialized forms.

The genera of the Pseudorthoceratidae fall into three subfamilies as listed below: (Generic characters are shown diagrammatically in fig. 16. on p.)

Dolorthoceratidae Flower, n. subf.

Anastamoceras Flower, n. gen.

Diagoceras Flower, 1936

Dolorthoceras Miller, 1931

Spyrocera Hyatt, 1884

Geisonoceroidea Flower, n. gen.

Petryoceras Flower, n. gen.

Palmeroceras Flower, 1936

Cryptorthoceras Flower, n. gen.

Sceptrites Flower n. gen.

Fusicoceras Flower, n. gen.

Adnatoceras Flower, n. gen.

Euloxoceras Miller Dunbar and Condra, 1933

Pseudorthoceras Flower, n. subf.

Pseudorthoceras Girty, 1910

Mooreoceras Miller, Dunbar and Condra, 1933

Paraloxoceras Flower, n. gen.

Bergoceras Flower, n. gen

Cayutoceratinae Flower, n. subf.

Cayutoceras Flower, n. gen.

Bradfordoceras Flower and Caster, 1935

No deposits are known within the siphuncles of Palmeroceras, Diagoceras, Geisonoceroides, Sceptrittes or Cryptorthoceras. However, the deposits are developed only in the adapical portion of the phragmocone, and apical portions of species of these genera have not as yet been obtained in a good enough state of preservation to show internal structure. These genera are placed in the Pseudorthoceratidae on the basis of the similarity of the outline of the siphuncle with Dolorthoceras and Adnatoceras, from which they are set apart by variations in the form of the conch and the ornamentation of the exterior.

The Pseudorthoceratidae comprises the only group of cyrtochoanitic orthoceracones known in the Devonian of America with the exception of a few species of Ormoceras Stokes and related forms. In the Devonian of Europe a few actinosiphonate orthoceracones occur, such as Laumontoceras Foerste, Jovellania Bayle, Tripleuroceras Hyatt,⁸⁷ but these lack the generalized features of

87. Foerste, A.^{F.}, Actinosiphonate, trochoceroid and other cephalopods, Dennison Univ. Bull., Sci. Lab., Jour., vol. 21, 1929, pp. 305-311.

section and form which characterize Devonian Pseudorthoceratidae. The family Pseudorthoceratidae is known to range from the Lower Devonian into the Permian.⁸⁸

88. I am indebted to Dr. Curt Teichert, vide litt., for information on the occurrence of Pseudorthoceras in the Fossil Cliff limestone of the Irwin River district of Australia, considered of Lower Artinskian age.

Ancestral forms are found in the Silurian, and the lower boundary of the family has been drawn rather arbitrarily at the appearance of cyrtochoanitic siphuncular outlines. Two changes are involved: a change in the mode of growth of the annulosiphonate deposits, and a change from orthochoanitic to cyrtochoanitic siphuncular outline. The change in the mode of growth of the deposits has been noted in Middle Silurian species which have been regarded as ancestral. Here the annulosiphonate deposits grow around over the connecting ring independent of the growth of cameral deposits, and finally fuse to form a complete lining within the siphuncle. This is the pseudorthoceroid type of siphonal deposit. By definition only cyrtochoanitic forms are placed in the Pseudorthoceratidae. The abrupt appearance of cyrtochoanitic siphuncular segments in the Lower Devonian may be more apparent than real. As yet no members of the genetic stock are known intermediate in age between the Middle Silurian orthochoanitic forms and the Devonian cyrtochoanitic forms. There is very little information available concerning the internal

structure of Upper Silurian orthoceracones. It is quite probable that when Upper Silurian orthoceracones are better known that intermediate stages between the orthochoanitic and cyrtchoanitic outline will be found in orthoceracones with pseudorthoceroid deposits. This is suggested by the gradual change in the ontogeny of the Pseudorthoceratidae and also by the gradual nature of the change of outline in other groups of orthoceracones.

Three subfamilies may be recognized within the Pseudorthoceratidae. Transitional features may be seen at certain points, but the groups are apparently of genetic significance and serve to clarify the relationships existing within the family.

The Dolorthoceratinae is characterized by siphonal deposits which show little dorso-ventral differentiation; in short, of the Dolorthoceras type. A continuous ring is formed at the septal foramen before adjacent segments fuse to form a continuous ventral lining. The siphuncular outline is slender, the segments are never as wide as long and are generally more or less barrel-shaped. The genera included in this group are listed above. This is a generalized group from which the others are derived, and it is not surprising that it is the oldest, appearing in the Lower Devonian and persisting into the Pennsylvanian.

The Pseudorthoceratinae is characterized by the fusion of adjacent segmental deposits on the venter before any trace of siphonal deposit appears on the dorsum. The segments of the siphuncle are broader than in the Dolorthoceratinae, and are fusiform to subspherical. Pseudorthoceras and Mooreoceras form the nucleus of the family. Paraloxoceras develops radial canals, and is a derivative of Mooreoceras. Bergoceras is a cyrtconic derivative of Paraloxoceras in which the dorso-ventral differentiation in the growth of the siphonal deposits seem to be lost. It is included tentatively in the Pseudorthoceratinae, although as pointed out elsewhere, it is possible that Paraloxoceras and Bergoceras may eventually be set off in another subfamily when more material has been studied than is available at present.

The Cayutoceratinae is characterized by the development of a double deposit, consisting of discrete calcareous annulosiphonate deposits covered by a carbonaceous deposit which appears to be continuous when fully developed, but which is actually composed of fused segmental elements. This group is confined to the Upper Devonian where it is represented by Cayutoceras and Bradfordoceras.

The essential characters of the genera of the Pseudorthoceratidae are given in the table below.

Generic characters in the Pseudorthoceratidae

	I	II	III	IV	V	VI	VII	VIII
Anastamoceras	1,2	1	1:0:0	1	1-2	1	1	1
Diagoceras	(1)	2	2:1:1	1-2	2	1	1	1
Dolorthoceras	1	2-3	2:2:1	1-2	1-2	1	1	1
Spyroceras	1	2-3	2:1:1	1-2	1-2	1	2+5	1
Sceptrittes	(1)	2	2:1:1	3	1	3	?	?
Palmeroceras	(1)	3-4	2:2:2	1	1	1	3+4	?
Geisonoceroïdes	(1)	3	2:2:1	1	1	1	2+4	?
Petryoceras	1	3	2:2:1	1-2	1-2	1	6	1
Cryptorthoceras	(1)	3-4	2:1:1	2	2	2	1	?
Fusicoceras	1	3	2:2:1	4	4	4	1	?
Adnatoceras	1	4	2:2:2	1-2	1-2	1	1	1-2
Euloxoceras	1	5	2:3:3	3	3	1	1-3-5	2
Pseudorthoceras	3	6	2:1:1	1	1	1	1	1
Mooreoceras	3	6	2:1:1	1-2	1-2	1	1-(5?)	1
Paraloxoceras	3*	6	2:2:2	2	2	1	1	1
Bergoceras	3*	6	2:2:2	2	2	3	1	1
Cayutoceras	4	3	2:1:1	1	1	1	1	2
Bradfordoceras	4	6	2:1:1	2	2	1	1	1

Key.

1. Siphonal deposits
 1. Dolorthoceras type
 2. Anastamoceras type
 3. Pseudorthoceras type
 4. Cayutoceras type
 - () denotes assumption. evidence lacking
 - * denotes development of connective rings.
2. Siphuncular outline
 1. Anastamoceras type
 2. neanic Dolorthoceras type
 3. ephebic Dolorthoceras type
 4. Adnatoceras type
 5. Euloxoceras type
 6. Pseudorthoceras type

Hyphenated forms have intermediate ephebic type of Siphuncular outline.
3. Ratio of length measurement of neck: brim: connecting ring.

Numerical valuse approximate. intended to show ratio among various genera as well as within genus; hence 2:2:2 indicates equal development of neck, brim, and area, with neck equal to that designated as 2 elsewhere.
4. Section of conch
 1. circular
 2. depressed
 3. compressed
 4. subtriangular, depressed, dorsum flattened.
5. Position of siphuncle
 1. central
 2. ventrad of center
 3. dorsad of center
 4. close to ventral margin
6. Form of conch
 1. orthoceracone
 2. orthoceracone with contracted aperture
 3. cyrtoceracone
 4. brevicone
7. Surface
 1. smooth, or with lines of growth
 2. annuli
 3. longitudinal ribs
 4. transverse lirae and striae

5. longitudinal lirae and striae
 6. transverse bands of zig-zag lirae
- Commas indicate specific variations of ornament in the genus; plus signs indicate patterns.
8. cameral deposits
 1. mural
 2. episeptal and hyposeptal

SPECIFIC CHARACTERS

The specific characters are derived largely from the proportions of the conch. Certain methods of expressing the proportions have been found convenient.

Rate of expansion.- This may be expressed in two ways. The apical angle may be measured, or the rate of expansion in a known length may be given. The author has found the apical angle rather cumbersome, and it is further undesirable because the rate may vary from one part of the conch to another. Measurements are taken, whenever possible in multiples of 10 mm. lengths. Larger units are desirable particularly where the differences are small.

Curvature and depth of septum.- The depth of the septum is considered here in relation to its diameter. Another method frequently employed is the expression of the curvature of the septum as a portion of an arc of a circle. This has been found cumbersome and there is a considerable possibility of error.

Curvature of sutures.- Sutures are only slightly modified in Nautiloidea. Obliquity is sometimes expressed as an angle made by the plane of the suture with a transverse plane. Sinuosity is expressed in terms of lobes and saddles as elsewhere in the Cephalopoda.

Depth of camerae.- It has been found convenient

to consider the depth of camerae in connection with the diameter of the conch. This has been conventionally expressed in terms of the number of camerae in a length equal to the diameter of the conch, the number of camerae being measured apicad (never orad) of the point at which the diameter is taken. As the proportion may vary among various parts of the conch it is best to give actual measurements rather than proportions. Further, in conchs which are not circular in section it is necessary to specify whether the dorso-ventral or transverse diameters are used.

Gerontic camerae are usually markedly contracted, and their relation to the diameter is therefore very different from that found in the rest of the conch. The position of the gerontic camerae in relation to the diameter is often important in fixing the size of the species.

Siphuncle.— The diameter and position of the siphuncle are measured at the septal foramen, i.e., the passage of the siphuncle through the septum. In cyrtochoanitic forms it is necessary to know the relationship of the maximum and minimum diameters of the segments and also its length. As proportions vary from one part of the phragmocone to another, it is desirable that the diameter of the conch be stated for the region at which the measurements of the siphuncle are taken.

The relative length of the septal neck, the brim and the area of adnation supply important characters which are discussed in connection with the types of siphuncle outlines.

Living chamber.— Immature living chambers furnish no information other than the length in relation to the basal) diameter and the condition of the aperture. The mature living chamber may have different proportions. The rate of expansion is normally greatly reduced, and in some forms, as in the species of Geisonoceroides the aperture may contract very slightly orad. The interior of the shell is normally thickened constricting the interior, usually just orad of the middle. The position form and extent of the constriction are important specific characters. The lobation of the aperture is expressed in terms of crest and sinuses. The mid-ventral sinus, which is often the only one developed corresponds in position with the hyponome and is known as the hyponomic sinus.

Variability of the proportions of the early part of the conch from one region to another and the relation of the proportions of the mature living chamber to a definite size make it necessary that the proportions be expressed in terms of actual measurements in most cases. This results in rather unwieldy descriptions, but what is lost in brevity is gained in accuracy.

SYSTEMATIC DESCRIPTIONS

Subfamily Dolorthoceratinae Flower, N. Subfam.

(For a graphic tabular presentation of the genera
see Text pg. 16, pp.)

The subfamily Dolorthoceratinae constitutes simple Pseudorthoceratidae characterized by the development of a complete annulus before the segmental deposits of the siphon fuse on the venter. The siphuncular segments vary from the scarcely cyrtochoanitic condition found in Anastamoceras, and the complex cyrtochoanitic segments of Euloxoceras. The segments are uniformly slender, never wide than long, and with the expansion usually more or less localized near the ends of the segment.

As a linear arrangement is essentially artificial, the genera below are arranged in a somewhat empirical sequence.

I Externally simple forms

Anastamoceras

Diagoceras

Dolorthoceras

II Ornamented derivatives of Dolorthoceras

Spyroceras

Palmeroceras

Geisonoceroides

Petryoceras

III Form deviations

ScreptritesCryptorthocerasFusicoceras

IV Internal specialization-increase in siphuncular expansion

AdnatocerasEuloxoceras

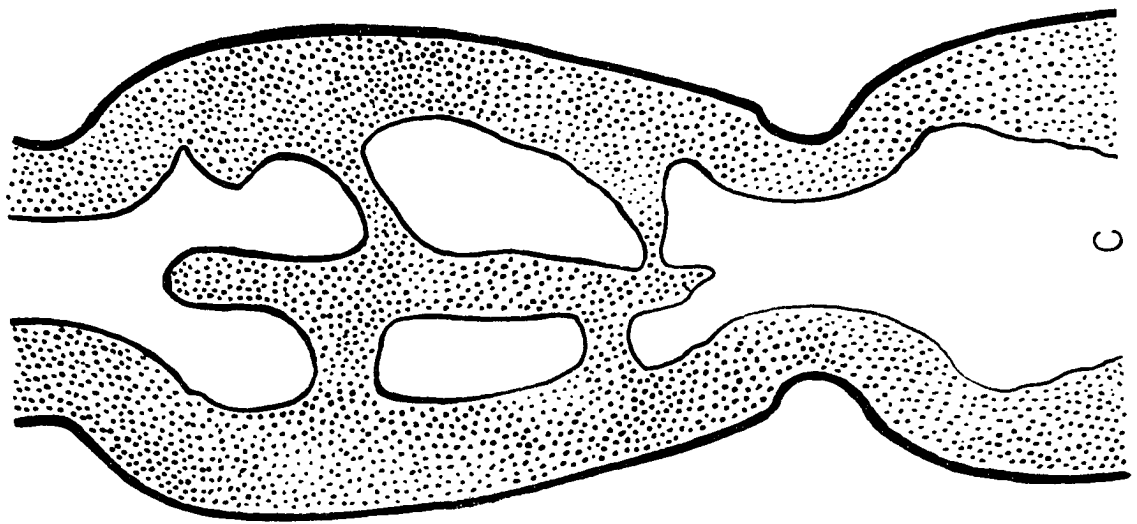
ANASTOMOCERAS FLOWER, n. gen.

Genotype: Anastomoceras mirabile Flower

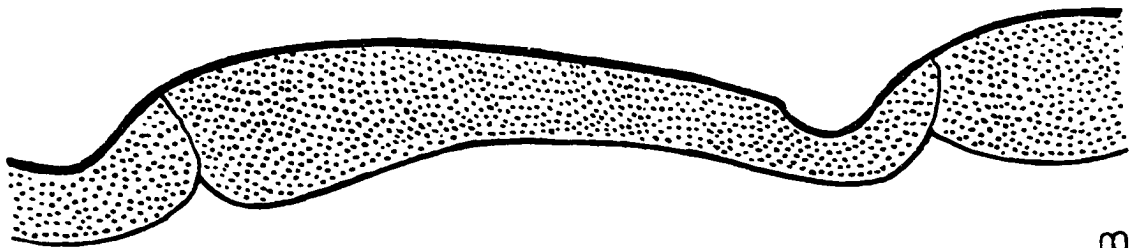
This genus contains orthoceracones of circular section and straight transverse sutures. The central siphuncle is cyrtochoanitic but the segments are slender as in Dolorthoceras. The brims are less than half the necks, and are sometimes obscure, the greater part of the expansion of the siphuncle being due to the connecting ring rather than the neck. The segments may be variously shaped; the genotype they are fusiform with the diameter increasing rapidly from the necks to a point orad of the middle, and decreasing more gradually to the preceding septum. In A. rudis (Hall) the segment is more clindrical. The connecting ring joins the preceding septum within the neck, so that there is no area of adnation.

Fig. 14. Ontogenetic stages of the siphonal deposits of
Pseudorthoceras knoxense (McChesney)

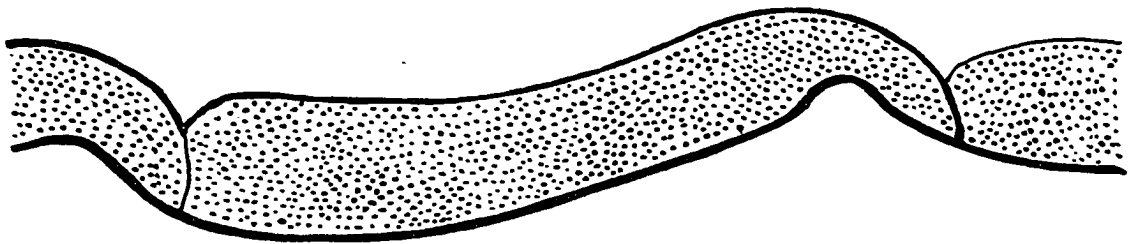
- A. Deposits formed as annuli at the septal foramina appear only on the venter, and grow adorally. The deposits are still discrete in this stage, which represents the Michelinoceras type of deposit.
- B. Cross section of segment A at the above stage.
- C. The deposits shown in A have fused along the venter forming a pseudorthoceroid deposit. This is accompanied and followed by lateral growth of the deposit.
- D. Cross section of segment A at the same stage showing the lateral growth of the deposit.
- E. The deposits have grown laterally until the lobes meet and fuse on the dorsum. The advancing edges of the deposit are variously lobed. The deposit closed at the ends first. Frequently, as in segment C, a lobe in segment B, no such lobe may be present, but the deposit may gradually encroach on the wall of the segment from the ends. Segment A shows complete closure.
- F. Cross section of segment A at the above stage.



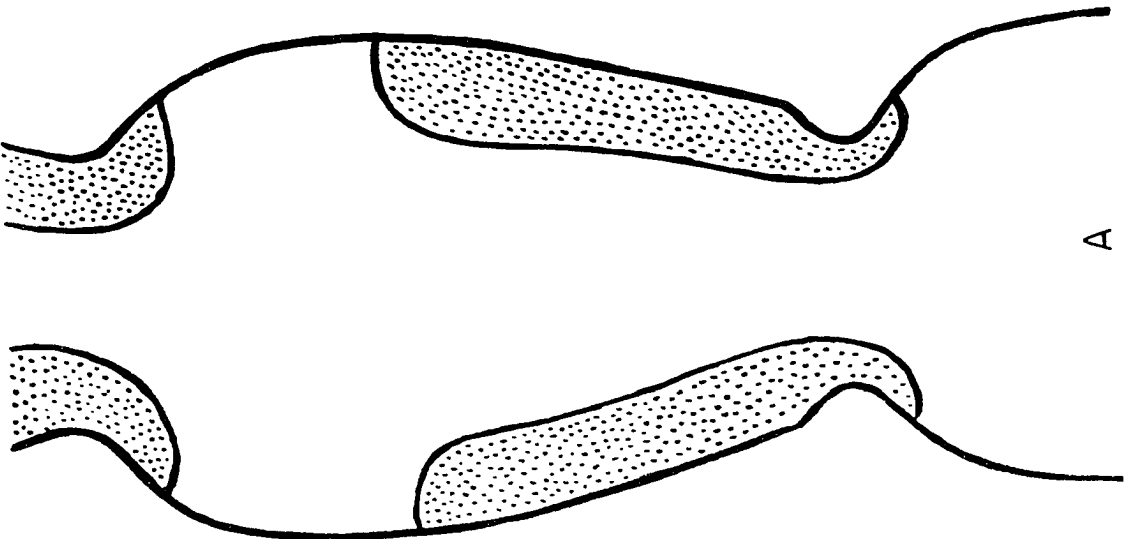
C



B



A



The deposits within the siphuncle are pseudorthoceroid. In the early stage the deposits are somewhat thicker over the septal necks than are those of other genera of this family. There is some dorso-ventral differentiation in the development of the deposits, but it is slight. The gerontic deposits consist of irregular anastomosing processes connecting the continuous pseudorthoceroid deposit with a central tube which occupies the middle of each segment and surrounds the central canal. This tube is not continued through the septal foramen. (Text fig. 3, 13.)

Discussion.- The genus is unique among the Pseudorthoceratidae in the gerontic development of the deposits; it appears that siphonal secretion is uncontrolled, and that the excess material is deposited in portions of the siphuncle which are not otherwise needed.

The outline of the segments of the siphuncle is adequate for the identification of the genus. The necks are less recurved than is typical of the nepionic Dolorthoceras type of outline, and no area of adnation is developed.

The only species which are known to belong to this genus are from the Helderbergian of New York. The genotype A. mirabilie Flower, n. sp. and A. rudis (Hall) are described below. A third species, Orthoceras

longicameratum Hall⁸⁹ from the same general locality

89. Hall, J., 1861, Paleontology of New York, vol. 3, p. 343, pl. 79, fig. 1 Not pl. 71, fig. 1, 5.

and horizon, will probably prove to be an Anastomoceras when better known. Only one of the three figured types shows the siphuncle. Its segments are consistent in outline with other Anastomoceras as far as can be determined from the original illustration. I have not been able to ascertain the location of the types.

Anastomoceras mirabile Flower, n. sp.

Pl. 5, fig. 1, 4-7.

This species is represented by a single specimen which has been somewhat flattened by pressure. The preserved portion of the conch reveals an expansion of from 20 to 21 mm. in a length of 15 mm., which indicates an unusually slender conch in its undistorted condition. The section appears to have been originally circular. The camerae and sutures are not well preserved save that one suture at the apertural end of the specimen shows a transverse and straight course. The depth of the camerae is known from the segments of the siphuncle; there are two and one-fourth camerae in a length equal to a horizontal or greater diameter of 20 mm. The siphuncle is

large in proportion to the diameter of the conch. Where the diameter of the conch in its crushed condition is 20 mm. at its greatest, the siphuncle is 4 mm. in diameter at its passage through the septum, and expands to 6 mm. within the camera. The length of the segment is 10 mm. The segments are elongated and slightly pyriform, the greatest diameter lying orad of the center of the segment. The necks are long, one fifth the length of the segment, and bear obscure brims which are about one-third the necks.

The deposits within the siphuncle at once set this genus apart from all others. In the adapertural end of the specimen two camerae show in section annulosiphonate rings so prolonged adorally as to form a continuous lining within the siphuncle. The deposits retain signs of their segmental origin through^{out}, and are slightly swollen at the adoral end. (Pl 5, fig. 6) Apicad of these segments the structure is lost by distortion in the holotype, but it is clear in the two apical segments. In a longitudinal section which does not quite attain the center, an apparently central core is present in the middle of each segment. The core does not pass through the septal necks but terminated close to them. It is connected with the pseudorthoceroid deposit by irregular radial anastomosing processes. These structures appear

to be uniform in texture with the original deposit. The spaces between are represented by clearer calcareous material, and appear to represent infiltrated material. A cross section, shows that the "central core" is a part of the wall of a hollow cylinder, apparently the wall of a central canal, which is slightly depressed in section and filled with matrix. Obscure traces of the anastomosing processes can also be seen in this section, together with the infiltrated material between them.

The living chamber, aperture and ornament are unknown.

Discussion.- Even in its poor state of preservation this species can be readily distinguished from all others by its slender section, deep camerae and relatively large siphuncle. Externally, it might be confused with Michelinoceras pauciseptum (Hall) which occurs in the same horizon, but that species has an orthochoanitic siphuncle which is considerably smaller in proportion to the diameter of the conch and its camerae are deeper.

Type.- Holotype: Pal. Res. Inst., no. 5817.

Occurrence.- From the Helderbergian near the Indian Ladder, Albany County, New York. From the lithology it appears that the specimen is from one of the more calcareous layers of the New Scotland.

Anastomoceras rudis (Hall)

Pl. 5, fig. 2-3; Pl. 7, fig. 12

Orthoceras rudis Hall, J., Paleontology of New York,
1861, vol. 3, p. 346, pl. 72, fig. 4.

This is an orthoceracone which sometimes attains a diameter of 40 mm. in an undistorted state. The section is circular and the rate of expansion is about 3 mm. in a length of 40 mm. The sutures are straight and transverse. There are three camerae in a length equal to the adapertural diameter. The septa are about one-fifth the diameter of the conch in depth, being 5 mm. deep where the diameter is 27 mm. The siphuncle is central in position and is 3 mm. in diameter where the diameter of the conch is 29 mm.

The siphuncle is poorly preserved, and the connecting rings are usually absent. Where the depth of the camerae is 6 mm., the septal necks are .8 mm. in length and are bent back at an angle of about 110 degrees and only slightly curved. The brim is about half the neck. The connecting rings are partially preserved in one specimen in conjunction with deposits, and join the septum at the apical end of the camera with no area of adnation. The outline of the siphuncle is known for several weathered and partly crushed specimens which are hardly adequate for

measurement of the expansion. It appears that the outline is roughly like that of Dolorthoceras, and there is no trace of the fusiform condition of Anastamoceras mirabile. The deposits within the siphuncle are pseud-orthoceroid. Only an early stage of development has been seen within the species. The first trace of deposits is seen at the sixteenth septal neck from the living chamber. Here the deposit is small, present only on one side, which is assumed to be the venter, and is equally developed orad and apicad of its center. Another specimen shows a more advanced condition. Here the deposit has not increased any apicad or centrad, but is extended orad for half the length of the camera. The deposits are thick at the septal necks, decreasing the diameter of the septal foramen by about one half. A trace of circumferential deposits can be seen in a camera in this specimen.

The living chamber is incompletely known. A fragment with a diameter at the base of 34 mm. is 68 mm. in length. The aperture and surface of the shell are unknown.

Discussion.- The holotype consists of a flattened portion of the phragmocone which is not suitable for either the proportions of the conch or the structure of the siphuncle. On the basis of the proportions, however, it has been possible to refer to this species a number of better preserved specimens upon which the above description

is based. In view of the variation of proportions due to distortion, which has more or less affected every specimen examined, it is not possible to use any finer divisions in distinguishing species from the lower Devonian of New York.

The outline of the septal necks and the absence of an area of adnation are typical of Anastomoceras. The deposits of the siphuncle show some peculiar features, but as a corresponding stage of Anastomoceras mirabile is not available for comparison and there is no justification for the erection of a new genus for the reception of this species.

Type.- Holotype: New York State Mus., Mo. 12401/1.
Hypotypes: Pal. Res. Inst., no. 5818, 5819, 5820.

Occurrence.- The holotype is from the "Central" portion of the Lower Helderberg group (Helderbergian; Lower Devonian,): Schoharie". which is the New Scotland limestone. The species seems to be widespread, as among the specimens examined there are several from the Helderberg escarpment in Albany County and others from near Catskill, New York.

DIAGOCERAS Flower

Genotype: Orthoceras aptum HallFlower, R.H., 1936, Bull. Amer. Paleont.,
vol. 22, p. 293.

This genus contains orthoceracones of circular or depressed section with markedly oblique sutures which slope adaperturally on the dorsum. The septa are oblique and very shallow as in Mooreoceras. The siphuncle is located about half way between the center of the conch and the ventral wall, and is markedly eccentric in the neanic stage of the genotype, the earliest observed. The neck is well developed, the brim is rudimentary and the free part of the connecting ring is faintly and nearly uniformly convex throughout its length. The poor preservation of all specimens examined leaves some doubt as to the condition of the area of adnation. It appears to be equal to the brim. No deposits are known within the siphuncle. Deposits within the camerae are mural and are normally well developed.

Discussion.- The nepionic Dolorthoceras type of segment is probably represented in the ephebic segments of this genus, but doubt concerning the area of adnation made it seem inadvisable to call this the Diagoceras type. It appears that Diagoceras is derived from primitive

species of Dolorthoceras in which this type of segment was an ephebic feature. Such forms may be found when better material of Onondaga and Schoharie orthoceracones has been studied.

The slender outline of the siphuncular segments of Diagoceras led to its inclusion in the Orthoceratidae. Further study has indicated that its relations are more probably with Anastomoceras and Dolorthoceras of the Pseudorthoceratidae. Only two species are known. The first, the genotype, has been recently described, and no new information has been obtained ⁿsince this redescription.⁹⁰

90. Flower, R.H., Ibid., p. 293, pl. 23, fig. 5-8; pl. 24, fig. 1.

The species is known only from the Cherry Valley limestone. A new species from the Tully limestone is described below.

The markedly oblique sutures and the condition of the siphuncle will serve to separate this genus from all others of the Pseudorthoceratidae. Externally it somewhat resembles Mooreoceras, from which it can be distinguished by the segments of the siphuncle.

Diagoceras tullium Flower, sp. nov.

plate 4, fig. 7.

Conch orthoceraconic, circular in section, with no trace of the slightest depression. The rate of expansion is between 2.5 mm. and 3 mm., in a length of 20 mm., with no gerontic decrease up to a diameter of 23 mm. The sutures are markedly oblique, sloping adaperturally on the dorsum. Where the diameter of the conch is 21 mm. at the dorsal portion of the suture, the ventral portion lies 7 mm. apical, so that the obliquity is one-third the diameter of the conch at that point, or equal to the depth of two camerae. The septum has not been observed. There are five camerae in a length equal to the adapertural diameter of 5 mm., the measurement being taken at the dorsal extent of the suture. This proportion is found in a much younger stage of D. aptum, but the camerae are closer shallower at a corresponding diameter in that species, as the increase in the depth of the camerae of aptum is slower than in tullium.

The position and structure of the siphuncle are unknown. The base of the living chamber is 21 mm. in diameter. The length of the living chamber is unknown as are the characters of the aperture. The external mold reveals no trace of fine surface markings, probably lines of growth,

such as occur in D. aptum.

Discussion.- This species is known only from the holotype which represents a portion of a phragmocone and the base of the living chamber. The species differs from D. aptum in the circular section, the slightly greater rate of expansion, the more rapid increase in the depth of the camerae, and by the much more oblique sutures.

Type.- Holotype: Pal. Res. Inst., no. 5821.

Occurrence.- From a loose block of the Tully limestone along the railroad track on the east shore of Cayuga lake, about five miles north of Ithaca, New York. Judged by the associated fauna it is from the Apulia member of the Tully. Collected by the author.

DOLORTHOCERAS Miller

Genotype: Dolorthoceras circulare Miller

Miller, A.K., 1931, Am. Jour. Sci., ser. 5, vol. 22, p. 419.

Miller, A.K., Dunbar, C.O., and Condra, G.E., 1933, Nebraska Geol. Surv., ser. 2, bull. 9, p. 94.

In Dolorthoceras, as here restricted, are placed smooth orthoceracones of circular or slightly depressed section. The sutures vary from straight and transverse to slightly oblique and sinuous. The siphuncle is central

in the early stages, but becomes slightly ventrad of the center in the ephebic stage of most species, though in a few it remains subcentral throughout life. The segments of the siphuncle are orthochoanitic at the earliest stage observed. Later segments show the Anastomoceras stage, the nepionic Dolorthoceras stage, and the ephebic segments are of the Dolorthoceras stage. The neck and brim are normally equal or nearly so. The area of adnation ceases to develop beyond the nepionic Dolorthoceras stage, so that in the normal adult segment it is one-half the brim, or may be even more reduced. The deposits of the siphuncle first appear as simple annuli. These develop into the Michelinoceras type of deposit and then into the Dolorthoceras type. The deposit is normally completed around the sipital foramen before the fusion of adjacent deposits takes place along the venter, but in one fragment of undetermined relationship, the fusion of successive segmental deposits has been noted along the venter before the deposit appears dorsally.

Deposits within the camerae are circumferential or mural and are heavier on the venter than on the dorsum.

The aperture has been observed only in certain of the Hamilton species. A hyponomic sinus is present, and the aperture may be trilobed. One of the lobes is slightly deeper than the others and probably represents

the hyponomic sinus. The surface of the conch may bear transverse striae or only fine lines of growth

Discussion.- The choice of D. circulare as a genotype is rather unfortunate, inasmuch as the presence and form of deposits within the siphuncle are unknown. The description of the species was based upon a single rather badly weathered specimen. As the species is from the Karakoram mountains of Asia, it seems unlikely that more material can be obtained for a study of the internal structure. On the basis of the present evidence it is impossible to detect any important difference between the genotype and the Devonian species here referred to Dolorthoceras except the presence of deposits in most Devonian species. Experience has shown that it is unwise to assume the absence of deposits within the phragmocone of a species on the basis of a single specimen, particularly when the specimen is fragmentary. Should D. circulare prove upon further study to lack deposits or to possess deposits of a different sort, a new name will have to be proposed for the Devonian species here included. However, the long ranges of other smooth shelled genera of the Pseudorthoceratidae, Adnatoceras, Pseudorthoceras and Mooreoceras, which also persist from the Devonian into the Pennsylvanian, make it seem probable that Dolorthoceras may also have a similarly extensive geological range.

In Dolorthoceras are included species with both the neanic and ephebic Dolorthoceras types of siphuncular outline in the mature stage. Species which retain the neanic Dolorthoceras outline throughout life are the oldest, and are not known to extend into the Eriean of the Middle Devonian. Gradation is such that a separation of such species into a distinct genus would only result in confusion.

The stratigraphic range of the know species of Dolorthoceras may be summarized as follows:

Lower Devonian

The Moose River sandstone of Maine, which is of Oriskanian age, contains Dolorthoceras parlenense (Williams). The species is described below.

Middle Devonian

Ulsterian.- No species from the Schoharie grit have as yet been recognized as members of this genus, owing to the absence of well preserved siphuncles.

Orthoceras rudicula Hall⁹¹ of the Onondaga limestone

91. Ibid., pl. 92, fig. 1.

of New York apparently belongs in Dolorthoceras Hall's illustration of the siphuncle suggests the nepionic Dolorthoceras type of outline, but is not clear enough to permit a conclusive statement.

Eriean.O In the Hamilton of central New York D. tersum (Hall), D. telamon (Hall) and D. exile (Hall) are fairly common. It is still doubtful as to just what Orthoceras bebryx is, but it is certain that a large species of Dolorthoceras has been included. The only Dolorthoceras from western New York so far recognized is D. revertum Flower, n. sp., in which the siphuncle is eccentric at an early stage and becomes central ephemerically. Dolorthoceras has not as yet been recognized from the Hamilton of Ontario or Maryland.

Upper Devonian

Senecan.- The tully limestone has yielded but one typical Dolorthoceras, D. solitarium, Flower, n. sp. The Ithaca has yielded only flattened specimens, and generic identification is largely impossible. A few specimens have shown Dolorthoceras-like siphuncular outlines, but these have been unidentifiable specifically. Dolorthoceras elegans Flower, n. sp. occurs in the Cashaqua shale of the Naples fauna.

Higher beds.- The only Dolorthoceras known from higher strata of the Devonian of New York is D. palmerae (Flower and Caster). The horizon of this species is uncertain. It may be Conneaut or Conewango.

Mississippian

A specimen from the Rockford limestone, Lower Mississippian, of Indiana, Dolorthoceras cf. icarus (Hall) is typical of the genus. No other species have as yet been recognized as typical Dolorthoceras from the Mississippian of America. It is possible that several of the species referred to Mooreoceras by Miller and Furnish⁹²

92. Miller, A.K. and Furnish, W.M., Lower Mississippian nautiloid cephalopods of Missouri, in Stratigraphy and paleontology of the lower Mississippian of Missouri, Part II, Univ. of Missouri Studies, vol. 13, no 4, 1938, p. 164-169.

may prove to be Dolorthoceras when the siphuncular outline and siphonal deposits have been made known. At the present time only the septal necks are known for some of the species which are not sufficient to form a basis for generic determination.

Of the orthoceracones of the Mississippian of Belgium described and illustrated by de Koninck, only one can be recognized as a Dolorthoceras from the descriptions and illustrations. This is Dolorthoceras goldfussianum de Koninck⁹³ of the Vise limestone.

93. De Koninck, L.G., Faune du Calcaire Carbonifère de la Belgique, 2me partie, Ann. du Musée Royal d'Hist. Nat. de

Belgique, série Paléontologique, tome V, 1880, pl 66,
pl. 38, fig. 8,9.

Pennsylvanian

The genotype, Dolorthoceras circulare Miller is from
the Pennsylvanian of the Karakoram mountains of Asia.

Doloroceras ciscoense Miller Dunbar and Condra⁹⁴ of the

94. Ibid., p. 96, pl. 1, fig. 1-3.

Cisco formation of Texas is removed to Adnatoceras on the
basis of the siphuncular outline. D. (?) dubium Miller
Dunbar and Condra⁹⁵ of the Weeping Water limestone, basal

95. Ibid., p. 95, pl.1, fig. 10-11.

Shawnee, of Nebraska as indicated in the original des-
cription is doubtfully referred to the genus owing to
the poor preservation of the holotype, which is the only
known representative of the species.

Key to American Devonian species of Dolorthoceras

- A. Siphuncular segments not passing beyond the nepionic Dolorthoceras stage
 - B. Size small; rate of expansion about 1 mm.
in 10 mm.....parlenense
 - BB. Size larger; rate of expansion at least 3 mm.
in 10 mm..... rudicula
- AA. Siphuncular segments attaining ephebic Dolorthoceras stage.
 - C. Small species; maximum diameter attained 30 mm.
 - D. Siphuncle subcentral throughout.
 - E. 5 camerae in length equal to adoral diameter; septum $1/5$ diameter in depth.
 - F. Length; width siphuncular segments 2:3
Rate expansion 3 mm. in 10 mm.;
Base mature living chamber beyond 16 mm.
.....solitarium
 - FF. Length; width siphuncular segments 1:2
Rate expansion 4 mm. in 10 mm.;
Base mature living chamber at 20 mm.
.....tersum
 - EE. 4 camerae in length equal to adoral diameter; septum $1/4$ diameter in depth;
 - G. Rate expansion 4 mm. in 10 mm.
Length; width siphuncular segments 3:2
.....palmerae
 - GG. Length to width siphuncular segment 2:1
Rate expansion 1 mm. in 10 mm.
 - DD. Siphuncle becoming eccentric at early stage
(about 7 mm. diameter)

- H. Siphuncle remaining eccentric throughout
.....exile
- HH. Siphuncle becoming central adorally
 - I. Gerontic living chamber at 20 mm.;
section subcircular; sutures straight.
 - II. Gerontic living chamber beyond 27 mm;
section depressed, sutures with lateral
lobes.....revertum
- CC. Large species; maximum diameter over 35 mm.
 - J. 4-5 camerae in length equal to diameter
in flattened specimen.....bebryx
 - JJ. 7-8 camerae in length equal to diameter
in flattened specimen.....cayuga

Dolorthoceras parlenense (Williams)

Orthoceras parlenense Williams, S.G., 1916, U.S.G.S.

Prof. Paper, no 89, p. 283, pl. 13, fig. 25.

Orthoceras cf. Orthoceras parlenense Williams, S.G.,

1816, U.S.G.S. Prof. Paper, no 89. pl. 25, fig. 21.

The original description was based upon a fragment of a phragmocone representing an immature portion. A second specimen was referred to the species with doubt, but is here regarded as conspecific on the basis of the similarity of proportions with those found in the later portion of the holotype.

The holotype is 25 mm. in length, increasing from 2 mm.

to 6 mm. in diameter. The section is circular. Sutures straight and transverse. Camerae increasing very slowly in depth, so that adapically one and one-half camera occupies a length equal to the adoral diameter of 3 mm., while adorally three occur in a length equal to the diameter of 6 mm. The siphuncle is slightly eccentric. Where it is 1 mm. in diameter it is 1.5 mm. from one side of the shell and 2 mm. from the other. Its structure is not shown on the holotype.

The other specimen is a natural section. It increases from 6 mm. to 9 mm. in 18 mm. Three camerae occupy a length equal to an adoral diameter of 8 mm. The septum has a depth of 3.5 mm. where the diameter is 8 mm. The siphuncle is made up of segments which are slightly expanded. A segment 3 mm. long increases from 1.4 mm. to 2 mm. in diameter. The outline appears to be of the nepionic Dolorthoceras type, though the condition of the area of adnation is obscure, and the possibility of the Anastomoceras type is not entirely eliminated. There are obscure traces of cameral deposits, though they must be regarded as doubtful due to the badly weathered condition of the specimen. The siphuncle shows traces of parietal annulosiphonate deposits.

Discussion.— This species occurs in a part of the section in which the Pseudorthoceratidae are very poorly

known, that is, in the interval comprising the upper part of the Lower Devonian and the lower part of the Middle Devonian. The earliest well preserved Dolorthoceras is Hamilton; the latest Anastomoceras is Helderbergian. A gradation between the genera is suspected in this time interval, a hypothesis to which this species lends some support. A slight area of adnation is suspected, though the poor preservation makes it necessary to admit that the evidence is not conclusive.

Types.- U.S.N.M. No. 59873.

Occurrence.- From the Moose River sandstone of the Oriskanian of the Lower Devonian, Detroit, Somerset County, Maine.

Dolorthoceras tersum (Hall)

Pl. 1, fig. 11; pl. 8, fig. 6; pl. 9, figs. 8 and 17

Orthoceras tersum Hall, J., 1879, Paleontology of New York, vol. 5, pt. 2, p. 286, pl. 84, fig. 5.

This is a small orthoceracone of subcircular section. The conch expands in a length of 27 mm. from diameters of 7.6 mm. and 8.5 mm. to 11.4 mm. and 12.6 mm.

The sutures are straight and transverse. The septa are evenly curved and are slightly less than one fifth their diameter in depth, being 2 mm. deep where the

diameter is 11 mm., or about equal to the depth of a camera. There are five camerae in a length equal to an adapertural diameter of transverse diameter of 8.5 mm. This proportion appears to lessen slightly so that where the diameter of the conch is 11 mm., there are four and three-fourths camerae in that length. At the base of the living chamber where the diameter is 14 mm., there are five and one-third camerae in a length equal to the adapertural diameter, indicating a beginning of the gerontic contraction of the camerae.

The siphuncle is slightly ventrad of the center of the conch. In an early portion it is .8 mm. in diameter and is 2.8 mm. from the venter and 4 mm. from the dorsum. At a later position it is 1.4 mm. in diameter and is 4 mm. from the venter and 5 mm. from the dorsum.

In section the segments of the siphuncle are cylindrical over the greater part of their length, and contract abruptly at the apices. Where the diameter of the conch is 11 mm., and the depth of a camera is 2 mm., the siphuncle is 1 mm. in diameter at the septal necks and expands within the camera to 1.4 mm. The necks are short and recurved, with the brim slightly less than the neck, though the proportions vary slightly from segment to segment. The neck is about one-tenth the depth of the camerae. The middle portion of the connecting ring is very faintly convex though the curvature is marked only at the

extremities. There is no area of adnation. No deposits are known within either the camera or the siphuncle.

The internal mold of the species shows the impression of a septal furrow. The living chamber is 12 mm. in diameter at the base and is 25 mm. in length on the hypotype. At the extremity there is a trace of contraction. The location of the contraction on this living chamber made it possible to correlate with the species some more nearly complete but isolated living chambers. One of these shows diameters at the base of 13.3 mm. and 14 mm., and is 30 mm. in length. The constriction begins about 18 mm. above the base. The aperture is not preserved. A slightly smaller specimen which appears to belong to the same species has diameters at the base of the living chamber of 12 mm. and 13mm. The constriction begins 20 mm. beyond the base of the specimen beyond a maximum diameter of 14.8 mm. At the middle of the constriction the diameter has decreased to 14 mm., but 28 mm. beyond the base of the chamber the former diameter is nearly resumed. None of these specimens preserved a good aperture.

A slightly larger living chamber which is referred to this species preserves a remarkably well preserved aperture. On the venter there is a large well defined hyponomic sinus. Two dorso-lateral smaller sinuses are present separated by a mid-dorsal crest. (Pl.9 fig. 8.)

Discussion.- The outline of the siphuncle of this species is typical for Dolorthoceras. No deposits are known in either the camerae or the siphuncle for this species, but the portion figured is only three camerae removed from the living chamber.

The dorsal furrow present in this species is the homologue of that found on the dorsum of Striacoceras typum Saemann, and not the homologue of the conchial furrow as Hall supposed. Consequently it has been necessary to reverse Hall's orientation of this species, and the siphuncle lies ventrad of the center and not dorsad as Hall believed.

Types.- Holotype: Amer. Mus. Nat. Hist., 4950/1.
Hypotypes: Pal. Res. Inst., no. 5822-5825.

Occurrence.- In the Skanneateles division of the Hamilton, Middle Devonian. The holotype and one hypotype are from the limestone in the upper portion of the Pompey member at Pratt's Falls, Onondaga County, New York. The free living chambers are from the Bembexia sulcomarginata horizon in the Delphi Falls member at Delphi Falls, New York.

Dolorthoceras exile (Hall)

Pl. 7. fig. 4; pl. 8, fig. 7.

Orthoceras exile Hall, J., 1862, 15th Ann. Rep.

Regents of the Univ. of the State of New York
on the condition of the State Cab. of Nat. Hist.,
etc., p. 78, pl. 8, fig. 5.

-----Hall, J., 1879, Paleontology of New York
vol. 5, pt. 2, p. 290, pl. 39, fig. 3. Not pl.
84, 85.

Conch orthoceraconic, slender, subcircular in section. The hypotype is 107 mm. in length and represents a gerontic individual which retains the basal portion of the living chamber. The neanic and ephêbic portions of the conch possess diameters which vary by about .5 mm, and the rate of expansion is between 1.5 mm. and 2 mm. in a length of 20 mm. In the adapertural portion of the specimen this is decreased to 1 mm. in the last 20 mm., the measurements being 14.5 mm. and 15.5 mm.

The sutures are straight and are inclined about 10 degrees from the horizontal. The proportion of the depth of the camera to the diameter varies during the growth. In the neanic stage, where the diameter is 10 mm. or less, there are three camerae in a length equal to the adapertural diameter. Where the diameter is 14 or 15 mm., there

are three and one-third camerae in that length. In the genontic portion of the phragmocone there are four and one-half camerae in a length equal to the adapertural diameter of 16 mm.

The septum is between one-third and one-fourth the diameter of the conch in depth. Where the diameter is 8 mm., the septum is 2.2 mm. in depth; where the diameter is 13 mm., the depth has increased to 4 mm.

The siphuncle is about twice as far from the dorsum as from the venter throughout the known portion. It is 1.8 mm. in diameter where the conch is 8 mm. in diameter. The septal necks are less than one-tenth the length of the segment, and are sharply recurved forming a brim which is slightly greater than the neck. The connecting rings are unknown, but from the similarity of this species to Dolorthoceras tersum (Hall) and Dolorthoceras telamon (Hall) with which it is associated, it is believed that the condition is that of Dolorthoceras rather than of Adnatoceras. In the adapical end of the specimen the camerae show faint traces of deposits against the outer wall. Deposits are not known in the siphuncle.

The mature living chamber is known from the lectotype, which is slightly crushed and not suitable for measurements, and from a hypotype. The hypotype consists of a living chamber which is 14 mm. in diameter at the

base, and which is 41 mm. in length. The gerontic constriction begins 29 mm. above the base of the chamber, and the former diameter is not attained at the aperture. The surface of the shell is smooth and without ornament, though fine lines of growth may have been originally present.

Discussion.- This species differs from Dolorthoceras tersum in the eccentric siphuncle and more slender form. The species closely resembles Dolorthoceras telamon, but that species attains a much larger size. Of the specimens which Hall figured as exile, only two belong to the species. Of the others, one is clearly a living chamber of Adnatoceras spissum (Hall),⁹⁶ and the other is a crushed

96. Type of Paleontology of New York, vol. 5, pt. 2, pl. 85, fig. 15. New York State Museum, no. 12365/3.

fragment which cannot be identified with certainty, but which appears to belong to D. telamon.⁹⁷ No figure

97. Ibid., pl. 85, fig. 14. New York State Museum, no. 12365/2.

accompanies the original description, and it cannot be definitely stated which of the specimens is that upon which the original description was based. The first specimen figured is recognizable and has been taken as typical D. exile. Specimen no. 4943/1 of the American

Museum of Natural History, the type of pl. 85, fig. 1-2, of the Paleontology, is an immature living chamber with a few camerae attached. This may be D. telamon, but be identified generically or specifically with certainty. The specimen is from Cumberland Maryland. In the catalogue of the American Museum the specimen is listed as "Internal cast which was used in the original description." Hall's final description shows clearly that while he may have had that specimen at the time when he described Orthoceras exile, it played a minor part if any in his conception or description of the species, for under the heading of formation and localities he says: "Hamilton group, on the south shore of Lake Erie; at Cayuga Lake, and at Cazenovia, Madison County, N.Y. It has also been identified in the rocks of this formation at Cumberland, Maryland.

Types.- According to the catalogue of the New York State Museum, another specimen was used at the time of the original description. This specimen, the one figured on plate 39, figure 3 of the Paleontology of New York, specimen no. 12365/1 of the New York State Museum, is hereby selected as the lectotype of the species.

It is uncertain whether 4943/2 of the American Museum of Natural History is to be regarded as a paratype of a hypotype. The hypotypes upon which this redescription is largely based are Pal. Res. Inst., no. 5826, 5827.

Occurrence.- Probably widespread in the Hamilton shales of New York. The lectotype is from Cazenovia, New York. The American Museum specimen is from ten miles south of Buffalo, New York. The hypotypes of the Paleontological Research Institution were collected by the author from the Pompey member of the Hamilton at Pratt's Falls, Onondaga County, New York.

Dolorthoceras telamon (Hall)

Pl. 2, fig. 10; pl. 4, fig. 10-11;
pl. 8, fig. 9-10.

Orthoceras telamon Hall, J., 1879, Paleontology of New York, vol. 5, pt. 2, p. 291, pl. 85, fig. 3,4, 12.

Conch orthoceraconic, slender, subcircular in section. The diameter increases at a rate of 2 mm. to 2.5 mm. in a length of 20 mm. The transverse diameter throughout the late neanic and ephebic stages.

The sutures are straight and transverse in the young but are more or less oblique in the late ephebic and gerontic stages. At the base of the gerontic living chamber the diameter is 19.5 mm. and the obliquity is 5 mm., though this appears to represent an extreme case.

The camerae vary somewhat in proportion, as the depth

increases more slowly orad than the diameter of the conch. There are three and one-half camerae in a length equal to an adapertural diameter of 9 mm., and three camerae at a later stage where the diameter is 14 mm.

The septa are evenly curved, and in the early stage the depth is slightly more than one-fourth the diameter. In the ephebic portion this may increase to one-third, where the diameter of the conch is 13 mm.

The siphuncle is nearly central in the youngest known stage but becomes rapidly eccentric. Where the diameter is 8 mm., the siphuncle is 3.5 mm. from one wall and 4.5 mm. from the other. Where the diameter is 12.5 mm., the siphuncle is 1.5 mm. in diameter and is 4 mm. from the venter and 7 mm. from the dorsum. At the base of the gerontic living chamber the siphuncle is 2 mm. in diameter and is 5 mm. from the venter and 12.5 mm. from the dorsum.

The outline of the siphuncle is known from a fragment representing a relatively early portion of the conch. Where the diameter of the conch is 8 mm. the siphuncle is .8 mm. in diameter at the septal foramen and expands to a maximum diameter of 1.4 mm. within the segment. The outline is typical of Dolorthoceras. The brim and neck are subequal and about twice the area of adnation. The free part of the connecting ring is

faintly convex over the middle portion but strongly curved at the ends. No trace of any organic deposit has been found within the siphuncle. Well defined circumferential deposits are present within the camerae, and these are clearly better developed on the ventral side than on the dorsal side.

The mature living chamber is 20 mm. in diameter at the base and is 59 mm. in length. The aperture is unknown. A shallow elongate constriction occupies the outer third of the chamber on this specimen. The surface of the conch is ornamented by obscure lines of growth which show no trace of a hyponomic sinus.

Discussion.— In its slender form this species resembles Dolorthoceras exile (Hall) from which it can be distinguished by the more gradual increase in depth of the camerae, the movement of the siphuncle from a sub-central position in an early stage to a markedly eccentric one in the gerontic stage, and in the deeper septa.

Mature living chambers are of a much larger size. The dorsal carina is normally well developed in this species.

The early stage of this species may be confused with Dolorthoceras tersum which has shallower camerae and septa, and which expands more rapidly.

Types.— Lectotype: New York State Museum, no. 12410/2. Paratype: New York State Museum, no. 1240/1. Hypotypes:

Pal. Res. Inst., no. 5828-5834.

Occurrence.- In the Hamilton shales of New York, apparently wide ranging. The types are from Menteth's Point, Canandigua Lake, New York, probably from the Ludlowville shales. The hypotypes are from the limestone on the top of the Pompey member at Pratt's Falls, New York and from the shales of the Delphi member at Delphi Falls, New York.

Dolorthoceras revertum Flower

Pl. 8, fig. 2-3; pl. 9, fig. 18.

This species attains a moderate size, and is characterized by the position of the siphuncle, which is closed to the venter in the early portion, but comes to lie only slightly ventrad of the center in the ephebic portion. The section is slightly depressed throughout, with the venter moderately flattened in the ephebic portion. The holotype expands from 10.5 mm. and 11 mm. to 16 mm. and 17 mm. in the basal 48 mm.; to 18 mm. and 22 mm. in the next 45 mm., and to 24 mm. and 27 mm. at the adoral end of the specimen in the next 48 mm. The sutures are exposed only in the adoral part of the specimen. They are sinuate, having lateral lobes separating dorsal and ventral saddles, and are slightly inclined

orad on the venter. There are four and one-half camerae in a length equal to the dorso-ventral diameter of 22 mm., and this relation holds throughout the ephebic portion. The septum has a depth of 8 mm. where the diameters are 19 mm. and 22 mm.

The center of the siphuncle is 9 mm. from the dorsum and 1.5 mm from the venter at the apex, but where the dorso-ventral diameter is 19 mm., the siphuncle is 8 mm. from the venter and 11 mm. from the dorsum. Here its diameter at the septal foramen is 2mm.

The outline of the siphuncle is known for the apical portion of the specimen. The segments are of the *Dolorthoceras* type. Where the transverse diameter of the conch is 11 mm., the segment is 3.2 mm. in length, and expands from .9 mm. to 1.5 mm. The septal neck is .3 mm., the brim is less than the neck and twice the area of adnation. Well developed deposits of the *Dolorthoceras* type line the siphuncle. Heavy mural deposits occupy the camerae.

No trace of ornament can be seen on the holotype. The surface of the shell must have been smooth or nearly so. The living chamber is unknown. Up to a transverse diameter of 27 mm., there is no trace of the living chamber or of the shortened camerae which indicate a mature condition.

Discussion.- The peculiar course of the siphuncle will serve to distinguish this from other species of Dolorthoceras. D. revertum can be distinguished from other Hamilton species by its size. The siphuncle of "Orthoceras" erlense is central, and that species is even larger. Dolorthoceras bebryx cannot be compared, because the undistorted section of that species is not known.

Type.- Holotype: Buffalo Museum of Science.

Occurrence.- From the Pleurodictyum bed, Wanakah member, Ludlowville shale Hamilton stages, Middle Devonian. Collected at Wanakah, New York, by I. G. Reimann.

Dolorthoceras sp. indet.

Pl. 2, fig. 8-9.

Orthoceras subulatum Hall, J., 1879, pl. 84, fig. 4, 6-10.

Among the various specimens which Hall placed in Orthoceras subulatum there are a number of more or less crushed apical portions of phragmocones from Platt's Falls, Onondaga County, New York. These occur in the soft shales at the bottom of that section, and identical forms are numerous at Delphi Falls. A number of the

specimens from Delphi Falls have yielded siphuncles which are sufficiently clear to show that the specimens are representatives of Dolorthoceras. The distortion makes specific identification impossible. It is probable that apical portions of Dolorthoceras tersum, Dolorthoceras telamon and Dolorthoceras exile are represented. Certainly there is variability in the depth of the camerae which seems to indicate that several species may be represented. One specimen, (pl. 2, fig. 9) is of interest in that the condition of necks and brims is typical of the nepionic Dolorthoceras outline, but the free part of the connecting ring is unusually straight in the middle. A second specimen (Pl. 2, fig. 8) is illustrated to show Michelinoceras stage in the development of the siphuncular deposit.

The specimens from Pratt's Falls and Delphi Falls cannot be distinguished, and are regarded as conspecific. The localities are only a few miles apart. The Delphi Falls specimens are from the Bembexia sulcomarginata zone of the Delphi Falls member of the Hamilton. The Pratt Falls material is from black shales which appear to represent the Delphi member rather than the Pompey member. There is no good boundary between these members. The typical Pompey consists of more arenaceous grayer shales which increase in the amount of silicious material upward,

passing through sandy beds which are rich in pelecypods, and capped by a shell limestone characterized by a great abundance of Nyassa arguta Hall. It is from this limestone band that the well preserved cephalopods were collected upon which the revised descriptions of D. exile, D. tersum, D. telamon and A. spissum are based. There is probably no faunal break.

Types.— Pal. Res. Inst., no. 5836, 5837.

Occurrence.— From the Delphi member of the Skaneateles division of the Hamilton, Middle Devonian, from Pratt's Falls and Delphi Falls, New York.

Dolorthoceras aff. exile (Hall)

Pl. 1, fig. 5.

The type consists of a portion of a phragmocone of circular section which expands from 7 mm. to 9 mm. in diameter in a length of 18 mm. The interior of the camerae is occupied by coarsely crystalline calcite which obscures the septa and the cameral deposits. The length of the siphuncular segments indicates that there were about four camerae in a length equal to an adapertural diameter. At the adapical end of the specimen the siphuncle is slightly ventrad of the center. It is .6 mm. at the septal foramen and is 3 mm. from the

ventral wall of the conch. The segment expands to a maximum diameter of 1.2 mm. and is 2 mm. in length. In outline the segments are intermediate between the nepionic ephebic Dolorthoceras types. The area of adnation is less than the brim, the brim is still slightly less than the neck, and the free part of the connecting ring is more convex at its ends than in the middle.

The siphuncle, though distorted and broken, preserves its internal structure well. At the adapertural end of the specimen the Michelinoceras type of deposit is seen on the venter only. In more adapical segments successive stages in the fusion of the deposits can be seen. In the two adapical segments the deposits are fused along the venter, and appear to occupy half of the interior of the siphuncle. No deposits are noted against the dorsal wall.

Discussion.— The specific relation of this fragment remain a matter of doubt. The depth of the camerae excludes D. telamon and D. exile. The rate of expansion is more slender than that of D. tersum, and by the condition of the deposits, the fragment belongs to a species which attained a considerably greater size than does tersum. It may be that this belongs to the species for which I proposed the name Michelinoceras noveboracense, The species is unfortunately known from the living chamber which is of exceptional length, and from a few gerontic

camerae. Undistorted specimens retaining the phragmocone and siphuncle are not known as yet.

The confinement of the siphuncular deposit to the ventral side of the conch suggests Pseudorthoceras. The thick condition of the deposit may indicate a more primitive condition. It is possible that this species may be directly ancestral to Pseudorthoceras which appears in the upper Devonian.

Types.— Pal. Res. Inst., no. 5835.

Occurrence.— From the limestone at the top of the Pompey member of the Skanneateles of the Hamilton, at Pratt's Falls, New York.

Dolorthoceras solotarium Flower, n. sp.

Pl. 1, fig. 9; pl. 4, fig. 6.

This is a slender orthoceracone of slightly depressed section. The dorso-ventral diameter increases from 11 mm. to 14 mm. in a length of 20 mm., and the transverse diameter, as estimated, increases from 14 mm. to 17 mm. in the same length.

The sutures are straight and transverse. The septa are moderately convex apicad, the depth being about one-fifth the dorso-ventral diameter throughout. There are five camerae in a length equal to an adapertural

diameter of 15 mm., and four and three-fourths in a length equal to a diameter of 13 mm.

The siphuncle is central. Where the dorso-ventral diameter of the conch is 15 mm. and the camera 2.5 mm. in depth, the siphuncle expands from a diameter of 1 mm. at the septal neck to 1.8 mm. within the camera. Necks and brims are subequal. The area of adnation is slightly less than half the brim. The free part of the connecting ring is convex throughout, attaining its greatest diameter arad of the middle of the segment.

Nothing is known of the living chamber, aperture or ornament of this species. The holotype shows no trace or organic deposits within the camerae or siphuncle.

Discussion.- This species may be distinguished from all others in the Tully by the much greater relative width of the siphuncular segments. Its markedly depressed cross section will serve to distinguish it from any Hamilton species of Dolorthoceras.

Type.- Holotype, U.S.National Museum, no. 96778.

Occurrence.- In the West Brook member of the Tully limestone, Upper Devonian, from the north-east corner of the Pitcher Quadrangle, New York. Collected by J.S. Williams.

Dolorthoceras elegans Flower, n. sp.

Pl. 9, fig. 15-16.

The holotype is a small orthoceracone of circular section and of a uniform rate of expansion throughout. In the adoral 30 mm. the conch expands from 10 mm. to 14 mm. The sutures are apparently straight and transvers. There are four camerae in a length equal to the adapertural diameter throughout the specimen. The septum is one-fourth the diameter of the conch in depth, being 2.5 mm. where the diameter is 10 mm.

The siphuncle is subcentral in position. In a nearly dorso-ventral section the diameter of the septal foramen is .8 mm., and it is located 4 mm. from the venter and about 4.2 mm. from the dorsum. The segments are of the Dolorthoceras type in outline. Where the segment is 3.5 mm. in length it expands from .8 mm. to 1.4 mm. The neck and brim are subequal, though their relation tends to vary rather erratically in the small portion of the specimen sectioned. The area of adnation is slightly less than the brim. The most adapical segments show the typical nepionic Dolorthoceras outline, with the brim scarcely more than half the neck. Deposits are present in the siphuncle. In the portion sectioned they can be seen forming a continuous lining on the venter,

though occasionally absent at the septal foramina. In part this is due to the removal of the deposit at the foramina by abrasion of invading sediments. On the dorsal side the deposits are present, but have not developed sufficiently to form a continuous pseudorthoceroid lining within the siphuncle. The connecting rings are preserved only where they are strengthened by the deposits of the siphuncle, a not uncommon condition.

Deposit within the camerae are mural and are well developed being concentrated on the venter. There is evidence of the progression of the ventro-lateral lobes to the dorsal side of the siphuncle as in Pseudorthoceras.

The shell is preserved only in part. The surface shows no trace of ornamentation of any kind. The living chamber of the holotype is incomplete. It is only 9 mm. in length and has a basal diameter of 14 mm. The adoral camerae are not contracted, indicating that the species attained a larger size than is indicated by the holotype.

Discussion.— This belongs to the ecological group of orthoceracones which have deposits, both of the siphuncle and of the camerae, markedly heavier ventrally than dorsally. This is, as usual, found in connection with a subcentral siphuncle. The completion of the siphunal deposit first on the venter is not an uncommon feature in Dolorthoceras. The development of dorso-ventral

differentiation is greater than usual in this species, and suggests that it is not far removed from the Pseudorthoceras type, which appears for the first time in Pseudorthoceras from the same general locality and horizon as this Dolorthoceras. The sectioned portion of the specimen represents five camerae, and is separated by seven camerae from the base of the living chamber.

Although the size attained in a mature representative of this species is not known, the uniform depth of the camerae throughout the holotype indicates an ephebic condition, and the proportions should remain adequate for the recognition of the species. It is the only species in the Naples which can be referred to Dolorthoceras with certainty at the present time.

Type.- Holotype: New York State Museum

Occurrence.- Parrish limestone, Cashagua shale, Senecan stage, Upper Devonian, from Naples, New York.

Dolorthoceras palmerae(Flower and Caster)

Pl. 1, fig. 7.

Pseudorthoceras palmerae Flower and Caster, 1935,
Bull. Amer. Paleont., vol. 22, p. 227, pl. 21,
fig. 1-3.

The original description of the species is adequate,

and the reader is referred to it for specific characters. It is now evident that the species belong in Dolorthoceras rather than in Pseudorthoceras.

The outline of the segments of the siphuncle is of the Dolorthoceras type. In comparable portions of Devonian Pseudorthoceras the Pseudorthoceras type of outline is already developed. Further, the siphonal deposits are of the Dolorthoceras type, showing practically no dorso-ventral differentiation in development.

The species is still known only from the holotype which is supposedly of Panama (Lower Conewange, Upper Devonian,) age.

Dolorthoceras (?) bebryx (Hall)

Orthoceras bebryx Hall, 1876, Illustrations of Devonian Fossils: Cephalopoda. Expl. of pl. 39, fig. 1-2.

-----Hall, 1879, Paleontology of New York, vol. 5, pt. 2, p. 275, pl. 38, fig. 10; pl. 39, fig. 2; pl. 83, fig. 14; pl. 84, fig. 11-12.

Five specimens were figured under this name by Hall. All represent fairly large sized orthoceracones, and all except one are more or less flattened by pressure. Only one specimen among the types preserves the outline of the siphuncle, and it is highly improbable that

sectioning would reveal any internal structure in the other specimens. The first specimen figured under the name of O. bebryx is flattened, and is not adequate for identification. The rate of expansion, the section, the position and structure of the siphuncle are all unknown. At the time of the original description two specimens were figured as O. bebryx. The first one was later re-figured as O. bebryx var. cayuga, therefore the other must be taken as the type of O. bebryx, and is here selected as such.

Dolorthoceras (?) cayuga (Hall)

Orthoceras Bebryx Hall, J., 1876, Illustrations of Devonian fossils: Cephalopoda. Explanation of pl. 39.

Orthoceras Bebryx, var. Cayuga Hall, J., 1879, Paleontology of New York, vol. 5, pt. 2, p. 276, pl. 39, fig. 1; pl. 86, fig. 3-5; pl. 91, fig. 1-5; pl. 92, fig. 1-5.

All of the representatives of this species which are known to me are more or less flattened individuals, and it is not certain that there is not more than one species concerned. Specimens preserving the siphuncular segments of the Dolorthoceras type. Nothing is known

concerning the condition of the deposits within the siphuncle. The surface of the shell bears prominent lines of growth, which show a broad shallow sinus on the ventral side of the conch.

After some years of collecting in the Ithaca shales I am convinced that it is highly improbable that an uncrushed specimen with the internal structure well enough preserved for section, will ever be found. Even in the limestone lenses specimens are fragmentary and badly flattened. The available evidence indicates that the species may be placed in the genus Dolorthoceras. The possibility of a relationship to Cayutoceras is not, however, eliminated. The ornament is such that the form could be placed in either genus. However, Cayutoceras is known at present only from the Chemung, in the strict sense, with a possible extension of its range into the Canadaway and Conneant. Dolorthoceras, on the other hand, is already prolific in the Hamilton, and in general the species of the Ithaca fauna are derived from Hamilton forms.

The relationship of D. cayuga with "Orthoceras" bebryx cannot be determined because the latter species is too little known. At present the only similarities in a similarity in size, and a rough and very inexact correlation between flattened specimens.

Types.— Amer. Mus. Nat. Hist. no 4939/1. N.Y.S.M.

no. 12349/1-10.

Occurrence.- Widespread in the Ithaca shales, Nunda stage, Upper Devonian, from Ithaca, New York.

SPYROCERAS Hyatt

Hyatt, A., 1884, Proc. Boston Soc. Nat. Hist., vol. 22, p. 276.

Hyatt, A., 1900, Cephalopoda in Zittel-Eastmann Testb. Of Paleontology, 1st ed., vol. 1, p. 519. Reprinted in later editions.

Grabau, A.W. and Shimer, 1910, H.W., North American Index Fossils, vol. 1, p. 600.

Foerste, A.F., 1924, Denison Univ., Bull. Jour. Sci. Lab., vol. 20, p. 225.

Foerste, A.F. and Savage, T.E., 1927, Ibid., vol. 22, p. 38.

Foerste, A.F., 1929, Ibid., vol. 24, p. 162.

Foerste, A.F., 1932, Ibid., vol. 27, p. 95.

Flower, R.H., 1936, Bull. Amer. Paleont., vol. 22, p. 295.

Original description.- "Spyroceras, nobis, includes the longitudinally ridged longicones, which at some stage of their growth are also annulated. The annular costae are usually large, rendering the outline sinuous. The longitudinal ridges are present in the young, and

the annular costae are developed later. Includes groups 5, 6 of M. Barrande. Type, Spy. (Orth.) crotalum sp. Hall. Mus. Geol. Survey, Albany, N.Y. Silurian and Devonian."

Until recently this genus contained all annulated orthoceracones with longitudinal ornament. Foerste⁹⁸

98. Foerste, A.F., Black River and other cephalopods from Minnesota, Wisconsin, Michigan and Ontario, Part I, Denison Univ. Bull. Jour. Sci. Lab., vol. 27, p. 111. 1932.

separated Metaspyroceras, based upon Spyroceras ruedemanni Foerste, a species common to the Cedarville of Ohio and the Racine of Illinois. In this genus the siphuncle is orthochoanitic, the sutures slope adorally on the venter, while the annuli slope adorally on the dorsum.

More recently Shimizu and Obata⁹⁹ have proposed a

99. Shimizu, S. and Obata, T., New Genera of Gotlandian and Ordovician Nautiloids, Jour. Shanghai Science Institute, sec. 2, vol. 2, p. 3-5, 1935.

large number of genera which are summarized below.

Eospyroceras.- Characterized by arching or undulating annulations and fine longitudinal striae. Genotype: Orthoceras arcuoliratum Hall of the Trenton.

Hyposoyroceras.- Characterized by broad slightly

arching annulations and coarse longitudinal striae.

Genotype: Orthoceras teretiforme Hall (not Orthoceras tretiforme, which is a misprint,) of the Trenton.

Subspyroceras.- Characterized by more prominent annulations and coarser longitudinal striae. Genotype: Spyroceras middlevillense Foerste of the Trenton.

Annaspyroceras.- Distinguished from Spyroceras by its more crowded, stronger annulation. Genotype: Orthoceras anellum Conrad from the Beloit of Wisconsin.

Gorbyoceras.- Characterized by annulations sloping apicad and weakening on the venter. Genotype: Spyroceras gorbyi (S.A. Miller) of the Richmond.

All of these new genera together with Spyroceras are placed in a new family Spyroceratidae, characterized as annulated conchs with longitudinal markings and at least so the authors hope, orthochoanitic siphuncles. The siphuncle is not known for any of the species used as genotypes. At present, there seems to be little justification for the recognition of these genera which are established solely upon the characters of the surface of the shell.

Spyroceras Hyatt is based upon Spyroceras crotalum (Hall) and that species must stand as the genotype in spite of the fact that it is fairly certain that the specimens Hyatt had in mind were Spyroceras nuntium

(Hall). On the basis of a study of the genotype, together with two closely related species, S. Nuntium and S. caelamen (Hall) it appears that Spyroceras should be restricted as follows:

Annulated orthoceracones with slightly cyrtconic apices. The sutures are straight and transverse, the annuli may be straight or slightly inclined apicad on the venter. The surface is variously marked, but longitudinal lirae play a conspicuous part in the ornament from the earliest stage. The siphuncle may be central or slightly ventrad of the center. Its segments are of the nepionic Dolorthoceras type, with brims and area of adnation equal to half the neck, in the neanic stage, but the brims and necks of the ephebic portion are subequal and greater than the area of adnation, thus attaining the condition typical of Dolorthoceras. Siphonal deposits are of the Dolorthoceras type. Cameral deposits are mural. Both cameral and siphonal deposits are more delayed in development than in other genera of the Pseudorthoceratidae, and are therefore confined to more apical regions of the conch.

Discussion.— Owing to the delayed development of the deposits of the phragmocone and the rarity of fragments sufficiently apicad of the living chamber, the structures are rarely observed. Siphonal deposits have so far been

observed only in one species, S. oppletum, Flower, n. sp., of the Tully limestone of the upper Devonian. Cameral deposits occupy a greater proportion of the phragmocone and are known for a greater number of species.

Of the annulated conchs which have been referred to Spyroceras in the past, only those which possess siphuncles of the nepionic or ephebic Dolorthoceras types can be considered as typical representatives of the genus. Other generic names must be employed for orthochoanitic Ordovician and Silurian forms.

Only a few of the Devonian species which possess spyroceroid ornament have yielded.

The condition of the siphuncular outline is known for only a few of the Devonian species of spyroceroid aspect. These include S. crotalum (Hall), S. caelamen (Hall) and S. nuntium (Hall), all of the Hamilton shales of the Middle Devonian. In addition the siphuncular outline is known for most although not all of the Tully species. There remains a large number of described species for which the siphuncular outline is not as yet known. In view of the fact that no orthochoanitic conchs of spyroceroid aspect are known in the Devonian, the reference of these species to Spyroceras as well seems beyond reasonable doubt.

Inasmuch as the greater number of specimens of

Spyroceras found in the Devonian of New York are more or less completely flattened, the rate of expansion, the spacing of the septal in relation to the diameter of the conch and other such features which can only be ascertained from undistorted specimens are of little use. However, the spacing of the annulations and the nature of the sculpture of the shell can be used as specific criteria, and it is upon those features that the recognition of species depends to a very large extent. Formerly the spacing of annuli has been used somewhat loosely, and confusion has resulted from the very different aspect presented by undistorted and flattened individuals. As all known Spyroceras species are circular in section, it has been apparent diameter in completely flattened specimens and thereby restore the original proportions of the conch.

DEVONIAN SPECIES OF SPYROCERAS

Spyroceras (?) thoas (Hall)	Schoharie - Onondaga
S. (?) multinctum (Hall)	Schoharie grit
S. (?) geneva (Clarke)	Onondaga - Cherry Valley
S. (?) incarcerationum (Clarke)	Stafford
S. (?) staffordense (Clarke)	Stafford limestone
S. nuntium (Hall)	Hamilton

S. crotalum (Hall) Hamilton
S. caelamen (Hall) Hamilton
S. nuntioides (Clarke) Hamilton
S. (?) rudens (Hall) Onondaga
S. thestor (Hall) Hamilton
S. (?) idmon (Hall) Hamilton
S. (?) lima (Hall) Hamilton
S. oppletum Flower, n. sp. Tully
S. pertestum Hall Ithaca.

Space does not permit an adequate illustration of the known species of Spyroceras at this time. Only the genotype and one new species, both of which are important because of their known internal structure, are discussed below.

Spyroceras crotalum (Hall)

Pl. 9, fig. 11-12.

Orthoceras crotalum Hall, 1861 Descriptions of

New Species of Fossils etc., p. 50.

-----Hall, 1862, 15th Rep. New York State
 Cab. Nat. Hist., 1862, p. 78. pl. 8, fig. 1.

-----Hall, 1876, Illustrations of Devonian
 Fossils, pl. 42.

-----Hall, 1879, Paleontology of New York, vol.
 5, pt. 2, p. 296, pl. 42, fig. 1-9, 11, 12; pl. 82,
 fig. 1-6; pl. 93, fig. 13.

A topotype agreeing with the original description and such of the types as have been examined, but which is unflattened, furnishes the basis for the following redescription of S. crotalum:

Conch circular in section, the apex slightly and uniformly cyrtoconic. Conch expanding from 6 mm. to 13 mm. in a length of 60 mm. Sutures straight and transverse. Septa increasing in depth orad, depth one-fifth the diameter of the conch at a diameter of 7 mm.; slightly more than one fourth the diameter at 12 mm. Siphuncle subcentral, the segments ranging from the nepionic Dolorthoceras type at a diameter of 6 mm., to the ephebic Dolorthoceras type at a diameter of 12 mm. Siphuncle subcentral, the segments known only at a diameter of 6 mm., where they are typical of the nepionic Dolorthoceras type. They are unusually short and broad at this stage, having a length of 1.1 mm., and expanding from .6 mm. to .9 mm. No siphonal deposits are present, but vestigial mural deposits can be seen in the camerae at this stage. There are four camerae in a length equal to an adoral diameter of 9 mm. and three and a half in a length equal to an adoral diameter of 10 mm.

The wall of the conch is corrugated into narrow rounded annuli with broad concave interspaces. Four annuli occur in a length equal to the adoral diameter of

the conch up to a diameter of 13 mm. The surface of the shell bears numerous fine subequal longitudinal lirae, about eight in the width of 1 mm. Finer obscure transverse lirae occur, but cannot be seen in many specimens.

Judging solely from flattened specimens, the annuli become much more distant in the later part of the conch, so that three and a half or even as few as two occur in a length equal to the adoral diameter. The spacing of annuli is evidently rather variable in this species as in many others.

Occurrence.- The species appears to be best developed in the Skanneateles shale of the Hamilton, and is best represented in central New York in the region between Cayuga lake and Hamilton. The Holotype is from Pratt's Falls, Onondaga County, New York.

Types.- The first specimen figured, which is here selected as a lectotype, is in the New York State Museum, no. 12359/1. Hypotypes are nos. 12359/2, 10, in the same museum, and Paleontological Research Institution, no. 5866.

Spyroceras oppletum Flower, n. sp.

Pl. 9, fig. 9-10.

The holotype consists of a portion of a phragmocone of circular section which expands in a length of 18 mm. from 6 mm. to 9 mm. The sutures are straight and transverse. The septa are about one fifth the diameter in depth. Throughout the known portion, there are four and one-half camerae in a length equal to an adapertural diameter. The siphuncle is eccentric, and supposedly ventral in position. At the apex of the specimen the siphuncle is 2 mm. from the venter and 4 mm. from the dorsum, while at the adapertural end it is 4 mm. from the venter and 5 mm. from the dorsum.

In section the siphuncle is of the nepionic Dolorthoceras type. Where the diameter is 7 mm. and the length of the camera is 1.8 mm., the siphuncle expands from .6 mm. at the septal foramen to 1 mm. within the camerae. The brims are one-half the necks, and the area of adnation is subequal to the brim. The free part of the connecting ring is faintly and evenly convex within the camera. The siphuncle contains calcareous material which suggests pseudorthoceroid deposits in lying close against the wall on one side, but which is probably adventitious inasmuch as it does not pass over the septal necks. The camerae, however, contain

well developed circumferential deposits which are more strongly developed on the siphonal than the antisiphonal side.

The surface of the shell and the internal mold are marked by low obscure annulations which appear to be straight and transverse. These occur in a regular arrangement with the septa, each annulation lying just orad of the point at which the free part of the septum joins the wall of the conch. The ornament consists of relatively prominent longitudinal lirae of which there are two in the width of 1 mm., and finer transverse lirae of which there are five or six in a length equal to the width between two of the longitudinal lirae. The shell is very thin, and the spaces between the low annuli are faintly concave.

Discussion.— This species belongs in a very small group of species of Spyroceras characterized by subcan-cellate ornament. Spyroceras geneva (Clarke) of the Onondaga and Cherry Valley limestones has much finer lirae and more prominent annulations. S. pertextum Hall, of the Ithaca shales of the Upper Devonian, has much finer and more closely spaced lirae, and more elevated and more distant annulations.

Type.— Holotype: Paleontological Research Institution, no. 5867.

Occurrence.- In the West Brook member of the Tully limestone, Upper Devonian, from the most easterly of the three quarries south of Borodino, New York.

GEISONOCEROIDES Flower, n. gen.

Genotype: Geisonoceroides woodae Flower, n. sp.

This genus is erected for the reception of species which differs from Dolorthoceras chiefly in ornament and aperture. The conch is orthoceraconic, with simple septa and straight transverse sutures. The siphuncle is slightly ventrad of the center of the conch, and is of the Dolorthocera type of outline. As only adapertural portions of the phragmocone are known, the deposits have not been observed. The ornament consists of transverse rounded ridges with equal concave interspaces. The fine ornament may vary, but in the genotype consists of fine distant transverse striae. The ridges are slightly oblique, sloping adapically from dorsum to venter, but there is no lobation to form a definite sinus.

Discussion.- This is another of the ornamented derivatives of middle Devonian Dolorthoceras, and one which bears the same relation to Dolorthoceras which Geisonoceras was thought to have to Orthoceras in the old sense. G. woodae and G. cylinoticum are the only species which can

be placed in Geisonoceroides with certainty. It is suspected that Orthoceras aulax Hall of the Hamilton and Orthoceras anguis Hall of the Ithaca may be related, but both are still known only from flattened specimens, and retain none of the siphuncular structure. Consequently it is not possible to refer these species to any genus. They are both most inadequately known, even for species of Orthoceras in the old sense.

Geisonoceroides woodae Flower, n. sp.

Pl. 3, fig. 4; pl. 7, fig. 11; pl. 9, fig. 4

Conch orthoceraconic, circular in section, and remarkably slender. The living chamber expands from 30 mm. to 31 mm. in a length of 80 mm. The sutures are straight and transverse. The septum has a depth of 8.6 mm where the diameter is 30 mm. which is equal to the depth of one and one-half camerae. There are normally four camerae in a length equal to the diameter of the conch. There are four and one-third camerae in a length equal to the diameter at the base of the living chamber, indicating approach of a gerontic condition in the plesiotype.

The siphuncle is 3 mm. in diameter near the base of the living chamber, and is 11 mm. from the venter and

15.5 mm. from the dorsum. The segments are of the Dolorthoceras type. The greatest diameter of the segment lies well orad of the middle and contraction is gradual apicad and more abrupt orad of it. The brims and necks have not been observed; they are probably subequal or nearly so. The area of adnation is neblibible, the connecting ring contracting to nearly the diameter at the septal foramen before joining the adapical septum. A segment 7 mm. in length expands from 2.5 mm. to 3.5 mm.

The condition of the deposits is unknown, either for the camerae or siphuncle. Only the eight adoral camerae are present on the plesiotype.

The incomplete living chamber has a basal diameter of 30 mm. and is 95 mm. in length. The ornament consists of transverse rounded ridges with equal concave interspaces, with seven or eight ridges in a length of 10 mm. No trace of longitudinal ornament can be made out, though the surface is well preserved. Fine narrow transverse striae occur sparsely and rather irregularly placed, averaging three in the space between the crest of two of the ridges. The aperture is not preserved. The condition of the ornament shows that the aperture was inclined to the section, sloping adapically on the venter, but was without any distinct lobation.

Color markings The dorso-lateral area of the shell

of the holotype shows traces of a color pattern unlike those previously noted on orthoceracones. A lateral or dorso-lateral light area represented by white calcite meets a dorsal black area on one dorso-lateral area. The transition between the two is abrupt, forming a faintly irregular longitudinal line. The remainder of the shell shows no conclusive color markings. The other dorso-lateral area shows patches of light calcite which may represent the other light lateral area. No traces of color are found on the venter at all.

Discussion.- The presence of fine transverse ornament and the absence of longitudinal ornament distinguish this from Orthoceras aulax Hall of the Hamilton, which it otherwise resembles in ornament. Hall's species is based upon a flattened specimen, and it is impossible to compare the proportions of the conch or the structure of the siphuncle. Our species is represented by two specimens, both undistorted from western New York. It is remarkable for its very slender form. Complete specimens must have attained a length of nearly three feet, unless the adapical portion is much more rapidly expanding than the portions which have been available for study.

Type.- Holotype: Buffalo Museum of Science,
Paratype: Buffalo Museum of Science.

Occurrence.- Both of the types, the only specimens

I have seen, are from the Pleurodictyum beds of the Wanakah member of the Ludloville shale of the Hamilton, collected at Wanakah, New York, by Mr. Irving G. Reimann.

Geisonoceroides cylindricum Flower, n. sp.

Pl. 3, fig. 5; pl. 6, fig. 7.

This species differs from G. woodae, which it resembles closely, in its very shallow camerae and its slightly depressed cross section.

The holotype consists of a part of a mature living chamber and one camera, the whole having a length of 65 mm. and expanding from 26 mm. and 28 mm. to 28 mm. and 32 mm. The markedly depressed condition of the adoral end is probably due to pressure. The condition at the basal end is probably normal. Here the venter is slightly flattened.

The sutures are straight and transverse. The septum has a depth of 11mm. , which is slightly more than one-third the diameter. The only camera preserved is 4 mm., but a paratype has two such camerae showing that the condition is probably not gerontic, as the shallow gerontic camerae are rarely of equal length. There should be between seven and eight camerae in a length equal to the diameter of the conch. The siphuncle is 4 mm. in diameter

at the septal foramen, and is 9 mm. from the venter, lying slightly ventrad of the center of the conch. The living chamber of the holotype is only 62 mm. in length, but the paratype has a living chamber, apparently complete, which is 130 mm. in length. The transverse basal diameter of this specimen is 28 mm., identical with the measurement of the holotype. The specimens, as can be seen, is badly weathered.

The ornament consists of oblique rounded ridges with equal concave interspaces as in the genotype. There are between seven and eight ridges in a length of 10 mm. The aperture, as indicated by the ornament, is as in the genotype.

Dicussion.- This species attains a slightly smaller size than G. woodae, from which it can also be differentiated by the shallow camerae, the deep septa, and the slightly flattened venter.

Types.- Buffalo Museum of Science. Holotype: no. ; paratype: no. .

Occurrence.- The holotype is from the pleurodictyum beds of the Wanakah member, at Wanahak, New York, the paratype from the Titchenor limestone, Smoky Creek, Win-don, N.Y. Both are from the Hamilton.

Geisonoceroides cf. cylindricum

Pl. 3, fig. 6.

Under this heading is figured a specimen believed to represent a nearly complete living chamber of this species. It has a basal diameter of 30 mm., and is 16.5 mm. in length. There is a broad shallow indistinctly outlined contracted area occupying nearly a quarter of the length and lying just orad of the middle of the specimen. The diameter at the adapertural end is 30 mm. A part of the aperture is preserved, which appears to be straight but oblique. The last septum is not preserved, so the living chamber may have been even longer than is indicated by this specimen.

Type.- Buffalo Museum of Science.

Occurrence.- South Shorecliff, Lake Erie. From the Tichenor limestone, Hamilton stage, Middle Devonian.

Geisonoceroides aulax (Hall)

Orthoceras aulax Hall, 1879, Paleontology of New York, vol. 5, pt. 2, p. 293, pl. 84, fig. 18.

The holotype is a portion of a flattened conch 80 mm. in length, which is essentially cylindrical and with no appreciable expansion of the conch. The width of the

flattened specimen is 28 mm. The surface bears regular low rounded ridges with equal concave interspaces, of which there are eight to ten in a length of 10 mm. Close examination of the type has failed to reveal any trace of the fine longitudinal ornament described by Hall.

Discussion.- The type is not sufficient to warrant the identification of this species. G. woodae and G. cylindricum described above do not differ from each other or from this species in ornament or the obviously slight rate of expansion. G. cylindricum is distinguished from G. woodae by the much shallower camerae and the longer living chamber. As the type of G. aulax does not retain the camerae, and the fragment is short enough to represent a part of a living chamber of either species, identification is impossible.

Type.- New York State Museum, no. 22347/1.

Occurrence.- "Hamilton beds, Hamburg, Erie County, New York," Probably from the Wanakan member of the Ludlowville shale, Hamilton stage, Middle Devonian.

Geisonoceroides anguis (Hall)

Orthoceras anguis Hall, 1879, Paleontology of New York, vol. 5, pt. 2, p. 312, pl. 89, fig. 9.

The holotype is an aseptate fragment 60 mm. in length,

flattened, expanding from 10 mm. to 12 mm. in width. Its surface is marked with numerous closely spaced rounded ridges with equal interspaces. These are spaced about 15 in 10 mm. They are straight, but slightly oblique. No trace of the phragmocone is known.

Discussion.- Though the species is still known only from flattened individuals there can be little doubt that it is a Geisonoceroides, as is indicated clearly by the ornamentation. It is unique in the close spacing of the ridges.

Type.- Holotype: New York State Museum, no. 12344/1.

Occurrence.- From the Ithaca shales, Nunda stage, Upper Devonian. The holotype is from Cascadilla Creek, Ithaca, New York.

PETRYOCERAS Flower, n. gen.

Genotype: Orthoceras thyestes Hall

Conch orthoceraconic, circular or slightly depresses in section. The sutures are straight and transverse, the septa are apparently evenly curved, and the siphuncle is subcentral in position or slightly ventrad of the center of the conch. The siphuncle is similar to that of Dolorthoceras in outline in the ephebic portion of the

conch. The nepionic Dolorthoceras type of structure has been observed in an earlier portion. No deposits have been seen within the siphuncle. Mural deposits are present within the camerae, The surface of the conch is marked by fine bands of short oblique zig-zag striae and lirae. There is no trace of a hyponomic sinus in the ornamentation.

Discussion.- The genus is set apart from Dolorthoceras by the remarkable ornament which is unlike that known from any other cephalopod. Two species are placed in Petryoceras. Both of these are from the shales of the Sherburne of the upper Devonian. Petryoceras is probably a specialization of Dolorthoceras. I have named this genus for Professor L.C. Petry of the department of Botany of Cornell University who found the remarkably well preserved specimens of the genotype which made possible a description of the genus and accurate knowledge concerning the species.

Petryoceras thyestes (Hall)

Pl. 8, fig. 15; pl. 9, fig. 13.

Orthoceras thyestes Hall, J., 1879, Paleontology of New York, vol. 5, pt. 2, p. 306, pl. 88, fig. 2.

Orthoceras sp. indet. Hall, J., 1879, Paleontology of New York, vol. 5, pt. 2, pl. 89, fig. 7-8.

This is an orthoceracone which sometimes attains considerable size but which usually occurs in a badly crushed condition. The section is believed to have been slightly depressed; a fragment preserved in a concretion has diameters of 27 mm. and 28 mm., and a rate of expansion of about 2 mm. in a length of 20 mm.

The sutures are straight and transverse. The septa are shallow and evenly curved; where the dorso-ventral diameter of a slightly compressed specimen is 35 mm. the septum is 9 mm. in depth. There are five camerae in a length equal to an apertural dorso-ventral diameter of 26 mm. Where the dorso ventral diameter is 36 mm., the siphuncle is 14 mm. from the venter. Here it expands within the camera from a diameter of 2 mm. at the septal neck to one of 3 mm. The segment is 4.5 mm. in length. The necks are short and sharply recurved, the connecting

rings are faintly convex throughout the middle, contracting abruptly at the extremities. There is no area of adnation. No deposits are known in either the siphuncle or the camerae.

The proportions of the living chamber are not known, all of the available living chambers being badly crushed. The aperture is not preserved.

The ornament, often impressed upon the internal mold, consists of close set transverse rows of broken zig-zag lirae and striae of which there are about nine in the length of 5 mm.

Discussion.- This species is very characteristic of the Sherburne horizon of Ithaca, New York, and the same facies, of approximately the same age, in the Seneca Lake section. The holotype is a badly flattened specimen which shows no trace of surface markings. Another specimen, that figured on pl , fig. of this paper, retains identical proportions but show traces of the ornament. Through this it was possible to connect the holotype with better preserved specimens which made possible a study of the siphuncle.

Crushed fragments of the shell are apt to bear obscure traces of the ornament, and if the shell is not preserved the markings of the suface may be impressed upon the internal mold. In amny instances the continuity

of the transverse bands of broken diagonal markings can not be made out, and the effect is one of an oblique cancellation. It was apparently such a specimen that Hall mistook for an orthoceracone covered with Bryozoa. Though Bryozoa have been found on this species, as they have on many others of the lower and Middle Devonian, none are of a type which would result in such an appearance.

The species apparently has a very short vertical range. Numerous fragments have been obtained from the Sherburne, but extensive collecting has failed to reveal this species either in the overlying Ithaca or the underlying Genesee.

Types.— Holotype: New York State Museum, no. 1246/1. Hypotypes: Pal. Res. Inst., no. 5843-5847.

Occurrence.— The holotype is from "the soft shales of the Portage group near Watkins, at the south end of Senaca Lake." Hall included in his Portage only the lower part of the section of the Senaca and Cayuga valleys which contained a predominance of black shale. The holotype is from such a facies in the Senaca section, while the hypotypes are from the Sherburne sandstone, Nunda stage, Upper Devonian, of Taughanock gorge on Cayuga Lake. Numerous fragmenary specimens have been found in the upper beds of the Sherburne at various localities near Ithaca, New York.

Petryoceras (?) atreus (Hall)

Orthoceras atreus Hall, J., 1879, Paleontology of New York, vol. 5, pt. 2, p. 305, pl. 88, fig. 1, pl. 89, fig. 10, 11.

The specimen first figured, and selected here as the lectotype, represents a large orthoceracone in a badly flattened condition. In its present condition the conch is 280 mm. in length and expands from 66 mm. to 80 mm. in 125 mm., which constitute the phragmocone. The living chamber is about 140 mm. in length. In the basal 110 mm. it expands to a diameter of 80 mm. and contracts noticeably beyond. The aperture is not preserved. There are five camerae in a length equal to an apertural diameter of 80 mm. in the present condition of the specimen. The sutures are straight and transvers. The siphuncle is not preserved on the lectotype.

The surface of the holotype bears a fine ornament identical with that of Petryoceras thyestes, (Hall), and is placed in Petryoceras on the basis of the ornament.

Discussion.-- Though the proportions are not accurately known for this species it can readily be distinguished even in a crushed condition, for the camerae are relatively deep. Petryoceras thyestes has between seven and one half and eight camerae in a length equal to an

adapertural diameter in a crushed specimen. The ornament is believed to be sufficient for the generic diagnosis. It is known only in these two species which are associated in the upper Devonian, and it would be remarkable if they differed in internal structure.

The septum figured by Hall and referred to O. thyestes with doubt probably belongs to that species. Among the Taughannock material I have observed other similar septa with eccentric siphuncles; the larger ones are depressed in section. The siphuncle of O. thyestes is subcentral in position.

Types.— Lectotype: New York State Museum, no. 12346/1. Paratypes, American Museum of Natural History, no. 4938/1. This number includes two specimens.

Occurrence.— "In the calcareous layers of the Portage group, at Penn Yan, Yates County, and in the shales at Rogers' Bridge on the Genesee River, below Portageville, N.Y." From this it would appear that Hall's types are from the lower part of the Upper Devonian, certainly not higher than the Cashaqua shales. Other specimens have been observed in the Sherburne at Taughannock Falls, Cayuga Lake, in association with Petryoceras thyestes (Hall).

PALMROCERAS Flower

Genotype: Orthoceras fustis Hall

Flower, R.H., 1936, Bull. Amer. Paleont., vol. 22,
p. 328.

This genus contains orthoceracones of circular section and straight transverse sutures. The siphuncle is central, and is of the Adnatoceras type. The brim is nearly twice the neck and the area of adnation is nearly as great as the brim. The free part of the connecting ring is abruptly curved at the ends, and is slightly convex over the middle portion, and not perfectly straight as is normal in the Adnatoceras type of outline. The surface of the shell bears fine cancellate markings which recall the orientation of Protokionoceras Grabau and Shimer. The aperture is trilobed. One of the lobes is slightly deeper than the other two and probably represents the hyponomic sinus. The mature living chamber bears upon its interior a series of constrictions which increase in prominence toward the aperture. Deposits have not been noted in either the siphuncle or the camerae.

Discussion.- This genus is set apart from the rest of the Pseudorthoceratidae by its ornament, which suggests the Kionoceratidae. The outline of the siphuncle

suggests a relationship with Adnatoceras, but the convex free part of the connecting rings and the trilobed aperture suggest Dolorthoceras, and it is believed that the condition of the brim and area of adnation represent a development parallel to that of Adnatoceras but independent of it. The genus is regarded as a derivative of Dolorthoceras.

Only one species, the genotype, is included in this genus. This species is known only from the mature living chamber and the adapertural portion of the phragmocone. Deposits of the siphuncle and camerae never occur in the adapertural part of the phragmocone and their absence here cannot therefore be considered as of any significance.

Palmeroceras fustis (Hall) has been recently refigured and redescribed. The species is known only from the Cherry Valley limestone of the middle Devonian. For further information the student is referred to the
¹⁰⁰
redescription.

100. Flower, R.H., Cherry Valley Cephalopods, Bull. Amer. Paleont., vol. 22, p. 329, pl. 24, fig. 4; pl. 26, fig. 1-2; pl. 29, fig. 3, 1936.

ADNATOCERAS Flower, n. gen.

Genotype: Orthoceras spissum Hall

This genus is erected for the reception of orthoceracones which resemble Dolorthoceras, but differ from that genus in possessing an area of adnation which is at least equal to the brim.

The conch is orthoceraconic, normally slightly depressed in section. The neanic sutures are straight, and this condition may continue into the ephebic portion of some species, but in the genotype the sutures become sinuous, lateral saddles appearing which separate dorsal and ventral lobes. When the sinuosity is well developed the dorsal lobe becomes the deeper of the two. The siphuncle is normally slightly ventrad of the center of the conch though central in the early stages. In the earliest stage available the brim is slightly greater than the neck, and the area of adnation is subequal to the brim. The free part of the connecting ring expands sharply from the ends, but the middle portion is straight. In the late ephebic and gerontic portions of the siphuncle, this type of structure disappears. The diameter of the septal foramen increases more rapidly than the maximum diameter of the segment, bringing about a marked reduction of brim and area of adnation until the nepionic Dolorthoceras type of

structure appears. The brim and area of adnation remain subequal, but become slightly less than one-half the neck. Meanwhile the free part of the connecting becomes more faintly and uniformly curved throughout.

Deposits within the siphuncle are known from the genotype and one other species. They are annulo-siphonate in origin, only slightly better developed on the venter than the dorsum, and are of the Dolorthoceras type, eventually meeting to form a continuous lining within the siphuncle. It appears to be characteristic of the genus that the deposits are confined to the extreme apical part of the phragmocone.

Deposits in the camerae are variable. All Devonian species which show these structures possess mural deposits, Adnatoceras ciscoense (Miller, Dunbar and Condra)¹⁰¹ has episeptal and hyposeptal deposits. It differs

101. Ibid., p. 96, pl. 1, fig. 1-3.

from the Devonian species in no other important particular.

Discussion.- In possessing the Adnatoceras type of siphuncular outline this genus is intermediate between Dolorthoceras and Euloxoceras. The genus can be distinguished from Dolorthoceras by the equal brim and area of adnation in all stages, as well as by the relation of the brim and neck impliedⁱ in the Adnatoceras type

of outline as previously defined. Euloxoceras differs from Adnatoceras in the compressed section, the greater development of brim and area of adnation, and by the faintly concave outline of the middle of the siphuncular segment.

The late ephebic and gerontic reversion to a more primitive type of outline has so far not been noted in any other genus of the Pseudorthoceratidae. The changes which take place are a modification of the outline of the segment, and an increase in the septal foramen at the expense of the brim and area of adnation.

Adnatoceras appears in the Hamilton where it is represented only by the genotype, A. spissum (Hall). The genus is better developed in the Upper Devonian. The Tully limestone has yielded three species. Adnatoceras has not been definitely recognized in the Ithaca shales, where orthoceracones are flattened and the internal structures destroyed. Two species have been recognized from the Naples fauna, and numerous fragmentary specimens indicate that more were probably present. The genus has not been found as yet ⁱⁿ higher strata of the Upper Devonian. The only species known as yet from the Mississippian is Adnatoceras cf. neglectum (De Koninck) from the Tournai limestone, of the Mississippian of Belgium. Adnatoceras ciscoense is the only known

Pennsylvanian species. A key to the American species of *Adnatoceras* is given below.

Key to American species of *Adnatoceras*

- A. Section depressed; camerae always shallow.
 - B. Difference in ephebic maximum and minimum diameters 1 mm.; Sutures scarcely sinuous.
 - C. Cameral deposits mural.....spissum
 - CC. Cameral deposits episeptal and hyposeptal.....ciscoense
 - BB. Difference in ephebic maximum and minimum diameters 4 mm.; Sutures markedly sinuous..wellsi
- AA. Section circular.
 - D. Length of brim and area of adnation greater than length of neck at least up to a conchial diameter of 20 mm.
 - E. Size large; gerontic contraction of camerae beyond a conchial diameter of 35 mm..... napalense
 - EE. Size small; gerontic contraction of camerae at a conchial diameter of 23 mm. clarkei
 - DD. The brim and area of adnation reduced to one-half the length of the neck at a conchial diameter of 20 mm.
 - F. Siphuncle subcentral; 5 camerae in diameter equal to adoral diameter of conch.....cryptum
 - FF. Siphuncle eccentric; 3 camerae in length equal to adoral diameter of conch.....cooperi

Adnatoceras spissum (Hall)

Pl. 1, fig. 8; pl. 4, fig. 8; pl. 7, fig. 10.

Orthoceras spissum Hall, J., 1879, Paleontology of New York, vol. 5, pt. 2, p. 287, pl. 85, fig. 6-9.

Orthoceras exile Hall, J., Ibid., pl. 85, fig. 15. not p. 290, pl. 39, fig. 3; pl. 84, fig. 3; pl. 85, fig. 1-2.

This is a moderate-sized orthoceracone of slightly depressed section. The conch enlarges at a rate of 6-7 mm. in a length of 20 mm. throughout the known portion. There is a difference between the diameters of 1 mm. from the earliest known stage, where they are 10 mm. and 11 mm. The sutures are straight and transverse in the early stages, but in the latter portion of the phragmocone slight lateral saddles separate dorsal and ventral lobes. The septum is shallow, its depth being about one-fifth the diameter, or 4 mm. where the transverse diameter is 19 mm. The camerae are uniformly shallow. In the early portion of the conch there are five in a length equal to an adapertural transverse diameter of 20 mm, but the depth varies slightly erratically. The siphuncle is subcentral where the dorso-ventral diameter is 10 mm., but is ventrad of the center in the later

portion. Where the dorso-ventral diameter is 19 mm., the septal foramen is 1.2 mm. in diameter as exposed at a septum, and is located 7 mm. from the ventral wall of the conch.

The outline of the siphuncle varies markedly. The earliest stages are not available, and the typical Adnatoceras type of outline appears where the conch has a dorso-ventral diameter of 10 mm. Here the siphuncular segment is 2 mm. in length, and expands from a diameter of .6 mm. at the septal foramen to one of 1.3 mm. within the camera. The necks are very short, about .2 mm. in length. The brim and area of adnation are subequal and slightly over .3 mm. The free part of the connecting ring is sharply curved to a vertical position just apical of the septal neck, so that the greater part of the segment of the siphuncle is cylindrical, and not faintly convex as in Dolorthoceras. The connecting ring contracts abruptly as it approaches the adapical septum which it joins to form an area of adnation.

The later segments of the siphuncle show a very different sort of outline. Where the diameter of the conch is 17 mm. dorso-ventrally, the segment of the siphuncle is 3 mm. in length. The diameter is 1 mm. at the septal foramen and 1.9 mm. within the camera. The brim and area of adnation are equal but less than

one half the neck, the neck being .7 mm. and the brim and area of adnation measuring .3 mm. The free part of the connecting ring is faintly convex throughout.

The adapical segments of the hypotype show the deposits in an early stage of development, forming minute annulosiphonate rings. The most apical of these show a slight adoral prolongation. The deposits are slightly better developed on the venter than on the dorsum. The siphuncular deposits are visible on the venter on the 25th camera from the living chamber, while the first trace of the deposit on the dorsum appears two camerae apical of this.

Deposits of the camerae are concentrated on the ventral side of the conch and are circumferential. The exact position of the first trace of deposits is not known, but they are developed at the 17th camera.

The living chamber of the hypotype has a transverse diameter at the base of 22 mm., and is 29 mm in length. The internal mold bears a constriction 9 mm. beyond the base which extends for 11 mm. The constriction is moderate; the diameter decreasing from 20 mm. to 18 mm., and returning to its original size just before the aperture. The aperture is straight and transverse with not trace of the hyponomic sinus. The surface of the shell is smooth, without even perceptible lines of growth.

Discussion.- The depressed section and shallow camerae serve to distinguish this species from the other Hamilton species, which can further be distinguished by the differences between Dolorthoceras and Adnatoceras. The living chamber can be recognized by its brevity and the absence of a hyponomic sinus. The proportions of the phragmocone and the condition of the sutures will serve to distinguish this species from congeneric forms of the Tully and higher horizons.

The species attains a maximum diameter of about 20 mm., and was probably about 150 mm. in length when complete. The internal holds of some specimens show a well developed dorsal carina. The living chamber of this species was referred by Hall to Dolorthoceras exile, but a specimen which retains both the phragmocone and the living chamber has made it possible to correct this error. The living chamber of D. exile is much more slender and bears a well defined hyponomic sinus.

Types.- Of the two syntypes figured by Hall only one can be located. This, upon which the first two figures of the species are based, is here selected as the lectotype. It is no. 1948/1 in the collection of the American Museum of Natural History. The hypotypes are in the Paleontological Research Institution, no 5840-5842.

Occurrence.- From the upper limestone band of the pompey member of the Hamilton, at Pratt's Falls, Onondaga County, New York, and from Norton's Landing, on the east shore of Lake Cayuga, New York. The species is probably fairly widespread in the Hamilton, but uncrushed specimens which can be placed in this species with certainty are not commonly found.

Adnatoceras wellsi Flower, n. sp.

Pl. 4, fig. 1-4.

Conch orthoceraconic, slender, slightly depressed in section. The diameters of the holotype increase from 20 mm. and 24 mm. to 24 mm. and 28 mm. in a length of 40 mm., giving a rate of expansion of 1 mm. in 10. The sutures are sinuate, with low lateral crests which separate a shallow ventral lobe and a slightly deeper dorsal lobe. The depth of the septum is about one-fourth the dorso-ventral diameter throughout the known portion, which includes only the late ephebic portion of the phragmocone. There are five camerae in a length equal to an adapertural dorso-ventral diameter of 24 mm., and six in a length equal to the corresponding transverse diameter of 28 mm.

The siphuncle is ventrad of the center. At the adapertural end of the specimen it is 3 mm. in diameter,

and is located 8 mm. from the venter and 13 mm. from the dorsum. The segments of the siphuncle are of the nepionic Dolorthoceras type, which is characteristic of the later segments of Adnatoceras. Where the dorso-ventral diameter of the conch is 24 mm., the siphuncular segment expands from 1.5 mm., to 3.5 mm. and is 6 mm. in length. The neck is 1 mm., one sixth the length of the segment. The brim is slightly more than half the neck and equal to the area of adnation. The free part of the connecting ring is faintly convex. Deposits are not known in either the siphuncle or camerae of this species. The living chamber and aperture are unknown. The surface is poorly preserved, and shows no sign of ornament

Discussion.- This species differs from A. spissum (Hall) in its larger size, more depressed section and more sinuate sutures, as well as in the proportions of the conch. The sinuate sutures and depressed section will separate it from other Tully species placed in Adnatoceras. This form appears to be intermediate in size and the sinuosity of the sutures between A. spissum of Hamilton and A. napalense of the Naples, though it differs markedly from the Naples species in its shallow camerae. This species is named for Dr. J.W. Wells.

Type.- Holotype: Pal. Res. Inst., no. 5849.

Occurrence ,- In the Tully limestone, from the

most easterly of the three quarries south of Borodino, New York. Collected by Dr. J.W. Wells.

Adnatoceras cooperi Flower, n. sp.

Pl. 7, fig. 6-7

Conch orthoceraconic, circular in section. The holotype is a specimen 174 mm. in length which attains a maximum diameter of 50 mm. The rate of expansion varies between 2 mm. and 3 mm. to a length of 40 mm. The sutures are straight and transverse. The depth of the septum increases from one-fifth a diameter of 30 mm. to slightly over one-fourth a diameter of 37 mm. There are four camerae in a length equal to the adapertural diameter throughout the known portion of the phragmocone.

The siphuncle is 21 mm. from the dorsum and 16 mm. from the venter. Where the camera is 9.4 mm. in length the siphuncle increases in diameter from 2.5 mm. at the septal foramen to 3.5 mm. within the camera. The necks are about .5 mm. in length and are slightly re-curved forming brims which are about half the necks. The connecting ring is faintly convex throughout its free portion and is adnate to the adapical septum for an area slightly greater than the brim.

The surface of the shell is not preserved. The outside of the internal mold bears longitudinal slickensides-

like markings which are adventitious. The aperture is not known. The basal diameter of the living chamber is 42 mm. and the chamber is incomplete and 45 mm. in length. The aperture is not preserved. The absence of gerontic contraction and any decrease in the depth of the camerae indicate that the specimen is not mature.

Discussion.— The outline of the siphuncle agrees with that found in the latest segments of A. spissum (Hall) from which this species can be distinguished by the much larger size and the much deeper camerae. The reduction of brim and area of adnation is such that this form might readily be confused with certain species of orthochoanitic affinities, but in such forms the necks are shorter and there is no area of adnation. The holotype is the specimen listed by Cooper and Williams as ¹⁰²Protokionoceras marcellense (Hall). Striacoceras

102. Cooper, G.E. and Williams, J.S., Tully formation of New York, Geol. Soc. Amer. Bull., vol. 46, p. 859. 1935.

The species, now properly Striacoceras typus (Saemann) was erroneously spoken as Striacoceras typum throughout the study of the Cherry Valley cephalopods, Bull. Amer. Paleont., vol. 22, no. 56, 1936.

possesses no area of adnation and is properly orthochoanitic.

Type.- Holotype: U.S. National Museum, no. 90758.

Occurrence.- In the Tully limestone at Carr's quarry near Tully, New York. Collected by J.G. Williams.

Adnatoceras cryptum Flower, n. sp.

Pl. 8, fig. 4.

This is a moderate sized orthoceracone of circular section. The diameter increases from 20 mm. to 24 mm. in a length of 40 mm. The sutures are straight, and are nearly transverse, being very faintly inclined orad on the dorsum. The septa are between one-fourth and one-fifth the diameter of the conch in depth. There are five camerae in a length equal to an adepertural diameter of 24 mm. The siphuncle is subcentral in position, and is rather poorly preserved in the holotype. Where the diameter of the conch is 20 mm., the segment is 3.5 mm in depth and expands from a diameter of 1.5 at the septal foramen to one of 2.4 mm. one-third the distance to the preceding septum, where the diameter is greatest. The neck is one-sixth the depth of the camera. The brim is about one-half the neck, and the area of adnation is slightly greater. The free part of the connecting ring is convex throughout, but attains its

widest point orad of mid-height.

The holotype consists of a portion of a phragmocone 51 mm. in length, representing a mature or nearly mature portion. The surface appears to be smooth.

Discussion.- In the central position of the siphuncle this is the simplest of the species referred to Adnatoceras. This and the circular section will serve to distinguish A. cryptum from other species of the genus.

Type.- Holotype: Pal. Res. Inst., no 5850.

Occurrence.- In the Tully limestone at the most easterly of the three quarries south of Borodino, New York.

Adnatoceras napalense Flower, n. sp.

Pl. 3, fig. 2.

This is a large orthoceracone apparently of slightly depressed section. The holotype is a portion of a phragmocone which is enclosed in a concretion so that none of the features of the surface are shown. The specimen has been ground down to the siphuncle, and the surface shown appears to be slightly oblique to the dorso-ventral plane so that more of the venter than of the dorsum is removed. The specimen is 124 mm. in length and expands

at a rate of 5 mm. in a length of 40 mm.

The sutures appear to be slightly oblique in section, sloping adaperturally on the ventral or siphonal side. The camerae occur three and one-half in a length equal to an adapertural diameter throughout. At the apical end of the specimen the siphuncle is 2 mm. in diameter and is separated from the two walls exposed in section by 8 mm. and 9 mm. respectively. The maximum distance of the siphuncle from the wall of the conch is 10 mm., and is inclined about 50 degrees from the plane of the section taken. At the other end of the specimen the siphuncle is 5 mm. in diameter and is 13 mm. and 17 mm. from the two walls, and its maximum distance is increased to 21 mm.

In the adapical part of the specimen the siphuncle is of the Adnatoceras type, with subequal brim and area of adnation which are greater than the neck. The connecting ring is cylindrical over the greater part of its length and contracts abruptly at its ends. In the adoral third of the specimen the brim and area of adnation are slightly less in proportion to the brim, and the free part of the connecting ring becomes faintly convex in outline. Where the camera is 10 mm. in depth the siphuncle expands from 3 mm. to 5 mm. in diameter. The neck is 1 mm. in length, and bears a brim which is 1.3 mm.

The area of adnation is slightly greater than the brim.

Organic deposits within the siphuncle and camerae are not known. The siphuncle shows in its adapical portion the phenomena of the incomplete internal mold supplemented by calcite. The dark matrix presumably represents the lower side of the conch as it lay in the sediments, and which invaded only the adapertural portion of the siphuncle, decreasing apicad in extent, and giving place there to the infiltrated calcite.

The living chamber, aperture and surface are unknown.

Discussion.- The specimen upon which this species is based was originally labeled Orthoceras bebryx but that species, one of uncertain affinities is not known from the upper Devonian. The species which has been called Orthoceras bebryx var. cayuga Hall and which is probably specifically distinct from O. bebryx is discussed below. The large size, deep camerae, and the relatively late retention of the Adnatoceras stage will separate this species from all others. It is approximated in size only by A. cooperi, which shows the gerontic type of siphuncular segment at a much earlier stage.

Type.- Holotype: New York State Museum.

Occurrence.- In the Naples of the upper Devonian, at Naples, New York; probably from the Cashaqua shale.

Adnatoceras clarkei Flower, n. sp.

Pl. 7, fig. 2.

Conch orthoceraconic, circular in section, expanding at a rate of 3 mm. in a length of 20 mm. The sutures are straight and transverse. The septa are less than one third their diameter in depth, being 6 mm. deep where the diameter is 21 mm. The depth of the camerae increases more rapidly than the diameter of the conch up to the ephebic stage as is shown in the following measurements:

diameter	17 mm.	18 mm.	20 mm.	22 mm.
camerae	$4\frac{1}{4}$	4	$3\frac{1}{2}$	4

The siphuncle is slightly ventrad of the center of the conch. At the apex of the specimen it is 7 mm. from the venter and 9 mm. from the dorsum. The outline is typical for Adnatoceras. The brim is slightly less than the neck; the area of adnation is slightly greater than the brim. A segment which is 6.5 mm. in length expands from 1.9 at the septal foramen to 4 mm. within the camerae. In the first two camerae the deposits of the siphuncle can be made out. They are small simple annuli, the oldest one showing slight adoral prologation. The deposit is only slightly heavier on the venter than on the dorsum. The deposits of the camerae are markedly

stronger on the venter than on the dorsum. They are episeptal, lying mainly against the free part of the septum.

The surface, aperture and living chamber are unknown. The specimen represents a portion of the phragmocone approaching the gerontic condition. This is shown by the contraction of the adoral camerae which measure 7.5 mm., 6 mm. and 5.4 mm. respectively.

Discussion.- This species recalls in proportions A. napalense, but is much smaller, more rapidly expanding, and the relation between the diameter and the depth of the camerae is not constant here. The proportions of the camerae recall A. cooperi of the Tully limestone, but that species attains a much greater size, the rate of expansion is less, and the relation between the depth of the camerae and the diameter is less variable.

Type.- Holotype: New York State Museum, no.

Occurrence.- Parrish limestone member of the Cashaqua shales, Senecan stage, Upper Devonian, from the Parrish gulley, near Naples, New York.

Adnatoceras cf. neglectum (De Koninck)

Pl. 8, fig. 1.

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Adnatoceras cf. neglectum (De Konick)

Pl. 8, fig. 1.

Orthoceras neglectum de Konick, 1880, Ann. Musée
Royale d'Hist. Nat. de Belgique, t. 5, 2 me.
partie, p. 55, pl. 34, fig. 2.

The specimen illustrated here consists of a portion of a phragmocone 27 mm. in length, which expands dorso-ventrally from 8 mm. to 11 mm. The transverse diameter is 1.5 mm. greater throughout. The specimen contains sixteen camerae which are spaced five to six in a length equal to an adoral dorso-ventral diameter. The sutures slope orad on the dorsum. The septum is shallow, measuring 1.5 mm. in depth at a diameter of 10 mm.

The siphuncle is subcentral in the early portion, being 1 mm. in diameter within the segment and 3 mm. from both the dorsum and venter. The distance from the venter remains nearly constant in the later part, while the distance from the dorsum increases, so that at the adoral end the siphuncle is 1.5 mm. in the camera and is 3 mm. from the venter and 5.5 mm. from the dorsum. In form the segments are typical of Adnatoceras in outline, but are a little broader at the septal foramen than is usual in the genus, and the contraction at either end of the siphuncle is more abrupt than has been noted in any

other species. A segment 2 mm. in length expands from 1.1 mm. to 1.5 mm. The brim and area of adnation are subequal and very slightly greater than the neck. The recrystallized condition of the interior is such that it is impossible to say whether any organic deposits were originally present in the camerae or siphuncle.

Discussion.- The specimen illustrated agrees in general with deKonick's description and figure of Q. neglectum. It has been impossible to make a critical study of this or other species from the Belgian Mississippian on the basis of the little material available for the present study. The specimen is of interest, however, in that it establishes the presence of the genus Adnatoceras in the Tournai limestone, Middle Mississippian, of Belgium.

Type.- The figured specimen is no. 8776 in the collection of the University of Cincinnati.

Occurrence.- From the Tournai limestone of the Mountain limestone (Mississippian,) Tournai, Belgium.

Adnatoceras ciscoense (Miller Dunbar and Condra)

Dolorthoceras ciscoense Miller, Dunbar and Condra,
1933, Nebraska Geol. Surv., ser. 2, bull. 9,
p. 96, pl. 1, fig. 1-3.

The original description and illustration of this species is quite adequate, and the reader is referred to it for details. The siphuncular segments are expanded at the ends, but straight in the middle. The brim and area of adnation are both slightly greater than the length of the neck. Siphonal deposits are of the Dolorthoceras type. The cameral deposits are episeptal and hyposeptal. This character alone will distinguish A. ciscoense from other members of Adnatoceras.

Occurrence.— Cisco formation, Pennsylvanian, from a locality north of Browwood, Texas.

EULOXOCERAS Miller Dunbar and Condra

Genotype: *Euloxoceras greeni* Miller Dunbar and Condra

Miller, A.K., Dunbar, C.O. and Condra, G.E., 1933,
Nebraska Geol. Surv., ser. 2, bull. 9, p. 97.

In this genus are placed orthoceracones which may be circular in the earlier stages, but which differ from most of the Pseudorthoceratidae by a laterally compressed ephebic section which may be oval or subquadrangular. The sutures are sinuous and slope slightly adaperturally on the ventral or antisiphonal side. The normal suture pattern consists of prominent lateral lobes separating

dorsal and ventral saddles. The sutures of the mid-dorsal and mid-ventral region may be straight and transverse or may possess rudimentary lobes as in E. milleri n. sp.

The siphuncle is located half way between the center of conch and the dorsal wall. The segments are sub-cylindrical over the greater part of their length, but contract abruptly at the septal foramen. The brim is more than twice the neck. The area of adnation is less than the brim but greater than the neck. The free part of the connecting ring is transverse at either end, continuing the expansion of the siphuncle. The turn of the connecting ring to a longitudinal position is abrupt. The greater part of the length of the free part of the connecting ring is either cylindrical or faintly concave.

The deposits of the siphuncle are of the Dolorthoceras type and are relatively thick. Stages leading to the fusion of the adjacent segmental deposits have been observed, and show that the annulosiphonate ring is complete before fusion. The thickness of the deposit and the great constriction of the siphuncle at the septal foramen reduce the endosiphuncular cavity to a small perforation at the septal neck, which enlarges gradually oradas the thickness of the deposit decreases, and then decreasing rapidly in diameter as the succeeding septal foramen is approached. The deposits of the siphuncle

show only a slightly greater development on the venter than on the dorsum. Deposits within the camerae are episeptal and hyposeptal, and are markedly heavier on the venter than on the dorsum.

Miller Dunbar and Condra regarded the siphuncle as ventral in position in this genus. The presence of a well defined dorsal carina on the siphonal side of the conch together with the greater development of cameral and endosiphuncular deposits on the antisiphonal side of the conch lead to the conclusion that the siphuncle is dorsal in position.

The surface of the shell of the genotype is unknown. E. milleri which is described below, shows low longitudinal ridges separated by flat or slightly concave interspaces. The longitudinal ornament is slightly impressed upon the internal mold, enough so to obscure any trace of a ventral carina which may be present. The aperture is unknown.

Discussion.- This genus contains but two recognized species. The genotype, Euloxoceras greeni. Miller Dunbar and Condra¹⁰³, appears to be fairly widespread in the

103. Ibid., p. 99, pl. 1, fig. 12-15.

Pennsylvanian of North America. Euloxoceras milleri of the Jackborough limestone may be distinguished by

the more nearly transverse and more sinuous sutures, the more quadrangular section, smaller size, and deeper camerae.

Euloxoceras represents the climax of one type of siphuncular enlargement, an enlargement by an increase in the brim and area of adnation while the middle portion of the segment tends to become first cylindrical and then slightly concave. An increase of brim and area of adnation together with the straightening of the middle of the connecting ring produce Adnatoceras from Dolorthoceras. An accentuation of the same characters will produce the siphuncle of Euloxoceras from that of Adnatoceras. It must, however, be derived from a relatively simple Adnatoceras with a subcircular section and a subcentral siphuncle, as the genera differ markedly in section and position of the siphuncle in the early stages.

Euloxoceras milleri Flower, n. sp.

Pl. 2, figs. 1-3, 12-14.

This is a small compressed orthoceracone which is slightly flattened on the dorsal and ventral faces and strongly flattened laterally, giving it a subquadrangular section. The holotype is a portion of a phragmocone

35 mm. in length, the adapertural portion of which is slightly compressed by pressure. The adapical portion, which is slightly if at all distorted, expands from 4 mm. and 5 mm. to 6.5 mm. and 7 mm. in a length of 20 mm. The sutures are transverse but undulate. There is a shallow ventral lobe between ventrolateral saddles. The lateral faces are occupied by conspicuous lobes. The dorsum is occupied by a broad saddle which is flattened in the middle.

The septa are shallow, being 1 mm. deep where the diameters are 4 mm. and 5 mm. The number of camerae in a length equal to an adapertural dorso-ventral diameter increases from three at 6 mm. to three and one-half at 7 mm. The gerontic condition of the camerae has not been observed. The siphuncle is dorsad of the center and faintly compressed at its passage through the septum. Where the dorso-ventral diameter of the conch is 5 mm., the siphuncle is 1 mm. in diameter as shown on the septum, and is 1.6 mm. from the dorsum.

In dorso-ventral section the siphuncle expands abruptly on either end of the septal foramen, and is slightly concave in outline within the camerae. The expansion of the segment apicad of the septum is made up of the brim and a portion of the connecting ring. Orad from the free part of the septum is it made up of an

adnate part of the connecting ring and a free transverse portion. The siphuncle expands from a diameter of .5 mm. to one of 1.5 mm. where the segment is 2 mm. in length. The dorso-ventral diameter of the conch at this point is 6 mm. The necks are very short, less than one-tenth the length of the segment. The brim is slightly more than twice the neck and the area of adnation is twice the neck. The effective expansion of the siphuncle at the region of the brim and area of adnation which consists of portions of the ends of the free part of the connecting ring is three times the brim.

The deposits of the siphuncle are of the Dolorthoceras type, but present a slightly different aspect than do the deposits of Dolorthoceras due to the more marked constriction of the siphuncle at the septal foramen. The deposits are clearly annulosiphonate in origin, and dorso-ventral differentiation of the development of the deposit is slight. Some segments of the holotype show the adjacent segmental deposits fused on the venter but still discrete on the dorsum. Each segment of the deposit grows thin as it~~x~~ adoral end is approached. This gives the endosiphuncular cavity a curious appearance. It is widest in the adoral third of each siphuncular segment and contracts abruptly orad and more gradually apicad to a small perforation at the septal foramen.

4
The camerae contain episeptal and hyposeptal deposits. Though enough material of the species is not available to permit a careful study of the lobation of the deposit by means of cross sections, it is apparent that the deposit is very heavy on the ventral side, almost completely filling the camera ventrad of the siphuncle, while only a thin lining of the septa is present on the dorsal side. The holotype further shows traces of complicated lobes projecting inward, similar to the inner pair of lobes of Pseudorthoceras. The episeptal and hyposeptal deposits show a well defined pseudoseptum in one specimen.

The internal mold bears a well defined dorsal carina. The surface of the shell is ornamented by fine raised lirae with flat interspaces. There are spaced about .8 mm. apart in the holotype. A faint faceting of the internal mold appears to be an internal expression of the ornament of the exterior. It is sufficient to obscure any trace of a true ventral carina which may be present. The living chamber and aperture of this species are unknown.

Discussion.- This species differs from E. greeni Miller Dunbar and Condra in the more approximate septa the presence of obscure mid-ventral lobes, the more quadrangular section and the transverse condition of

sutures. E. greeni has only two camerae in a length equal to an adapertural dorso-ventral diameter, whereas E. milleri has three or more in such a length.

Types.- Holotype: Pal. Res. Inst., no. 5851
Paratypes: Pal. Res. Inst., no. 5852-5854.

Occurrence.- From the Jackborough limestone, Pennsylvanian, Jack County, Texas.

CRYPTORTHO CERAS Flower, n. gen.

Genotype: Cryptorthoceras productum Flower, n. sp.

Up to the development of the gerontic aperture the conch is a depressed orthoceracone. The sutures are straight and either transverse or very slightly inclined orad on the dorsum. The septa show no unusual features. The siphuncle is located slightly ventrad of the center of the conch. The segments are slender, faintly expanding within the camerae. The brim and area of adnation are equal and less than the neck, in a gerontic siphuncular segment. Ephebic segments unknown.

The mature aperture is turned abruptly ventrad, the dorsal wall being arched over the normal position of the aperture. The dorsal margin of the aperture is broadly arched, the lateral portions strongly rounded,

the central portion like the dorsla side laterally, but with a prominent V-shaped hyponomic sinus in the middle.

Discussion.- This genus is erected from the reception of a single species which, by reason of its unique aperture, can be placed in no previously described genus. The affinities of the genus are obviously with simple orthoceracones. The outline of the siphuncle as known is not all that might be desired, as it probably represents a gerontic condition. The gerontic outline of Adnatoceras is similar, as is also the neanic Dolorthoceras outline. The aperture, though admittedly aberrant, suggests a relationship with orthoceracones with trilobed apertures, such as Dolorthoceras telamon (Hall) or Palmeroceras fustis (Hall). Were the apertures of such forms turned toward the venter and the form of the lobation slightly modified the aperture of Crypt-orthoceras would result.

The early portion of the phragmocone is unknown, therefore the deposits of the camerae and siphuncle have not been observed.

The aperture and the form of the siphuncular segments are sufficient to show that this genus is a member of the Dolorthoceratinae of the Pseudorthoceratidae. It was probably derived from Dolorthoceras near to the point from which Palmeroceras and Adnatoceras sprang from the

same genus.

Cryptorthoceras productum Flower, n. sp.

Pl. 4, fig. 12-15.

The holotype represents a mature living chamber and part of a phragmocone of a large orthoceracone of depressed section which is remarkable for the contracted aperture which is turned abruptly ventrad.

The phragmocone, 60 mm. in length, expands from 45 mm. and 60 mm. to 50 mm. and 72 mm. at the base of the living chamber. The living chamber is 120 mm. in length, attaining diameters of 65 mm. and 80 mm. 75 mm. above the base, at the level of the hyponomic sinus.

The sutures are straight and transverse. Although the specimen is apparently mature, the last camerae are not contracted. In a length equal to the transverse diameter of 72 mm. at the base of the living chamber there are about four and one-half camerae; in a length equal to the corresponding dorso-ventral diameter of 50 mm. there are about three and three fourth camerae. The siphuncle is located ventrad of the center. Where the diameters of the conch are 60 mm. and 45 mm., the siphuncle is 4 mm. in diameter and is 17 mm. from the venter and 22 mm. from the dorsum.

The siphuncle is preserved only in the earliest segment of the type. It is cylindrical within the camera and contracted abruptly at the ends as in Adnatoceras. The condition of the septal neck is obscure, but evidently the brim and area of adnation are considerably less than the neck, as in the gerontic stage of Adnatoceras.

The basal 100 mm. of the living chamber expands uniformly, but at this point the dorsal wall curves over the adoral surface, the sides contracting, so that the aperture is on the ventral side of the specimen. The aperture is a transverse oval with a V-shaped hyponomic sinus interrupting the ventral side for the middle third of its width. The sinus occurs 80 mm. above the base of the living chamber. The aperture measures 55 mm. and 70 mm. It is surrounded by a slightly produced lip which bears prominent lines of growth. No ornament is preserved elsewhere on the shell.

Discussion.- The holotype is a specimen preserved in a concretion, and it at first seemed that the unique characters of the aperture might represent a fortuitious placing of septaria, but a careful working out of the aperture revealed its symmetry and the continuity of the shell over the whold of the specimen. Portions of this species and genus not preserving the aperture

closely resemble ordinary orthoceracones, and in fact cannot be distinguished from them. A portion of a specimen representing the basal part of the living chamber and the adoral part of the phragmocone was figured by Hall¹⁰⁴ as Orthoceras eriense. It can be

104. Hall, J., Paleontology of New York, vol. 5, pt. 2, pl. 87, fig. 1-2. 1879.

recognized as conspecific by the apparently originally depressed section, the slightly eccentric position of the siphuncle, and the depth of the camerae. The specimen represents a part of a mature individual.

Type.- Holotype, Buffalo Museum of Science, no. E9013.

Occurrence.- From the Wanaka member of the Ludlowville, Hamilton group, collected at Bay View Creek, Collected by Mr. I.G. Reimann.

SCEPTRITES Flower, n. gen.

Genotype: Orthoceras sceptrum Hall

The conch is slightly compressed throughout and slightly cyrtconic. The sutures are straight and transverse in the young, tending to develop slight lateral lobes in the later portion of the phragmocone. The siphuncle is subcentral in position, lying slightly

closer to the convex side in sceptrum and closer to the concave side in carteri. The segments are apparently of the nepionic Dolorthoceras type. No deposits are known in the siphuncle. S. carteri possesses well defined cameral deposits which are mural and concentrated against the concave side of the conch. The aperture is unknown. no trace of the surface of the shell is known and the internal mold shows no indication of any ornament.

Discussion.- It is uncertain whether the genus is endogastric or exogastric in the absence of internal carinae and apertural characters. The position of cameral deposits suggests an endogastric condition. The only two species placed in the genus are both from the Onondaga of New York. Orthoceras ohioense Hall shows a curvature which, if natureal, suggests Sceptrites, but the absence of compression is inconsistent with the genus, and it is far from certain that the curvature is original

Key to species of Sceptrites

- A. Living chamber clavate.
 - B. Sutures transverse; $5\frac{1}{2}$ camerae in length equal to diameter; living chamber gibbous S. claviformis.
 - BB. Sutures sloping apicad on convex; $6\frac{1}{2}$ camerae in length equal to diameter; living chamber scarcely gibbous.....S. oblicus
- AA. Living chamber not clavate.

- C. Size large; 7 camerae in length equal to diameter of 44 mm., 6 in length equal to 73 mm.
S. sceptrum.
- CC. Size small; $4\frac{1}{2}$ camerae in 22 mm., 5 in 40 mm.
S. carteri.

Sceptrites sceptrum (Hall)

Pl. 6, fig. 3, pl. 9, fig. 1.

Orthoceras sceptrum Hall, J., 1888, Paleontology
 of New York, vol. 5, pt. 2, suppl., p. 26,
 pl. 117, fig. 2.

The two specimens upon which this revised description is based agree in their large size, slightly compressed section, and subcentral siphuncle. Slight differences in the rate of expansion and proportions of the camerae are attributable to the slight distortion which has affected both specimens to some extent.

The conch is compressed, very slightly curved throughout. The holotype has a length of 440 mm., in which the rate of expansion shows considerable variation. The dorso-ventral diameter only is known. The conch expands 15 mm. in the first 100mm., from 35 mm. to 50 mm., 20 mm. in the succeeding 100 mm., 18 mm. in the next 100 mm., and 15 in the last 100 mm., attaining a maximum dorso-ventral diameter of 95 mm. The hypotype, a slightly smaller specimen shows the following diameters at

intervals of 100 mm. 40 mm. and 34 mm., 51 mm. and 48 mm., 68 mm. and 55 mm. and 85 mm. and 70 mm. At the adapical 50 mm. the conch expands more rapidly, increasing from 35 mm. and 30 mm. (estimated) to 40 mm. and 34 mm.

The sutures are transverse to the curving axis of the conch and are straight adapically, tending to develop slight lateral lobes in the adoral portion. The septum, as known from the hypotype, is slightly less than one fifth the dorso-ventral diameter in depth, being 9 mm. at 41 mm. and 15 mm. at 59 mm.

The siphuncle is located slightly closer to the convex than to the concave side of the conch. Where the dorso-ventral diameter of the conch is 39 mm. the segment is 4 mm. in diameter at the septal foramen and is 15 mm. from the convex and 20 mm. from the concave side of the conch. The segment expands from 4 mm. to 6 mm. in the camera and is 6 mm. in length. The segment is of the nepionic Dolorthoceras type, with brimless than neck and subequal to the slight area of adnation. No deposits within siphuncle or camerae are yet known in this species.

The living chamber of the holotype has a basal dorso-ventral diameter of 90 mm. and has a maximum length of 156 mm. The aperture is not preserved. The hypotype, representing a younger individual, has diameters at the

base of the living chamber of 78 and 68 mm., and retains only the basal 40 mm. No trace of the surface of the shell is retained on any specimen known.

The camerae occur six in a length equal to an adoral dorso-ventral diameter of 73 mm., but increasing slightly in frequency apicad so that there are seven at 44 mm. in the hypotype. In the holotype the proportion is rather more variable, showing six and one half at 41 mm., the same number at 50 mm., five and one half at 67 mm. and five at 85 mm. Whether the adoral increase in depth is due to pressure or not is uncertain.

Discussion.- The very large size and the shallower camerae distinguish this species from S. carteri.

Types.- Holotype: New York State Museum, no. 12403/1. Hypotype: Buffalo museum of Science, no. E8997.

Occurrence.- From the Onondaga limestone of New York. The holotype is from Cherry Valley, Otsego County, the hypotype is from the Federal Crushed Stone Quarry near Lancaster, Erie County.

Sceptrites carteri Flower, n. sp.

Pl. 6, fig. 4.

The holotype has a total length of 285 mm., and

lacks the extreme apex and the greater part of the mature living chamber. 39 mm. from the apex, which is somewhat crushed, the diameters are 19 mm. and 22 mm. In 140 mm. the conch expands to 40 mm. and 28 mm., and in the next 120 to 55 mm. and 35 mm. Curvature is slight and uniform. The sutures are straight and transverse. The septum has a depth of one-fourth the dorso-ventral diameter of 21 mm. The camerae occur four and one-half in a length equal to a dorso-ventral diameter of 22 mm., but five in a length equal to the dorso-ventral diameter throughout the later portion except in the region of the last camera which shows gerontic contraction, the last two measuring 9 mm. and 6 mm. at a dorso-ventral diameter of 50 mm.

The siphuncle is known only at a dorso-ventral diameter of 22 mm. The siphuncle is 10 mm. from the convex and 11 mm. from the concave side of the conch. Here the segment is $4\frac{1}{2}$ mm. in length, and expands from 2 mm. to 3 mm. The segment is poorly preserved, but appears to be of the Dolorthoceras type. Mural deposits are present in the apical 13 camerae of the specimen, leaving eighteen camerae without deposit. The fragment of the living chamber is 40 mm. in length, and evidently represents not much more than the basal half.

Discussion.- The smaller size and deeper camerae

at once distinguish this from the large Sceptrites sceptrum (Hall) the only associated form which resembles it remotely.

Type.- Holotype, collection of Mr. Alec Carter, Buffalo, N.Y., to be deposited in the Buffalo Museum of Science.

Occurrence.- Onondaga limestone, Federal Stone Quarry, south of Lancaster, Erie County, New York. The species was collected by Mr. A. Carter for whom it is named.

Scep trites claviformis Flower, n. sp.

Pl. 6, fig. 2.

This Sceptrites is differentiated by the relatively rapid expansion of the apical portion, to which curvature is confined, and the fusiform condition of the living chamber. The holotype has a length of 1340 mm. The dorso-ventral diameter is 8 mm. greater than the transverse diameter is the apical part of the specimen, but increases to 10 mm. in the adoral half. The conch expands at a rate of about 7 mm. to 9 mm. in 40 mm. in the phragmocone; this decreases to nothing over the living chamber and contraction occurs in the adoral half. Measurements of the dorso-ventral diameter taken at intervals

of 40 mm. are as follows: 36 mm., 40 mm., 52 mm., 60 mm., 67 mm., 73 mm., 75 mm., 72 mm. 70 mm., The living chamber has a length of 140 mm. and increases in the basal 55 mm. from 72 mm. and 58 mm. to 75 mm. and 65 mm. and contracts in the next 85 mm. to 70 mm. and 60 mm.

The sutures described broad lateral lobes but are transverse to the axis of the conch. Five and a half camerae occupy a length equal to the diameter in the apical part up to a diameter of about 50 mm., where the number increases to six. The last three camerae measure 12 mm. 10 mm. and 8 mm., showing a gerontic condition. The siphuncle is not known nor is the depth of the septum.

Discussion.- The fusiform condition of the conch and the straight condition of the living chamber characterize this species. The rate of expansion is greater than that of S. sceptrum with which it agrees most closely in size, further, that species is more uniformly curved and the depth of the camerae is more constant.

Type.- Holotype: U.S. National Museum, unnumbered.

Occurrence.- From the Columbus limestone, near Columbus, Ohio.

Sceptrites obliquus Flower, n. sp.

Pl. 6, fig. 1.

This species, from the same locality as the preceding, may be distinguished by the less gibbous form of the living chamber, and the oblique condition of the sutures. The dorso-ventral diameter changes as follows at intervals of 40 mm.: 41 mm., 50 mm., 65 mm., 60 mm., 75 mm., 75 mm., 74 mm. The obscurity of the adoral sutures leaves some doubt as to the exact position of the base of the living chamber. Its maximum possible length is 190 mm. It expands from 62 mm. and 50 mm. to 74 mm. and 67 mm. in the basal 120 mm., and contracts to 74 mm. and an estimated horizontal diameter of 62 mm. at the aperture.

The sutures are straight and oblique, sloping apicad on the venter in the apical portion, becoming more nearly transverse toward the living chamber. The depth of the camerae is the same as in the preceding species, ranging from six camerae at a diameter of 50 mm., to six and a half camerae at 70 mm., At the apex of the specimen the siphuncle is 4 mm. in diameter at the septal foramen and is 18 mm. from the concave side of the conch. No trace of cameral deposits is shown.

Discussion.- This species differs from the preceding in the less gibbous form of the living chamber, the larger size, and the oblique sutures, which together

seem sufficient to warrant regarding this form as distinct.

Type.- Holotype: U.S. National Museum, no. 37228.

Occurrence.- From the Columbus limestone, Middle Devonian, from Columbus, Ohio.

FUSICOCERAS Flower, n. gen.

Genotype: Fusicoceras erienne Flower, n. sp.

The conch is breviconic, slightly curved exogastrically, and subtriangular in section with the dorsum transverse. The greater part of the living chamber is unknown, but slight cessation of expansion is marked at its base, which is indicative, together with the rapid expansion of the apical portion, of a breviconic condition.

The sutures bear broad low lobes on the dorsum which are well rounded centrally, and deeper lobes on the venter, which are less rounded in the median portion. The siphuncle is located close to the ventral wall and is of the Dolorthoceras type, both in outline and the form of the deposits. No cameral deposits are known.

Discussion.- Even the absence of the aperture this genus can be readily separated from all other breviconic genera by the outline and internal structure of the

siphuncle. The genotype, the only known species of the genus, resembles Endoplanoceras Flower¹⁰⁵ somewhat in

105. Flower, R.H. Devonian brevicones of New York and adjacent areas, *Paleontographica Americana*, vol. 2, no. 9, 1938, p. 53.

form, but has a subtriangular section, a marginal siphuncle and lacks longitudinal markings. The section is more angular than that of Brevicoceras Flower which is suggested by the sutures, and the dorsal concavity and the ventral lobes furnish other differences, as does the structure of the siphuncle. The genus is separated from other Pseudorthoceratidae by the marginal siphuncle and the breviconic condition. No other genus of brevicones has as yet been recognized as having affinities with this family.

Fusicoceras eriense Flower, n. sp.

Pl. 6, fig. 5-6; pl. 7, fig. 1.

The holotype is a portion of a conch 80 mm. in length consisting of a part of a phragmocone and the base of a living chamber. The section is strongly depressed, subtriangular, with the venter strongly arched, obscurely keeled, and the dorsum transverse and scarcely convex.

In vertical outline the dorsum is slightly concave throughout, becoming straighter anteriorly, the venter is uniformly convex, the sides diverge uniformly to the base of the living chamber, where the outline becomes faintly convex. The conch expands from 57 mm. and 33 mm. to 69 mm. and 35 mm. in a ventral length of 67 mm.

The sutures bear broad shallow dorsal lobes, transverse centrally. The ventral lobes are slightly deeper, and strongly curved in the median portion. Six camerae occur in the apical 55 mm., increasing from 7 mm. to 11 mm. in depth. The one remaining camera is gerontically contracted to a depth of 7 mm.

The siphuncle lies close to the venter, being 5 mm. in diameter at the apex and separated from the venter by 4 mm. A transverse section ground through the siphuncle, not, however, attaining its greatest diameter, shows segments of the Dolorthoceras type. As exposed a segment 8 mm. long expands from 2 mm. at the septal foramen to 4 mm. in the camera. Neck and brim are subequal and one-eighth the length of the segment. The apical two septal necks show evidence of a deposit of the Dolorthoceras type.

In the apical segment the lining is very nearly continuous but in the next segment the condition is still immature, although the Michelinoceras stage is past.

Succeeding adoral segments are not preserved.

Discussion.- In proportions this species does not agree with any described forms, and is easily characterized by the development of the ventral lobes of the sutures from other brevicones. Other distinguishing characters are discussed under the genus, of which this is the only known representative.

The absence of cameral deposits is not surprising in a brevicone, which was apparently a floating form. Evidently the development of deposits in the siphuncle is more rapid than in most Pseudorthoceratidae. The specimen exhibits a stage indicative of early maturity, but definitely pre-gerontic.

Type.- Buffalo Museum of Science,

Occurrence.- From the Wanakah member of the Ludlowville, Idlewood Cliff, near 18 Mile Creek, Lake Erie.

PSEUDORTHOCERATINAE Flower, n. subfam.

Siphonal deposits fuse ventrally to form a continuous lining before appearing on the dorsum. The Pseudorthoceras type of deposit characterizes the subfamily.

Pseudorthoceras is the simplest member of the subfamily, and the longest ranging one. The genus persists from the lower part of the Upper Devonian through the Pennsylvanian and into the Permian.¹⁰⁶ The thinning of

106. Teichert, C. fide litt., 1938.

the siphonal deposit from Devonian to Pennsylvanian time is slight. Mooreoceras makes its appearance slightly higher in the Devonian. Devonian species possess a rather thick siphonal deposit on the ventral side. Closure of the deposit on the dorsum has not been observed, and may not occur. Pennsylvanian species possess a much thinner deposit, which is scarcely thicker at the expanded region of the siphuncular segment than at the septal foramen.

Paraloxoceras Flower, n. gen. is a Mississippian derivative of Mooreoceras. The siphuncular segments become more expanded and the deposits more massive. In them can be seen traces of a radial canal system. Bergoceras Flower, n. gen., is evidently a cyrtconic derivative of Paraloxoceras, and if De Koninck's figures are to be relied on the deposits develop equally on the dorsal and ventral sides of the siphuncle. On the basis of this character the genus cannot be said to be typical of the Pseudorthoceratinae. It is highly probable that the best solution would be the separation of Paradoxoceras and Bergoceras in a new subfamily characterized by thick siphonal deposits in which radial canals are developed. Material of Paraloxoceras has been limited to one specimen,

and no material of Bergoceras was available. It has seemed best to delay the proposal of a new subfamily until more material can be examined.

PSEUDORTHOCERAS Girty, 1911

Genotype: Orthoceras knoxense McChesney

This genus contains slender orthoceracones of circular or subcircular section in which the apex shows a very slight exogastric cyrtconic curvature. The sutures are straight and transverse, the septa are moderate in depth and evenly curved, and the siphuncle is central or subcentral in position. In outline the siphuncle undergoes a marked ontogenetic development. A "false cyrtchoanitic condition" is followed by a Michelinoceras stage. This gives way shortly to the Anastamoceras stage. The nepionic and ephebic Dolorthoceras stages follow in turn and give place to the Pseudorthoceras stage. Here the brim and neck are subequal and the area of adnation is half the brim or less. The free part of the connecting ring is convex, forming segments which vary between pyriform and subglobular in outline. The siphuncle contains deposits which are annulosiphonate and pseudorthoceroid. Deposits fuse along the venter forming a continuous lining before being circumferentially continuous

at the region of the septal foramen.

The camerae contain well defined mural deposits which show remarkable circumferential lobation which has been described in an earlier portion of this paper see text figure 14. The internal mold retains the dorsal carina, but I have not been able to observe the ventral carina in any specimen of Pseudorthoceras.

Discussion.- The genus is characterized by the generalized features of the phragmocone, the outline of the siphuncle and the form of the siphuncular deposits. The numerous specimens of Pseudorthoceras from the Pennsylvanian are referred to P. knoxense which appears to be a rather variable species. New species from the Naples fauna of the upper Devonian are described below.

Pseudorthoceras knoxense (McChesney)

Pl. 1, fig. 6; pl. 2, fig. 11; pl. 8, fig. 5, 11-12.

The synonymy and a good description of this species have been recently given by Miller Dunbar and Condra¹⁰⁷

107. Ibid., p. 81.

and need not be repeated here. The absence of the living chamber in this species which is represented by abundant phragmocones throughout the Pennsylvanian has been

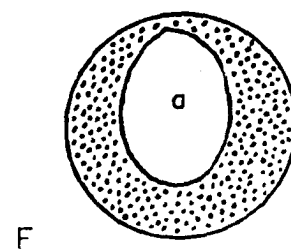
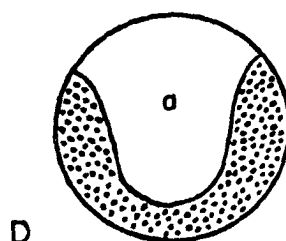
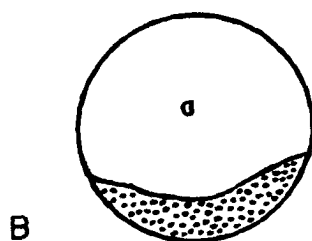
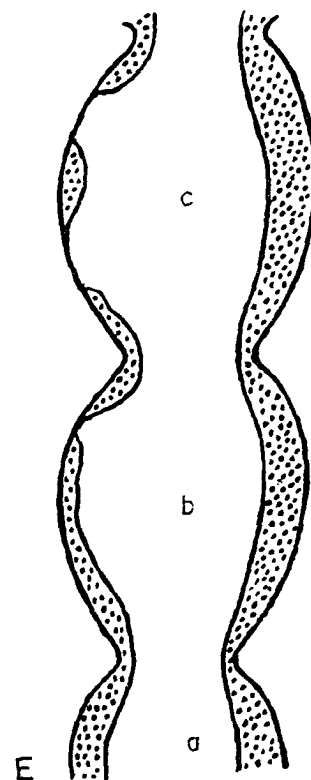
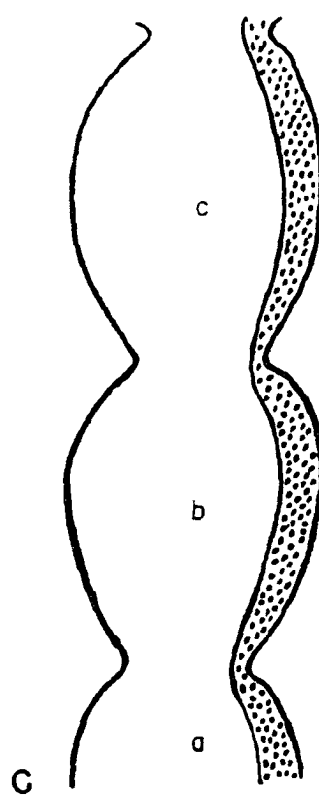
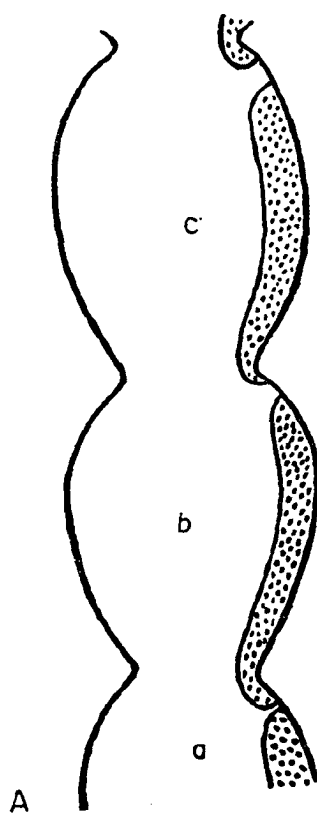
Fig. 13. Development of siphonal deposits in Anastamoceras.

The sections are dorso-ventral and show the complete absence of dorso-ventral differentiation in the development of the deposits.

A. Siphonal deposits have formed as complete rings at the septal foramina and have developed orad along the connecting ring forming the Mechelinoceras type of deposits.

B. Further growth of the deposits orad has resulted in the fusion of adjacent deposits to form a continuous lining within the siphuncle. This is the Pseudorthoceroid type of deposit. The equal development of the deposit on dorsum and venter result in the Dolorthoceras type of deposit.

C. Further deposition results in a central core which is attached to the pseudorthoceroid deposit of B by irregular radial pillars. The section shown is not quite central, and fails to show the perforation of the central core which allowed the main blood vessels to run the length of the siphuncle.



commented on but not explained. The species seems to characterize facies in the Pennsylvanian which are rich in clastics, and normally occurs in a more or less crushed condition. A typical specimen will consist of a portion of a phragmocone which is undistorted adapically but which becomes progressively more and more flattened adaperturally. If such a specimen is sectioned it will be found that there exists a very definite relationship between the extent of the deposits of the camerae and the degree of distortion. The adapical portion in which deposits are pronounced is practically undisturbed by pressure, while the adoral portion in which the deposits are immature has been flattened to an extent which varies inversely with the amount of cameral deposit present. It is now known that in orthoceracones the cameral deposits are formed in the adpical part of the phragmocone and not at the base of the living chamber, and that the point at which deposits begin is separated from the base of the living chamber by a considerable number of empty camerae. It would follow that in a typical specimen of P. knoxense not only the living chamber but also a considerable number of the adapertural camerae are lost.

For this reason the earliest stages of the development of the deposits of camerae and siphuncle have not been observed in this species. The earliest available stage

of the siphuncular deposit shows the deposits which originate at the septal necks markedly developed aperturally so that they extend about half way to the next adoral septal neck. Following this can be seen stages leading to the fusion of the deposits of adjacent segments along the venter. No deposits appears against the dorsal wall of the siphuncle at this stage. Cross section taken at a stage at which the fusion of the deposits along the venter is complete shows that the structure is confined to the ventral third of the siphuncle and is thickest at the mid-ventral region. (Fig. 14 B) Beyond this stage material is added to the sides of the deposit until they meet along the dorsum. The advancing lateral margins of the deposit are lobed and are rather variable. Normally the two ends at the region at or near the septal neck are completed first and then the middle portion, indication that the lateral margins of the deposit are trilobed. (Fig. 14 C) Two specimens have been seen which in cross section show mid-dorsal mass of deposit which is isolated from the main mass. Enough material showing this phenomenon has not been available to demonstrate whether this dorsal body is really isolated or whether it represents an independant adoral extension from the deposit which is completed circumferentially at the septal neck.

The lateral growth of the deposits is shown diagrammatically in fig. 14. The characteristic features are the fusion of adjacent segments of the deposit along the venter followed by an encroachment of the deposit laterally and finally dorsally. Though the completed deposits are similar to those of Adnatoceras, Euloxoceras and Dolorthoceras, the developmental stages are very different and the annulosiphonate origin of the structure is not at once apparent in Pseudorthoceras, as the annuli at the septal foramen are not completed until a pseudorthoceratoid deposit is complete ventrally, thereby obscuring the resemblance.

It has been noted that in several adapical portions of P. knoxense the deposit is not closed on the dorsal side, though normal closure occurs in more adapertural segments of the same individual. In such specimens the failure to develop the dorsal wall of the siphuncular deposit is found in segments in which the cameral deposit has nearly filled the camerae. This is of interest as it supports the belief that the pseudorthoceroid deposit when completed serves to sever the connection between the siphon and camerae, thereby controlling the extent of the development of the cameral deposits. In P. knoxense the heavy cameral deposits must have been important hydrostatically, while the thin siphuncular

deposit could have had little direct significance, as it is not massive enough to affect the balance of the organism to any extent.

The radial distribution of the deposits of the camerae has been discussed in detail in morphological section of this paper, and need not be repeated here. (See fig. 14 p. , also pl. 1, fig. 8.)

Of particular interest is the preservation of the original micro structure of the cameral deposits in some specimens from the Hazleton Bridge limestone¹⁰⁸ of the

108. C.A. Mallot, ms.

upper Pennsylvanian of western Indiana. Although the specimens are now completely composed of calcite, the original pattern is retained in considerable detail.

Types.— The specimens here figured are deposited in the Paleontological Research Institution, nos. 5859-5864.

Occurrence.— The species is widespread in the Pennsylvanian of America, apparently occurring throughout.

Pseudorthoceras senecum Flower, n. sp.

Pl. 1, fig. 1-3.

Conch orthoceraconic, presumably originally circular

or subcircular in section. The holotype is badly flattened, with one side ground away. The greater diameter of the specimen increases from 8 mm. to 11.5 mm. in a length of 26 mm. The sutures are straight and transverse. The septa, in their present condition, are less than one-seventh the diameter in depth. There are four camerae in a length equal to an adapertural diameter of 10 mm.

The ground surface of the specimen represents a nearly dorso-ventral section as is shown by the slightly eccentric siphuncle and the uneven distribution of deposits. The siphuncle is 4.5 mm. from the venter and 5.5 mm. from the dorsum. Where the depth of the camera is 215 mm., the siphuncle expands from .6 mm. to 1.5 mm. The necks are about one-sixth the depth of the camera and are evenly recurved so that the brims and necks are equal. The connecting rings are convex throughout, though more strongly so at their apices than in the middle portion. There is no area of adnation. The interior of the siphuncle bears on the right or ventral side of the specimen continuous lamellar deposits. On the left side the deposits are rudimentary.

The camerae bear well developed mural deposits which are better developed on the ventral than on the dorsal side of the specimen.

Discussion.- In the organization of the deposits and the outline of the siphuncle this species is a typical Pseudorthoceras. It differs from the genotype in the less pyriform outline of the segments, a character which suggests the possibility of an origin of the genus in some of the middle Devonian species of Dolorthoceras.

The asymmetrical position of the siphuncle and the distribution of the deposits in the siphuncle and camerae indicate that the section shown is dorso-ventral or nearly so. The surface is ground parallel to the plane of the bedding, and shows that the uneven distribution of the deposits is not due to inorganic agencies. Frequently orthoceracones are found in which the lower portion of the siphuncle is occupied by sediments while the upper portion which was left vacant at the time of burial was later filled in by infiltrated material. Schindewolf¹⁰⁹

109. Schindewolf, O. H., Bemerkungen zur Ontogenie der Actinoceren und Endoceren (Cephal., Nautil.). Neues Jahrbuch für Mineralogie etc. Beil.-Bd. 74, Abt. b, p. 96, fig. 6. 1935.

has figured a condition found in the apical end of Pseudorthoceras knoxense which suggests such a phenomenon, but the presence of a similar asymmetrical structure in the Devonian specimen shows clearly that this is

characteristic of the stock, as such an explanation cannot apply to a horizontally made section.

The extent of flattening of the specimen is not known, as it came into my hands with one side ground down to the siphuncle. The septa appears to be largely undisturbed in the plane of the section which is in the plane of the bedding. The depth of the camerae and the outline of the siphuncle are not modified. It is questionable whether flattening has increased the dorso-ventral diameter. The septa show unusually few irregularities for a distorted specimen and suggest that vertical pressure may not have resulted in the usual horizontal expansion.

The species can be distinguished from P. anomalum the only other Devonian species of Pseudorthoceras so far known, by the shallower camerae and the broader siphuncular segments.

Type.— Holotype: Pal. Res. Inst., no 5858.

Occurrence.— In the Cashaqua shales of the Upper Devonian, Naples, New York.

Pseudorthoceras anomalum Flower, n. sp.

Pl. 4, fig. 9.

The holotype represents a portion of a phragmocone including the neanic and early ephebic stages, so that the adapical and adapertural ends of the specimen differ markedly in proportions as well as in the form of the siphuncle. The section is circular throughout. The specimens is 70 mm. long, expanding from 5 mm. to 15 mm., with the conch expanding from 10 mm. to 15 mm. in the last 25 mm.

The sutures are straight and transverse. The septum 3 mm. deep where the diameter is 12 mm., or one-fourth the diameter. It is shallower adapically. The camerae are deep adapically but become rapidly shallower adorally. The number of camerae in a length equal to an adoral diameter varies from three at 6 mm., to five at 10 mm. and seven at 14 mm. The siphuncle is subcentral in position throughout. In the earliest segments the outline is that of the Dolorthoceras type except for the somewhat greater development of the area of adnation which is scarcely less than the brim. The connecting ring is convex over its free portion, with the greatest diameter in the adoral fifth of its length. Such a segment is 1.8 mm. in length, and expands from .8 mm

to 1.4 mm. Later segments retain the 1:1:1 ration of neck, brim and area of adnation, but the converging sides of the free part of the connecting ring apicad of the greatest diameter become straight. This type of outline is essentially the Adnatoceras type, except that the straight sides converge apicad, producing a segment which is more pyriform than cylindrical. This type of outline is developed where the conch is 8 mm. in diameter. The segment is 2 mm. in length, and expands from .8 mm. to 1.4 mm. as before. Orad of this the segments become more convex in outline, producing the typical early pyriform segment of Pseudorthoceras. This is developed at a diameter of 9 mm. The segment is 2 mm. in length, and expands from 1 mm. to 2 mm. The segments orad of this region are poorly preserved and fragmentary. The area of adnation remains equal to the brim, but apparently the convexity of the connecting ring increases still further.

The deposits of the siphuncle are well developed in the adapical part of the specimen. The specimen is sectioned nearly transversely, but at a point where the section passes through the dorsal wall of the siphuncle is shown that the deposit is of the Pseudorthoceras type, the adjacent segment of the deposits fusing ventrally and then growing toward the dorsum. Adoral segments demonstrate the annulosiphonate origin of the

structure, and show its ontogeny from the earliest stage. Mural deposits occupy the camerae. The deposit can be seen adjacent to the outside of the connecting ring in the adapical camerae, which is taken to represent the development of the inner pair of lobes of the ventro-lateral masses. Transverse sections of Pseudorthoceras knoxense show similar phenomena.

The living chamber and surface of the shell are unknown. The ventral side of the specimen has been removed by grinding. It was studied previous to grinding. The shell was removed by weathering, also the mural part of the septa. The deposits had partly been weathered, and were less resistant than the matrix of the camerae, with the result that the ventral sinus of the deposits could be seen. The lobation of the ventro-lateral masses was indistinct.

Discussion.- On the basis of the outline of the latest known segments of the siphuncle and the form of the siphuncular deposits this species is referred to Pseudorthoceras. It is unique in the retention of the strong area of adnation throughout. This feature might be carried through from a nepionic Dolorthoceras stage. In view of the fact that the area of adnation is strong where the segments are of the typical Dolorthoceras outline, it appears that it represents the failure to

suppress the nepionic character of the area of adnation in the ephebic Dolorthoceras type of segment, and that the feature is merely continued.

The imperfect similarity of later segments to Adnatoceras appears to be accidental. Rather it seems that the straight form of the apically converging portions of the connecting ring are the logical origin of the Pseudorthoceras pyriform outline. The stage has not been observed in P. knoxense, but acceleration might cause it to be omitted in this later form. Sufficiently early stages of P. senecum to determine whether there is a similar condition in that species, are lacking. However, the holotype of senecum does show suggestions of the flattening of the siphuncular outline.

This species can readily be distinguished from P. senecum by the much shallower camerae in the ephebic portion. The shallow camerae of the adapertural end seem to indicate that this was originally a small species, though the gerontic condition has not been observed.

Type.— Holotype, New York State Museum.

Occurrence.— From the Parrish limestone member of Cashaqua shales, Upper Devonian, Parrish gulley, Naples, New York.

MOOREOCERAS Miller Dunbar and Condra

Genotype: Mooreoceras normale Miller Dunbar and Condra

Miller, Dunbar and Condra, Nebraska Geol. Surv.
ser. 2, bull. 9, p. 85.

In this genus are placed orthoceracones which are similar to Pseudorthoceras, but differ from that genus in having a depressed section, oblique or sinuate sutures and an eccentric siphuncle. The section is circular in the young and in some species may remain so in the ephebic stage, though typical specimens are definitely depressed. The sutures in the early portion are straight and transverse but later normally slope adaperturally on the dorsum and are more or less sinuous, showing faint lateral saddles separating dorsal and ventral lobes. The septum is very shallow even in the younger stages, and serves as a good criterion to distinguish early fragments of Mooreoceras from Pseudorthoceras. The siphuncle is central in position in the younger stages but is ventrad of the center in the ephebic portion of the conch. The outline of the ephebic segments varies among the species. in some forms it is subglobular, but it is more typically pyriform, with the greatest diameter orad of the center and contracting more gradually apicad than orad. Occasionally the segments are slender enough to resemble

those of Dolorthoceras, but they can be distinguished by the pyriform condition, which is not known in typical Dolorthoceras.

Siphonal deposits are of the Pseudorthoceras type. Thus far stages up to and including the fusion of adjacent deposits on the venter have been noted, but no specimen has been found which shows the closure of the deposits on the dorsum. It is possible that in Mooreoceras the deposits may not be developed dorsally at all, but at the present time enough material has not been examined to justify such a conclusion.

The deposits of the camerae are concentrated on the ventral side of the conch. One internal mold has been observed which retains the dorsal hiatus and the ventral sinus, but the differentiation between the dorso-lateral bands and the ventro-lateral masses is not marked.

The surface of the shell is smooth. Mooreoceras appears to have a thicker shell than Pseudorthoceras. The internal mold bears well defined impressions of the conchial furrow and the septal furrow.

Discussion.- Mooreoceras is probably derived from Pseudorthoceras as is shown by the similarity of the siphonal deposits and the siphuncular outlines. The depressed section, and the eccentric siphuncle and the sinuous sutures represent a more specialized condition

than that of Pseudorthoceras. The similarity between Mooreoceras and Dolorthoceras in section, sutures and occasionally in the form of the siphuncular segments is due to isomorphism.

The oldest known representatives of Mooreoceras are two species M. bradfordoides Flower n. sp. and M. ruedemanni Flower, n. sp. described below, from the Wellsburg monothem, which constitutes the upper half of the Chemung stage of the Upper Devonian of New York.

Mooreoceras is present in the Mississippian of America, though apparently not well developed there. A fragmentary specimen from the Salem limestone of the Middle Mississippian is described and illustrated below. Miller and Furnish¹¹⁰ have described and illustrated

110. Miller, A.K. and Furnish, W.M., Lower Mississippian nautiloid cephalopods of Missouri in Stratigraphy and paleontology of the Lower Mississippian of Missouri, Univ. of Missouri studies, vol. 13, no. 4, pp. 164-169. 1938.

several new and old species which are referred to Mooreoceras. Fusiform siphuncular segments are reported for M. chouteauense (Swallow) and M. cliftonense Miller and Furnish.

Several species figured by de Koninck¹¹¹ and Foord¹¹²

111. De Koninck, L. G., Faune du calcaire carbonifere de la Belgique Ann. de Musee Royal d'Hist. Nat. de Belgique, Serie Paleontologique Tome V, 2 me partie. 1880.

112. Foord, A. H., Monograph on the Carboniferous Cephalopoda of Ireland, Part I, Family Orthoceratidae (in part), Paleontographical Soc., vol. 51, p. 12, pl. 5, fig. 4a-c. 1897.

from the Mississippian of Belgium and Ireland respectively recall Mooreoceras in section, sutures and the eccentric siphuncle. In particular O. hindei Foord appears to be a Mooreoceras, for the siphuncular outline as shown is correct for the genus. It is doubtful, however, whether the continuous lining within the siphuncle figured by Foord represents an organic or an inorganic deposit. Without knowledge of the siphuncle outline it is not possible to determine the generic position of the other species figured. Paraloxoceras can be distinguished by its much more expanded siphuncular segments, even in the absence of siphonal deposits.

I have made no attempt here to redescribe the Pennsylvanian species of Mooreoceras, and such as are figured are used here for purely morphological purposes. All of the Pennsylvanian species known to belong to Mooreoceras have been recently and quite adequately

described. These and many new ones are at present being studied by Mr. Richard Schweers of the University of Indiana. I am indebted to Mr. Schweers for an opportunity to study his undescribed material and to figure such specimens as were required.

Mooreoceras ruedemanni Flower, n. sp.

Pl. 1, fig. 4; pl. 7, fig. 3; pl. 8, fig. 8.

The holotype consists of a portion of a phragmocone containing seven camerae, 22 mm. in length. It has been ground so as to expose a surface inclined about twenty degrees from the dorso-ventral plane. Conch depressed in section, expanding from 9 mm. and 14 mm. to 12 mm. and 18 mm. as nearly as can be estimated. Sutures oblique, sloping strongly orad on the dorsal or antisiphonal side. Septa shallow, having a depth of 1.5 mm. on the venter and 3 mm. on the dorsum. There are three and one half camerae in a length equal to the adapertural dorso-ventral diameter of 12 mm., and six camerae in a length equal to the corresponding transverse diameter of 18 mm.

Siphuncle fusiform in outline, located ventrad of the center of the conch. Its distance from the venter increases from 4 mm. to 5.5 mm. in 22 mm. Septal neck strongly recurved, the neck slightly greater than the

brim. Where the segment is 4 mm. in length the diameter at the septal foramen is .8 mm. This increases to a maximum diameter of 3 mm. one-third the distance to the preceding segment, then contracting gradually apicad, producing a strongly fusiform outline. Area of adnation minute, about one-half the brim.

The deposits of the siphuncle are of the Pseudorthoceras type and are well developed on the ventral side, but can not be distinguished clearly on the dorsal side. Deposits of the camerae are mural and well developed. The surface, aperture and living chamber are unknown.

Discussion.- The holotype, the only representative of this species which has come to my attention, represents an adapical portion of the phragmocone, as is shown by the development of the deposits. It is an internal mold, originally badly weathered, so much so that the measurements of the conch are only approximate. The outer part of the mural deposits of the camerae have been for the most part removed. Nevertheless, the species can be recognized by the very shallow camerae, which will distinguish it from the species of Bradfordoceras which also occurs in the Upper Devonian with the exception of B. gomphoides Flower and Caster, the siphuncular structure of which is unknown.

The cameral spaces of the holotype are filled with white calcite; the cameral deposits are strongly limonitic. The deposits of the siphuncle appear to be some greenish iron compound, and have partly been dissolved. They can be distinguished from the matrix of the siphuncle only with difficulty.

Type.- Holotype, New York State Museum no. 1753.

Occurrence.- "From iron ore bed in the Chemung, Austinville, Bradford County, Pennsylvania." Dr. K.E. Caster has very kindly supplied a statement as to the horizon which is quoted: "From the matrix of the material from the Upper Devonian of Bradford County, Pennsylvania, I would judge that it came from one of the local iron-limes or coquinities in the Wellsburg monothem. The iron ore bed near Austinville apparently lies near the horizon of the "Burlington limestone" of the Second Survey (Pa.) reports, for which Willard, 1936, suggested the name Luthers Mills coquinite."

Mooreoceras bradfordoides Flower, n. sp.

Pl. 7, fig. 7.

Conch orthoceraconic, depressed in section, with the venter more flattened than the dorsum and a ventral siphuncle. The conch expands from 5.5 mm. and 7 mm. to

9 and 11 mm. in the first 20 mm. of the holotype. In the next 20 mm., the conch expands to 13 mm. and 17 mm. The sutures are straight and transverse in the earliest part of the conch but develops lobate pattern consisting of dorsal and ventral crests separated by lateral lobes. The dorsal crest is the higher of the two, giving the suture and septum a slightly oblique aspect. The septa are shallow. At diameters of 9 mm. and 11mm. the depth is 2.5 mm.

Throughout the known portion of the conch there are five camerae in a length equal to an adapertural dorso-ventral diameter, and six in a length equal to the corresponding transverse diameter.

The siphuncle is close to the ventral wall of the conch. Where the dorso-ventral diameter is 5.5 mm. the siphuncle is .6 mm. in diameter and 1.6 mm. from the venter. Where the diameter has increased to 9 mm., the siphuncle is 1.5 mm. in diamter and 2 mm. from the venter. In section the segments are fusiform, expanding to their greatest diameter orad of the center of the segment. The brim appears to be considerably less than the neck, and there is no area of adnation. A segment which is 2.4 mm. in length expands from .6 mm. at the septal foramen to 1.4 mm. Deposits within the siphuncle are of the Pseudorthoceras type, and have been observed only on the

ventral side. The anterior of the sectioned camerae show the segmental deposits yet unfused; in the more apical portion adjacent segments have joined and their boundaries cannot be made out. The deposits is thick in the interseptal space, and it occupies nearly half of the siphuncle, so that the endosiphuncular cavity is nearly straight on the ventral side. Deposits within the camerae are mural. They extend along the free part of the septum nearly to the siphuncle on the venter, and are not massive peripherally. The internal mold shows little lobation, but the ventral hiatus is well preserved. Deposits have not been observed on the dorsum. A well defined dorsal carina is present.

The living chamber, aperture and surface are not known.

Discussion.- The species is remarkable for its resemblance to Bradfordoceras in the lobation of the sutures, and suggests that some of the specimens referred to Bradfordoceras by Flower and Caster without knowledge of the siphuncular structure may eventually prove to belong to Mooreoceras instead. The specimen is of interest first for the heavy concentration of the deposits of camerae and siphuncle on the venter, and second for the effect that this had on the conch after the death of the organism. The specimen was still imbedded in its matrix

when it came into my hands, and was contained in a small block one side of which showed considerable evidence of weathering. This appears to be the upper side. The conch rests with the venter on the opposite or lower side of the block, which is just what is to be expected in view of the condition of the cameral deposits. The deposits of the siphuncle are strongly replaced, and the margin of the deposit is irregular in the adapical end of the specimen. Were it not for the segmental condition of the deposit in the anterior portion, and were there no indication of the position of the conch in the sediments, such structures might be interpreted as the supplemental infiltration to an incomplete internal mold of the siphuncle. The specimen occurs in a highly ferruginous and micaceous sandstone, and is replaced with calcite, limonite and some unidentified iron silicates.

The species differs from M. ruedemanni in the more sinuate and less oblique sutures. So far as can be determined from the other species, the depth of the camerae is about the same.

Type.- Holotype, New York State Museum, no.

Occurrence.- This bears the same locality number as the preceeding, and like it, is probably from the Wellsburg monothem. The matrix sent to Dr. Caster is from this specimen. Both are undoubtedly from the same

horizon as is indicated by the preservation, matrix, and the minerals in the siphuncles.

Mooreoceras sp.

Pl. 4, fig. 5.

This consists of a small fragment of an orthoceracone which does not furnish enough information to merit the use of a new specific name. Only three camerae are preserved, and these are too fragmentary to furnish either the section of the conch or the rate of expansion. The total depth of the camerae is 6.2 mm., and the apertural diameter is 12 mm. The curvature of the septum in section is equal to the depth of a camera. Where the camera is 2 mm. in depth the siphuncle expands from 1 mm. at the septal foramen to 2 mm. within the camera. The necks are short and recurved, the brim appearing slightly less than the neck, and the connecting ring is convex throughout, not more curved at the ends than in the middle, and meeting the preceding septum with no area of adnation. Deposits are not known in either the camerae or the siphuncle.

Discussion.— This species is referred to Mooreoceras for the outline of the siphuncle is similar to that of certain species referred to that genus, though in many

species the siphuncle is more expanded. The outline of the connecting ring is too convex for Dolorthoceras, or other Mississippian limestone of Indiana agree with this species in the outline of the siphuncle or in the very shallow camerae. The specimen is of interest in that it established the existence of Mooreoceras in the Mississippian; previously described species are of Pennsylvanian age.

Type.— Pal. Res. Inst., no. 5865.

Occurrence.— From a loose block of Salem limestone on the campus of the University of Indiana, collected by the author. The block is one of several which was removed when digging the foundation of the Biology building, which would place it in the lower or middle part of the Salem, probably not over 40 ft. above the top of the Harrodsburg limestone.

Pennsylvanian species of Mooreoceras

Mooreoceras normale Miller Dunbar and Condra
Orthoceras colleti Morse, 1931, (not S.A. Miller)

Kentucky Geol. Surv., ser. 6, vol. 36, pp. 300,
325, 326, pl. 54, fig. 1-2.

Mooreoceras normale Miller Dunbar and Condra, 1933, Nebraska
Geol. Surv., ser. 2, bull. 9, p. 87, pl. 2, fig. 5-7.

Mooreoceras normale var. angusticameratum

Miller Dunbar and Condra

Mooreoceras normale var. angusticameratum Miller, Dunbar and Condra, 1933, Nebraska Geol. Surv., ser. 2, bull. 9, p. 89, pl. 2, fig. 8-10.

Mooreoceras tuba Miller Dunbar and Condra

Mooreoceras tuba Miller, Dunbar and Condra, 1933 Nebraska Geol. Surv., ser. 2, bull. 9, p. 90, pl. 2, fig. 2-4.

Mooreoceras bakeri Miller Dunbar and Condra

Mooreoceras bakeri Miller Dunbar and Condra, 1933, Nebraska Geol. Surv., ser. 2, bull. 9, p. 92, pl. 2, fig. 11-13.

Mooreoceras conradi Newell

Mooreoceras conradi Newell, N.D., 1936, Jour. Paleont., vol. 10, p. 483, pl. 69, fig. 3a-e.

Mooreoceras sp. (1)

Pl. 7, fig.

A fragment of a Mooreoceras from the Winterset limestone is illustrated to show the form of the siphonal deposits which are developed at the stage illustrated on the ventral side only. Mural deposits appear in the camerae. This specimen belongs to a species soon to be described by Mr. Richard Schweers, formerly of the University of Indiana, where this specimen is deposited.

Mooreoceras sp. (2)

Pl. 2, fig. 4-7.

A sectioned specimen of a Mooreoceras from the Kansas city group, Pennsylvanian, of Kansas City Missouri, is illustrated to show the ontogeny of the siphuncular outlines, which can be seen grading from the Michelinoceras condition to the Pseudorthoceras outline typical of mature Mooreoceras. This species belongs to a group in which the siphuncular outline remains fusiform throughout. University of Cincinnati, no. 22251.

PARALOXOCERAS Flower, n. gen.

Genotype: Paraloxoceras konincki Flower, n. sp.,

Conch orthoceraconic, slightly depressed in section. Sutures oblique, sloping slightly orad on the dorsum and generally faintly sinuate. The siphuncle is ventrad of the center in the ephebic stage, though possibly central in the early stage. Its segments are subspherical, slightly broader than long in the genotype. The brim is slightly shorter than the neck and equal to the area of adnation. Siphonal deposits are typical of the Pseudorthoceratinae in their mode of development, i.e. forming a continuous lining on the venter and then

growing toward the dorsum, but differ in form. The deposits are massive, leaving as a cavity within the siphuncle only a cylindrical central tubular cavity when complete. The inner free margins of the complete deposit are essentially straight. On the ventral side of the deposits of the genotype radial canals can be seen, a single one in each siphuncular segment, which pass obliquely apicad from the central canal to the connecting ring.

Paraloxoceras konincki Flower, n. sp.

Pl. 5, fig. 8-9.

cf. Orthoceras breynii de Koninck, 1880, Ann. Mus. Royal d'hist. Nat. de Belgique, T. 5, 2^{me} partie, p. 73, pl. 38 fig. 11a-c.

Non Orthoceratites breynii Martin, 1809, Petrifacta Derbiensia fig. 17-18, pl. 39.

Conch orthoceraconic, slightly depressed in section. The holotype is 38 mm. in length and expands from 13 and 14.5 mm. to 19 mm. and 21 mm. in that length. The specimen was faintly compressed by flattening adorally, resulting in a slight decrease from normal of the transverse diameter and also in a slight modification of the course of the adoral septa. The sutures are faintly inclined

orad on the dorsum. No sinuate suture pattern is apparent. The septum has a depth of about one-sixth the dorso-ventral diameter throughout the specimen. There are five to six and one-half camerae in a length equal to an adoral dorso-ventral diameter throughout.

The siphuncle is located ventrad of the center, and becomes more eccentric adorally. At the apical end it is 1 mm. at the septal foramen and is 4 mm. from the venter and 7 mm. from the dorsum. At the adoral end it is 1.5 mm. in diameter and is 5 mm. from the venter and 12.5 mm. from the dorsum.

The siphuncular segments are numuloidal, slightly broader than long. A segment 3.2 mm. in length expands from 1.5 mm. to 4.5 mm. The brim and area of adnation are in successive adapical camerae the space becomes progressively smaller, and is finally reduced to the proportions of a radial canal such as is found in the Actinoceroidea, (Pl. 5, fig. 9.) subequal and slightly less than the neck, which is about one eighth the length of the segment. Siphonal deposits are annulo-siphonate, pseudorthoceroid, and of the Pseudorthoceras type by their manner of growth. The first trace of a deposit on the dorsum appears in the third camera from the adoral end of the specimen, and on the venter in the same segment the adjacent deposits are barely

discrete. The deposit is massive on the venter. In the earliest stage observed it extends for about two thirds in length of the segment in the form of a broadly rounded lobe extending orad from the septal neck. The vacant space remaining is semi-crescent shaped in section. In the two apical segments the radial canal bifurcates just before reaching the connecting ring. It is not known how many radial canals there may have been nor how they may have been distributed radially. As the radial canals do not show in every segment, they were probably discrete. The deposits on the dorsum increase from the third to the sixth segments. Apicad of the sixth segment, the deposits vary slightly in size, but variation is erratic. This suggests very strongly that the deposit does not close on the dorsum. An identical condition has been found in the neanic stage of Pseudorthoceras.

Cameral deposits are mural, moderate in development and are seen only in the four apical camerae of the holotype. The surface of the shell is smooth and without ornament.

Discussion.- The whole interior of the specimen has been recrystallized and the original structures are somewhat obscured. It is doubtful whether a slight variation in color of the crystalline material close to the connecting ring on the venter represents a perispatium or

not. If so, this genus shows a remarkable parallelism in structure with the Actinoceroidea. The strong dorso-ventral differentiation and mode of growth of the siphonal deposit is opposed to an Actinoceroid origin. The strong resemblance of the structure of this genus to that of Mooreoceras has already been discussed.

The only specimen available for the present study is the one figured and described above. Its specific name involves several problems. It is closely allied if not conspecific with a species which de Koninck described as Orthoceras breynii Martin. The camerae in de Koninck's specimens are slightly shallower, but they represent slightly later portions of the conch than does the specimen studied.

O. breynii, the genotype of Loxoceras McCoy is known only from the original description and figure. Although various authors have attempted a redescription, it appears that until and unless the original type is examined, no specimen can be referred to the species with any certainty. Further, the lack of knowledge of what O. breynii is makes it impossible to refer any species to the genus Loxoceras McCoy which was based upon it, and further the family Loxoceratidae is one to which no genus other than Loxoceras can be referred.

It is evident that on purely nomenclatorial grounds

a new name must be proposed for de Koninck's specimen. Further, if Martin's original drawing of O. breynii was accurate, de Koninck's specimen is not conspecific, for there is a clear difference in the depth of the camerae, those of O. breynii Martin being considerably longer than those of O. breynii de Koninck.

De Koninck's species differs from O. breynii as originally illustrated by Martin in having much shallower camerae and less sinuate sutures, and the two are probably quite distinct.

Type.— Holotype, University of Cincinnati, no 8738.

Occurrence.— From the Visé limestone, of the Upper Mississippian, Visé, Belgium.

Bergoceras Flower n. gen.

Genotype: Cyrtoceras antilope de Koninck 1880, Ann. Mus. Royal d'Hist. Nat. de Belgique, vol. 5, 2^{me} partie, p. 36, pl. 37, fig. 1. Visé limestone, Mississippian, Visé, Belgium.

Pl. 9, fig.

Conch cyrtconic, exogastric, depressed in section. Sutures straight and transverse to the curving axis of the conch. Siphuncle ventrad of the center, composed

of subspherical segments which are broader than long, and closely resemble the condition found in Paraloxoceras. Annulosiphonate deposits are as in Paraloxoceras except that dorso-ventral differentiation is not apparent.

Surface with rounded longitudinal lirae separated by fine striae. Aperture unknown.

Discussion.- This is presumably a curved derivative of Paraloxoceras. The curvature, ornament, and the lack of dorso-ventral differentiation of the deposit distinguish the genus. From other cyrtoceracones it can be separated by the nature of the siphonal deposits.

Subfamily Cayutoceratinae Flower, n. subfam.

This subfamily is characterized by a siphonal deposit which is differentiated into two layers. An outer layer consists of discrete calcareous annuli of the Michelinoceras type. The inner layer, apparently originally carbonaceous, consists of fused segmental deposits which form a continuous lining within the siphuncle.

Two genera, both simple orthoceracones, are placed here. The subfamily appears in the Cayuta shale, lower Chemung, Upper Devonian where it is represented by

Cayutoceras. Bradfordoceras is characteristic of the Conewango, of the Upper Devonian, where it is represented by a variety of species. As yet the subfamily had not been recognized outside of the Penn-York Embayment.

CAYUTOCERAS Flower, n. gen.

Genotype: Cayutoceras casteri Flower, n. sp.

Conch orthochoanitic, circular or slightly depressed in section. The sutures are straight and transverse and the septa are evenly curved. The diameter of the siphuncle in section is slightly less than one-seventh that of the conch. In the early portion it is central; in later portions it may lie slightly ventrad of the center. The segments are of the Dolorthoceras type, (see p.) though slightly broader than in typical Dolorthoceras. The brim and neck are equal and the area of adnation is less than half the brim. The free part of the connecting ring is strongly curved at the ends and faintly convex in the middle. The segments are more or less barrel-shaped. The necks are short, less than one-tenth the length of the segment. The interior of the siphuncle bears a double deposit. Calcareous annuli develop into the Michelinoceras type of deposit. The adapertural end

of the deposit may continue orad for over half the length of the segment, but the adjacent deposits are not known to fuse. The calcareous deposit is covered by a carbonaceous deposit which appears to be continuous, though its segmental origin can be made out. This appears first as a thin black coating of the calcareous annulus. Where well developed it is continuous, lining the inside of the siphuncle, and is thickened markedly orad of the greatest development of the calcareous deposits, where it is massive and rather irregular. Both deposits are much heavier on the venter than on the dorsum, but the deposits appears on the dorsal side before the carbonaceous deposit is continuous on the ventral side from segment to segment.

The aperture of this genus is not known. The surface is poorly preserved in all specimens examined, but show no trace of any ornament.

Discussion.- The deposits within the siphuncle are unlike those of any Actinoceroid, but the double nature of the deposit suggests the type of structure which Teichert¹¹³ has figured for Westonoceras. In view of

113. Teichert, C., Untersuchungen an actinoceroiden Cephalopoden aus Nordgrönland. Meddelelser om Grønland udgivne af Kommissionen for videnskabelige undersøgelser i Grønland, bd. 92, nr. 10, p. 36, fig. 18, 1934.

the very different structure of the septal necks and the difference in the position of the break between the segmental deposits it is probable that the resemblance is isomorphic and is not indicative of any relationship. The genus suggest a relationship with Bradfordoceras if the deposits within the siphuncle of that genus have been interpreted correctly.

Cayutoceras is monotype. It is known only from the Cayuta shale of the Upper Devonian.

Cayutoceras casteri Flower, n. sp.

Pl. 1, fig. 10; pl. 3, fig. 1.

This is a moderate sized orthoceracone of subcircular section. The conch enlarges at a rate of 3-4 mm. in length of 20 mm. No gerontic cessation of enlargement has been noted, though specimens with a diameter of 50 mm. have been found.

The sutures are straight and transverse. There are five camerae in a length equal to an adapertural diameter of 23 mm. The septa are evenly curved and moderate in depth. Where the diameter of the conch is 21 mm, the septum is 4 mm. deep, slightly less than the depth of a camera. The siphuncle is subcentral in position in the

earlier stages and is very slightly eccentric in the later portion, so that where the diameter of the conch is 40 mm. the siphuncle is 4 mm. in diameter at the septal foramen and is 17 mm. from the supposed venter.

Where the conch is 21 mm. in diameter the camera is 5 mm. in depth. The siphuncle at this point is central. It expands from 2.5 mm. at the septal neck to 3 mm. within the camerae. The neck is about one-sixth the depth of the camera and the brim is equal to the neck. The connecting ring is faintly convex in the middle and curves more rapidly at its ends. The area of adnation is about one-half the brim, but the connecting ring is only narrowly separated from the septum for a greater distance, giving an appearance of a much greater area of adnation than is actually present. The internal deposits of the siphuncle have been described under the generic discussion. The camerae contain well defined episeptal and hyposeptal deposits which are concentrated on the ventral side.

The largest fragment of a living chamber observed for this species has a diameter at the base of 40 mm. and is 90 mm. in length. No trace of the aperture has been found. Several fragments of the shell which adhere to the internal mold show no trace of ornament.

Discussion.- This species appears to be widespread in coquinites of the Cayuta shale, but most of the

specimens obtained represent relatively small fragments of phragmocone.

So far as known Cayutoceras casteri is the only representative of Cayutoceras, although it is possible that ¹¹⁴Orthoceras palmatum Hall may belong here also. That

114. Hall, James, Paleontology of New York, vol. 5, pt. 2, p. 312, pl. 90. fig. 9-10. 1879.

species has a depressed section and much deeper camerae than C. casteri. The horizon and locality of O. palmatum are virtually unknown. Hall recorded it from "semi-calcareous beds of the upper member of the Chemung group, in southern New York."

Types.- Holotype: Pal. Res. Inst., no. 5855.

Paratypes: Pal. Res. Inst., no. 5856-5857.

Occurrence.- In coquinites of the Cayuta shale from 2 miles south of Owego, New York, and from a road cut three miles west of Bainbridge, New York.

BRADFORDOCERAS Flower and Caster

Genotype: Bradfordoceras transversum Flower and Caster.

This genus contains orthoceracones of slightly depressed section. The sutures slope adaperturally on the dorsum and are more or less sinuous. When the sinuosity is well developed the suture pattern consists of lateral saddles which separate a shallow ventral lobe from a deeper dorsal lobe. The septum is shallow as in Mooreoceras.

The siphuncle is located ventrad of the center of the conch. The condition of the early segments has not been observed. The ephebic segments are of the Pseud-orthoceras type of outline, and may be pyriform or globular. In the genotype the segments are as wide as long.

Deposits within the siphuncle are of the Cayutoceras type, consisting of discrete annulosiphonate rings which are only slightly better developed orad than apicad. These rings are overlaid by an apparently continuous deposit of calcite which is believed to correspond to the carbonaceous deposit of Cayutoceras.

The surface of the shell bears obscure lines of growth. The aperture bears a broad shallow hyponomic

sinus.

Discussion.- Bradfordoceras resembles Mooreoceras somewhat in section, sutures and position and outline of the siphuncle. The genera can readily be distinguished by the endosiphuncular deposits; those of Mooreoceras are of the Pseudorthoceras type while those of Bradfordoceras are of the Cayutoceras type. Each genus represents the end development of a different line; Mooreoceras being a specialization derived from Pseudorthoceras, while Bradfordoceras is probably more closely related to Cayutoceras than any other genus.

Bradfordoceras is definitely known only from the Conewango series of the upper Devonian. Seven species were referred to the genus when it was first described. In the Salamanca conglomerate there are numerous fragmentary specimens which were described as variants of B. hector (Hall). It is highly probable that when these forms have been studied from additional material they may prove to be of specific rank.

The structure of the deposits of Bradfordoceras is known only from a few propitiously preserved fragments of the genotype. The structures present were recognized as organic, but the continuous deposits which were at first compared to the deposits of Pseudorthoceras are more probably the homologue of the carbonaceous deposits of

Cayutoceras.

Bradfordoceras transversum Flower and Caster

Pl. 5, fig. 10-11.

Bradfordoceras transversum Flower, R.H. and Caster ,
K.E., 1935, Bull. Amer. Paleont., vol.22, p. 230,
pl. 17 fig. 1-5; pl. 18, fig. 1; pl. 19, fig. 1;
pl. 20, fig. 3; pl. 22, fig. 3-4.

The portion of the original description dealing with the external features and general proportions of the conch needs no revision; however, the internal structure needs further comment.

The internal structure is preserved in four specimens the camerae of which are completely filled with crystalline calcite. The endosiphuncular cavity is occupied for the most part by matrix, and the septa, margins of the deposits and the connecting ring are variously represented by calcite and limonite.

A paratype, Pal. Res. Inst., no 5023, shows the simplest condition. Here the siphuncle is filled with calcite. The annulosiphonate deposits are not developed, but the second deposit, that corresponding to the

continuous carbonaceous deposit of Cayutoceras is represented by a limonitic band. In another specimen, likewise a paratype (Pal. Res. Inst., no 5015,) the siphuncle is occupied for the most part by a matrix of yellowish sand. In the adapical part of this specimen the annulosiphonate rings are still calcareous, and they are covered by a thin layer which is carbonaceous adapically, limonitic adaperturally and in places seems to be destroyed by the invading matrix.

Unfortunately the holotype, which was selected largely because of the undistorted section and the outline of the siphuncle, represents an atypical condition. The carbonaceous deposit of Cayutoceras is here represented by a band of calcite lined on either side with limonite. This encloses spaces which correspond to the annulosiphonate deposits but which are occupied by a red sandstone, apart of the matrix. This must be broken at some point to permit the entrance of the sand into the annulosiphonate spaces.

It seems impossible that the structures present here could be of inorganic origin, even when not considered in the light of the two paratypes mentioned above. The band of calcite enclosing annulosiphonate spaces filled with sand cannot be explained in terms of any sedimentary process of the filling of the siphuncle with matrix;

rather it must represent a space which could not be filled with sand because it was occupied by some tissue or some deposit. After burial the original structure was dissolved out and replaced by calcite, doubtless from percolating waters.

Types.- Holotype: Pal. Res. Inst., no 5014. Paratypes: Pal. Res. Inst., no 5015-5023, and Acad. Nat. Sci. Philadelphia, Second Geol. Survey Pennsylvania Coll., no. 9602.

Occurrence.- Lewis Run sandstone member, Venango stage, Conewango series, Upper Devonian, from Lewis Run, Bradford County, Pennsylvania, and in the Salamanca sandstone of northern Pennsylvania.

Bradfordoceras moderatum Flower, n. sp.

Pl. 3, fig. 8.

The holotype represents a portion of a mature specimen including most of the living chamber and several attached camerae. The conch is slightly flattened, the pressure being directed about 25 degrees from the dorso-ventral diameter. Flattening is slight. The conch expands from 20 mm. and 27 mm. to 29 mm. and 35 mm. in the first 40 mm., which includes the lower part of the

living chamber. Just beyond this there is a marked decrease in the rate of expansion. The phragmocone is 24 mm. in length and contains six camerae. The sutures are only partially preserved. A broad evenly rounded dorsal saddle and lateral lobes can be seen. A ventral saddle shallower than the dorsal one must have been present, and is indicated by the slight anterior direction of the ventro-lateral part of the suture. The camerae increase rapidly in depth, except the last which is contracted. The last four measure 3 mm., 4.4 mm., 5 mm., and 4 mm. respectively. There were seven camerae in a dorso-ventral diameter of 26 mm. at the base of the living chamber, and eight or nine in a corresponding transverse diameter of 32 mm. The siphuncle in the present specimen is 2 mm. in diameter at the base, the only point where it can be seen, and is 3 mm. from the ventral wall. Oblique distortion results in the siphuncle being 12 mm. from one side and 13 mm. from the other.

The living chamber has diameters at the base of 26 mm. and 32 mm., and is 67 mm. in length. A small portion of the aperture is preserved. A little below mid-height, the rate of expansion decreases abruptly, giving the conch a faintly gibbous aspect. A marked constriction, probably only internal, appears in a region 55 mm. to 60 mm. from the base of the living chamber. Only the lateral

part of the aperture is preserved. The constriction of the interior preserves the apertural pattern, a rather unusual feature, showing a well developed hyponomic sinus and a shallower and narrower lateral sinus.

Discussion.- The species is unique in the proportions and characteristic constriction of the internal mold of the living chamber. The sutures and the depth of the camerae are intermediate between B. transversum Flower and Caster and B. sinuatum Flower having a better developed ventral saddle than typical transversum, and lacking the mid-dorsal flattening of sinuosum to which it is closer in size and cameral proportions.

Type.- Buffalo Museum of Science, no. .

Occurrence.- In the Lewis Run sandstone, at Lewis Run, Pennsylvania. Collected by I.G. Reimann.

Bradfordoceras giganteum Flower, n. sp.

Pl. 3, fig. 7.

The holotype is a large specimen which has been crushed dorso-ventrally in such a way as to produce a transverse fold in the septa throughout. The dorso-ventral diameter is decreased, but the transverse diameter has apparently not been increased. The conch expands in

the first 56 mm. from 32 mm. and 25 mm. to 37 mm. and 44 mm., and in the next 60 mm., to 60 mm. and 51 mm.

The depth of the septa has been destroyed and is of no value. The sutures are sinuous, producing rounded ventral and dorsal lobes, the ventral lobe low and well rounded, the dorsal lobe higher and less flattened in the median region. The depth of the camerae is uniform throughout the phragmocone. There are nine to ten camerae in a length equal to the transverse diameter, and eight to nine in a length equal to the dorso-ventral diameter. The siphuncle, as exposed at the septa is 3 mm. in diameter and 10 mm. from the venter at the base of the specimen where the diameters are 25 mm. and 32 mm. At the base of the living chamber the siphuncle is 4 mm. in diameter and is 16 mm. from the venter, measuring in each case the distance along the distorted septum. The form of the segments is unknown.

The living chamber has diameters at its base of 60 mm. and 51 mm. It is incomplete, but 70 mm. are present. One side of the apertural end is missing. The dorso-ventral diameter is 62 mm. The estimated transverse diameter is 80 mm.

The internal mold shows traces of irregular growth lines as in other species of Bradfordoceras.

Discussion.- This species is unique both for its

large size and its rapid rate of expansion. The shallow camerae recall Bradfordoceras multicameratum Flower and Caster¹¹⁵ of the Salamanca, but the holotype of that

115. Flower, R.H. and Caster, K.E., Ibid., p. 234, pl. 21, fig. 6.

species is much smaller and represents the gerontic portion of the phragmocone. Further the rate of expansion is not as large as it appears, for the specimen is badly flattened, while B. giganteum is only slightly flattened. The reference to Bradfordoceras rests upon the marked sinuosity of the sutures and the prominent growth lines, both of these features are absent in Mooreoceras with which Bradfordoceras is easily confused.

Types.- Holotype: Buffalo Museum of Science no.

Occurrence.- The specimen is labeled as follows: Conewango group? From Allegheny State Park. Donated by J.W. Ruobloch. Collector unknown. The form is preserved in a light colored very hard sandstone, normally yellowish but weathering lighter, which recalls the Salamanca very strongly.

Bradfordoceras fusiforme Flower, n. sp.

Pl. 7, fig. 9.

The holotype is a fragment 110 mm. long consisting of a mature living chamber and twelve camerae. The conch is depressed in section expanding in the apical 40 mm. from 15 mm. and 17 mm. to 24 mm. and 28 mm. The conch expands at a nearly uniform rate to the middle of the living chamber which is slightly inflated, and the aperture is contracted.

The sutures described broad lobes on the dorsum, rising orad on the ventro-lateral area as far as observed. The mid-ventral part of the suture has not been preserved. The septum has a depth of 5 mm. where the transverse diameter is 24 mm. and the estimated dorso-ventral diameter is 22 mm. The siphuncle has not been observed, but must lie well ventrad of the center. The camerae occur five in a length equal to a transverse adoral diameter of 26 mm. The last two camerae are slightly shorter.

The living chamber has basal diameters of 25 mm. and 28 mm. and is 60 mm. in length. In the basal 30 mm. the conch expands to 28 mm. and 32 mm., beyond which it contracts and is nearly cylindrical to the aperture where the diameters are 28 mm. and 28 mm. The apertural

margin is not preserved.

Discussion.- The gibbous form of the living chamber suggests B. gomphoides, which is amuch larger species with much shallower camerae.

Type.- Holotype: Buffalo Museum of Science, no.

Occurrence.- From the Lewis Run sandstone, Lewis Run, Pennsylvania.

PART IV

PHYLOGENY

Relationship Of The Pseudorthoceratidae

1. The outline of the mature segments of the siphuncle and the annulosiphonate nature of the siphonal deposits suggests that the Pseudorthoceratidae might be allied to the Annulosiphonate of the Cyrtchoanites in which may be included the Actinoceroidea and a few forms of doubtful affinities.

The Pseudorthoceratidae and the Actinoceroidea possess several features in common, but the differences are such that the two groups are believed to be merely isomorphic. The following features are common to the two families:

(1). Cyrtchoanitic adult siphuncular segments. So far as the outline of the siphuncle is concerned it might be possible to derive the Pseudorthoceratidae from the Sactoceratidae of the Actinoceroidea.

(2). Deposits within the siphuncle are annulosiphonate. Here the resemblances cease. The following differences are found:

(1). The nepionic segments of the siphuncle approach the orthochoanitic form in all Pseudorthoceratidae and attain it in the earlier and simpler genera. The earliest siphuncular stages of the Actinoceroidea are greatly expanded and definitely cyrtchoanitic. Simplification of the siphuncular outline in the Actinoceroidea occurs in the latest

not the earliest segments.

(2). Deposits within the siphuncles of Actinoceroid forms are pendant and are normally extended about equally oral and apical of the center of deposition at the septal foramen. The deposits of the Pseudorthoceratidae are parietal, scarcely developed apical, and elongated oral for the length of the segment.

(3). The central and radial canals of the siphonal vascular system together with the perispatium are characteristic of the Actinoceroidea but are absent throughout the Pseudorthoceratidae. It is believed that this indicates a fundamental difference in the organization of the siphon.

(4). The dorsal hiatus, well developed in all of the Pseudorthoceratidae is largely absent in the Actinoceroidea, being known only in a specialized group of Upper Ordovician Ormoceras.

(5). The apical end of the siphuncle is open in the Actinoceroidea but is closed by a siphonal caecum in the Pseudorthoceratidae, in which that family agrees with other stenosiphonate cephalopods.

2. Another cyrtchoanitic annulosiphonate group is comprised in the family Westonoceratidae Teichert. Here again the resemblances with the Pseudorthoceratidae seem to be isomorphic. The segments are cyrtchoanitic, the deposits are annulosiphonate. But the perispatium is lacking and there is no trace of the radial canal system of

the Actinoceroidea. The deposits resemble those of the Pseudorthoceratidae in that they are parietal and consist of two layers, the outer layer calcareous and the inner one carbonaceous. The condition recalls that of Cayutoceras Flower and Bradfordoceras Flower and Caster.

The condition recalls that of the Cayutoceratinae. However, the calcareous deposits of the Westonoceratidae are recumbent and both ends of the connecting ring are broadly adnate to the free part of the septum, features which are opposed to anything known in the Pseudorthoceratidae. Further, it may be noted that the Westonoceratidae are confined to the Ordovician, while the Pseudorthoceratidae do not put in an appearance until the Devonian. The Pseudorthoceratidae which are closest to the Westonoceratidae stratigraphically are those which have simple and slender siphuncular segments. Euloxoceras approximates the condition of the Westonoceratidae in its siphuncular outline more closely than does any other genus of the Pseudorthoceratidae, and this genus is known only from the Pennsylvanian. The structural and stratigraphic discrepancies between the two families seem to indicate that the resemblance between them has no genetic significance.

3. Among the cyrtochoanitic cephalopods which are not annulosiphonate there are several possible relatives which must be considered. One is Troedssonoceras Foerste¹¹⁷

117. Foerste, A. F., American arctic and related cephalopods. Denison Univ. Bull., Soc. Lab., Jour., vo. 23, p. 40. 1928.

which possesses longitudinal ornament like that of Kionoceras, but which has remarkedly cyrtochoanitic siphuncular segments. The siphuncle contains lamellar deposits which superficially resemble the completed deposits found in the Pseudorthoceratidae. Teichert¹¹⁸ has figured the siphuncle of

118. Teichert, C., Untersuchungen an Actinoceroiden Cephalopoden aus Nordgrönland, Meddelelser om Grønland, bd. 92, nr. 10, p. 41, fig. 20. 1934.

Troedssonoceras striatum (Troedsson). His figure shows lamellar deposits in which super imposed layers can be made out, while the layers are slightly irregular they are apparently not of segmental origin but seem to extend unbroken from segment to segment. The structure suggests rather that of Stokesoceras balticum Teichert and seems to support Teichert's¹¹⁹ suggestions that the genus may be

119. Teichert, E., Einige actinoceroide Cephalopoden aus dänischen Diluvialgeschieben und aus dem Gotlandium Skandnaviens, Meddelelser fra Dansk Geologisk Förening, bd. 8, hft. 4, p. 387, pl. 8, fig. 3. 1934.

related to the Discosouridae.

It might be noted in passing that Troedssonoceras is based upon Orthoceras turbidum Hall and Whitfield¹²⁰ of the

120. Hall and Whitfield, Geol. Surv. Ohio, vol.2, pt. 2, Paleontology, p. 100, p. 3, fig. 1.1875.

Maysville.

At the time of the original description of the genus, Foerste referred to it two species from the Cape Calhoun bed of the Middle Ordovician of Greenland, Sactoceras (?) lineatum Troedsson and S. (?) striatum Troedsson.¹²¹

121. Troedsson, G.T., On the middle and upper Ordovician faunas of northern Greenland, I., Cephalopods, Jubileks-
peditionen nord om Grønland 1920-23, nr. 3. 1926, p. 79, 80,
pl. 1, fig. 7; pl. 47, fig. 1-7.

More recently Shimizu and Obata¹²² have made S. striatum

122. Shimizu, S., and Obata, T., New genera of Gotlandian and Ordovician nautiloids, Jour. Shanghai Sci. Inst., 1935, sec. 2, vol. 2, p. 6-7.

the type of a new genus Striatoceras which is placed in a new family Ohioceratidae, based upon the new genus Ohioceras of the same paper, while S. lineatum is made the genotype of the new genus Greenlandoceras which is placed in the new family Greenlandoceratidae of which it is the solitary member. From the descriptions it appears that the genera

and families are separated because the segments of Striatoceras are "ormoceratoid" while those of Greenlandoceras are "actinoceratoid." Troedsson's figures show that the differences in the outlines of the siphuncle are mainly concerned with the width of the siphuncle at the septal foramen. In *S. lineatum* the area of adnation is slightly greater and the segment on the whole is slightly broader in proportion to its length. The differences between the genera are such as might occur between different parts of the same species, though it is apparent here that the species are distinct. The differences are not however sufficient to warrant generic or family distinctions. Both genera are here regarded as synonyms of Troedssonoceras Foerste of which Shimizu and Obata appear to be ignorant. Kobayashi¹²³ has proposed the family name Troedssonoceratidae

123. Kobayashi, Teiichi, On the Stereoplasmoderatidae, Japanese Jour. Geol. Geogr., vol. 13, no. 3-4, pp. 230-242, pl. 26, 1936.

and suggested that the family might be related to the Stereoplasmoderatidae, rather than to the Discosouridae. A relation between all three families is not impossible.

4. Kobayashi's family Stereoplasmoderatidae presents another possible relationship. In a revision of the family by its author¹²⁴ it is defined as follows:

"Longiconic orthoceracone(s), smooth or annulated; siphuncle elliphoanoidal, more or less expanded between the septal necks; intracameral stereoplastic deposit present; and if the stereoplastic deposit is present in the siphuncle it is more or less tubular."

The siphuncular outline of the family ranges from a nearly orthochoanitic type of outline which recalls the primitive pseudorthoceroid condition of Anastamoceras through forms with nummuloidal and definitely cyrtochoanitic segments. Deposits within the siphuncle are continuous and not segmental, as far as can be determined from published figures, and in this respect differ from the Pseudorthoceratidae. There is a wide stratigraphic gap between the two families. The Stereoplasticoceratidae appear to be largely if not entirely confined to the Lower and Middle Ordovician. The Pseudorthoceratidae appear in the Devonian. Kobayashi¹²⁵ referred Pseudorthoceras to the Stereoplas-

125. Kobayashi, T., Ibid., pp. 233-234.

moceratidae on the basis of the similarity of the siphuncular outlines and the continuous deposits within the siphuncle. However, it was not apparent at that time that the deposits of Pseudorthoceras and its allies were of annulosiphonate origin. Now that this has been demonstrated, it appears that the Stereoplasticoceratidae and Pseudorthoceratidae are perfect isomorphs, if only portions of the

phragmocone containing mature siphonal deposits are considered.

5. The remaining possibility for the origin of the Pseudorthoceratidae seems to be the Orthochoanites, and indeed the majority of the evidence favors such a hypothesis:

(1). The early segments of Dolorthoceras and Pseudorthoceras and indeed the segments of all Pseudorthoceratidae for which the ontogeny of the siphuncular outline is known, are consistent with the origin of the family in the Orthochoanites and the "Orthoceratidae" in the old sense.

(2). The annulosiphonate deposits are parietal in the Pseudorthoceratidae and also in Michelinoceras Foerste and Geisonoceras Hyatt of the "Orthocerntidne".¹²⁶

126. Teichert and Miller. What is Orthocerns? Amer. Jour. Sci., vol. 31, 1936, pp. 352-362. The authors have shown that the genotype of Orthoceras was probably a Rudistid and Orthoceras and Orthoceratidae cannot be used legitimately for cephalopods. Their proposal of the use of the old name Orthoceros and the proposal of a new family name Orthocerotidae seems inadivseable, inasmuch as the name suggests on the part of the original author a typographical error. Further it appears that the slightrness of the change will cause more confusion than it will eliminate.

(3). The Pseudorthoceroid deposit is the ultimate development of the orthoceroid deposit, and in all

Pseudorthoceratidae the deposit passes through an ontogenetic Michelinoceras stage identical with the condition found in many orthochoanitic genera.

(4). The conchinal furrow and the septal furrow are typically developed in both the "Orthoceratidae" and the Pseudorthoceratidae.

(5). Species are known which form a transition between the two families, exhibiting the pseudorthoceroid type of siphonal deposit in conjunction with an orthochoanitic siphuncular outline. One is Orthoceras palemon Barrande¹²⁷. The deposits are parietal as in the

127. Barrande, J., System Silurien du centre de la Boheme, vol. 2, Cephalopodes, 4th ser., pl. 394, fig. 6. 1870.

Pseudorthoceratidae and show the Dolorthoceras type of structure. Their primitive condition is shown by the clarity with which the segmental nature is evident from the outline of the mature deposits. Related species are not uncommon in the Middle Silurian of America, though because internal structures have not been closely studied in past they have gone unrecognized. These include not only smooth orthoceracones referred in the past to Orthoceras, but also forms referable on the basis of ornament to Protokionoceras.

The points upon which the families differ are as follows;

(1). The ephelic segments of the siphuncle of the

Pseudorthoceratidae are cyrtochoanitic.

(2). The deposits of the siphuncle of the orthochoanites are limited in extent, as is discussed elsewhere, being commensurate with the development of the cameral deposits against the connecting ring. The pseudorthoceroid deposit is not thus confined.

Summary

From the evidenc reviewed here it appears that the closest affinities of the Pseudorthoceratidae are with the orthochoanitic annulosiphonate cephalopods. Indeed, so close is the similarity that there is probably not a good genetic break between the groups and the position of the boundary might be questioned. For convenience in definition and recognition the Pseudorthoceratidae are limited to cyrtochoanitic forms. At the present time there is a good break between the orthochoanitic Silurian forms and the cyrtochoanitic Lower Devonian forms. But there is a stratigraphic break also, and it is quite possible that when Upper Silurian cephalopods are better known both will be eliminated. Certainly there is ontogenetic and adult gradation in the siphuncular outlines of Devonian species, and there is not reason to assume that the gradational nature of the development of the siphuncular segments should be confined to the Devonian in the Pseudorthoceratidae and their immediate ancestors.

EVOLUTION OF THE PSEUDORTHOCERATIDAE

The changes which took place in the development of the Pseudorthoceratidae had to do mainly with the modification of the siphuncular outline and the specializations of the siphonal deposits. The section of the conch and the position of the siphuncle are sometimes helpful, but seem to be matters of secondary importance which vary too much within a genus to serve as reliable criteria by themselves. Oblique and sinuous sutures are isomorphic characters, and accompany any modification from the generalized subcircular section. The aperture is of use only in rare instances, largely because it is unknown for many of the genera.

The outline of the siphuncle of various representatives of the family can be arranged in a series of stages ranging from the simple orthochoanitic type to the various expanded cyrtochoanitic types. These have been described in detail under the discussion of the siphuncle and are shown in text fig. 3. They need only be summarized here. The siphuncular outlines seen in the Michelinoceras, Anastamoceras, neanic Dolorthoceras and ephebic Dolorthoceras types represent an evolutionary sequence. Beyond the Dolorthoceras type there is a division of the stem. One line passes through the Adnatoceras type to the Euloxoceras type, while two others show an almost identical change from the Dolorthoceras to the Pseudorthoceras type. The following table summarizes what is known and what is suspected of the various siphuncular outlines of the various genera.

Known and assumed changes of siphuncular
outline in the Pseudorthoceratidae

	1.	2.	3.	4.	5.	6.	7.
Anastamoceras	xxxxxxxx-						
Diagoceras	????????	xxxxxxx					
Spyroceras	????	xxxxxxxxxxxxxx					
Dolorthoceras	xxxxxxxxxxxxxxxxxxxxxx						
Sceptrites	????????????xxx						
Fusicoceras	????????????????xxxxxx						
Cryptorthoceras	????????????????xxxxxx						
Palmeroceras	????????????????xxxxxx						
Petryoceras	????????xxxxxxxxxxxxxx						
Gelsonoceroides	????????????????xxxxxx						
Adnatoceras	????????????????xxxxxxxxxxxxxx						
Euloxoceras	????????????????????????????xxxxxx						
Cayutoceras	????????xxxxxxxxxxxxxx						
Bradfordoceras	????????????????xxxxxx-----xxxxxx						
Mooreoceras	???xxxxxxxxxxxxxxxxxxxxxx-----xxxxxx						
Pseudorthoceras	xxxxxxxxxxxxxxxxxxxxxx-----xxxxxx						
Paraloxoceras	-----xxxxxx						
Bergoceras	-----xxxxxx						

1. Michelinoceras type
2. Anastamoceras type
3. Neanic Dolorthoceras type
4. Ephebic Dolorthoceras type
5. Adnatoceras type

6. Euloxoceras type7. Pseudorthoceras type

x= observed outline ?= supposed outline (early stages not known) -= outline type absent.

The structure and development of the siphonal deposits have likewise been discussed in an earlier part of this paper. The following types are recognized:

1. The primitive annulus, which occurs in the early stages of all genera.

2. The Michelinoceras type, which occurs in the early stages in all genera.

3. The Dolorthoceras type. This occurs in all Dolorthoceratinae where deposits are known. In Anastamoceras it is ephebic, and is modified gerontically into the Anastamoceras type. Owing to the lack of suitably preserved parts of the phragmocones, it has not been noted in Sceptrites, Cryptorthoceras, Palmeroceras or Diagoceras.

4. The Anastamoceras type. Confined to gerontic Anastamoceras.

5. The Pseudorthoceras type. This is characteristic of the genera placed in the Pseudorthoceratinae, Pseudorthoceras and Mooreoceras.

6. The Cayutoceras type. In the Cayutoceratinae, comprising Cayutoceras and Bradfordoceras.

The first two appear in all genera, but are modified in the Pseudorthoceratinae. A complete ring is not formed there in the early stage of a deposit, because of the great retardation of development of the deposit on the dorsum. The incomplete ring on the venter, however, recapitulates these stages. These two types are not ephebic characters in any members of the family, but are the ontogenetic expression of the ancestral condition of the family, as is discussed elsewhere.

Anastamoceras is the earliest of the true Pseudorthoceratidae, being the only representative of the family known from the Helderbergian of the Lower Devonian. By its siphuncular outline it is the most primitive genus of the family, but the gerontic siphonal deposits are complex. The deposits in the ephebic stage are those of the Dolorthoceras type. In the gerontic stage, however, a central sheath and irregular radial pillars are added, which result in the more complex Anastamoceras type. (Fig.3, 13.)

So far as the family Pseudorthoceratidae is concerned the Anastamoceras type of deposit might be taken as the logical beginning of a progressive thinning of the siphonal deposit. In the transition to Middle Devonian Dolorthoceras the excessive gerontic deposits are lost. In contemporaneous and later forms there is noted a thinning of the deposit at the septal foramen, a necessary accompaniment

to the increase in expansion of the siphuncular segments. In later forms the remainder of the deposit thins, so that all that remains is a very thin uniform siphuncular lining, the segmental nature of which is not at once apparent to the eye. This is a gradual and continuous process, and can be well seen by comparing Devonian and Pennsylvanian species of Mooreoceras or Pseudorthoceras. This is a significant process and is one indicative of some interesting changes of the functions of deposits.

The primitive annulosiphonate deposit had a dual function. First it apparently served as a depository for excess calcareous material, and was excretory in this sense. Second, the deposits were significantly heavy. Being concentrated apically, they undoubtedly served to weigh down the apex of the shell. This permitted active typonmic swimming by weighting the tip of the shell. Further, by both ventral and apical concentration, it counteracted the buoyant effect of gas in the camerae and permitted a horizontal mode of life. This was the function of the deposits of the phragmocone taken as a whole. The relative importance of cameral and siphonal deposits as excretory and especially hydrostatic factors varied with their mass, as is explained in another section of this paper. When the continuous lining of the siphuncle developed it became a controlling agent for the development of cameral deposits, for cameral deposition could not continue after

the cameral tissues had been separated from the siphonal tissues by the pseudorthoceroid deposit. The gradual thinning of the siphonal deposit, which can be traced from the Middle Silurian through the Pennsylvanian, indicated that the siphonal deposits gradually came to be more and more exclusively devoted to their new function. The very thin siphuncular lining found in Pennsylvanian Mooreoceras could have had little significance due to its own weight, but its main function was that of a valve, separating the siphonal and cameral tissues when growth was complete in any siphuncular segment.

Yet it does not follow that the development of the Anastamoceras type of deposit is the beginning of this series. That it may not be is suggested by two lines of evidences. First, it must be remembered that the gerontic Anastamoceras type of deposit is developed only in the genotype, A. mirabile. There is not enough evidence to show whether it is really absent in other Helderbergian species or whether the apparent absence is due only to meagre material.¹²⁸

128. A nomenclatorial problem is also involved. If the gerontic deposits should prove to be confined to only a part of Anastamoceras as here delimited, a new genus might be proposed for species lacking the gerontic deposit. The practical difficulties involved as well as the uncertainty of the interpretation under discussion make such a step

undesirable at the present time.

A consideration of the ancestral Silurian types shows that it is not necessary to include the gerontic Anastamoceras type of deposit in the direct line indicated by the orthogenetic thinning of the siphonal deposits. The group of O. palemon Barrande is well represented in America, although it has not previously been noted owing to the lack of study of the internal structures of Silurian Orthochoanites. Such forms are now being studied, and are found to include both smooth and ornamented species in the Laurel limestone of the Middle Silurian of Indiana, and judging from the affinities of associated cephalopods, it will be remarkable if this group is not found to be widely distributed in the Middle Silurian of East-Central North America. The siphonal deposits form a continuous lining of segmental origin, and the deposits are thicker at the region of the septal foramina than elsewhere in the segments. This thickening is a primitive condition which harkens back to the Michelinoceras type of deposit from which it was derived. In the ephebic deposits of Anastamoceras the foraminal thickening is eliminated; in Dolorthoceras the deposits become thinner at the septal foramina than elsewhere, and general thinning follows in later forms. The Anastamoceras type of deposit might be an independent offshoot from this line. It is the type of variation which is met with again and again in the early history of genetic groups:

erratic development of a structure which later becomes stabilized and subject to only minor variation.

Dolorthoceras and its immediate relatives follow.

The siphuncle becomes more expanded in the camerae, largely by virtue of the increase of the brim and the development of a slight area of adnation, and the siphonal deposits are becoming thinner and more regular. In Dolorthoceras the Anastamoceras type of outline, which is without definite brim or area of adnation, is followed by the neanic Dolorthoceras type, in which the brim and area of adnation are slightly and subequally developed. The transition to the ephebic Dolorthoceras type is marked by an increase in the brim while the area of adnation remains stationary. The earliest well preserved and abundant material of Dolorthoceras which has been available for study is of Hamilton age. There Dolorthoceras is prolific, and further with it are associated several of its ornamented or otherwise specialized derivatives, suggesting that the origin of the genus must be looked for in Ulsterian or more probably Oriskanian strata. Further, it is to be expected that in pre-Hamilton species the neanic Dolorthoceras type of outline may be found to appear as an ephebic character. Dolorthoceras parlenese (H.S. Williams) of the Moose River sandstone of the Oriskanian of Maine, shows in general a type of outline which is very similar to that shown in the neanic stages of later Dolorthoceras. The poor preservation

of the only specimen known which shows the siphuncle leaves some doubt as to the exact condition of the area of adnation and the extent of the brim, but is adequate to show that this species must be considered as an advanced Anastamoceras or a primitive Dolorthoceras. Dolorthoceras rudis (Hall) of the Onondaga seems to represent a typical neanic Dolorthoceras condition.

In the Middle Devonian, and more particularly in the Hamilton, Dolorthoceras gave rise to many specializations, which find their expression in a variety of form and ornament. Probably each of these specializations is quite independent of the others. The variations of ornament will be considered first:

Two genera proclaim their early development from Dolorthoceras by the retention of the neanic Dolorthoceras type of siphuncular outline. Diagoceras is specialized in section, sutures and in the development of a pattern of fine rhythmically spaced striae. It appears in the Cherry Valley limestone in the basal Hamilton and its reappearance in the Tully limestone at the top of the Hamilton suggest that it is a form which favors a limestone facies. Spyroceras, characterized by annulations and longitudinal ornament, is prolific in the Hamilton, is well developed in the Tully and the latest known species are found in the Ithaca shales of the Upper Devonian in association with a fauna the other members of which are also presumably

of Hamiltonian affinities and origin. Ulsterian species which agree in form and ornament are probably congeneric, though their internal structure is not known. Whether the one Helderbergian annulated orthocerasone, "Orthoceras" tenuiannulatum Hall,¹²⁹ which was referred to Spyroceras

129. Hall, J., Paleontology of New York, vol. 3, p. 345, pl. 72, fig. 1. 1861.

by Foerste,¹³⁰ really is a representative of the genus is

130. Foerste, A. F., American orthoconic Silurian cephalopods, Denison Univ. Bull., Sci. Lab., Jour., vol.23, p. 285. 1928.

very doubtful though not impossible. If so, an even earlier origin than is here suggested must be accepted.

Geisonoceroides possesses siphuncular segments showing the epebic Dolorthoceras condition. The genus is characterized by low annuli and transverse striae, suggesting both Cycloceras and Geisonoceras. The genus is doubtfully present in the Onondaga, is typically developed in the Hamilton of western (but not eastern,) New York, and persists into the Ithaca.

Palmeroceras suggests by its siphuncle that it originated close to the point at which Adnatoceras developed from Dolorthoceras. Its trilobate aperture suggests Dolorthoceras rather than Adnatoceras. The ornament is

essentially that of the Silurian Protokionoceras, and strangely enough Palmeroceras is associated with the Devonian development out of that genus, namely Striacoceras Flower, in which the longitudinal ornament is lost in the ephebic stage.

Petryoceras is the last of the ornamented derivatives, and the most singular of them all, its surface being marked with transverse bands of zig-zag striae and lirae. Although known only from the Sheburne sandstones and shales of the Upper Devonian, the siphuncular outline shows that the genus is derived from Dolorthoceras.

Three Middle Devonian genera serve to show that form is not more constant than ornament. Sceptrites of the Onondaga differs from Dolorthoceras in being a compressed cyrtoceracone. The orientation is not definitely known, but the cameral deposits suggest endogastric curvature. Fusicoceras of the Hamilton is a derivative of Dolorthoceras by the form and deposits of the siphuncle. It is a brevicone and is strikingly similar to Brevicoceras Flower¹³¹ in

131. Flower, R. H., Devonian brevicones of New York and adjacent areas. *Paleontographica*, vol. 2, no. 9, p. 24, 1938.

form and sutures. The siphuncular segments of Brevicoceras are subspherical and contain actinosiphonate deposits.

Cryptorthoceras is the most singular of the form types

produced in the family and is without a duplicate elsewhere in the Nautiloidea. It is clearly derived from some such trilobate Dolorthoceras as D. tersum (Hall) by exaggeration of the mid-dorsal crest of the aperture, slight inflation of the living chamber, and a revolving of the aperture so that it opens on the ventral side.

The Middle Devonian development of the Pseudorthoceratidae is essentially one of the ornament and form. Most of the ornament patterns known for orthoceracones are developed. The ornament is no longer adequate for the reference of a species to a supposedly orthochoanitic genus. Further, one cyrtoceracone and one brevicone develop. None of these specialized types survived the last development of the Hamilton faunas, namely that of the Ithaca facies of the Upper Devonian. Dolorthoceras itself lived on into the Mississippian and Pennsylvanian apparently without change, but it never again attained the variety or abundance of species which is found in the Hamilton.

A continuation of the siphuncular expansion which has been already noted produces Adnatoceras from Dolorthoceras. The increase in the brim is slight, the increase in the area of adnation is great. The expansion of the siphuncular segment becomes concentrated at its end and the middle part loses the faintly convex outline found in Dolorthoceras and becomes essentially straight. Adnatoceras appears in the Hamilton, but does not become prolific until Upper

Devonian time. It is the most abundant genus of the Tully and the fragmental evidence suggests that it is also the dominant orthoceracone in the Ithaca fauna.. The genus is not met with in higher strata until the Pennsylvanian A. ciscoense Miller Dunbar and Condra is reached. Here the only new feature developed is the appearance of hyposeptal deposits. Euloxoceras carries the siphuncular expansion by marked increase at the ends of the segment to its final development. The genus agrees with A. ciscoense in having episeptal and hyposeptal deposits, but is unique in its compressed form and dorsal siphuncle. Further, fragments of the shell suggest a Kionoceroid ornament.

In the entire line which has been traced, which constitutes the Dolorthoceratinae, there is no essential change in the structure of the siphonal deposits. In the Upper Devonian two new stocks develop which are characterized by modifications of the pseudorthoceroid deposit.

The Pseudorthoceratinae are characterized by a dorso-ventral differentiation in the development of the siphonal deposits. In many orthoceracones with central siphuncles the annulosiphonate deposits are more strongly developed on the venter than on the sorsum; further in such forms the deposit in any given segment appears on the venter before it appears on the dorsum and an important feature of growth of the annulosiphonate ring is the addition of material to its lateral extremities until they meet and

fuse dorsally. The development of the extreme differentiation found in Pseudorthoceras would doubtless not have been possible in a series of forms with siphuncles close to the venter. The ventral concentration of deposits is well marked in some Hamilton Dolorthoceras but the condition in which the ventral lining is completed before any deposit appears on the mid-dorsal region is not attained until Upper Devonian time, where it is accompanied by an increase in the convexity of the connecting ring, thereby producing Pseudorthoceras. It is apparently true that wherever a subcentral siphuncle occurs there is some ventral concentration of the siphonal deposit, but the condition is rarely advanced, and the condition cannot be traced as a permanent character through any considerable series. The causes bringing it about are partly, at least, mechanical. But in the Pseudorthoceratinae the condition has become a genetic factor, for it is retained in Mooreoceras, a derivative of Pseudorthoceras in which the siphuncle is relatively close to the venter, and in which there is no mechanical reason for the retention of the unusual mode of growth. The peculiar modification of the ontogeny has all the earmarks of the genetic preservation of an acquired characteristic.

Before such a hypothesis can be accepted it is necessary to examine the evidence more closely. First of all it must be determined whether the dorso-ventral differentiation can be explained as a mechanical modification which is

the necessary accompaniment of the form of the conch and the subcentral position of the siphuncle. It is a fact that among orthoceracones wherever the siphuncle lies close to the venter little dorso-ventral differentiation is found, but where it becomes central a marked ventral concentration is to be expected. This is found in the Orthochoanites as well as in the Actinoceroidea. Probably more than a hydrostatic factor is involved here. In the Pseudorthoceratidae the cameral deposits are more affected by the position of the siphuncle than are the siphonal deposits, and while it is probable that the changes producing the Pseudorthoceras type of siphonal deposit could not have occurred in an orthoceracone with a ventral siphuncle is the essential factor. The other great difference between Dolorthoceras and Pseudorthoceras, namely the development of the pyriform siphuncular outline from the barrel shaped one, suggests no solution to the problem.

Possible the appearance and retention of the character are due to coinciding but independent elements. In a stock of forms with central siphuncles inherent variation might evolve a type in which dorso-ventral differentiation of the siphonal segments was marked. The development of coenogenetic character already noted in Pseudorthoceras, the failure of the deposit to complete the siphonal lining dorsally in neanic segments, might be a factor in the

retention of the mode of growth. From this it would appear that the explanation of the origin is not entirely satisfactory, as it invokes a generalization which is known not to hold in the later members of the Dolorthoceratinae to any great extent. However, if by chance this structure was developed, and we have evidence that it was, it is quite possible for another character, for the appearance of which we have no really convincing explanation, to form a pattern of which the first character is an essential part, resulting in its genetic preservation.

Pseudorthoceras appears in the Naples fauna of the Upper Devonian. In Chemung time it gives rise to Mooreoceras, which is now definitely known from the Wellsburg monothem of the upper Chemung, as not restricted. Both genera persist into the Pennsylvanian, with a thinning of the siphonal deposit the only apparent change.

Paraloxoceras, which appears in the Mississippian, represents a new specialization derived from Mooreoceras. It differs from that genus in the more expanded siphuncular segments, a thickening of the siphonal deposits, and the development of a radial canal system. Bergoceras is a cyrtconic derivative of Paraloxoceras, which shows no trace of the ventral concentration of the siphonal deposits in their growth stages.

The Cayutoceratinae are characterized by the differentiation of the siphonal deposits into a primary and

a secondary layer. This is again foreshadowed in Hamilton Dolorthoceras. Cayutoceras is known only from the Chemung. The siphuncle is essentially of the Dolorthoceras type, though slightly broader than usual. The inner layer of deposits is irregular and the camerae contain episeptal and hyposeptal deposits.

Bradfordoceras is definitely known only from the Conewango, though its presence in the Conneaut is suspected on the basis of the similarity of the suture patterns of crushed specimens in the Chadokoin shale to those of crushed specimens of Bradfordoceras transversum Flower and Caster. Bradfordoceras is more specialized than Cayutoceras in the depressed section, eccentric siphuncle, and the development of oblique and sinuous sutures. Mooreoceras is developed from Pseudorthoceras in the same way. Bradfordoceras is further specialized in the development of subspherisal siphuncular segments. It is generalized in that the deposits are mural, as in most Pseudorthoceratidae, and not episeptal and hyposeptal as in Cayutoceras. Doubtless forms combining the simpler features of the two genera await discovery.

It is significant that in this stock the dorso-ventral differentiation of siphonal deposits is essentially mechanical. It is to be found in Cayutoceras where the siphuncle is central, and is quite pronounced there. No dorso-ventral differentiation has been noted in Bradfordoceras

where the siphuncle lies close to the venter.

The accompanying diagram illustrates the phylogeny and known distribution of the genera of the Pseudorthoceratidae. The three groups typified by the three main types of siphonal deposits lend themselves well to subfamily groups. Known and assumed range are differentiated, and some attempt has been made to designate the relative abundance of the various groups in different times. Although our knowledge of the Pseudorthoceratidae is as yet very incomplete there is a remarkable correlation between the appearance of the genera in the stratigraphic column and the phylogeny as based on the structures. (Text figs. 14, 15.))

POSSIBLE DERIVATIVES OF THE PSEUDORTHOCERATIDAE

It is the purpose of this section to call attention to several groups which it has not been possible to investigate thoroughly, but which is suspected may be closely related to the Pseudorthoceratidae.

Among orthoceracones the genus Neocycloceras Flower and Caster¹³² of the Upper Devonian, a genus

132. Ibid., p. 210.

which is possibly also present in the Lower Mississippian, possesses annulations and transverse ornament. The siphuncle of the genotype is known only in the ephebic portion. The segments are subspherical. In the apical end

of N. harrisi the segments are tubular and apparently orthochoanitic. The poor preservation of all specimens in Upper Devonian sandstones has made it impossible to determine whether any organic deposits are present in the siphuncle. On the basis of stratigraphic occurrence it appears probable that the genus may belong to the Pseudorthoceratidae, for no other stenosiphonate cyrtoceraconic orthoceracones are known in the Upper Devonian, or in any strata after the Ordovician for that matter.

Originally the Pseudorthoceratidae were conceived as a family of orthoconic forms. However in the Devonian Sceptrites is a cyrtoceracone which by the form of the siphuncular segments can hardly be placed anywhere else. Fusicoceras is evidently a breviconic derivative of Dolorthoceras and the aberrant Cryptorthoceras, an orthoceracone with the aperture contracted and bent ventrad, is probably a derivative of the same genus.

Cyrtospyroceras Flower¹³³ may easily belong to the

133. Flower, R.H., Devonian brevicones of New York and adjacent areas, Paleontographica Americana, vol. 2, 1938 p. 212.

family as well, and may represent a specialization out of Spyroceras from which it differs mainly in curvature, depressed section, and the ventral position of the siphuncle.

The Mississippian of Ireland and Belgium contains a large number of cephalopods which are of uncertain affinities. Some of these possess slender cyrtochoanitic siphuncles and may belong to the Pseudorthoceratidae.

Dolorthoceras, Adnatoceras Pseudorthoceras and Mooreoceras are to be expected, as these genera extend in range from the Devonian into the Pennsylvanian. Our material has been meagre and the illustrations of internal structure are few in number and not always sufficiently detailed. Adnatoceras is represented by A. cf. neglectum (De Koninck), described and illustrated in the systematic portion of the present paper. Orthoceras sollasi Foord¹³⁴ may be an

134. Foord, A. H., Monograph of the Carboniferous Cephalopoda of Ireland, Part I, Family Orthoceratidae (in part), Paleontographical Society, vol. 51, 1897, pl. 8, fig. 1

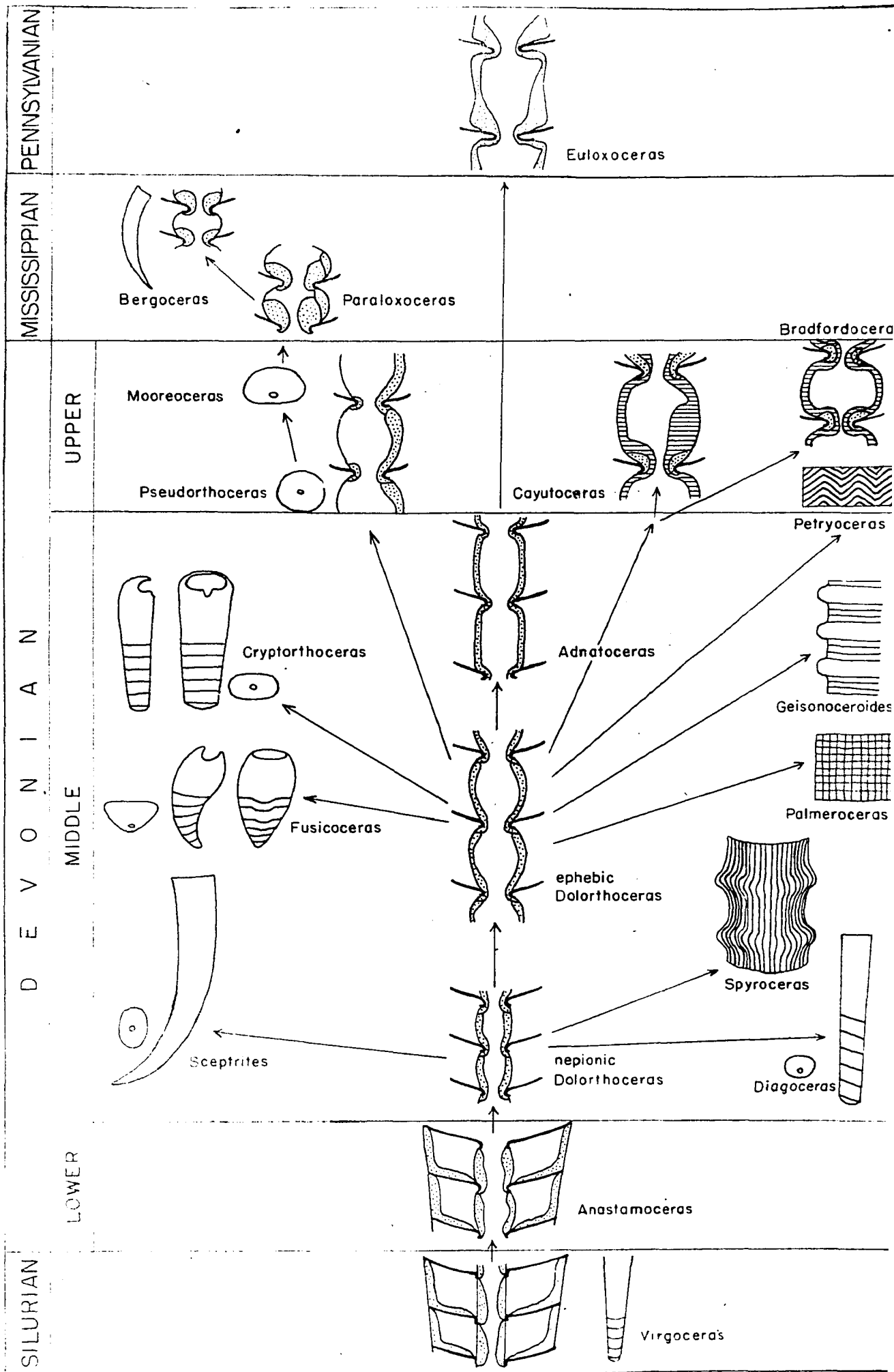
Adnatoceras or a Dolorthoceras, by the outline of the siphuncle.

Paraloxoceras Flower n. gen., and Bergoceras Flower n. gen., show that the Mississippian development of the Pseudorthoceratidae is characterized by new developments of both form and internal structure. There are numerous cyrtoconic species described the internal structure of which has not been sufficiently investigated. Foord¹³⁵

135. Ibid., pl. 15.

Fig. 15. Genetic relationship and geological range of the genera of the Pseudorthoceratidae. The known occurrence of the genera is indicated in black; the inferred range is indicated by oblique lines. Solid lines connect genera where the genetic relationship and the time of development are beyond reasonable doubt. Broken lines are used where the time element is uncertain.

1. Development of cyrtosiphuncular outline.
2. Early derivatives of Dolorthoceras, retaining the nepionic Dolorthoceras siphuncular outline.
3. Cayutoceratinae.
4. Pseudorthoceratinae.



has figured a section of Poterioceras fusiforme (Sowerby) which shows a continuous lining within the siphuncle and mural deposits within the camerae. Both features suggest the Pseudorthoceratidae, and indicate that Poterioceras may represent another deviation from the generalized orthoceraconic form.

At the present time it appears that the development of the Pseudorthoceratidae was centered in Europe in Mississippian time and that only occasional strays reached America. A restudy of the Nautiloidea of the Mississippian of Europe should yield rich morphological and taxonomic results, and may serve to disclose modifications of the Pseudorthoceratidae in form, structure and ornament of which the two genera Paraloxoceras and Bergoceras already show some indication.

CONCLUSIONS

I Morphological

1. The deposits of the camerae and siphuncle are laid down upon the surfaces of specialized secreting tissues, functional mantles, similar to the mantles which secrete the shell wall and the speta. On structural grounds the connecting ring appears to be mesodermal and to be laid down with the tissues.

2. The tissues of the camerae and siphuncle may be traced through similar cycles of (1) areal growth without differentiation of tissues, (2) development of secreting surfaces, (3) increase in surface and folding and invagination of the tissue, sometimes with resorbition, and regional differentiation of secretion of calcareous deposits terminating in a cessation of deposition.

3. Cessation of deposition of the cameral and siphonal deposits appears to be controlled by the axial gradient in generalized forms.

4. In the Pseudorthoceratidae the continuous lining within the siphuncle serves to sever the connection between the cameral mantle and the rest of the organism, thereby controlling the extent of development of the cameral deposits. This is advantageous, as is shown by

the development of such a lining in the Ordovician in the Westoniceratidae, Troedssonoceratidae, Discosouridae and Stereoplasmodoceratidae, and in the Devonian in the Pseudorthoceratidae.

5. Deposits may have had originally an excretory function, but have been modified to serve a hydrostatic function. The apical concentration permits the orthoceracone with air-filled camerae to occupy a horizontal position; further the weighted tip of the shell permits effective hyponomic swimming. The concentration of deposits on the venter serves to orient the conch with the venter beneath.

6. Orthoceracones without deposits may have occupied a vertical position, or may have lived horizontally with little or no gas in the camerae.

7. The relation of color bands to the dorsum or venter is at present not conclusive. In most instances the complemental filling of the internal mold by calcite dictates the region of the conch on which color bands are preserved, and for that reason they are commonly found only on one side of the shell.

8. In generalized orthochoanitic orthoceracones of the Silurian there is a continuous surface of secretion of deposits in the phragmocone, partly in the siphuncle and partly in the camerae. It is conceivable

that all other types may have been derived by the up-setting of this relation, permitting excessive development of cameral or siphunal deposits with numerous variations and specializations.

9. The relationships of tissues within the phragmocone and their deposits are of great systemic value, inasmuch as they reflect fundamental physiological and morphological conditions.

10. The cameral deposits are bilaterally symmetrical. Details of lobation are specific. They have not as yet been used in the definition of genera, which purpose is served by the siphonal deposits, but in many instances they appear to be constant in generic or higher groups.

11. On the basis of siphonal deposits, siphuncular outline, and gross features of the shell a total of eighteen genera of Pseudorthoceratidae are recognized.

12. Orientation even of fragmentary shells is possible on the basis of continuous conchial ventral furrow which corresponds to the ventral aponeurotic bands of Nautilus, or the dorsal discontinuous septal furrow.

II Systematic

1. In the ontogeny of the siphuncle and annulo-siphonate deposits the Pseudorthoceratidae show indications

of a derivation from the Orthoceratidae (in the old sense) in Silurian time.

2. The cyrtochoanitic cephalopods are polyphyletic isomorphs and the term cyrtochoanitic is useful for systemic purposes, but is without taxonomic value.

3. Even with the present incomplete data the genetic sequence of genera corresponds to a remarkable degree with the appearance of the genera in the stratigraphic column. The family can be traced from the Silurian ancestors through the development of most of the generic types in Devonian time, to the disappearance of the family in the early Permian.

4. The development of the family is orthogenetic in regard to (1) the development of a thin continuous siphuncular lining from a series of thick annulosiphonate deposits, and (2) the development of expanded cyrtochoanitic segments. The Middle Devonian types are remarkable for divergence in form or ornament; the Upper Devonian types for modifications of the siphonal deposits.

5. Siphonal deposits in the Pseudorthoceratidae are isomorphic with the Troedssonoceratidae and Stereoplasmoceratidae of the Ordovician, but differ in being of segmental origin. The deposits of the Cayutoceratinae are almost perfect isomorphs with the Westonoceratidae of the Ordovician.

EXPLANATIONS OF PLATES

Note.- Original plates are made $6\frac{1}{2} \times 10$. Slight reduction has been necessary for incorporation in the present form.

PLATE I

Figures

1-3. Pseudorthoceras senecum Flower, n. sp.....

Three views of the holotype: (1) dorso-ventral section of the specimen, with plane of section parallel to bedding, x 3; (2) fourth siphuncular segment from apical end, x 14; The siphonal deposit (white calcite) is thick against the ventral wall, on right. The two adjacent deposits shown on the opposite side of the siphuncle, have not completely joined on the dorsal wall. The deposit is developed more than usually apical of the septal neck. (3) Second segment from apical end of the same specimen, x 14. In this segment the siphonal deposit is only very meagerly developed on the dorsal wall. Pal. Res. Inst., no. 5758. Cashaqua shale, Senecan series, Upper Devonian, from Naples, New York.

4. Mooreoceras ruedemanni Flower, n. sp.....

Portion of the siphuncle of holotype, x 14. The venter is on the left. The light material in the siphuncle represents the organic deposit, which is present here only on the ventral side. See also plate 7, fig. 3, and plate 8, fig. 8. New York State Museum no. . Wellsburg monothem, Chemung stage, Chautauquan series, Upper Devonian, from Austinville, Bradford County, Pennsylvania.

5. Dolorthoceras aff. exile.....

Dorso-ventral section through siphuncle, with venter on the right, x 14. The siphonal deposits are unlike those of typical Dolorthoceras; in their extreme ventral concentration. They resemble the Pseudorthoceratinae, while the apparent differentiation into a calcareous (light) and a carbonaceous layer (dark) suggests the Cayutoceratinae. Pal. Res. Inst., no. 5835. Pompey member, Hamilton stage, Middle Devonian, Pratt's Falls, Onondaga County, New York.

6. Pseudorthoceras knoxense (McChesney).....

Cross section through a camera, about x 20. The siphuncle in the center shows mature siphonal deposits. Beneath the siphuncle the ventral sinus of the cameral

deposits is seen. The two processes of the ventro-lateral masses are assymetrical and partially embrace the siphuncle. The cameral deposits show traces of the original structure, although the specimen is a calcite pseudomorph. Pal. Res. Inst. no. 5853. Hazelton Bridge limestone, Pennsylvanian, West Indiana.

7. Dolorthoceras palmerae (Flower and Caster).....

Enlargement of siphuncle of holotype, x 14. Horizontal section. Antioch College, Yellow Springs, Ohio. Horizon doubtful, lowermost Conewango or upper Conneaut, Upper Devonian, Howard quarry, Erie County, Pennsylvania.

8. Adnatoceras spissum (Hall).....

Hypotype: siphuncular segments showing outline and the Michelinoceras stage of the siphonal deposits, x 14. Pal. Res. Inst., no 5840. Pompey member, Hamilton stage, Middle Devonian, from Pratt's Falls, Onondaga County, New York.

9. Dolorthoceras solitarium Flower, n. sp.....

Holotype: enlargement of siphuncle, x 14. See also plate 4, fig. 6. U.S. National Museum, no. 98778. West Brook member, Tully limestone, basal Upper Devonian, from the northeast corner of the Pitcher Quadrangle, New York.

10. Cayutoceras casteri Flower, n. sp.....

Holotype: enlargement of 5th and 6th siphuncular segments of the dorso-ventral section, venter on left, showing differentiation of siphonal deposit into two layers, one dark and rich in organic matter, the other light and calcareous, about x 9. Pal. Res. Inst., no. 5855. Cayuta shale, Chautauquan series, Upper Devonian, two miles south of Owego, New York.

11. Dolorthoceras tersum (Hall).....

Hypotype: portion of phragmocone showing siphuncular outline, x 3. See also pl. 8, fig. 6; pl. 9, fig. 8.

Pal. Res. Inst., no 5822. Pompey member, Hamilton stage, Middle Devonian, Pratt's Falls, Onondaga County, New York.

Note: In these and all succeeding longitudinal sections the conventional orientation is retained, with the adoral end at the top.



PLATE II

Figures

1-3. Euloxoceras milleri Flower, n. sp.....

(1) Dorso-ventral section of holotype showing siphuncular outline, siphonal and cameral deposits, x 9. Venter on right. Pal. Res. Inst., no 5851. (2) Dorso-ventral section of paratype at a slightly later stage Pal. Res. Inst., no 5852. (3) Enlargement showing detail of siphuncular outline of the preceding, x 15. See also fig. 12-14 below. Jackborough limestone, Caddo formation, Canyon group, Pennsylvanian, Jack County, Texas.

4-7. Mooreoceras sp.....

(4) Late siphuncular segments, 6th and 7th from adoral end of specimen, showing typical fusiform outline of Mooreoceras. No siphonal deposits, x 16. (5) 12th and 13th segments from adoral end. The siphuncular outline is of the Dolorthoceras type. Siphonal deposits present only on ventral side (right) x 16. (6) 20th and 21st segments from adoral end. The Adnastamoceras type of siphuncular outline, containing well defined deposits on the venter (right) x 16. (7) The complete specimen sectioned dorso-ventrally of which the above three figures are enlargements, x 1½. University of Cincinnati, no. 22251. Kansas City group, Pennsylvanian, Kansas City, Missouri. Note: The white lining of camerae and siphuncle is of morganix nature. The siphonal deposits shows in black in the adapical end; the well developed cameral deposits do not show in this figure.

8-9. Dolorthoceras sp.....

Early stages of unidentifiable fragmentary specimens, showing early siphuncular stages x 14. (8) Siphuncular outline intermediate between the Anastamoceras and the Michelinoceras types. Siphonal deposits of Michelinoceras type. (9) Siphuncular outline of the nepionic Dolorthoceras type; siphonal deposits of Michelinoceras type. Pal. Res. Inst., no. 5836, 5837. Delphi member, Hamilton stage, Middle Devonian, Delphi Falls, Onondaga County, New York.

10. Dolorthoceras telamon (Hall).....

Enlargement to show form of ephebic siphuncular segments, x 10. No siphonal deposits are developed. Same specimen as pl. 4 fig. 10. Pal. Res. Inst., no. 5831. Pompey member, Hamilton stage, Middle Devonian, Pratt's Falls, Onondaga County, New York.

11. Pseudorthoceras knoxense (McChesney).....

Dorso-ventral section with venter on right, showing outline of ephebic siphuncular segments and the concentration of deposits first on the venter, x 10. Pal. Res. Inst., no 5859. Hazelton Bridge limestone, Pennsylvanian, southwestern Indiana.

12-

15. Euloxoceras milleri Flower, n. sp.....

(12) Holotype, lateral aspect. (13) Holotype, dorsal aspect. (14) Paratype, lateral aspect. Pal. Res. Inst., no. 5851, 5852. Jackborough limestone, Pennsylvanian, Jack County, Texas.

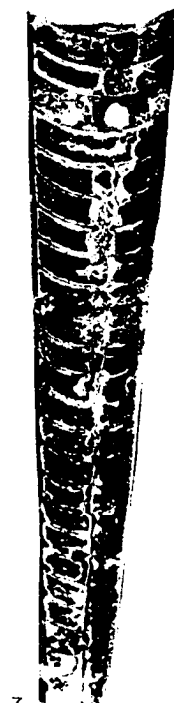
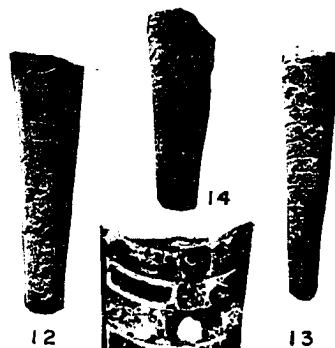


PLATE III

Figures

1. Cayuoceras casteri, Flower, n. sp.....

Holotype: vertical section with venter on right x $2\frac{1}{2}$
Septa are destroyed on right, but the margins of epi-
septal and hyposalal deposits can be traced. See
also pl. 1, fig. 10. Pal. Res. Inst., no 5855.
Cayuta shale, Chautauquan series, Upper Devonian,
two miles south of Owego, New York.

2. Adnatoceras napalense Flower, n. sp.....

Holotype: Note the phenomenon of the incomplete in-
ternal mold shown in the siphuncle indicating in-
vasion of mud (black) from adoral end, x $2\frac{2}{3}$. New
York State Museum no. Cashaqua shale, Nunda
stage, Senecan series, Upper Devonian, Naples,
New York.

3. Virgoceras palemon (Barrande).....

Reproduction of Barrande's original illustration of
a dorso-ventral section through the phragmocone
showing pseudorthoceroid siphonal deposits, x 1.
Venter on left Etage E, Middle Silurian, from Lock-
now, Bohemia.

4. Geisonoceroides woodae Flower, n. sp.....

Natural section through phragmocone of holotype, x $1\frac{1}{2}$
See also pl. 7, fig. 10 pl. 9, fig. Buffalo
Museum of Science, no E9013. Strophalosia bed,
Wanakah member, Ludlowville shale, Hamilton stage,
Middle Devonian, shore of Lake Erie, Wanakah, Erie
County, New York.

5. Geisonoceroides cylindricum Flower, n. sp.....

Holotype, x 1 Buffalo Museum of Science, no.
See pl. 6, fig. 7. Tichenor Limestone, Hamilton
stage, Middle Devonian. Smoky Creek, Windom, New York.

6. Geisonoceroides cf. cylindricum Flower, n. sp.....

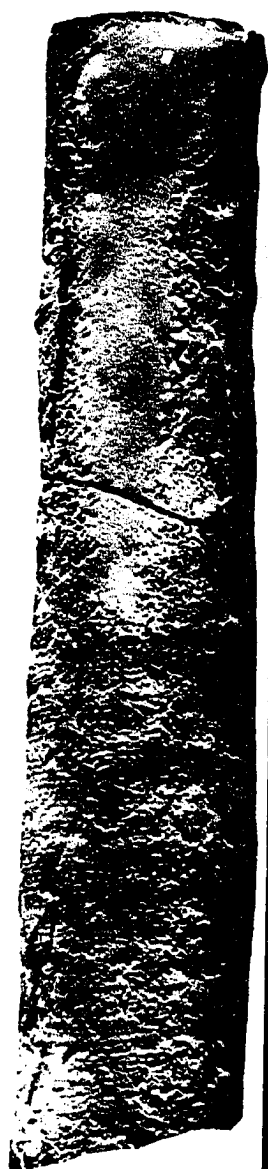
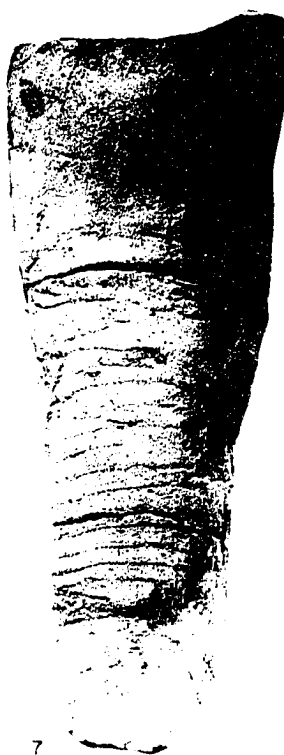
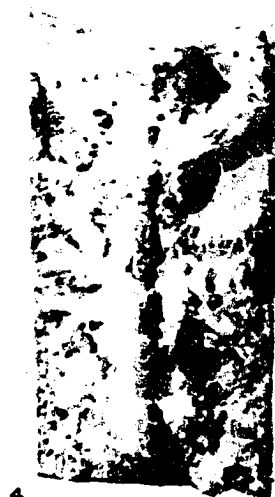
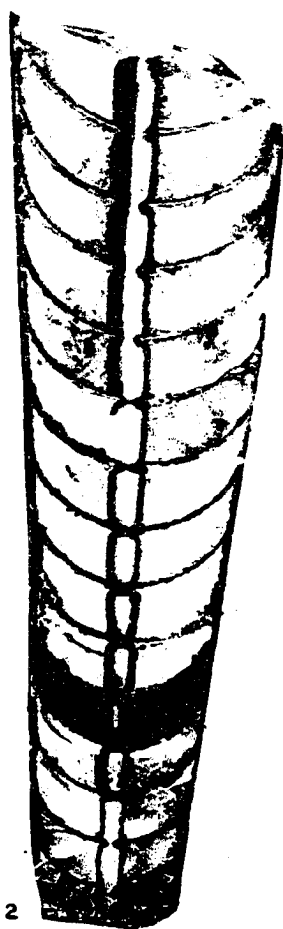
Margin of aperture of living chamber apparently complete. Referred with doubt to the preceding species, x 1. Buffalo Museum of Science, no. Tichenor limestone, Hamilton stage, Middle Devonian, South Shore cliffs, on Lake Erie, Erie County, New York.

7. Bradfordoceras giganteum Flower, n. sp.....

Holotype, x $\frac{1}{2}$. Ventral aspect. Buffalo Museum of Science, no. . A sandstone of the Conewango series, Upper Devonian, Allegheny State Park, New York.

8. Bradfordoceras moderatum Flower, n. sp.....

Holotype, xl, Ventral aspect. Buffalo Museum of Science, no. Lewis Run sandstone, Conewango series, Upper Devonian, Lewis Run, Bradford County, Pennsylvania.



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PLATE IV

Figures

1-4. Adnatoceras wellse Flower, n. sp.....

Holotype: (1) ventral aspect, x 1; (2) left lateral aspect x 1; (3) adoral aspect, xl; (4) vertical section through siphuncle, x $2\frac{1}{2}$. Pal Res. Inst., no. 5849. West Brook member, Tully limestone, basal Upper Devonian, Bordino, New York.

5. Mooreoceras sp.....

Section of phragmocone showing siphuncular outline, x $2\frac{1}{2}$. Section horizontal. Pal. Res. Inst., no. 5865. Salem limestone, Middle Mississippian, University of Indiana campus, Bloomington, Indiana.

6. Dolorthoceras solitarium Flower, n. sp.....

Holotype: horizontal section, x $1\frac{1}{2}$. See also pl. 1, fig. 9. U.S. National Museum, no 96778. West Brook member, Tully limestone, basal Upper Devonian, north east corner of the Pitcher quadrangle, New York.

7. Diagoceras tullium Flower, n. sp.....

Holotype: ventro-lateral aspect, xl. Pal. Res. Inst. no 5821. Loose block of Tully limestone basal Upper Devonian, east shore of Cayuga Lake near Portland Point, New York.

8. Adnatoceras spissum (Hall).....

Hypotype: adapical portion, vertical section with venter on left, about x $2\frac{1}{2}$. Pal Res. Inst., no. 5840. See pl. 7, fig. 10. Pompey member, Hamilton stage, Middle Devonian, Pratt's Falls, Onondaga County, New York.

9. Pseudorthoceras anomalum Flower, n. sp.....

Holotype; vertical or nearly vertical section, venter on left. Slightly more than x 2. The sides

of the specimen are weathered below the plane of the section, obscuring the form of the cameral deposits. New York State Museum, no. . Parrish limestone Nunda stage, Upper Devonian, Naples, New Yor.

10-

11. Dolorthoceras telamon (Hall).....

Hypotypes: (10) dorso-ventral section, venter on right x 2; Pal. Res. Inst. no 5831. (11) exterior of phragmocone of another specimen, x 1. Pal. Res. Inst. no 5830. See pl2, fig. 10; pl. 8, fig. 9-10. Both specimens are from the Pompey member, Skaneateles shale Hamilton stage, Pratt's Falls, Onondaga County, New York.

12-

15. Cryptorthoceras productum Flower, n.sp.....

Holotype: (12) adoral aspect, x $\frac{1}{2}$; (13) ventral aspect, showing hyponomic sinus x $\frac{1}{2}$; (14) adoral portion right lateral aspect, x 1; (15) left lateral aspect, x $\frac{1}{2}$. Buffalo Museum of Science, no. E9013. Wanakah member, Ludlowville shale, Hamilton stage, Bay View Creek, Erie County, New York.



PLATE V

Figures

1. Anastamoceras mirabile Flower, n. sp.....

Holotype: internal mold, x 1. See also figs. 4-7, below. Pal. Res. Inst., no. 5817. Helderbergian, New Scotland or Kalkberg(?) series. Lower Devonian, Albany County, New York.

2-3. Anastomoceras rudis (Hall).....

Hypotype: (2) weathered surface x 1; (3) enlargement of anterior end after grinding, showing traces of siphuncular outline and cameral and siphonal deposits, x $1\frac{1}{2}$. Pal. Res. Inst., no 5818, New Scotland Helderbergian series limestone, Lower Devonian, Schohaire, New York.

4-7. Anastomoceras mirabile Flower, n. sp.....

Holotype: (4) anterior two siphuncular segments, showing Dolorthoceras type of siphonal deposits, x 2; (5) enlargement of apical five siphuncular segments after grinding, x 2; (6) Enlargement of septal foramen of fig. 4, showing septal necks and the point of fusion of adjacent deposits, x 14; (7) second segment from apex showing the wall of the central canal and the radial pillars, x 14. See figure 1, above.

8-9. Paraloxoceras knnicki Flower, n. sp.....

Holotype: dorso-ventral section showing siphuncle and siphonal deposits, x $2\frac{1}{2}$; (9) enlargement of a segment of the same specimen, showing the septal necks, the broad area of adnation and the radial canal penetrating the siphonal deposit, x 14. Univ. of Cincinnati, no. 22253. Visé limestone? Mississippian Visé, Belgium.

10-

11. Bradfordoceras transversum Flower and Caster.....

Holotype: (10) section of siphuncle, showing character of siphonal deposits, x 5; (11) enlargement, showing spetal neck, area of adnation and connecting ring, x 20. Pal. Res. Inst., no. 5014. Lewis Run sandstone, Venango stage, Conewango series, Upper Devonian, Lewis Run, Bradford County, Pennsylvania.

12. Mooreoceras sp.....

Dorso-ventral section through siphuncle showing siphonal deposits on the ventral side (left) only. Note absence of connecting ring on dorsum. Ventral wall of conch lost. About x 6. Collection of Mr. Richard Schweers, Univ. of Indiana. From the Winterset limestone, Kansas City group, Pennsylvanian, Kansas City, Missouri.



PLATE VI

Figures

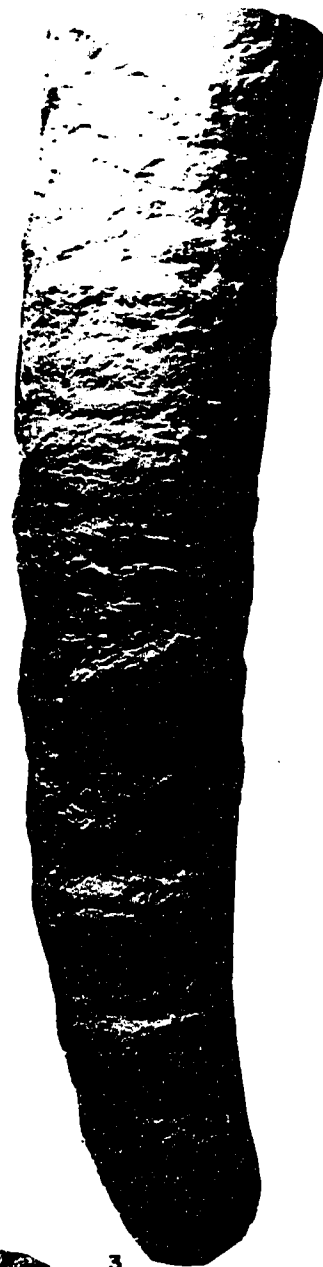
1. Sceptrites obliquus Flower, n. sp.....
 Holotype: lateral aspect, x $\frac{3}{5}$. U.S. National Museum, no 37228. Columbus limestone, Middle Devonian, Columbus, Ohio.
2. Sceptrites claviformis Flower, n. sp.....
 Holotype: lateral aspect x $\frac{3}{5}$. U.S. National Museum unnumbered. Columbus limestone, Middle Devonian, Columbus, Ohio
3. Sceptrites sceptrum (Hall).....
 Holotype: lateral aspect, x $\frac{1}{2}$. Buffalo Museum of Science. Onondaga limestone, Middle Devonian, Federal stone quarry, Lancaster, Erie County, New York.
4. Sceptrites carteri Flower, n. sp.....
 Holotype: lateral aspect, x $\frac{3}{5}$. Collection of Mr. Alec Carter, to be deposited in the Buffalo Museum of Science. Onondaga limestone, Middle Devonian, Federal stone quarry, Erie, County, New York.
- 5-6. Fusicoceras eriense Flower, n. sp.....
 Holotype: (5) right lateral aspect, (6) ventral aspect, Siphuncle retouched, xl. Buffalo Museum of Science, no. .Wanakah member, Ludlowville shale Hamilton stage, Idlewood cliff, shore of Lake Erie, near eighteen mile Creek, New York.
7. Geisonoceroides cylindricum Flower, n. sp/.....
 Holotype: lateral aspect, x 1. Buffalo Museum of Science. Wanakah member, Ludlowville shale, Hamilton stage, Middle Devonian, Wanakah, New York.



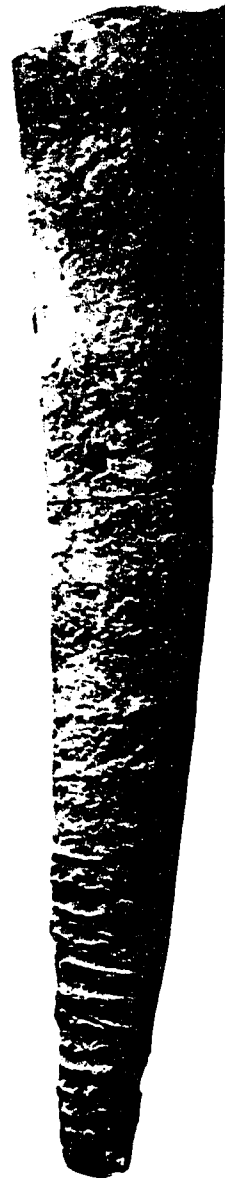
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PLATE VII

Figures

1. Fusicoceras erienne Flower, n. sp.....

Holotype; enlargement of horizontal section through siphuncle x 2. See also plate 6, fig. 5-6. Buffalo Museum of Science, no. . Wanakah member, Hamilton stage, Middle Devonian, Wanakah, New York.

2. Adnatoceras clarkei Flower, n. sp.....

Holotype: Section, slightly oblique from horizontal, x $1\frac{1}{2}$. New York State Museum. Parrish limestone, Nunda stage, Senecan series, Upper Devonina, Naples, New York.

3. Mooreoceras ruedemanni Flower, n. sp.....

Holotype: vertical section, venter on left, x $2\frac{1}{2}$. The ventral wall is missing owing to solution of both the shell wall and the cameral deposits. See pl. 1, fig. 4; pl8, fig. 8. New York State Museum, no. . Same horizon and locality as the preceding.

4. Dolorthoceras exile (Hall).....

Phragmocone and base of living chamber of a mature individual, x 1. Pal. Res. Inst., no 5826. Pompey member, Skaneateles shale, Hamilton stage, Middle Devonian, Pratt's Falls, Onondaga County, New York.

- 5-6. Adnatoceras cooperi Flower, n. sp.....

Holotype: (5) showing proportions, x $\frac{1}{2}$; (6) vertical section showing position and outline of siphuncle, x $1\frac{1}{2}$. U.S. National Museum, no. 90758. West Brook member, Tully limestone, Upper Devonian, Tully, New York.

7. Mooreoceras bradfordoides Flower, n. sp.....

Holotype: sectioned surface, slightly inclined from the vertical. Venter on right, x $2\frac{1}{2}$. Cameral deposits

are clearly shown, as are the outline and deposits of the siphuncle. New York State Museum, no. . Wellsburg monothem, Chemung stage, Chautauquan series, Upper Devonian, Austinville, Bradford County, Penna.

8. Geisonoceras teichertii Flower, n. sp.....

Holotype: phragmocone sectioned showing organization of cameral and siphonal deposits, x 2/3. See pl. 9, fig. 19. New York State Museum, no. . Onondaga limestone, Middle Devonian, western New York.

9. Bradfordoceras fusiforme Flower, n. sp.....

Holotype: dorsal aspect, x 1; Buffalo Museum of Science, no. . Lewis Run sandstone, Venango stage, Conewango series, Upper Devonian, Lewis Run, Bradford County, Pennsylvania.

10. Adnatoceras spissum (Hall).....

Hypotype: a nearly complete unflattened individual, x 1. The basal portion of the living chamber has been partially restored. Ventral aspect. Pal. Res. Inst., no 5840. Pompey member, Skaneateles shale, Hamilton stage, Middle Devonian, Pratt's Falls, Onondaga County, New York.

11. Geisonoceroidees woodae Flower, n. sp.....

Holotype: living chamber, dorso-lateral c 1. Buffalo Mus. of Sci., no E9013. Strophalosia bed, Wanakah member, Ludlowville shale, Hamilton stage, Middle Devonian, shore of Lake Erie, Wanakah, Erie County, New York.

12. Anastomoceras rudis (Hall).....

Hypotype: Largest and most complete specimen observed, x 1. The living chamber extends for an additional 40 mm. in a flattened condition. Pal. Res. Inst., no 5819. New Scotland limestone, Helderbergian Series, Lower Devonian, Catskill, New York.



PLATE VIII

Figures

1. Adnatoceras cf. neglectum (de Koninck).....

Vertical section, venter on left, x $2\frac{1}{2}$. Univ. of Cincinnati, no 2252. Tournai limestone, Lower Mississippian, Tournai, Belgium.

2. Dolorthoceras revertum Flower, n. sp.....
3

Holotype: adoral portion x 1; (2) right lateral aspect, x 1; (3) dorsal aspect, x 1. Buffalo Museum of Science no. . Pleurodictyum bed, Wanakah member, Ludlowville shale, Hamilton stage, Middle Devonian, Wahakah, New York.

4. Adnatoceras cryptum Flower, n. sp.....

Holotype: right lateral aspect, x 1. Pal. Res. Inst., no 5850. West Brook member, Tully limestone, Upper Devonian, Borodina, New York.

5. Pseudorthoceras knoxense (McChesney).....

Vertical section through phragmocone, showing the relatively thin cameral deposits (light) on the dorsum (left), x 10. The deposits on the venter are massive and extend almost to the siphuncle but are poorly defined owing to crystalization (they are largely dark). Siphonal deposits are mature. Pal. Res. Inst., no. ,5860. Hazelton Bridge limestone, Pennsylvanian, southwestern Indiana.

6. Dolorthoceras tersum (Hall).....

Internal mold of living chamber, showing position and character of internal constriction, x 1. Pal. Res. Inst., no. 5823. Delphi member, Skaneateles shale, Hamilton stage, Middle Devonian, Delphi Falls, Onondaga County, New York.

7. Mooreoceras ruedemanni Flower, n. sp.....

Holotype: lateral aspects, xl. Same specimens as pl. 1, fig. 4; pl. 7, fig. 3. New York State Museum no. . Welsburg monothem, Chemung stage, Upper Devonian, Austinville, Bradford County, Pa.

8. Dolorthoceras exile (Hall).....

Hypotype: living chamber preserving the aperture, x 1. Pal. Res. Inst., no 5827. Pompey member, Skaneateles shale, Hamilton stage, Pratt's Falls, Onondaga County, New York.

9-
10. Dolorthoceras telamon (Hall).....

Hypotype: living chambers, x 1; (9) a partially crushed specimen showing the surface of the shell; (10) an internal mold of a mature living chamber showing the gerontic constriction. Pal. Res. Inst., nos. 5831, 5832. Delphi member, Skaneateles shale, Hamilton stage, Middle Devonian, Delphi Falls, Onondaga County, New York.

11. Pseudorthoceras knoxense (McChesney).....

Hypotype: dorso-ventral section not attaining the siphuncle, showing the extent of the ventro-lateral masses (on left side) beyond the middle of the camerae, x $1\frac{1}{2}$. Pal. Res. Inst., no 5864. Jackborough limestone, Pennsylvanian, Jack County, Texas.

12. Cf. Pseudorthoceras knoxense (McChesney).....

A pyritized specimen showing the septal furrow, x $1\frac{1}{2}$ Pal. Res. Inst., no 5863. Pennsylvanian, southern Indiana. Exact locality and horizon unknown.

13. Striacoceras typus (Saemann).....

Ventral aspect showing the three conchial furrows unusually well developed, xl. New York State Museum no. 12381/2. Cherry Valley limesonte , Hamilton stage, Middle Devonian, Manlius, New York.

14. Virgoceras cancellatum Flower, n. sp.....

Longitudinal section of adoral end of specimen, showing the pseudorthoceroid deposits in the orthochoanitic siphuncle, x $2\frac{1}{2}$. Laurel limestone, Middle Silurian, Westport, Indiana.

15. Petryoceras thyestes (Hall).....

Hypotype: flattened individuals showing characteristic appearance and proportions, x $\frac{1}{2}$. Pal. Res. Inst., no. 5845. See also pl. 9, fig. 13. Sherburne sandstone, Nunda stage, Upper Devonian, Taughannock Falls, New York.



PLATE IX

Figures

1. Sceptrites sceptrus (Hall).....

Hypotype: dorso-ventral section through siphuncle, x $1\frac{1}{2}$, same specimen as pl. 6, fig. 3. Onondaga limestone, Middle Devonian, Federal Stone quarry, Erie County, New York.

2-3. Nautilus pompilius Linnaeus.....

(2) enlargement of a portion of the base of the ventral side of the living chamber showing the aponeurotic bands(below), which disappear beneath the mural part of the septum (central zone of figure) above which the concave part of the septum is seen.

(3) enlargement of dorsal wall of phragmocone, with septa removed, showing the septal furrows, x 2. Univ. of Cincinnati, no B4390.

4. Geisonoceroides woodae Flower, n. sp.....

Holotype: lateral aspect, natural color, showing traces of the original color pattern, slightly less than x 1. Note abrupt but irregular transition from dark on the left to light on the right of the specimen at the center. Buffalo Museum of Science, no. E9013. Same specimen as pl. 7, fig. 10 and pl. 3, fig. 4. Strophalosia bed, Wanakah member, Ludlowville shale Hamilton stage, Middle Devonian, from the shore of Lake Erie, Wanakah, New York.

5-7. Bergoceras antilope (De Koninck).....

Reproduction of De Koninck's original figures. (5) exterior, x $\frac{1}{2}$; (6) section, x 1; enlargement of two camerae, x 2. Visé limestone, Mississippian, from Visé, Belgium.

8. Dolorthoceras tersum (Hall).....

Ventral aspect of a living chamber preserving the hyponomic sinus, x 1. Pal. Res. Inst., no 5825.

Pompey member, Hamilton stage, Middle Devonian,
Pratt's Falls, Onondaga County, New York.

9-

10. Spyroceras oppletum Flower, n. sp.....

Holotype: (9) exterior, showing ornament, x $2\frac{1}{2}$.
(10) section through siphuncle, showing neanic
Dolorthoceras siphuncular outline and siphonal de-
posits of the Dolorthoceras type, x 14. Pal. Res.
Inst., no 5867. West Brook member, Tully limestone,
Upper Devonian, from Borodina, New York.

11-

12. Spyroceras crotalum (Hall).....

Hypotype: (11) phragmocone directly orad of the
portion sectioned, x 1; (12) enlargement of early
siphuncular segments showing nepionic Dolorthoceras
type of outline. Pal. Res. Inst., no 5866. Pom-
pey member, Skaneateles shale, Hamilton stage,
Middle Devonian, Pratt's Falls, Onondaga County,
New York.

13. Petryoceras thyestes (Hall).....

Hopotype: a flattened specimen showing the ornament
characteristic of the genus, x 2, Pal. Res., Inst.,
no 5847. See also pl. 8, fig. 15. Sherburne sand-
stone, Nunda stage, Upper Devonian, Taughannock
Falls, New York.

14. Cayutoceras casteri Flower, n. sp.....

Paratype: Weathered section, showing siphuncular
outline, x 1. Pal. Res. Inst., no. 5857. From a
coquinte in the Cayuta shale, Chemung stage,
Chautauquan series, Upper Devonian, Bainbridge, New
York.

15-

16. Dolorthoceras elegans Flower, n. sp.....

Holotype: (15) adoral portion of phragmocone, x 1;
(16) vertical section through siphuncle, with venter
on left, showing outline and the greater development

of siphonal deposits on the venter, x 14. New York State Museum. Parrish limestone, Nunda Stage, Senecan series, Upper Devonian, from Naples, New York.

17. Dolorthoceras tersum (Hall).....

Hypotype: a nearly complete internal mold of a living chamber showing the internal constriction. Pal. Res. Inst., no.5824. Delphi member, Hamilton stage, Middle Devonian, Delphi Falls, Onondaga County, New York.

18. Dolorthoceras revertum Flower, n. sp.....

Holotype: section (see also fig. 8 above) through siphuncle showing early (Michelinoceras) stage of the siphonal deposits, x 14. Buffalo Museum of Science, unnumbered. See also pl. 8, fig. 2-3. Pleurodictyum beds, Wanakah member, Hamilton stage, Middle Devonian, from Wanakah, New York.

19. Geisonoceras teichertii Flower, n. sp.....

Holotype: enlargement of apical end of the specimen shown on pl. 7, fig. 8, showing the continuity of the surface of the cameral and siphonal deposits, and the carbonaceous band representing the original position of the cameral mantle, in part. New York State Museum. Onondaga limestone, Middle Devonian, "western New York".

