

MEMOIR 13

Nautiloid Shell Morphology

By ROUSSEAU H. FLOWER

STATE BUREAU OF MINES AND MINERAL RESOURCES
NEW MEXICO INSTITUTE OF MINING AND TECHNOLOGY
CAMPUS STATION SOCORRO, NEW MEXICO

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DEDICATION

To the memory of those students of the fossil Cephalopoda who approached them as organisms rather than as medals of creation, and whose efforts have contributed so materially to the understanding of the shell morphology, evolution, and classification of the Nautiloidea:

Joachim Barrande, whose numerous sections brought to light internal structures, largely previously unknown, who recognized the organic nature of cameral deposits and contributed generally to knowledge of internal structures

Alphaeus Hyatt, who brought us from a classification of form genera to a more natural one, employing the evidence of ontogeny and internal structures

Gerard Holm, whose studies particularly of the Endoceratida and *Bathmoceras* contributed materially to our knowledge of morphology

Rudolf Ruedemann, whose studies form the basis of the modern understanding of the complex endoceroid siphuncle, as well as of the Actinoceratida

August F. Foerste, whose labors reduced the mountain of undescribed American species and brought to light a number of then novel and now very significant structures in the older Nautiloidea

They have refused to look upon these fossils as, to paraphrase Huxley, a savage looks at a ship, as something strange beyond his comprehension, and have thereby laid a significant groundwork for our still imperfect modern investigations. Often one finds that their work was ahead of their time and indicated avenues of investigation which were not pursued further for thirty to fifty years. Though in some instances future work has modified some of their suggestions, it has found others remarkably sound. I am particularly indebted to Dr. Ruedemann, whom, had he lived, I would have asked to serve as joint author in this work which certainly profited from his discussions and notes.

Abstract

The fundamental parts of the nautiloid shell are (1) conch, (2) septa, (3) connecting ring, (4) siphonal deposits, and (5) cameral deposits. It is important to recognize that the septal neck and connecting ring, ordinarily considered the two hard parts of the siphuncle universally developed, are discrete structures. Classification of siphonal deposits by shape separates homologous structures and unites unrelated ones. A better approach in terms of composition, textures, and mode of secretion is not yet possible, but it is evident that some "de-

posits" are true parts of the rings; others are derived from the ring, but now distinct from it; still others are distinct from the ring, cenogenetic in the various orders, and secreted within the siphonal strand; and some are possibly secreted as mantle deposits on its surface. Evidence being ambiguous in some instances, the siphonal deposits are treated in terms of their evolution, in terms of the orders or parts of orders in which they develop. New observations on a number of structures are included.

Introduction

GENERAL PURPOSE

The present work is a restatement and, to a considerable extent, a revision of the shell morphology of the Nautiloidea. It embodies some new observations and others currently described in several works, now in such an advanced stage that it is difficult to say whether they will precede or follow the present work in publication. The particular need for restatement, however, involves a necessary emphasis of matters of structure rather than of form. The last fifteen years of investigation have brought to light new facts indicating increasingly the need of an approach to nautiloid shell morphology in terms of composition, and textures of parts, and, particularly, their mode of secretion. Already, investigation of such matters has contributed to an understanding of relationships where the evidence supplied from form rather than structure seemed ambiguous and open to more than one interpretation, and present findings indicate that further inquiry into such matters will yield even greater rewards.

In a group such as the Nautiloidea, represented by one living genus, and with some highly significant structures known only in long-extinct lineages of the Paleozoic, it may be argued that fossilization forbids our ever being absolutely sure of original composition, that textures may be lost or altered in replacement, and that any possible conclusions as to mode of origin of the various shell parts are necessarily inferential. However, even from the present imperfect observations, it is possible to approach conclusions on these matters as a sort of geometric limit, even though they may never be attained perfectly, and the results have so far been most rewarding. Indeed, one hope leading to publication at the present time is that others may be influenced to conduct similar investigations, perhaps those having access to material not known or not available to the writer, and fuller understanding of these matters will thus be achieved more quickly.

Certainly it is time that it is realized that the nautiloid shell is an aggregate of various discrete parts. They were not all secreted in the same way and are not all the product of secretion on the surface of a tissue by specialized groups of epithelial cells—regions to which the term *mantles* has been given (Flower, 1939), though some are parts of the mantle proper and others are distinct from the original mantle.* Fur-

ther, each of these parts not only shows characteristics of texture and composition, but variations in both can be found as the shell parts are traced in their evolution within the Nautiloidea. For example, it was found (Flower and Teichert, 1957) that in the Discosorida the connecting ring had various specialized regions differentiated by texture and composition, and the recognition of such rings supplied a criterion of discosorid affinities. Without such evidence, it is possible that the distinctness of the order from the Oncoceratida could not have been demonstrated beyond question, and this evidence permitted the certain assignment of some genera to the Discosordia, the oncoceroid affinities of which could not have been completely disproved otherwise. Certainly it is time that it should be realized that these matters of texture and composition are original, and real and valid criteria in taxonomy; that they may be subject to alteration and even destruction where replacement or recrystallization in fossil material may be advanced is quite aside from the point.

The structures here treated as fundamental shell parts will seem novel.

They consist of (1) the conch, (2) the septa, (3) the ring, (4) siphonal deposits, and (5) cameral deposits. The siphuncle is omitted from this list for a very definite reason. The siphuncle is real enough as a structure, but it must be realized that the two hard parts preserved throughout the Nautiloidea, the septal neck and the connecting ring, have nothing to do with each other. The necks are mere topological modifications of the septa around the siphonal strand, the siphuncle proper. The rings, however, are secreted on or within the surface of the siphonal strand; rings are repeated segmentally, and, primitively at least, they join, forming a continuous tube to which the septal necks are merely external supporting structures. It has been found that the consideration of the septal neck and the ring as two parts of the "siphuncle" has led to some confusion. Though the matter has largely escaped publication,

*Perhaps not. In a sense the siphonal strands and cameral tissues were developed from the posterior part of the true mantle.

many paleontologists have accepted the implication that the neck and the ring are differentiated from a single primitive structure. It is now evident that the ring and neck are widely distinct from the earliest cephalopods. The idea was suggested that the long septal necks were primitive and that as the necks shortened, the rings were added to the general pattern. Ruedemann (1905) suggested that the rings might have developed from the endosiphoning. Indeed, Hyatt (1900) by placing his order Holochoanites, characterized by long necks, at the beginning of his classification implied some such possible relationship, and Foerste, in numerous works, expressed the opinion—which he later abandoned—that the holochoanitic neck was general in the older cephalopods. It is evident today that the holochoanitic necks—those extending essentially for the length of one siphuncle segment—are specialized and derived but are not primitive. Further, the endosiphoning, usually believed to be a general structure in the endoceroid endosiphuncle, was recognized largely on the basis of a structure which is now considered as inorganic, and a replacement phenomenon: the general presence in cross sections of an outer band of bundles of calcite fibers. The true lining is rare, developed only in highly specialized Endoceratida, and is, indeed, certainly known at the present time only in two genera, *Allotriceras* and *Mirabiloceras* of the Allotrioceratidae (Flower, 1955).

In addition to the conch, septa, and rings, there are structures in the siphuncle and camerae, here termed siphonal and cameral deposits. Cameral deposits develop complex surfaces, difficult to ascertain except under exceptional conditions of preservation; elaborate patterns of lobes, bosses, striae, and lamellae may be involved, always showing a bilateral symmetry. Siphonal deposits are simpler as to form but complex and varied as to textures, and were developed independently at several different points in the phylogeny of the Nautiloidea. The reference to these structures, both siphonal and cameral, as "deposits" seems partly responsible for the unfortunate impression that these structures are erratic in form and distribution, and unreliable guides to taxonomy. Any such view has been amply disproved by investigations of the last thirty years. These "deposits" are subject to regular laws of growth and conform, though not all in the same way, to the general growth of the shell as a whole.

Previous terminology and classification of the siphonal deposits has been based only on their shape. It is now apparent that this is misleading, for one structure may show various patterns of growth, and forms similar in shape are nonhomologous; the present information available suggests that they were different in composition, texture, and even in mode of secretion. For example, the parietal annular deposits and the endocones developed in the higher Discosorida are two different patterns of growth exhibited by a single structure; if the "deposit" grows only forward from its point of inception, a lining of fused annular elements is evident, much like that developed in the Pseudorthoceratidae (see Flower, 1939). However, if it grows in both directions, orad and apicad, from the point of inception, one deposit grows over an earlier one, and thus a series of endocones is developed. The deposit shows growth laminae and fibers normal to the growing surface, and suggests secretion by a siphonal mantle, and an original condition which was quite possibly dominantly calcitic rather than aragonitic. On the other hand, the endocones of the Endoceratida are phylogenetically distinct from those of the

Discosorida, show features indicating an originally aragonitic condition, and details can be explained only in terms of a structure secreted within the tissues of the siphonal strand. Annular deposits in the siphuncle developed independently in (1) the bulletes of the Discosorida, (2) the parietal annular deposits of the same order, (3) the annuli in the Actinoceratida, (4) annuli of the Michelinoceratida, and (5) as incipient phases of actinosiphonate deposits in many of the Oncoceratida.

What is needed is a classification of siphonal deposits in particular, in terms of original composition, texture and textural differentiation of parts, and mode of secretion. It is evident that some "deposits" are integral parts of the connecting ring extended into the cavity of the siphuncle. There is reason to believe that the annuli of the Actinoceratida are derived from the rings, but differentiated from them in texture and composition, and also that they are delayed in development beyond the secretion of the main part of the ring. Other deposits may be secreted as new structures, coenogenetic in their appearance, and such structures are possibly laid down within the tissue of the siphonal strand or are mantle secretions, laid down on the surface of the strand. Such a classification cannot yet be attained with certainty. The structures of the endoceroid endosiphuncles can be explained only in terms of material secreted within the tissues of the siphonal strand. The annuli of the Discosorida seem explicable instead as mantle deposits, but this conclusion seems still debatable. For some other structures, as annuli of the Michelinoceratida, linings, rods, either type of secretion seems possible, but it is evident that such structures have no phyletic connection with those of similar form in other orders, and show indications of different and often distinctive composition and texture.

Inquiry into matters of composition, texture, and origin of various shell parts is relatively young, and quite possibly future work will show that our present state of knowledge is most incomplete. For these matters, thinsection investigation is commonly needed. The best results are obtained from material of better than average preservation. To be sure, selection of such material is difficult, and perhaps not free from subjective matters.* Where structures commonly fail to show anything that approaches the original condition closely, some information can be obtained from the study of habit, a term I have used here for uniformly varying conditions of preservation under specific conditions of replacement and alteration. Thus, general loss of texture in conch and septa is an indication of an originally aragonitic condition, loss of texture accompanying alteration to calcite. The habit of the endosiphuncles of the Endoceratida is, although no specimens probably represent the original condition, indicative of an original composition of mainly aragonite, and contributes to understanding the mode of secretion.

While such thinsection investigations as are required for understanding morphology are not needed for identification, they promise to solve problems of evolution and relationship. Unfortunately, material needed to answer some crucial ques-

*Oddly, while one might expect the best preservation where matrix did not penetrate, it is true, from experience, that calcite-filling of the siphuncle may involve gross recrystallization and alteration of original parts, while matrix-filled siphuncles in the same association may show much less alteration.

tions has not been available to the writer. Some cephalopod types are extremely rare, and there are species, genera, and possibly families in which the known collected material consists exclusively of type specimens. Obviously, such specimens cannot be sacrificed for thinsection investigations, particularly when the reward is uncertain until the section has been made. Material of many crucial types needs examination. Holm (1899) devoted several pages to detailing his several disappointments in his search for one specimen of *Bathmoceras* well enough preserved internally to serve as the primary basis of his study. Material of the Mandaloceratidae needs study to determine whether the "obstruction rings" are bullettes or accessory deposits. Study of the Diestoceratidae is needed to determine whether they should be considered Discosorida or Oncoceratida. Fuller observation of the rings in the older Nautiloidea is generally needed, as well as investigation of segmental and nonsegmental linings in the Michelinoceratida, and possible differentiation within rings of the older Actinoceratida. As yet, no thinsection examinations have been made in the remarkable siphuncles of the Ascoceratida; even poor specimens are generally rare.

HISTORY

One will find in Hyatt (1900) a general statement of morphology and classification of the Nautiloidea which was scarcely surpassed for thirty years. This work, however, was merely a summary designed to bring the classification of the Nautiloidea into line with that of other fossils, and matters not essential to this aim were bypassed. Hyatt recognized the essential shell parts as conch or shell wall, septa, siphuncle, composed of septal neck and connecting ring, and various deposits in the siphuncle. Those noted there consist of the diaphragms of the Diphragmida (our present Ellesmeroceratida) and the endocones of the Endoceratida, and in the Cyrtocoanites he recognized annulosiphonate and actinosiphonate deposits as perfected within the two divisions of that group, the Annulosiphonata and Actinosiphonata. Annular deposits in the Orthoceratida (our present Michelinoceratida) were not stressed, for, although they had been made known by Barrande (1885, 1865-1877), they then seemed to have no impingement upon the taxonomy. Neither was extensive attention given to the structures within the endoceroid endosiphuncle. The work of Holm (1899) on *Bathmoceras* certainly appeared too late to be incorporated. Only the barest mention was made of cameral deposits which seemed to have no impingement on the taxonomy. One must remember in approaching this work that it was a mere summary; Hyatt's notes show that he was fully aware of the need for further understanding of some structures, as well as of further taxonomic investigations, but his next years were devoted to the Ammonoidea, and his untimely death prevented his returning to nautiloid investigations.

For twenty years there was almost no advance, and the nautiloids were largely neglected, though the work of Ruedemann (1905, 1906) is a welcome gleam of light in these otherwise dark ages. In the 1920's the works of Foerste began to appear, but they were at first largely devoted to reducing the vast amount of undescribed material needing attention. One may note Grabau's (1922) study of the remarkable piloceroid *Chihlioceras*, and mention his proposal (1919) of the homology of the endoceroid endosiphuncle with the conch of other nautiloids, a view which it is now necessary to abandon. In

the 1930's material advances were made in the understanding of internal structure; here should be noted the work of Foerste and Teichert on the actinoceroids (1930) and of Ulrich and Foerste (1933, 1936) who brought attention to some of the odd structures occurring in the older nautiloids. Kobayashi (1931-1940) made material advances in the understanding of structures in particularly the older nautiloids, based largely upon material from eastern Asia, bringing attention to the siphuncular bulbs of the Plectronoceratidae, the diaphragms in the ellesmeroceroids, and remarkable structures in some endoceroids and piloceroids. Teichert (1933) embodied some major advances in his study of the Actinoceratida, calling attention to the siphonal structures, the ecological role and organic reality of the cameral deposits, which had scarcely received mention since the work of Ruedemann (1906), and calling attention to the taxonomic importance of the general internal patterns involving both siphonal and cameral deposits, for the recognition of the major groups. Oddly, this work contains not one but two new taxonomic proposals, one the general if vague definition of orders, Endoceroidea, Actinoceroidea, Orthoceroidea, Cyrtoceroidea, Gompherocoidea, and Nautiloidea, the other proposing the Eurysiphonata and Stenosiphonata as major divisions of the Nautiloidea and possibly even of the Cephalopoda. The former proposal involved groups too vaguely defined to be used; the latter, two divisions which it is now impossible to recognize. Oddly, the assertion of the value of general internal morphological patterns was not put into practice; had it been, the bullettes of the Westonoceratidae and the annuli of the Actinoceratida would not have been confused. Strand (1933) pointed out the distinctness of these structures. Flower (1935, 1936, 1939) called attention to the cameral deposits, in particular, their growth relationships, surface patterns, apical concentration, their necessary secretion in closed camerae, and their hydrostatic significance, and used them and the siphonal deposits in tracing the phylogeny in the Pseudorthoceratidae. Further works (Flower, 1941, 1946, 1947, 1955) resolved more fully the perplexities surrounding the structure of the siphuncles of some of the older cephalopods, in particular, emphasizing the specialization of the holochoanitic condition which for a time was thought to be primitive and general, and contributed toward the understanding of the endoceroid endosiphuncles. He also (1954) described new material, reaffirming the validity of the siphuncular bulbs which Kobayashi had reported in the Plectronoceratidae. A study of the Discosorida (Flower and Teichert, 1957) brought this order into some degree of coherence, devoting much attention to the siphonal deposits and demonstrating the extremely specialized connecting rings that are peculiar to that order. The revision of the Ordovician Actinoceratida (Flower, 1957) showed the importance in that group of the evolution of the siphonal canal system, the spatial relationships of siphonal and cameral deposits in complete mature shells, not previously evident, and something of the early evolution of the order. Mutvei (1957), oddly, presented a revision of morphology involving a rather odd concept of orientation, a rather cumbersome terminology, a purely topological and incomplete treatment of siphonal deposits, ignoring variations in composition and apparent origin, and an odd assertion denying the possibility of any organic cameral deposits.

Some observations, either new or in works still in manu-

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script, are incorporated here. The more important points involve layers of the septa, complexities in the primitive thick rings of the older Actinoceratida, the rods of some specialized Baltoceratidae, carbonaceous apertures, possibly connected with the black layer of *Nautilus* in several Paleozoic groups, variations in the mural part of the septum, the problem of segmental and nonsegmental linings, and contributions to the understanding of the endoceroid endosiphuncles.

Before proceeding to the detailed morphology, it is necessary to emphasize the importance of further morphological investigations, involving (a) particularly well-preserved materials and (b) suites of materials showing the varied behavior of homologous structures under different histories of alteration and replacement. In particular, further thinsection investigations are needed for some crucial types for which adequate material has not been available, as the lobed rings of the Cyrtocerinae, more investigations of the thick and complex rings in Ellesmeroceratida, Actinoceratida, and Endoceratida, further investigation of the "obstruction rings" of the Mandaloceratidae, generally wider investigation of structures in the Michelinoceratida, and further observations of the varied "actinosiphonate deposits" of the Oncoceratida. It must also be emphasized that this work is nearer to being a beginning than an end in such investigations; indeed, the present work has been some five years in process, being constantly delayed in the hope of incorporating new materials, and is published now largely in the hope that it will stimulate similar investigations by others, and thereby accelerate a fuller understanding of the remarkable shell structures to be found in the Nautiloidea. Quite possibly there is no other fossil group in which more material advances will result from the increase of study by thinsections. Dr. A. G. Fischer has for some years been conducting thinsection study of the exceptionally well-preserved orthocones of the Buckhorn formation of the Pennsylvanian of Oklahoma, which is now near completion and will contribute materially to our knowledge of structures of the conch and septa, as well as to siphonal and cameral deposits. The material on which this study is based belongs largely if not exclusively to the Michelinoceratida.

General works for many years did not progress beyond the concept of morphology laid down by Hyatt in his summary of 1900. Discussion of morphology is to be found in Miller, Dunbar, and Condra (1933) with a useful glossary, but this work could not take into account essentially contemporary advances made in the early 1930's. A more advanced discussion of morphology and a glossary of terms is found in Flower (1946), but even this seems now somewhat antiquated in the light of later discoveries. Oddly, while for long no texts appeared involving modern advances, two appeared here in almost the same year (1952-53). Of these, that of Shrock and Twenhofel (1953) is the more accurate in general, though a better treatment of cameral deposits is found in Fischer *in* More, Lalicker, and Fischer (1952). This work involves an oddly reactionary classification, the origin of which is not made evident, all coiled forms being returned to the order Nautiloidea, which, strangely, includes the Oncoceratida as well. The recent paper of Mutvei has already received comment here. Dr. Basse (1952), in the French *Traite de Paleontologie*, has presented a very able summary of morphology and classification. Naturally, there are material advances made since these works, which are incorporated here.

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The present work contains no major revision of morphological terms, though such a revision would have certain advantages. It is now apparent that parts formerly thought to be of secondary importance are fundamental structures, as, for example, the septal neck and the connecting ring. Likewise, various types of "deposits" based only on shape supply an unwieldy terminology as well as one having unfortunate implications, as noted above. It is felt, however, that the present terminology is too firmly entrenched in the paleontological literature to be supplanted readily, and a new morphological terminology would probably fail to meet general acceptance, and if not, would cause more confusion than it would eliminate. Proposed changes are largely abbreviation and simplification of terms in general use, the meaning of which should, from the older terminology, be quite obvious. Thus *conch* and *shell wall* have been used largely synonymously in the past, and brevity suggests the former to be preferable. The term *septal neck* is conveniently shortened to *neck*, the *connecting ring* to *ring*, and some slight simplification, not altogether new, is employed for the siphonal deposits. New terms are confined to new structures or new types of structures.

Interestingly, Mutvei (1957) has proposed a radical revision of shell terminology. In part, it involves a concept of orientation and symmetry which seems not beyond question, but, in part, the terms are either new or involve the reviving of such archaic terms as "funnel." * His terminology seems unnecessarily unwieldy, fails to recognize the distinctness of neck and ring, regards all cameral structures as mantle deposits, and denies the organic reality of cameral deposits.

GENERAL SHELL ORGANIZATION

The matters here noted are not new and need only be summarized briefly. Figure i shows a dissected anterior portion of a shell of a straight nautiloid. The conch (C) appears as a simple conical structure. The aperture (A) may show various emarginations but only one is common, the hyponomic sinus (H), which marks the venter. On the inside of the living chamber, the conchial furrow (CF) marks the midventral region; it is ordinarily of slight relief and may not show in poorly preserved material.

At the posterior end of the living chamber are a series of septa, separating camerae or air chambers which together constitute the chambered portion of the shell, the phragmocone. Three parts of the septa are shown, the mural part (M), shown here as extending nearly, but not quite, the entire length of a camera, the free part (F), and the septal neck (N). The septal furrow (SF) is a middorsal linear region in which the mural part of the septum is wanting. The connecting ring (R) extends from the tip of one neck apicad to the tip of the next neck, as shown. Cameral and siphonal deposits, commonly wanting in the anterior portion of the shell, are not shown here. It must be emphasized that though orthocones

**Funnel* was used loosely and ambiguously in the late 1890's, though not extensively. It is difficult to determine whether in some instances the endocones of the Endoceratida or the septal necks, or possibly necks and rings are referred to, and the term is one which has been assigned to a justifiable oblivion. Its appearance in a modern paleontological work would find a parallel, perhaps, were a modern physics work to discuss combustion and heat under the term "phlogiston."

appear circular in section and radially symmetrical, bilateral symmetry is fundamental to the shell pattern. Forms with circular cross sections are specialized, not primitive, and even in these forms the symmetry is shown by the hyponomic sinus, the septal and conchial furrows, and is often displayed further by the suture, curvature of the septum, the position of the siphuncle, and the symmetry of siphonal and cameral

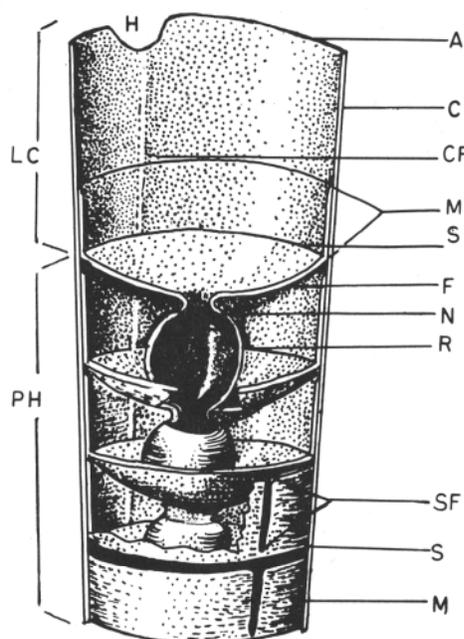


Figure 1

DISSECTION OF A SHELL OF *Orthonyboceras*, SHOWING RELATIONSHIPS OF SHELL PARTS

H. Hyponomic sinus	M. Mural part of the septum
A. Aperture	F. Free part of the septum
C. Conch	N. Septal neck
LC. Living chamber	R. Connecting ring, or ring
PH. Phragmacone	S. Suture
CF. Conchial furrow	SF. Septal furrow

The shell is viewed from a dorsolateral position, the dorsum; marked by the septal furrow, to the right of center, and the shell so dissected that the venter, in the back left, is viewed largely from the shell interior. No attempt has been made to include the muscle impressions which would occupy the base of the living chamber; cameral and siphonal deposits are absent in the adoral camarae here shown, but would be developed in more apical regions. Redrawn from Flower, 1946.

deposits.

A NOTE ON SHELL HABIT

Habit is here employed as a succinct term for the general pattern of behavior of a specific shell part under varied conditions of replacement. While of course specimens showing the least alteration are the most rewarding subjects of study, there are few instances of very perfect preservation of nautiloid shells, particularly in view of the susceptibility of aragonitic parts to alteration to calcite, and the selection of the "least altered" materials is a matter never completely free from subjective elements. It has been found that homologous shell parts show a general similarity of habits, and that non-

homologous parts may show profound differences, even though they may be similar in general form. Sometimes, the various aspects of a single structure, or of homologous structures, may supply some indications of original composition and texture and lead to significant conclusions as to mode of secretion. Oddly, we have had from time to time denials of the organic validity of such details as are not generally preserved, but this view now appears to be reactionary rather than merely conservative and is opposed by a significant mass of observation. It is necessary to remember that layers in the conch and septa should be present, comparable to those known in *Nautilus*, but possibly showing specializations peculiar to the various orders. Alteration of these aragonitic shell parts to calcite is commonly accompanied by the destruction of all traces of such layers, but their reality is not to be denied for this reason. However, the habit of the conch and septa, the general loss of structure and layering, is in itself an indication of the general, original, aragonitic condition, and such an exception as is found in the peculiar genus *Ecdyceras* (Flower, 1962) is certainly an indication of a departure from this general pattern. It is necessary, surely, to recognize the complexity of the original nautiloid shells and to realize the importance of fuller examination of layers, textures, and inquiry into mode of origin. Elsewhere the writer has found in a closer examination of endoceroid endosiphuncles that commonly endosiphosheaths are well preserved under calcite preservation, but blades may be obscured or destroyed and are best retained in specimens subjected to slight, gentle, incomplete silicification early in their history, evidently prior to alteration of the original aragonite to calcite. With further alteration, blades may be lost, but traced by shadows formed by the alignment of masses of botryoidal or fibrous calcite along the original blades, and such masses or the original blades may be emphasized by relatively late staining, connected with weathering. With extreme replacement, either by silica or by calcite, real blades or their shadows may be imperfect and may be complicated by completely adventitious patterns, possibly by further replacement along cracks, and considerable experience as well as a good assortment of specimens is needed to distinguish real from adventitious structures.

Often habit may indicate differences which it is yet difficult to evaluate. Cephalopods from the Whiterock beds from Ikes Canyon of the Toquima Range of Nevada show an odd contrast between general preservation in endoceroids and actinoceroids, indicating significant differences in the materials acted on in these two groups by similar events of deposition and subsequent alteration. Commonly, calcite in the endoceroids is so recrystallized that all structures in endosiphuncles are lost, and organic and inorganic calcite cannot be distinguished readily. Further, such alteration has commonly left only remnants of the connecting ring, which, from other evidence, is believed to be originally calcitic while other shell parts were aragonitic, and is commonly retained with considerable fidelity where aragonitic parts are grossly altered. However, in this material the rings are commonly destroyed or preserved as mere vestiges. It is believed that relatively late thrusting is responsible for the general recrystallization of calcite in such specimens. It is odd to find that the actinoceroids in the same beds show general retention of connecting rings and the canal system, and retain much of the pattern of cam-

eral and siphonal deposits under the same conditions of preservation. Certainly this fact is an indication of differences which still held at the time of recrystallization of the endoceroids, and probably indicated still greater differences in the original shells. Not unnaturally, the original differences cannot be fully estimated as yet, and one can only hope that wider observations and closer examination by thinsection and other methods,* may supply better answers than can now be offered. Similarly, the general retention of growth lines and lamellae normal to the secreting surface of discosorid parietal deposits, whether annuli or endocones, shows their general relationship as two aspects of a single structure, while the general loss of lamellae and endosiphosheaths (actually growth lines, resting stages in the development of the endosiphuncle) shows a profound difference in the endoceroid endocones,

indicative of a very different structure, and the blades require here a concept of origin of the parts as aragonitic deposits laid down within the tissues of the siphonal strand.

Of course the information supplied by habit where alteration is general or perhaps universal is limited and, as for the endoceroids and actinoceroids of the Ikes Canyon occurrence, indicates original differences which cannot at present be interpreted with certainty, but it may supply evidence in instances of alteration where, without it, there was even less information than now exists about the original shell condition.

*Dr. Charles Gregoire is conducting X-ray and electron microscope examinations which we hope may be rewarding even in considerably altered materials.

Conch

GENERAL FEATURES

The term *conch* is here used for the outer conical shell to which are later added septa, rings, and various "deposits." The term *shell wall* is synonymous, but *conch* is preferred here, first, because of brevity, and second, because of obvious homology with the gastropod shell to which this term was first applied. True, some gastropods add diaphragms closing off early whorls, but the development is minor and far from general.

The essential matters concerned with the conch involve (1) shell form, (2) composition and layers, (3) aperture, (4) ornament, (5) conch interior, and (6) the problem of the protoconch.

SHELL FORM

In general, the cephalopod shell is a cone, modified variously by variations in rate of expansion and by curvature, but in general, it is a bilaterally symmetrical structure and not a radially symmetrical one, as the use of the term *cone* might seem to imply.

It is now evident that the primitive shell form is that of an endogastric cyrticone, a shell curved but completing less than three quarters of a volution, curved with the venter concave, the dorsum convex. Indeed, with the exception of the Balkoceratidae and a few Protocycloceratidae, the order Ellesmeroceratida is composed of shells ranging from endogastric cyrtocoines to straight shells and a very few endogastric gyroconic genera. Endogastric form is also dominant in the older Discosorida, the Ruedemannoceratidae, Cyrtogomphoceratidae, and the derived Phragmoceratidae, and only endogastric to straight shells are found in the Endoceratida.

Exogastric curvature is now known to have developed in the Balkoceratidae, a family derived from the dominantly endogastric Plectronoceratidae in late Cambrian time. The group is a small one, with two genera and less than a dozen species known, and gave rise to nothing higher. The real beginning of exogastric curvature appeared in the Bassleroceratidae of the lower Middle Canadian. This family is the archaic stock of the Tarphyceratida, all exogastric coiled shells, and from the Tarphyceratida the Barrandeoceratida are derived. The Bassleroceratidae is likewise the point of origin from which sprang the Oncoceratida, and from that stock in turn were derived the Rutoceratida and, probably ultimately, the Nautilida. The Actinoceratida and Michelinoceratida are dominantly orthoconic, but examples of both exogastric and endogastric curvature develop there, though curvature in the Actinoceratida is slight and is pronounced only in *Cyrtonyboceras*.

The Ascoceratida, insofar as mature anterior ends are concerned is dominantly exogastric, but many forms are essentially straight and a very few appear endogastric. The rarely known early stages indicate a general gentle cyrtocoine exogastric curvature.

Derivatives of the Tarphyceratida are dominantly exogastric. Possible exceptions occur within the dominantly breviconic Oncoceratida. It is uncertain whether the endogastric Diestoceratidae of the Ordovician should be assigned to this

family or to the Discosorida, but other Ordovician types are exogastric. In the Silurian, however, forms of rather generalized aspect seem to run the gamut from exogastric breviconic cyrtocoines to straight shells to endogastric cyrtocoines. Apparent endogastric stocks occur in the Devonian. One such form, *Archiacoceras*, has revealed a septal furrow on the siphonal side, so the form has a dorsal siphuncle instead of being exogastric, but ancestral types involved in the migration of the siphuncle to the dorsum remain unknown. Probably the Devonian *Paraconradoceras* and *Bolloceras* are truly endogastric, as they develop shell form similar to that of *Phragmoceras*.

Until the revision of Hyatt (1883-1900), most nautiloid genera recognized were characterized by shape. Such genera, *Orthoceras* for straight shells, *Cyrtoceras* for curved shells, *Gyroceras* for loosely coiled shells, and *Nautilus* for shells coiled with the whorls grading from barely in contact to deep involution, were large, wide ranging, and had no phyletic significance. Before 1883 a number of genera were proposed for coiled nautiloids based upon variations in cross section, suture pattern, ornament, etc., but most other shells remained in the old, broad form-genera, though one may note the early recognition of the actinoceroid and endoceroid patterns, and genera for such bizarre shells as *Gonioceras* and *Ascoceras*. The matter is worth noting, for descriptive terms relating to shell form stem largely from these old form-genera. Thus, from *Orthoceras* come the terms orthocone, orthoconic and orthoceran (adj.), orthoceracone, and orthoceraconic. There is a real value in making a distinction between a shell which is straight, or seemingly straight, from a fragment (orthocone) and one which is completely straight (orthoceracone).

Cyrticone, cyrtoceracone, cyrtocoine, cyrtoceran, and cyrtoceraconic refer to gently curved shells. Properly the cyrtoceracone is one which at maturity completes less than a single volution; in practice (Flower, 1955A), we find that such shells rarely complete three quarters of a volution, and many describe between a quarter and a half volution. (See fig. 2B.)

Gyrocone, gyroceracone, gyroconic, gyroceran, gyroceraconic (fig. 2C) refer to shells of more than one volution, describing a spiral with the whorls free. Oddly, while there is some intergradation between cyrtocoine and straight shells and evolution must have progressed from the cyrtoceracone to the gyroceracone, although several such points of transition are known, there is no known gradation. The writer (Flower, 1955A) has suggested that the shells which crossed this transition found intermediate stages unstable, being, as they are, necessarily involved with a profound change in the mode of life, for the aperture of the cyrtocoine was directed obliquely downward and forward in life, while that of the coiled shell points directly forward. Such a change could hardly have taken place without being accompanied by profound changes in mode of life, and in particular, locomotion by hyponomic swimming and the gathering of food.

Nautilicone was used formerly for all coiled shells, but later various subdivisions have been given descriptive terms.

Of these, only a few are of general importance in relation to the nautiloids.

The tarphycone or tarphyceracone is one in which the whorls are in contact or in which involution is only most slightly developed. The name stems from the genus *Tarphyceras*, to which were assigned at first slender coiled shells with the whorls only slightly flattened in contact, or with, as is true for *Tarphyceras* as used in its present, more restricted, sense, a relatively shallow impressed zone. The impressed zone is a concavity developed on the outer whorl to embrace part of a preceding whorl. Its depth in relation to the outer whorl de-

pends upon a combination of two factors, the rate of vertical expansion, and the degree of involution. Figure 2E-H shows several selected examples of involution compounded with variations in the cross section of the shell. Figure 2H is obviously a nautilicone, but one can readily see how subtle is the transition from the tarphyceracone. In nautilicones, in which involution is advanced, the umbilical perforation is generally small, but there is wide variation from shells in which portions, at least, of early whorls are exposed to forms in which the outer whorl is extended to the center, and the umbilical callus closes the center of the coiled shell and obscures all

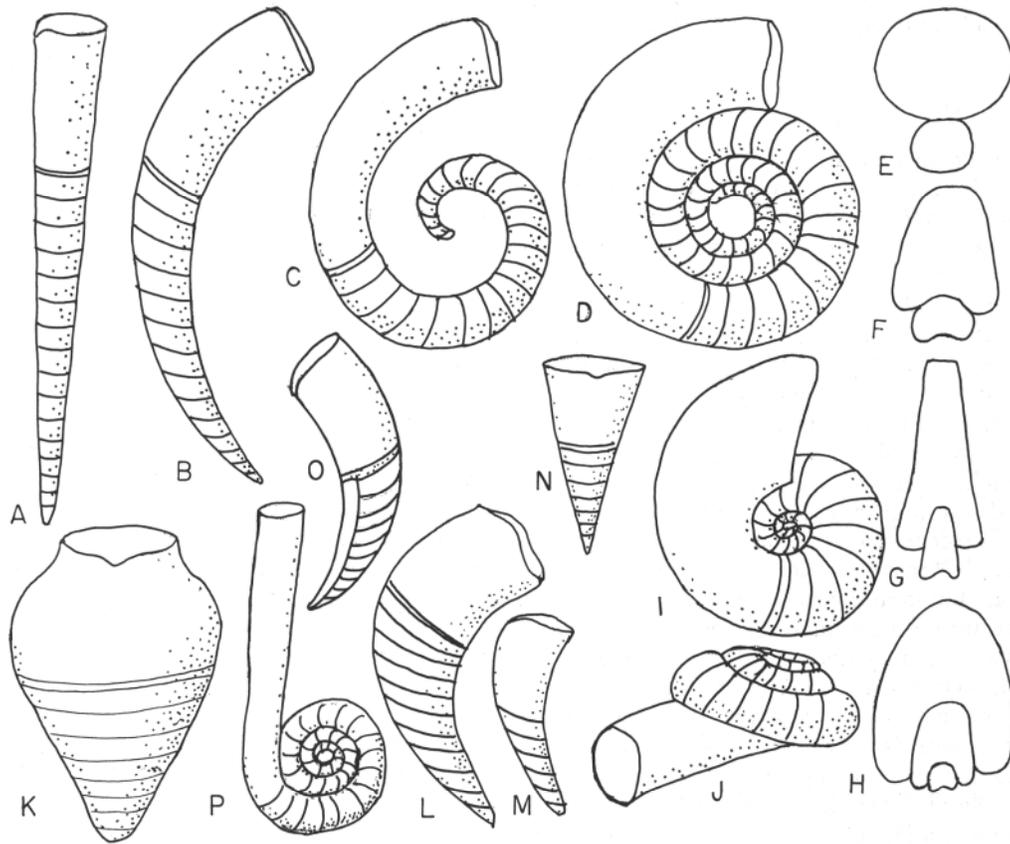


Figure 2
COMMON SHELL FORM TYPES IN THE NAUTILOIDEA

- A. Orthoceracone
- B. Cyrtoceracone (exogastric)
- C. Gyroceracone
- D. Tarphyceracone
- E. Cross section of tarphyconic shell showing whorls in contact, slight flattening, but no impressed zone
- F. Outer whorls of a *Tarphyceras*, showing slight development of an impressed zone
- G. Cross section of a nautilic shell with narrow whorls, rapidly enlarging vertically so that the impressed zone, though appreciable, is relatively low.
- H. Cross section of outer whorls of an involute nautilicone
- I. Nautilicone, lateral view. The shell, at maturity, shows a slight modification of the ventral profile, a feature of some nautiloids and developed also in many Devonian Ammonoidea
- J. Trochoceroide
- K. One type of brevicone, a straight shell with a contracted aperture, also a gomphoceroide
- L, M. Mature and immature specimens of an exogastric cyrtoceracone, in which the mature aperture is contracted
- N. An orthoconic brevicone with uncontracted aperture
- O. An endogastric cyrtoceracone, the basal part sectioned showing the position of the siphuncle
- P. A lituiticone. All side views, except M, have the shell oriented with the venter to the left

earlier whorls. Figure 2I represents a reasonable nautilicone of the earlier Paleozoic; there complete closure at the umbilicus is not attained. Such closure is approached, however, in the late Devonian *Carloceras* and is attained in the Permian *Stenopoceras*. It is more general in the Nautilina of the late Mesozoic and Cenozoic.

Coiled shells in which the whorl departs from the plane of symmetry are trochoceroids, though the earlier terms of *torticone* (twisted shell) was also applied. *Trochoceras* was a generic name applied to such shells at almost the same time by Barrande and Hall. It is an odd commentary on the punctiliousness with which priority had been observed that the genus was attributed to Barrande, who proposed it first, and *Mitroceras* Grabau (91o) was proposed for the first *Trochoceras* described by Hall, *T. gebhardi* of the Cobleskill limestone of New York. Subsequent investigation shows, however, that Barrande's proposal was unaccompanied by any described species, and actually Hall was the first to use this name in connection with any species which could possibly be a genotype, so this matter is one over which nomenclatorial fun and games will doubtless develop. Trochoceroids are termed sinistral or dextral on the basis of conventional gastropod orientation. A shell oriented with the spire above and the aperture facing the observer is sinistral when the aperture is to the left, as in Figure 2J, dextral when it is to the right.

The term brevicone is rather loosely used. It is a shell which is relatively short, but within that limit there is considerable scope. It may be a short, rapidly expanding shell, straight or curved; a straight shell of this type is shown in Figure 2N. *Gomphoceras* was widely used as a form genus for shells rapidly expanding in the young, but with a mature living chamber contracting as it approaches the aperture. Such shells, gomphoceroids, may be essentially straight (fig. 2K), exogastric (fig. 2L, M), or endogastric. L and M of Figure 2 are a mature and an immature specimen of an exogastric brevicone which at maturity has a contracted aperture and is thus also a gomphoceroid. A gomphoceroid is a brevicone specialized by a restricted aperture.

Possibly, had it been recognized earlier that endogastric cyrtocoines were archaic among the cephalopods, a special term for such shells would have been proposed; as it is, there is none.

COMPOSITION

Layers in the conch of *Nautilus* have been described by Hyatt (1875), Blake (1882), and Appellof (1892). There are generally recognized (1) an outer porcelaneous layer of aragonite prisms, generally opaque, and in which the color markings are integrated; (2) an inner, thicker layer of alternating layers of aragonite and thinner layers of organic material; and (3) a thin inner layer, the annulus layer, secreted not at the aperture but at the region of muscle attachment, near the posterior end of the living chamber. All these layers are dominantly aragonitic. In addition, a black, carbonaceous layer is secreted beneath the hood, and it is reported that in mature shells this layer may spread around the entire circumference of the aperture.

In fossil material, the conch is commonly replaced by calcite and shows in thinsection only irregular calcite crystals, all trace of original textures and layers being lost. In general, thinsection examination has proved most unrewarding, and attempts to study the conch by thinsection have largely been

given up.

In the experience of the writer, only two examples of fossil material are known showing any suggestion of layering in the conch. One (Flower, 1962) is found in the specialized genus *Ecdyceras*. Thinsections through the conch show lamellae sloping at a low angle forward from the inner to the outer surface. The presence of these lamellae in every section made suggests that *Ecdyceras* is specialized either in having a conch made of calcite rather than of aragonite or in containing, as in *Pecten*, alternating layers of calcite and aragonite. In view of the remarkable specializations on the interior of this genus, it is not surprising to find specializations in the conch. What is surprising is to find only oblique laminae, which seemingly have no relation to the orthodox layers which one would expect from accounts of *Nautilus*. Oddly, a second example of layers is found in a small part of the dorsal shell wall of the holotype of *Eremoceras magnum* (fig. 3). Here there are

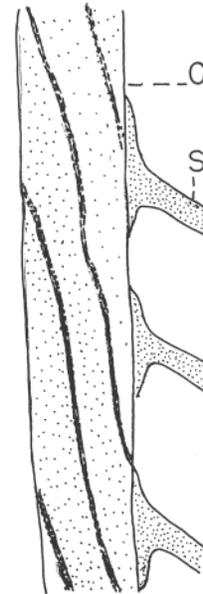


Figure 3
EREMOCERAS MAGNUM

Thinsection through a small part of the dorsal wall of the shell, showing the conch composed of steeply inclined laminae, in which thin dark and thick light bands alternate. Also shown is the buttress-like attachment of the septa, and the several septa shown indicate the extent of variation observed.

C. Conch.

S. Septum.

steeply inclined lamellae, consisting of thin, dark layers separated by broader, light layers; the light layers show irregular calcite crystals and were probably aragonitic. In comparison to *Ecdyceras*, these layers are steeply inclined forward from the inner to the outer surface. No additional outer or inner layers are developed. Possibly the short frills developed in *Barnesoceras* are external expressions of similar laminae, but the known material of this genus is confined to the Threadgill limestone of the Tanyard formation, and shows such ad-

vanced alteration that even the rings show no significant textural differentiation from the remainder of the shell parts and no trace of original texture remains in the conch.

The figures of Appellof (1892) and, though less clearly, those of Blake (1882) do, however, suggest a fantastic analogy with the shell of *Nautilus*. Appella shows quite clearly in the aragonitic prismatic layer growth lamellae which slope steeply forward from the inner to the outer surface. No such structure is found in the outer porcelaneous layer. Can it be that the conch of some if not all of these early Paleozoic types consisted only of the prismatic layer? Such a conclusion is suggested by the scant evidence now available. If so, where in the phylogeny the outer layer was added, is an interesting question. Alternate explanations involve exfoliation of the outer layer or its solution prior to burial, not convincing from the material observed. Quite probably in a group as large and as diverse as the Nautiloidea, there are to be found variations in the composition and layering of the conch; Fischer's current but yet unpublished studies of the orthocones of the Buckhorn beds seem to have little relationship to the meager findings reported here. Obviously, while some odd variations are indicated, our present data are too meager to permit their interpretation in terms of specializations in the orders, and such conclusions must await the study of more propitiously preserved material in a wider variety of forms.

In connection with the fine structure of the conch, note should be taken of Gregoire's (1957) fine study of topography of textures of mother-of-pearl in *Nautilus*. The textural details are shown by electron microscope pictures. These matters are not discussed here, inasmuch as the details are apparently too small to show as significant features in thinsections examined at ordinary optical magnifications.

APERTURES

The features of the aperture previously noted are concerned with its shape. Portions projecting forward are known as crests; backward, re-entrant portions, as sinuses. In many forms the aperture remains relatively transverse, but most commonly there is a sinus developed on the venter; this is termed the hyponomic sinus, and apparently it permits more ready extension of the hyponome in swimming, and must also facilitate circulation of water through the hyponome when the animal is retracted into its shell. A pair of lateral sinuses is also developed characteristically in the Lituitidae but also appears in other groups. Contraction of the apertures at maturity of the shell occurs in several distinct groups, and the apertures may be reduced to a series of slits. In such development, the hyponomic sinus is always prominent. Apertures of this type are best known in the Mandaloceratidae and Phragmoceratidae of the Discosorida, and again in the Hemiphragmoceratidae of the Oncoceratida, but domelike closure of the aperture over the front of the shell is developed, though less perfectly, in some other groups. In the Lower Canadian, tiny homeomorphs of *Phragmoceras* developed in the Ellesmeroceratidae;* in the Devonian were developed large shells of similar form, stemming from the Oncoceratida. Restricted apertures may be developed at maturity in members of the Tarphyceratida, Ellesmeroceratida, Discosorida, Michelinoceratida, Ascoceratida, and Oncoceratida.

In *Nautilus* a black deposit lies beneath the hood, and it is reported that at maturity the black material may be extended around the circumference of the aperture. A similar condition

seems to have escaped notice but can be found in Paleozoic Nautiloidea belonging to several groups. The writer has observed shells with the conch thinning toward a mature aperture and involving a change from granular calcareous material to a finer-grained black substance. Such apertures have been observed in *Actinoceras* from the Simard limestone of Lake St. John and in Endoceratida from several places in the Middle and Upper Ordovician. Again, they are quite generally developed in a group of Ordovician shells, mainly Oncoceratida but involving some Michelinoceratida, in the Middle Trenton of the Fairy River (originally Rivier du Fer) near the Falls of the Montmorency River of Quebec (pl. 1, fig. 6-1 r). Oddly, *Trocholites*, common in the same beds, fails to show a similar development clearly. A like phenomenon is shown most strikingly in the holotype of *Crypthoceras productum* Flower (1939) of the Pseudorthoceratidae, a species of the Wanakah shale member of the Hamilton. As yet, such development seems to show no phyletic significance, but our observations thus far are certainly most incomplete. Exceptionally good conditions of preservation are required, and certainly it is only at complete maturity that the carbonaceous aperture is developed. It has not, to the writer's knowledge, been observed in coiled forms of the Late Paleozoic or Mesozoic, where it would certainly be expected, for it is in these shells that the more immediate ancestors of *Nautilus* are to be found.

ORNAMENT

Inasmuch as terminology and form of ornament in nautiloids is general among shells, no survey need be made of the terminology. Ornament types are formed at the shell aperture, and in some instances frills, nodes, and spines may represent modifications of the aperture. In the Rutoceratidae, and to a lesser extent in some derived families, the frills, spouts, and nodes represent significant modifications of the aperture at resting stages in shell growth. Ornament types, once considered characteristic of genera, are now known to develop independently in different lineages. Thus, such genera as *Kionoceras*, *Spyroceras*, and *Cycloceras*, the former fluted, the second combining annuli and longitudinal markings, the third combining annuli and transverse markings, are known to be convergent homeomorphs, as defined on the basis of orthoconic form and shell exterior alone.

In general, the older Nautiloidea tend to have the shells relatively simple externally, showing surfaces which are smooth or marked only with growth lines. Short frills are known to appear in the lower Canadian *Barnesoceras* (Ellesmeroceratida), again in a few Tarphyceratida, and again in *Zitteloceras* (Oncoceratida) of the Ordovician. Shells with longitudinal ridges (*Kionoceras*) appear in the Ordovician, and again independently in the Late Paleozoic in *Euloxoceras* of the Pseudorthoceratidae and in *Thoracoceras*, a genus of still somewhat uncertain affinities. Shells with annuli first appear in the Protocycloceratidae, appearing in the Canadian, but develop again in several different stocks in the Ordovician, Silurian, and Devonian. Annuli are commonest in the Michelinoceratida but are known in the Endoceratida, Actinoceratida, and Discosorida, while some oncoceroid genera

**Burenoceras phragmoceroides* Flower 1963.

develop moderate annulations, and one may find them again in such coiled shells as the Silurian *Bickmorites* and the trochoceroids of the Lechritrochoceratidae and the Devonian genus *Sphyradoceras*. Prominent distant frills suggestive of varices of growth are not known prior to the development of the Rutoceratidae in the Devonian. Some years ago a note appeared in the *Journal of Paleontology* urging abandonment of the term *ornament* because its use implied that the animals "ornamented" their shells from some sense of beauty and personal adornment. Surely this is nonsense. The writer feels that any reader who expects the term to be used in relation to shells with this implication, fully deserves the surprise that he will get when he finds that it is not so.

CONCH INTERIOR

The interior of the nautiloid conch bears a series of characteristic markings consisting of the conchial furrow, a shallow furrow on the ventral side of the shell, the muscle impressions, thickening of the shell, confined to the basal part of the living chamber, and various modifications, most commonly a thickening of the shell interior near the aperture, a phenomenon developed only at maturity.

The conchial furrow (see fig. IC, F) is variable in development but is always a shallow furrow formed on the midventral part of the shell. In rare examples, three such furrows may be present. In *Striacoceras typus* (Saemann) of the Cherry Valley limestone (pl. I, fig. 12, 13) three such furrows are commonly evident, but the species is exceptional in this respect. Barrande has figured three similar furrows in a very few Silurian species, but it is not clearly evident whether this condition is general in those species or exceptional; the illustrations suggest the latter condition. Generally the furrows are shallow and are most commonly observed as carinae on internal molds so preserved that the surfaces appear polished. Only rarely, as in *Striacoceras typus*, do they show any very strong relief. Probably the conchial furrow is quite generally developed. Certainly it is common to the Michelinoceratida and the coiled orders. Suggestions of this structure have been found in the Endoceratida and Actinoceratida.* Unfortunately, most representatives of these orders, and also of the Discosorida, Ellesmeroceratida, and Tarphyceratida, occur most commonly with surfaces of internal molds rather poorly preserved, under conditions unfavorable for the preservation of the furrow.

Quite commonly, mature living chambers show an internal thickening shortly prior to the aperture. Such a thickening is quite marked in the Michelinoceratida, and internal molds of such shells in the Hamilton were the basis of *Orthoceras constrictum*. A somewhat similar thickening has been observed in the Actinoceratida. In some Ellesmeroceratida there is a similar but less pronounced thickening, which has been observed in *Ellesmeroceras*, *Annoceras*, and *Eremoceras*, and the cyrtoconic Ellesmeroceratidae show a similar feature. Just before the mature aperture, the profile of the living chamber commonly becomes faintly sinuate, the concave portions thickened slightly. No such thickenings have been observed in the Endoceratida, and observations made on large living chambers suggest that the structure is not developed in that order.

ture may be quite pronounced. A comparable development in the coiled orders is generally lacking, surprising in view of their relationship with the Oncoceratida, and only in the Rutoceratidae has such a thickening been observed. Commonly, instead, the smooth curve of the shell profile is modified, and the ventral profile becomes irregular in curvature, usually involving the development of a slight flattened zone, a feature found also in the older Ammonoidea and figured by Hall (1879) for *Agoniatites*. The general appearance of such shells is shown in Figure 21.

Orthoceratites regularis Schlotheim, which has been made the genotype of *Orthoceras* and may, by plenary powers of the International Commission, be made the type of *Orthoceras*, shows three prominent longitudinal internal thickenings at or just before midlength of the mature living chamber. Troedson (1931) has figured these structures quite adequately. Similar but more irregular thickenings were reported for the genus *Ctenoceras* Noetling. If Sweet (1959) is correct in his interpretation of that genus, its internal structure shows that it is not closely related to *Orthoceras*, for the siphuncle segments are expanded and contain a siphonal deposit. Noetling's (1889) illustrations show considerable distortion of the living chamber, and it may be that the internal thickenings in the genus are not real. Quite a similar appearance is presented by crushed living chambers of *Stereospyroceras* of the Chazyan of North America, in which certainly no such linear thickenings are developed.

Muscle scars occurring at the bases of living chambers form transverse bands orad of the mural part of the last septum in which the shell wall is slightly thickened; such bands have their anterior ends extended forward, and the band broadened to accommodate the large pair of retractor muscles. Mutvei (1957A) has summarized most previous observations and some new ones, but the value of his work is obscured by a novel and rather cumbersome terminology which is not completely valid, as noted below in the discussion of orientation. Oddly, while Mutvei is extremely careful to insist that the septum is dorsal in relation to the body of the cephalopod and calls the dorsum *anterior* and the venter *posterior*, he speaks of the muscle scars as annular "elevations." Surely an elevation is something that extends upward. It is not clear whether Mutvei visualizes the shell as cut longitudinally and unrolled, so that the shell at the muscle markings extends slightly upward, or whether he has reverted to the old conventional orientation of the shell, used for purposes of illustration, and considers the anterior margin of the elevation as extending orad from the septum. Sweet (1959), though retaining the terminology of "annular elevation," has abandoned Mutvei's ideas on the orientation of the shell and has thus presented a concept of the muscle impressions in more comprehensible and less cumbersome terms, and he has also added some very significant observations of his own. Mutvei claimed great phyletic value for the muscle markings, but the observations which he has accumulated seem inconclusive in this respect. Sweet (1959) finds instead a correlation between the types of muscle markings and the shape of the living chamber. He recognizes three types: ventromyarian, in which the muscle scar is broadened materially, its anterior margin swinging

**Nybyoceras ventrolineatum* Sweet and Miller (1957, pl. 3, fig. r) is the only actinoceroid so far known to show a prominent furrow.

Among the breviconic genera, both of the Discosorida and of the Oncoceratida, the thickening of the shell near the aper-

forward in paired lobes on the venter; pleuromyarian, in which the muscle scars are similarly broadened laterally; and dorsomyarian, in which the scars are similarly broadened dorsally. He finds the dorsomyarian type in essentially straight living chambers in general, the ventromyarian in exogastric coiled forms, though where the whorl is involute, the pleuromyarian type develops.

Muscle scars have not been observed yet in very many genera, but among the forms now known only the orders Endoceratida, Actinoceratida, and Ecdyoceratida remain unrepresented. No muscle markings are known in the older Ellesmeroceratida, but dorsomyarian scars are reported for *Baltoceras*. The Michelinoceratida, regarded as derived from the Ellesmeroceratida through the Baltoceratidae, are also dorsomyarian as far as is known; the samplings include "*Geisonoceras*" *scabridum* and "*Orthoceras*" *angulatum* of the Orthoceras limestone, and *Lyecoceras*, a Silurian genus. Sweet suggests that *Lyecoceras* is possibly allied to *Calocyrtoceras* of the Paraphragmitidae, but the writer would consider it as related instead to *Kionoceras*, to which it is allied in form of the siphuncle segment and in extreme retardation of development of siphonal and cameral deposits.

Oddly, for the Ascoceratida, which are derived from the Michelinoceratida, only *Billingsites* cf. *cleformis* is known to show muscle scars; they are ventromyarian. This form has an essentially straight living chamber, but with the forward swing of the sigmoid sutures, the natural place of attachment for retractor muscles would be in the deepest part of the living chamber, which is here ventral.

The older coiled stocks, the Tarphyceratida and Barrandoceratida, include the following forms known to have ventromyarian scars: *Estonioceras*, *Planctoceras*, *Discoceras*, *Uranoceras* (?) *longitudinale*, and *Charactoceras*. The Lituitidae, however, which develop straight living chambers at maturity, are dorsomyarian in pattern, as known from *Lituites* and *Rhynchorthoceras*.

The pattern in the Oncoceratida seems less firmly established. Sweet (1959) has found in the basal zone indications of muscle scars, but the writer feels that such a basal zone involved certainly the formation of gerontic septa which are marginal only, and that all such markings, which are common particularly on the Oncoceratida with contracted apertures, are not necessarily muscle scars also. Sweet figures a clear ventromyarian muscle impression for *Oncoceras* sp. from Cornwallis Island though the ventral widening is quite slight. He also shows a band in *Diestoceras* sp. which is narrow with quadrate protuberances around most of the shell, but more uniformly thickened over the venter, though the anterior margin is not extended forward. In the Rutoceratida, derived from the Oncoceratida, to which the former Solenocheilida is almost certainly allied,* the pattern is dominantly ventromyarian, though it is pleuromyarian in *Metacoceras*, where there are two large lobes on the lateral faces. *Casteroceras* shows a pattern suggestive of the ventromyarian, but the writer is uncertain that these extensive impressions (Flower, 1939) are muscle markings alone; palial markings may also be involved. Muscle markings are known for *Germanonautilus*, *Metacoceras* (*Metacoceras*), and *Metacoceras* (*Mojsvaroceras*) and *Pleuonautilus*, as well as for *Solenocheilus*. In the Nautilida the markings are dominantly pleuromyarian, and Sweet lists as showing such markings *Apheleceras*, *Cenoceras*, *Cimonia*, *Eutrephoceras*, *Grypoceras*, *Nautilus*, *Pseudaganides*, *Syringoceras*, and *Vestinautilus*. It is significant that two of these

genera, *Apheleceras* and *Vestinautilus*, belong to the lirate group of Mississippian genera, the Triboloceratidae. Probably the Liroceratina are derived from this lineage, as discussed elsewhere (Permian cyrtocoones of New Mexico, in press, Jour. *Paleontology*, 1962). *Coelogasteroceras* of this stock seems to have good pleuromyarian muscle scars.

The Discosorida is an odd group in relation to form, as the primitive endogastric forms give way in the Westonoceratidae and its descendants to exogastric shells. In this order, Sweet has found ventromyarian scars in *Parryoceras*, a member of the endogastric Cyrtogomphoceratidae. The writer has found in *Westonoceras alberta-saskatunae* (Flower and Teichert, 1957) a pitted band, narrow and parallel-sided, over dorsal and lateral areas, and though it is weathered ventrally and obscure as to details, it is certainly no wider there. A slight ventral widening of a possible muscle impression is found in *Sinclairoceras*. It should be noted that the Diestoceratidae, which show a distinct ventral area, though one which is narrow, may possibly be Discosorida rather than Oncoceratida as was previously thought, for they alone of the supposed Oncoceratida of the Ordovician are endogastric, and it has since been found that similar seemingly actinosiphonate structures may develop within the Discosorida, as in the Mandaloceratidae.

No muscle impressions have yet been recognized for the Actinoceratida or Endoceratida, though some well-preserved internal molds of living chambers have been examined. Presumably good muscle scars are found in shells which are mature if not gerontic, but Sweet (1959) regards his *Metacoceras* which shows such impressions as immature. Quite probably, the conditions required for clear development of muscle scars are not yet thoroughly understood for the Nautiloidea. It should be noted that, as Sweet has observed, all Ammonoidea known to show muscle scars show a dorsomyarian pattern. It should be noted also that Mutvei (1957A, p. 231, fig. 7c) represents *Apheleceras* as dorsomyarian but Sweet considers it similar to other Nautilida. Surely, more observations are needed. At present the distribution of the three form types of muscle scars accords approximately with the form of the living chamber, but not quite perfectly, and further investigations are needed. Particularly odd is the apparent ventromyarian condition on both endogastric and exogastric Discosorida. The reported muscle scars in *Amphoreposis* by Crick (1904) have not been mentioned by Mutvei or by Sweet. This is just as well. From a plastotype lent by the British Museum, the writer would conclude that the muscle scars are adventitious, being too deeply placed in an obviously weathered surface to be the result of any internal thickening of the conch.

PROTOCONCH

Early cephalopod works recognize two parts to the ammonoid shell, the conch and the protoconch. (See Clarke, 1893; Pocta, 1902.) Hyatt believed most Nautiloidea to have a protoconch that was not calcified and figured a shriveled protoconch on the apex of one of Hall's types of *Spyroceras*

*The family name Solenocheilidae is preoccupied by the older Aipoceratidae of Hyatt 1894. The writer has elsewhere considered the Aipoceratina as a suborder of the Rutoceratida.

crotalum. It is worth noting that Ruedemann (1912) has figured apical swollen protoconchs of orthocones from the middle Trenton Snake Hill shale. The writer has observed the external mold of a similar development in a tiny orthocone from the shales of the Skanneateles division of the Hamilton, from Pratts Falls, New York. Such observations pertain certainly to the one order Michelinoceratida. Similar bulbous protoconchs, larger than the shell part immediately following, are certainly wanting in the Ellesmeroceratida, Endoceratida, Discosorida, and Actinoceratida, though the best evidence indicates a small apical chamber for the Actinoceratida, fitting like a shallow dome over the much larger well-calcified apex of the shell; poor calcification is suggested from the fact that such observations have been made so far on only a very few specimens by Kobayashi (1937) and the writer (Flower, 1940).

Early stages of the Ellesmeroceratida and primitive Endoceratida involve blunt, rapidly expanding shell apices, but in higher Endoceratida some odd specializations as yet difficult to evaluate have been reported, but show in general no indication of a large apical protoconch detached from the remainder of the shell in outline. It is difficult to say in some instances whether large apical siphuncles were covered by camerae dorsally and laterally at least, as is certainly true for *Proendoceras* (Flower, 1941), or whether camerae are definitely delayed as in the form-genus *Nanno*. Oddities insofar as apices are concerned are (1) *Proterocameroceras*, in which the initially blunt siphuncle expands gently, then contracts, and later resumes expansion; (2) *Manchuroceras wolungense*, reported as having a notch separating a small apical portion from the remainder of the siphuncle; (3) *Chihlioceras nathani*, represented as having a small buttonlike protuberance on the apical end of the siphuncle; and (4) *Coreanoceras* kuni, interpreted as having a siphuncle conical apically, the one side strongly oblique, then becoming abruptly tubular (*see*

Kobayashi, 1937).

It now appears that the inflated protoconch developed in at least two lineages: (1) in the Michelinoceratida from which the Bacritidae and Coleoidea are developed and (2) in the development of the first coiled Ammonoidea from the Rutoceratida. Possibly the Clymeniida represented a third group, and there is some evidence suggesting derivation of that group from the Centroceratidae of the Devonian (Centroceratina, Nautilida).

In the Michelinoceratida, protoconchs are known from few specimens, and unfortunately, the taxonomy and structure of the species concerned are not adequately known, so it is impossible to say how general the development is in that order. It is, however, clearly common to the Michelinoceratidae in the broad sense and to the Pseudorthoceratidae. Oddly, while the protoconch is reported in the older Coleoidea, no trace of this structure was found in sections of *Hematites* (Flower and Gordon, 1959), an anomalous condition which seems best explained by resorption of the protoconch and, indeed, of the extreme apex of the phragmocone as the rostrum is developed.

Controversy continues to surround the origin of the Ammonoidea, but it appears that in spite of the discovery of slightly curved Bacritidae, there still remains a form gap between these shells and the early, properly coiled Ammonoidea. Examination of Devonian Rutoceratidae, in which the ancestors of the Ammonoidea probably lie, and of the Centroceratidae, in which probably the ancestors of the Clymeniida are to be found, have failed to show any trace of a swollen protoconch.

The present evidence suggests that apical chambers containing the siphonal caecum, the apical closed part of the siphuncle, are homologues of the swollen protoconch.

Septa

GENERAL STRUCTURE

As the shell grows at the aperture and the body mass of the animal moves forward in the shell, a series of septa are secreted behind the body mass. The body is here covered by a mantle, and the surface responsible for secretion of the septa was termed the *posterior mantle* (Flower, 1939). Reports indicate that in *Nautilus*, forward movement of the visceral mass is a gradual process and that behind the animal a preseptal space is occupied with air or gas.* At one time it was generally believed that *Nautilus* could vary the gas in the preseptal gas space, but observation has failed to substantiate this supposition; buoyancy of the animal can, however, be varied, so that the organism may either sink or float by expansion and contraction of the body mass.

COMPOSITION

The septum of *Nautilus* is composed of a layer of vertical fibers of aragonite. On its apical surface there is a layer of conchiolin, reported as formed just prior to the main aragonitic layer. Blake (1882) and Appella (1892) reported also a deposit formed in the anterior corner of the camera on the apical surface of the septum where it joins the shell wall at an acute angle. Indeed, Appella figures two distinct deposits there of different textures and apparently of somewhat different substances. No parallel to these structures has yet been found in fossil nautiloids. Their mode of secretion has not yet been explained. Appella shows the "membrane," the conchiolin layer, as extending along the posterior face of the septum and terminating on the siphuncle at essentially the point at which the anterior end of the ring appears. He does, however, show in one segment of the siphuncle a suggestion of the conchiolin membrane extending for a short distance between the anterior end of the ring and the outer surface of the septal neck.

Appella shows on the anterior face of the septum a thin layer of papillae or small pillars, the surfaces overlaid by a thin membrane. Relationships of this structure to others are somewhat puzzling; this layer extends certainly along the anterior face of the septum where it is bent into a neck; Appella's illustrations suggest a merging of this structure with the connecting ring. Oddly, Appella's study of *Spirula* showed no trace of either the apical conchiolin layer or the anterior layer with papillae.

In fossil material septa commonly show all loss of original fine structures, evidently as the result of the alteration of aragonite to calcite. No deposit at the anterior corner of the septum has been recognized in fossil material, and structures which might be homologues of the apical conchiolin layer or of the anterior papillate layer of *Nautilus* are confined to the two examples described below. Ordinarily septa in fossil Nautiloidea show only a composition of irregular calcite crystals. Some specimens have been observed showing in section a dark line along the middle of the septum, but this line, ordinarily about half way between the anterior and posterior surfaces, is irregular, shows no uniformity over any considerable series of septa, and commonly fails to continue into the septal neck. Such lines are certainly adventitious, and in part at

least, they represent incipient fractures along which, under further stress, the now stone-filled camerae would separate. Weathering can produce such fractures, as well as physical stress.

Our meager evidence suggests that the aragonitic condition of the septa is general, perhaps universal. In *Ecdyceras*, where lamellae of the conch suggest an originally calcitic condition, septa are altered as usual, suggesting that they have remained aragonitic.

Thinsection examination of septa in the Nautiloidea has not been very extensive, and most sections, made primarily for study of the siphuncle, fail to show any significant septal layers distinguishable by textures. However, the sections of the writer have shown two examples of structures of considerable complexity. Sections of *Faberocheras* from the Leipers formation of the Cumberland River of southern Kentucky have revealed some accessory layers shown in Figure 4 and in Plate 6, Figures 1, 3-5. Here the main part of the septum (s) is shown recrystallized, with only irregular calcite crystals apparent within. A narrow clear region (cr) separates a thick band of honey-yellow material showing a composition of vertical fibers (ac). This layer terminates in various ways, only one of which is shown here, where it joins an extension of the ring onto the anterior face of the septum. The clear layer disappears before the bending of the septal neck. A thin posterior clear region (per) is developed which is traceable for a distance between the vinculum of the ring and the septum.

A section of *Adamsoceras isabellae* from the Whiterock beds of Ikes Canyon, Nevada, shows some even more remarkable differentiation (fig. 5, also pl. 2, fig. 8). Here the main part of the septum again shows no original textures, but there are supplemental layers on both the anterior and posterior surfaces. On the posterior side is seen a very thin layer of light calcareous material which seems to extend the observed length of the septum from conch to siphuncle (though the section is incomplete at the margin) and this layer extends over the outside of the septal neck but is wanting on the excavated tip which holds the anterior end of the ring. On the anterior face there is a thicker layer of fine-grained brownish material, which, as in *Faberocheras*, one is tempted to interpret as conchiolin. When traced peripherally, toward the conch, this layer thins and disappears; it clearly does not continue even to the point of the suture, but when traced toward the siphuncle it is found to continue for some distance between the anterior surface of the septum as it bends apicad to form a neck and the apical end of the connecting ring, though it terminates before the tip of the ring is attained. Sweet (1958, p. 120-121, text fig. 15, pl. 20, fig. 3) has figured a siphuncle of *Rhynchorthoceras helgoyense* in which he interprets the ring as composed of two layers, a relatively thick, dark, inner layer and a lighter, generally thinner, outer layer. The outer

*The gas secreted is a mixture like air but richer in nitrogen; as *Nautilus* commonly lives at some depth, where solubility of nitrogen in blood is greater under some pressure, the effect is very much what one would expect under such circumstances.

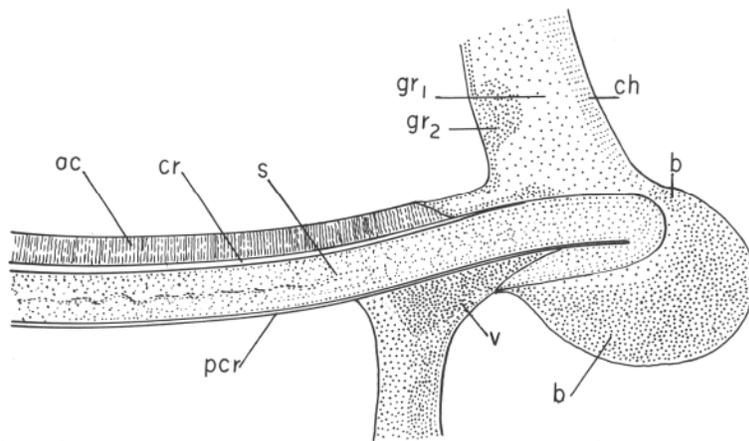


Figure 4
SECTION OF SEPTUM AND PART OF SIPHUNCLE OF *Faberoceras* sp.

s—septum proper, ac—anterior chitinoid layer, cr—clear region, pcr—posterior clear region, gr1—fine granular zone of ring, gr2—coarser granular zone of ring, ch—chitinoid zone, b—bullette, the two regions here poorly differentiated, v—vinculum. From material from the Leipers formation, Cumberland River, southern Kentucky, from sections in the collection of the writer.

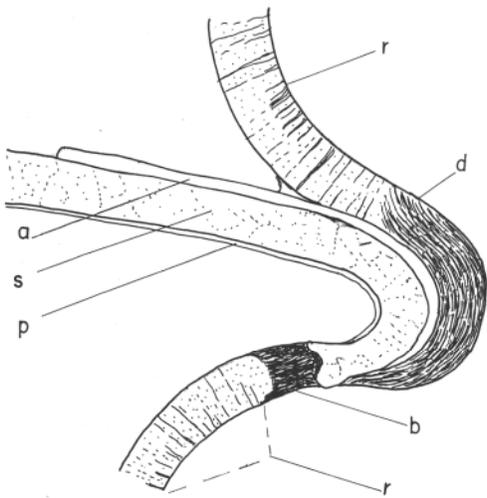


Figure 5
PORTION OF SEPTUM AND SIPHUNCLE WALL OF *Adamsoceras*

a—anterior layer; s—septum proper; p—posterior layer; b—basal zone of the ring, highly carbonaceous and showing obscure fine cancellate texture; r—main part of the ring, traversed by thin dark bands, possible pores; d—distal part of ring, with prominent lamellae and more obscure transverse structure.

layer is represented in his text figure as extending for an indefinite distance over the anterior face of the septum and is possibly comparable to the layer of papillae in *Nautilus* and to the layer noted on the anterior septal faces of *Faberoceras* and *Adamsoceras*. These are the only occurrences thus far reported or, as far as the writer knows, observed in fossil Nautiloidea showing more than a simple homogeneous septum. Possibly the layers evident in this specimen depend upon rather exceptional conditions of preservation; there is indication of slight silicification early in the history of this material, possibly prior to the general replacement of aragonite by calcite, a process generally destructive of fine textural features.

A search of younger and more specialized actinoceroids for similar layers has been made, but thus far has been fruitless.

REGIONS OF THE SEPTUM

In gross aspect, the septum is divisible into three main regions which Teichert (1933) named the mural part of the septum, the free part of the septum, and the septal neck. (See fig. 1.) Teichert indicated the mural part of the septum as extending forward along the interior of the conch for the length of a camera. This condition is quite general in the Actinoceratida, on which group his observations were mainly based, and again in the Endoceratida. In the Michelinoceratida a similar condition may be found but there are exceptions. In some Michelinoceratida the anterior thinning of the mural part of the septum leaves its anterior limits difficult to determine. In some species, particularly a group of forms with rather long camerae, internal molds will show a definite line which marks the anterior limit of the mural part of the septum a considerable distance apicad of the next adoral suture. Such camerae were figured by Hall (1879) for a group of species from the Schoharie Grit of New York typified by *Orthoceras procerus*.

Internal molds may show on the dorsal region of the phragmocone a series of faint lines, one on the middorsal part of the mural part of each septum. (See fig. 1, SF.) This structure was called the "ligne normale" by Barrande, and the English equivalent of normal line is to be found in the literature. Flower (1939) renamed this structure the *septal furrow* and concluded that this is a middorsal region in which the mural part of the septum is wanting. The structure is quite widespread, and in the group of *O. procerus*, where the mural part of the septum is short, it fails to extend orad beyond the anterior limit of that structure. It extends nearly, though not quite, apicad to the suture. Material of *Leurocyloceras bucheri* from the Laurel limestone of Indiana (pl. 1, fig. 15) shows the septal furrow marked by black material. Interest-

ingly, its alignment in the series of camerae is approximate, but imperfect.

The septal furrow is generally wanting in the Endoceratida and Actinoceratida. The structure is unknown in the Discosorida, and for a better reason; in that order the mural part of the septum is universally short. In the archaic Ellesmeroceratida the furrow has not been observed, and the length of the mural part of the septum is highly variable. In *Eremoceras magnum* (fig. 3) the septum extends forward only for about half the camera length, but at the septum it is thickened into a buttress, and the buttress extends the septum apicad along the interior of the conch for a distance which is appreciable though plainly rather variable. Thinsection examination of *Ectenolites* Firms has failed to show a comparable condition, and the section suggests that the mural part of the septum is relatively long. In *Palaeoceras* of the Plectroceratidae, thinsection material fails in general to show the conch, but clearly the septum increases gradually in curvature, beginning this development rather close to the shell margin, and the mural part can be traced for the full length of the camera. It would appear then that shortening of the mural part of the septum is possibly a specialized condition, one developed several times independently and in various of the nautiloid orders. Again caution must be recommended, for our present observations actually consist of a disparate series of isolated samples.

The suture is the point at which the free part of the septum bends forward as it joins the conch (*see* fig. 1); anterior to this region, the mural part of the septum is developed. There is no discontinuity of parts.* As yet, fossil material has not been known showing a deposit in the anterior corner of the camera at this point. The buttress noted in *Eremoceras* may represent such material, but such an interpretation is not supported by any laminae or textures. The suture is, of course, widely used in taxonomy. In many nautiloids it is relatively simple, but in higher forms may be bent forward into *saddles* or apicad into *lobes* of definite patterns. As previously noted (Flower, 1946), two sorts of patterns may be distinguished, the stable and functional sutures. In the stable suture, the suture is the function of the union of the conch with a septum of fairly simple and uniform curvature, so that in general lateral lobes are found in shells of compressed section; sutures may be straight where the section is circular, or dorsal and ventral lobes may develop where the section is depressed. The last condition, however, is not common, and in shells of depressed section, the curve of the suture is commonly less horizontally than vertically so that a straight suture results. It is largely in the higher coiled genera that functional suture develops. There the often elaborate suture patterns develop, which involve bending of the septum so that it departs markedly from being a portion of a surface of a relatively perfect sphere. In connection with the septum, it is worth noting that a peculiar vertical asymmetry of curvature occurs in the Ascoceratida, and indeed, it was this phenomenon which first suggested the affinities of *Montyoceras* and *Hebetoceras* with the Ascoceratida (Flower, 1941). Even odder asymmetry is, of course, developed in the specialized septa of the higher Ascoceratidae. Curious asymmetry is found again in the remarkable genus *Ecdyceras*, at first attributed on this basis to the Ascoceratida, but which, in the light of further knowledge of the shell, has been given an order to itself (Flower, 1962). Apparently anterior modifications of the septa in

Choartoceras are a development paralleling that of the Ascoceratida, but developed in an independent stock stemming independently from the Michelinoceratida. Odd septa, straight and conical rather than gently curved, have been reported in a few orthocones, but the morphology of such shells as show this structure is too inadequately known to permit a closer evaluation of their relationship than is indicated by assignment to the Michelinoceratida,

The septa' neck is merely a bending of the septum apicad about the siphonal strand. Except for the complications of the conchiolin layer and the anterior layer, known thus far from only *Faberoceras* and *Adamsoceras*, there appears to be no special structure distinguishing the neck from the free part of the septum, nor are there generally retained supplementary layers which show any difference between the neck and the rest of the septum. Foerste and Teichert (1931) and Teichert (1933) have regarded the longitudinal extension of the septum where it bends around the siphonal strand as the *neck*, and the extent of a recurved portion as a *brim*. These two units are convenient for measuring but are not distinct entities. Flower (1939) found their application useful to the Pseudorthoceratidae.

Use of the terms *neck* and *brim* in taxonomy must be approached with caution inasmuch as proportions of the two regions may vary markedly in ontogeny. Examples of such variation have been shown in several works. Flower (1957) showed marked changes in siphuncle proportions in the Actinoceratida; they were earlier noted within the Pseudorthoceratidae (Flower, 1939). Possibly one of the most singular changes is that shown in *Proteoceras* Flower (1955) in which strongly recurved necks and subspherical segments give way in later stages to perfectly tubular segments with the necks parallel to the shell axis.

Elaborate terminology has developed for various shapes and lengths of the septal necks. Hyatt (1900) recognized *holochoanitic* necks, those extending for the length of a siphuncle segment or more. *Ellipchoanitic* necks were shorter; later this term was generally replaced by *orthochoanitic*, for necks parallel to the shell axis, and *cyrtchoanitic*, for necks which are recurved. *Recumbent* necks (Teichert, 1933) are those so strongly recurved that they touch the free part of the septum. Flower (1946) used the term *suborthochoanitic* for short necks which are scarcely recurved, lying on the tenuous boundary between orthochoanitic and cyrtchoanitic. Ulrich and Foerste (1933, 1936) used the term *aneuchoanitic* for examples in which the neck is extremely short and scarcely developed, found largely in the Ellesmeroceratida. A more elaborate terminology was proposed by Teichert and Glenister (1954) involving the following emendations: *macrochoanitic*, a term for necks extending for considerably more than one siphuncle segment, formerly included in holochoanitic; *hemichoanitic*, necks extending for half to three quarters of the length of a segment; *loxochoanitic*, necks moderate in length, their tips pointing obliquely inward and backward toward the siphuncle as in *orthochoanitic*; *achoanitic* was proposed as a shorter term than *aneuchoanitic*.

Hyatt (1900) believed that in his Schistochoanites he had

*The conchiolin layer does not extend between the mural part of the septum and the conch in *Nautilus*, but as the conchiolin layer is rarely evident in fossil material, the matter seems unimportant paleontologically.

a group of nautiloids in which the septa and necks are not developed between the siphuncle and the ventral shell wall. Subsequent investigations have not corroborated this concept. On the contrary, septal structures between the conch and the most extremely ventral siphuncles have been found quite generally. Some difficulty in relation to this question was due, of course, to the fact that many readily extractable specimens appear as internal molds, and where the siphuncle is marginal, septal structures and the conch are commonly removed with the conch and with the external matrix.

The tip of the septal neck is usually simple and pointed, but examples of necks excavated at their tips for the reception of the anterior end of the ring have been observed. Such necks characterize *Proterocameroceras* of the Endoceratida (Flower, 1941; Teichert and Glenister, 1954) and are found in some actinoceroids. They are well shown in our section of *Adamsoceras* (fig. 5, and pl. 2, fig. 8).

Elongation of necks occurs in various stocks. Lengthening

which is progressive in ontogeny is, rather surprisingly, found in the more advanced genera of the archaic Plectronoceratidae; further, it has been found that there the lengthening is always more advanced ventrally than dorsally. Examples of lengthening have been found, though rare and apparently isolated instances, in the Ellesmeroceratidae. It is in the Endoceratida that lengthening of the necks is most commonly seen, and some complex patterns are achieved in the combination of elongated necks and rings, discussed more fully below. There are elongated necks in *Offeyoceras* of the Michelinoceratida. Elongation of the necks is not marked in the Paleozoic coiled orders, nor in the Mesozoic coiled genera, but *Aturia* of the Eocene attains essentially holocoanitic necks (Miller and Furnish, 1938), and much the same condition is shown in sections of the coleoid genus *Spiru/a* (Appella, 1892).

Connecting Ring

GENERAL STRUCTURE

The connecting ring is, in its simplest form, a cylindrical structure which is segmentally repeated in each camera; the segments together form a tube enclosing the main part of the siphuncle. Primitively, one ring extends apicad to the tip of the next, and the line of junction is generally aligned with the tip of the septal neck. However, there are wide variations in form, and this general pattern is subject to considerable modification.

Secretion of the ring is a source of some perplexity. In *Nautilus*, the ring is described as secreted on the outside of the siphonal strand. Flower (1939), in postulating the development of the cameral mantle, concluded that the primitive rings were necessarily secreted within the wall of a primitive siphonal strand, the outer tissues of which then came to form a part of the cameral mantle. He further suggested that the ring might even be mesodermal in origin. Oddly, Mutvei (1957) has misquoted this suggestion as a factual statement and has denied it as categorically.

The ring is, throughout its development in the various nautiloid orders, a structure quite apart from the conch and septa. It commonly retains textures where those parts show no such details, a condition which indicates a very different composition. From the fossil material one may conclude that the ring is dominantly calcitic while those other shell parts are aragonitic, a condition consistent with what is known of the ring in *Nautilus*. Considerable organic material is also involved. Appell (1892) has shown thinsections of the ring, which show it as consisting of a fine outer membrane on the cameral surface, a thicker inner membrane on the siphonal or inner surface, with a broad space between in which there are irregular calcitic pillars with cavities between them; fine, irregular, dominantly transverse membranes connect the pillars of the interior.* It should be also noted that a layer of papillae or tiny pillars, also covered by a membrane, lies on the adoral face of the septum at least near the connecting ring, and Appell's figure shows this material, when traced centrad, merging with the ring and joining it without any definite boundary.

The ring shows great variation in thickness, and it is surprising that it is mainly in the older Nautiloidea that the ring is commonly thick and shows various regions differentiated by distinctive textures. Such thick rings dominate the Ellesmeroceratida, Discosorida, Endoceratida, and Tarphyceratida. They are present only in primitive Actinoceratida, being simplified and thinned in higher members of the order. Oddly, simplification occurs in the transition from the Tarphyceratida (Bassleroceratidae) to the simplest of the Oncoceratida (Graciloceratidae), but in higher Oncoceratida the ring is thickened and extended into the siphuncle as "actinosiphonate deposits." The general pattern of evolution of the ring is shown in the accompanying Figure 6. Oddly, reduction of the ring to a thin, apparently homogeneous, structure occurs independently in several lineages; it develops apparently within the Actinoceratida, is perfected in the Michelinoceratida, and the beginning of such a trend is to be found in the ancestral Baltoceratidae of the Ellesmeroceratida. It is found again in

the transition from the Tarphyceratida to the Barrandeoceratida. Apparently the thickening of the oncoceroid ring, the secondary nature of which has been noted, is found in the older members of the derived Rutoceratida.

Thinsections are needed for the study of these structures, and of rather well-preserved material, for though the ring is more commonly preserved showing textures than are the shell parts previously noted, it, too, is subject to alteration under advanced conditions of replacement and recrystallization. Some anomalies and gaps remain in our knowledge of this structure. However, it is at this time possible to outline a broad pattern of evolution of the ring, in terms of the various older nautiloid orders.

The phyletic relationships of the rings are shown in Figure 6. Dashed lines indicate the distribution of the primitive thick rings, dots the secondary thin homogeneous rings. In the Oncoceratida the rings apparently thin primitively in the Graciloceratidae, and much the same condition maintains over many of the Oncoceratidae, though not the Valcouroceratidae of the Ordovician. The thickening of the ring is apparently cenogenetic and secondary; therefore, a different symbol is used for this group.

In general, we may recognize the following main types:

1. Thick rings showing obscure layering, rarely preserved, and presumably poorly calcified, found in the Plectronoceratina.

2. Thick, well-calcified rings, more or less lens-shaped, in longitudinal section, commonly showing differentiation of layers with dense amorphous material commonly as an inner layer on the siphonal surface of the ring, the remainder of granular material, though there are variations in this pattern.

3. Apical concentration of the dense inner layer, forming an eyelet, developed alike in the higher Endoceratida and in some Tarphyceratida.

4. The discosorid type of ring, confined to the order Discosorida, a structure of considerable complexity, described more fully below.

5. The lobed rings of the Cyrtocerina.

6. Thin homogeneous rings, developed in various orders as noted above.

PLECTRONOCERATINA

In this suborder, the necks outline tubular parts of siphuncle segments, between which are "siphuncular bulbs" in which the part outlined by the ring alone is expanded. Rings in this order show an appreciable thickness, but they are commonly destroyed; certainly they were poorly calcified. That *Plectronoceras* shows the necks commonly destroyed (Kobayashi figured a bulb in only one segment of *P. liaotungense*) led to the suggestion that the remarkable bulbs were adventitious, but they are better shown in the Wanwanian genera *Multicameroceras* and *Sinoeremoceras*, and were substantiated further by material of *Palaeoceras*.

*One wonders whether Appell's sections were made from a dried shell; if so, shrinking of original materials might contribute to the effect seen in his illustrations.

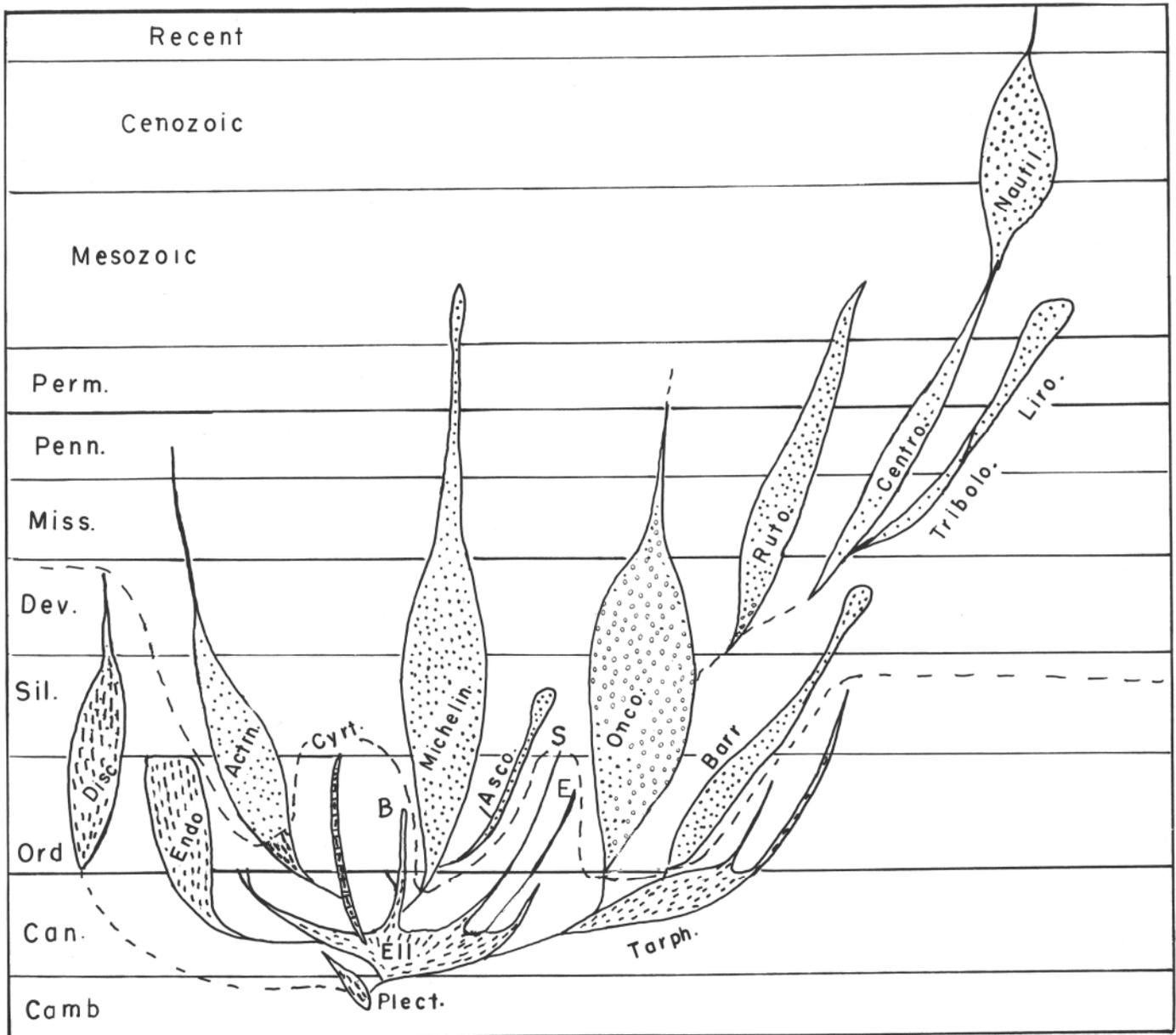


Figure 6

PHYLETIC RELATIONSHIPS OF THE VARIOUS TYPES OF RINGS

Primitive thick rings are indicated by short dashed lines; secondarily thin homogeneous rings, by dots. The apparently secondarily thickening of the ring in the Oncoceratida is indicated by circles. The full

dashed line indicates the general level in the various orders at which simplification occurs. Ordinal and significant lower category names are abbreviated:

- Disc.—Discosorida
- Endo.—Endoceratida
- Actin.—Actinoceratida
- B.—Baltoceratidae
- Ell.—Ellesmeroceratina
- Plect.—Plectronoceratina
- Cyrt.—Cyrtocerina

- Michelin.—Michelinoceratida
- Asco.—Ascoceratida
- S.—Shideleroceratidae
- E.—Ecdyceratida
- Onco.—Oncoceratida
- Tarph.—Tarphyeratida

- Barr.—Barrandoceratida
- Ruto.—Rutoceratida
- Centro.—Centroceratina (Nautilida)
- Naut.—Nautilina (Nautilida)
- Tribolo.—Triboloceratina (Nautilida)
- Liro.—Liroceratina (Nautilida)

Rings show considerable thickness. The type material of *Palaeoceras mutabile* shows a suggestion of a dark inner layer and a lighter outer layer in opaque section. Such differentiation is not generally observable, however, and the condition would have been dismissed as adventitious were it not that such differentiation is more general in the Ellesmeroceratina. In higher genera of the Plectronoceratina, there is gradual elongation of the necks with ontogeny. Rings in such instances still extend from the tip of one neck to the tip of the

next, continuing within the necks. Thus in *Palaeoceras*, there is a progression from the condition shown in Figure 7A to that of Figure 7B. Oddly, lengthening of the necks begins on the venter, and the neck is always longer ventrally than dorsally, at least until a holocoanitic condition is general, so externally a segment would have the rather odd appearance shown diagrammatically in Figure 7C.

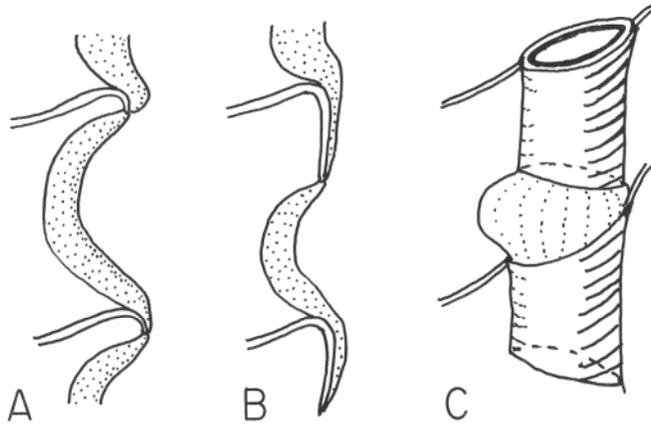


Figure 7
SIPHUNCLE AND RING IN THE PLECTRONOCERATINAE

A. Section showing short neck, thick ring outlining a large siphuncular bulb. B. Section through a segment showing lengthening of the neck and suppression of the bulb. C. Exterior view of a portion of the siphuncle from the anterior part of *Palaeoceras*, showing greater ventral elongation of the neck.

ELLESMERO CERATINA

In the archaic Ellesmeroceratina, the Ellesmeroceratidae, rings tend to be moderately thick and lens-shaped in section, the outer surface concave, the inner surface convex, and generally they are narrow adorally and variously widened adapically. With extreme widening, the apex of the ring is broadly attached to the next adapical septum, extending well outside the bending of the neck. Differentiation of layers shows some variation, part of which is apparently attributable to poor development of layering in early stages, or even mature stages of some small species. In general, with maturity, there may be either obscure differentiation of finer-grained, usually darker-colored layers on both the inner and outer surfaces, or of only such a layer on the inner surface. In *Ellesmeroceras bridgei* from Alaska, clear differentiation of a dark layer on the inner surface is shown (see text fig. 8E), which widens as it is traced apicad. However, another *Ellesmeroceras* from the Lower Canadian of Alaska shows in thinsection such fine-grained layers on both inner and outer surfaces, and they grade into the lighter, more coarsely granular material making up the bulk of the material of the ring (fig. 8F). As a similar pattern is found in *Cyrtocerinina*, shown in material which seems exceptionally well preserved, this pattern is certainly original; it may be that this particular ellesmeroceroid is one trending toward the development of the *Cyrtocerinina*, as the ring as unusual in thickness.

Material studied in opaque sections shows varied development of layering, and though it is hard to estimate the effects of alteration, it is clear that relatively advanced alteration is present in some of the specimens in which such layering is obscure or seemingly wanting in mature rings from adoral parts of phragmocones. Such alteration is certainly advanced in the holotype of *Ellesmeroceras scheii* (fig. 8A), though this species shows rings which are unusually thin and lack the tendency to widen at their adoral ends. An opaque section of the holotype of *Metaellesmeroceras anomalum* shows darkening of the inner surface of the ring, though the boundary of

such an area is obscure (fig. 8B).

In higher families, indications of layering have been found in *Pro tocyloceras* and *Catoraphiceras* of the Protocycloceratidae, and similar layering is present in the derived family Apocrinoceratidae, which is little more than Protocycloceratidae in which the siphuncle segments have become convex in profile and slightly expanded in the camerae. Indeed, it was such layering that showed the first indication that *Apocrinoceras* was an ellesmeroceroid and not a discosorid, to which group it had been assigned by Teichert and Glenister (1954; see Flower, in Flower and Teichert, 1957). In the Baltoceratidae, layering has been observed though imperfectly preserved, in *Rioceras* and *Baltoceras* (fig. 81). It is to this family that *Loxochoanella* is to be assigned, a genus originally attributed to the Ellesmeroceratidae. It shows specialization in that dense amorphous material is concentrated not only on thin layers on both the inner and outer surfaces but also at the tip of the ring (fig. 8G). *Cartersoceras* is, in most respects, little more than a *Murrayoceras* in which the siphuncle segments become slightly convex in outline, but a thinsection of *C. shideleri* shows a peculiar ring, composed of honey-yellow material, in which numerous fine, longitudinal laminae are visible, but with no differentiation of inner and outer layers. In the small family Cyclostomiceratidae, rings are convex, thickened apically, and show differentiation of a dark inner layer.

In summary, the Ellesmeroceratina show in general relatively thick rings in which there is some variation in the differentiation of layers, but such differentiation is generally developed in rings from mature parts of the shells, though generally wanting or poorly developed in young stages. There is indication of some variation in clarity and location of such layers, which requires further exploration as suitable material becomes available for sections, but it is possible now to recognize a general pattern that prevails throughout the Ellesmeroceratina.

Good material for the study of diaphragms by thinsection has been sparse, but in general, both opaque sections and thinsections indicate that the diaphragms are merely extensions of the rings across the cavity of the siphuncle. They are delayed beyond the secretion of the primary part of the ring, however, and may be confined to apical parts of siphuncles in some genera, though apparently they are distributed over a wider length of the siphuncle in such genera as *Robsonoceras* and *Boreoceras*. Color differentiation, though imperfectly indicated, is probably more general than present observations suggest, for loss of differentiation is logically associated with such alteration that certainly its loss is due in large part to loss or destruction of parts by alteration. That its presence might be an accessory staining effect due to inorganic phenomena is unconvincing in the light of the material so far examined. In some, but not all instances, diaphragms appear to be extensions of only the dense amorphous layer of the siphonal surface of the rings.

Diaphragms have been observed in the Plectronoceratidae, are general throughout the Ellesmeroceratidae, and are retained in late Canadian Protocycloceratidae, and may be general in that family, one of the two major post-Gasconade lineages of the Ellesmeroceratina, but are certainly wanting in the other major lineage, the Baltoceratidae.

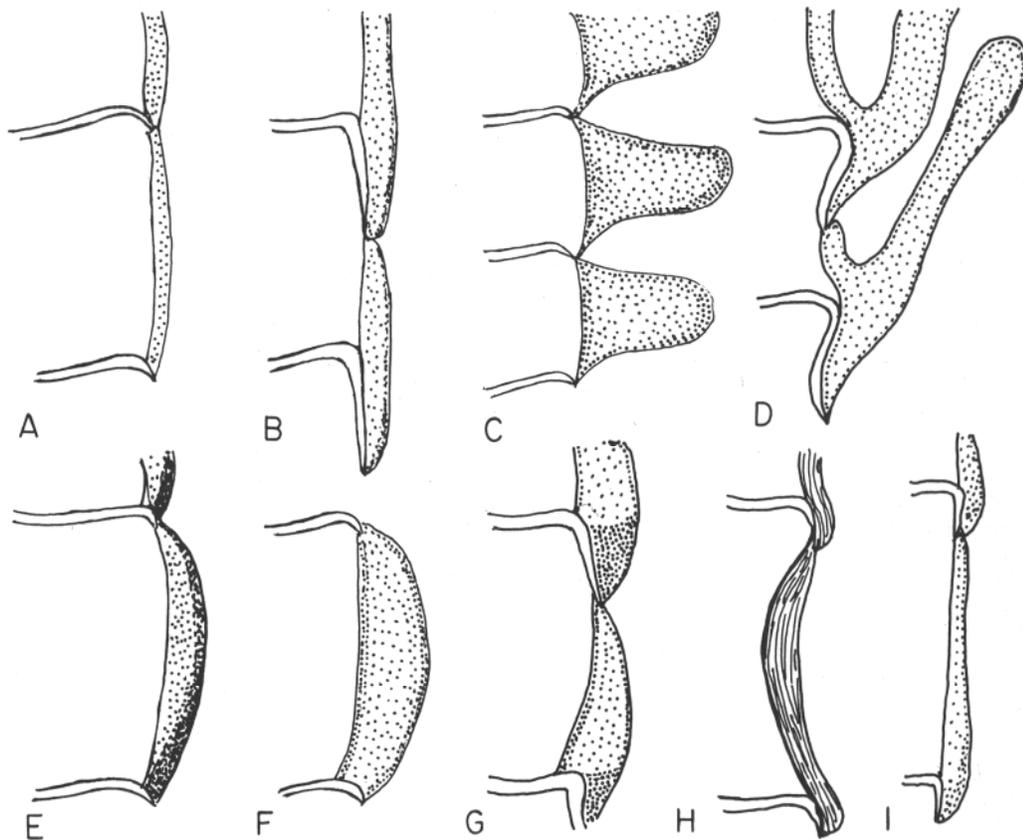


Figure 8

RINGS OF THE ELLESROCERATINA AND CYRTOCERININA

A. Apparent relatively thin and homogeneous ring as seen from an opaque section of the holotype of *Ellesmeroceras scheii*. B. Lengthening of neck and obscure differentiation of a dark inner portion, from an opaque section of the holotype of *Metaellesmeroceras anomalum* Flower. C. Inflated rings of *Cyrtocarina*, with differentiation of outer fine-grained portion and of inner more coarsely granular portion, but without clear differentiation of the regions. D. Reconstruction of *Bathmoceras*, after Holm, 1899. The indication of growth lines at the tip of the lobe of the ring is not fully substantiated. E. Differentiation of thin, dark, inner layer and thicker, outer, granular layer as seen in *Ellesmeroceras bridgei* Flower, 1941. F. More obscure differentiation of fine-grained marginal layers on both external and internal surfaces, from *Ellesmeroceras* sp. from Alaska. G. Differentiation of thin bands on inner and outer surfaces, and also at the tip in *Loxochoanella*, modified from Teichert and Glenister, 1954. H. Lamellate texture in the ring of *Cartersoceras*. I. Obscure differentiation of fine-grained, darker, inner surface, as indicated in *Rioceras* and *Baltoceras* of the Baltoceratidae.

CYRTOCERATINA

In this order, the rings are thickened and extended as lobes into the cavity of the siphuncle. As yet, only three genera are recognized, *Eothinoceras* of the Middle Canadian, *Bathmoceras* of the late Canadian and early Ordovician, and *Cyrtocarina*, known to range from the Lowville, early Mohawkian, to the close of the Ordovician. Teichert and Glenister (1954) have published a thinsection of *Eothinoceras*, but the enlargement is too small to show textures within the ring. In *Cyrtocarina*, it is clear that the rings are composed of granular material in the centers, grading to fine amorphous material on both the inner and outer surfaces. No growth lines are developed. From what can be learned from the published evidence, the condition in *Eothinoceras* is apparently closely similar. *Bathmoceras* was studied by Holm (1899), and only his illustrations are available. He shows rings extended into forward-pointing lobes of rather remarkable form. His sections show these lobes as true parts of the ring, with some differentiation of marginal materials. Their form is shown in Figure 8D. The growth lines suggested for the tip of the lobed rings are

theoretical. Mutvei (1957) has asserted that the lobed structures are independent of the true ring, and a supplementary "deposit," but as yet further substantiation of this conclusion has not been published. If this assertion is true, it will serve to lessen the morphological gap which now seems to exist between *Bathmoceras* and *Polydesmia*. The writer has postulated origin of the Actinoceratida through *Polydesmia* by development of the lobed "annuli" of *Polydesmia* from the lobed ring of *Bathmoceras*. Such a process involves retardation of development of what was originally the thickened part of the ring, with further textural differentiation.

ACTINOCERATIDA

As yet, few thinsections for the study of the ring have been made for the genera of the Actinoceratida. Previously, it was believed that such rings are universally homogeneous and, except for *Polydesmia*, relatively thin.

A section of *Adamsoceras* of the Wutinoceratidae was

made, in part, because it seemed that the Wutinoceratidae represent an intermediate stage from the ancestral thick ring of *Polydesmia* and the thin rings of Chazyan and younger Actinoceratida. The results, shown in Figure 5, and in Plate 27, Figure 8, were surprising, showing the ring to have a dense carbonaceous anterior end, set into a concavity of the tip of the neck. Beyond this there is a long free portion showing transverse structures. In part, such structures seem uniform between an inner and an outer margin; in part, there is a suggestion of such fibers or pillars different in size and spacing in inner and outer portions. Interpretation in terms of fibers or in terms of pores through the ring is not yet certain. The matter becomes of some interest in view of the fact that this is the only example so far found in a Paleozoic nautiloid showing something suggesting the pillars with spaces between, which Appellof figured for *Nautilus*. The apical part of the ring shows darker coloration and both longitudinal and transverse lines. Under the discussion of the septum, anterior and posterior layers of the septum were noted, of which the former extends for some distance between the apical part of the ring and the septal neck.

Sections of younger actinoceroids have been made. In the main, they have been unrewarding, but one section of an *Actinoceras* from the Chaumont of Watertown, New York (pl. 6, fig. 2), shows similar transverse structures in the main free part of the ring, though anterior and apical regions lack

the dark color or distinctive texture shown in *Adamsoceras*. The material suggests 'that rather exceptional conditions of preservation are required for the preservation of textures in the rings of the actinoceroids. Material from Newfoundland was sectioned, representing *Adamsoceras*, but shows more advanced silicification than the Nevada material, and differentiation within the ring is lost. Apparently, purely calcitic preservation may involve loss of structure also. A thinsection of *Polydesmia* would be of exceptional interest, for this is the oldest genus of the Actinoceratida yet known, and has rings so thick that they were interpreted as holochoanitic necks (Kobayashi, 1946), but material has not yet been available for such a study. The genus is rare, confined to eastern Asia, the known specimens are largely types, and obtaining more material from that region is not now possible.

ENDOCERATIDA

Primitive Endoceratida, the older Proterocameroceratidae, show necks and rings similar to those of the Ellesmeroceratidae. Width and differentiation of parts tend to vary, as in the Ellesmeroceratida, but in general the rings are widened, either lens-shaped in section or definitely widened apically, and there is some variable differentiation of a dark, thin, inner layer and a broader, lighter, outer layer (fig. 9A, B). With elongation of the septal neck (fig. 9C) there is a trend of the

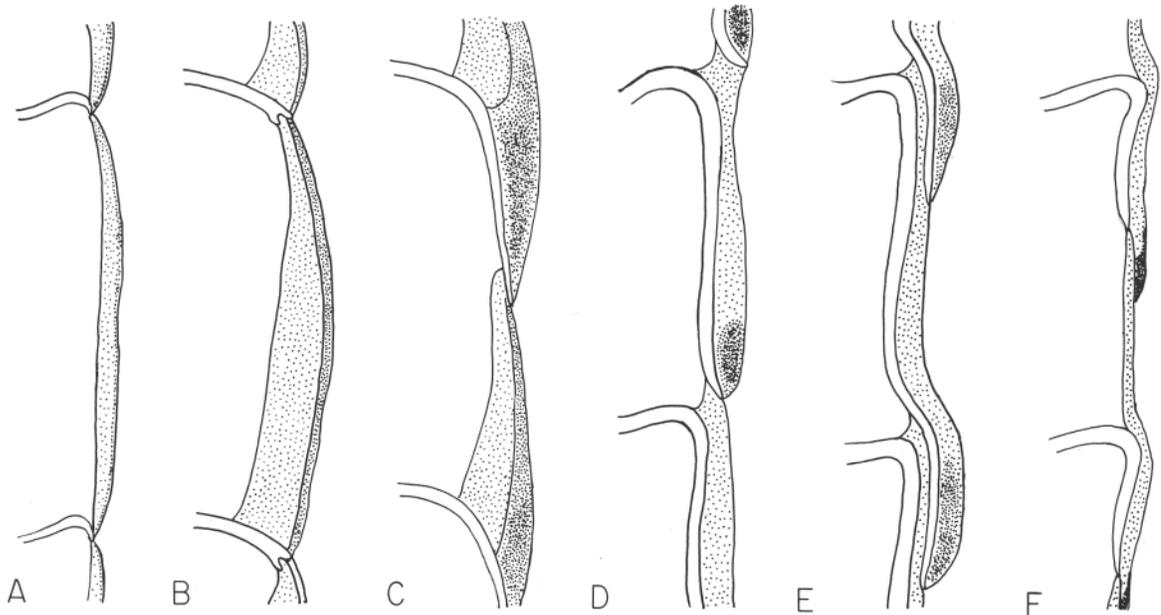


Figure 9

SIPHUNCLE WALLS IN THE ENDOCERATIDA

- A. Short necks, rings relatively thin, with poor differentiation of layers, from the early stages of *Proendoceras annuliferum*
- B. Short necks, excavata at the tips, ring greatly widened apically, with light, outer granular zone and thin dark zone, from *Proterocameroceras brainerdi* (Flower, 1941)
- C. Ring showing apical widening, with inner dark zone partially concentrated at the tip, an incipient stage in the development of the eyelet, from *Clitendoceras*
- D. Necks holochoanitic, dark material concentrated in a perfected eyelet, in the tip of the ring. From *Vaginoceras oppletum* Ruedemann
- E. Necks further elongated, with eyelet restricted as in D, from *Dideroceras*
- F. Septal necks only moderately elongated, but rings extended and lapping one on the other, with the eyelet in the tip of the ring, from *Williamsoceras*

dark inner layer to thin anteriorly, while at the same time it tends to be concentrated apically in the part of the ring lying within the adapical septal neck. With further development in this direction, all the fine, dense, amorphous material is concentrated apically in the *eyelet*, but the elongation of the eyelet is not equivalent to the length of the ring enclosed in a septal neck. With still further elongation, as in *Dideroceras* (pl. 3, fig. 4), the eyelet remains unlengthened. In *Williamsoceras*, the eyelet is commonly short; here necks are relatively short, and the end of one neck overlaps the base of the next, originally the next adapical ring.

TARPHYCERATIDA

Investigations of the rings in the Tarphyceratida rest as yet upon too few observations. It is evident, however, that in general the ring is similar to that of the Ellesmeroceratida and the primitive Endoceratida in a great part of the order, showing an outer granular zone and a dense amorphous zone, generally much thinner, on the inner surface (Flower, 1941). In *Eurystomites*, where the neck is slightly elongated, the amorphous material is concentrated apically into an eyelet, exactly as in the higher Endoceratida. It should be noted that Sweet (1958) has found thick complex rings in the Lituitidae, and on this basis has regarded that family as derived from the Tarphyceratida rather than, as was previously thought (Flower and Kummel, 1950) from the Barrandeoceratida. This conclusion seems eminently correct. Structures within the lituitid ring involve some peculiarities, including evident large pores in the ring, and extension of the outer (peripheral) layer of the ring along the anterior face of the septum. The evidence so far published fails to show the anticipated differentiation in the main part of the ring, other than the distinction of two sharply separated layers.

THE DISCOSORID RING

It has been found that the rings in the Discosorida show a peculiar differentiation of parts. What is known of such differentiation has been published to some considerable extent by Flower and Teichert (1957); there have been no significant additions to this information and it need only be summarized here.

Ruedemannoceras, the oldest and simplest genus so far known, shows a ring (fig. 10A) in which there is differentiated a broad anterior region of attachment, the vinculum (fig. RDA), beyond which the free part of the ring shows (b) an anterior granular zone, (d) an apical chitinoid zone of fine-grained yellow material set off at either end by curved bands of amorphous material (c, e) and followed by an apical part, the bullette, within which an inner layer (f) and an outer layer, the latter next to the septal neck (g), are differentiated. A thin section of *Westonoceras* shows closely comparable structures, with the vinculum (a), granular zone (b), chitinoid zone (d) bounded by curved amorphous bands (c and e), with the bullette here swollen, but still showing the two layers. Comparable parts have been found in such other Discosorida as have been sectioned. In general the apical bullette of two layers is distinguishable whether swollen or not, and the anterior vinculum is clear. There is evident some variation in the differentiation of the free parts of the ring which is greater than can be accounted for by inorganic factors of replacement

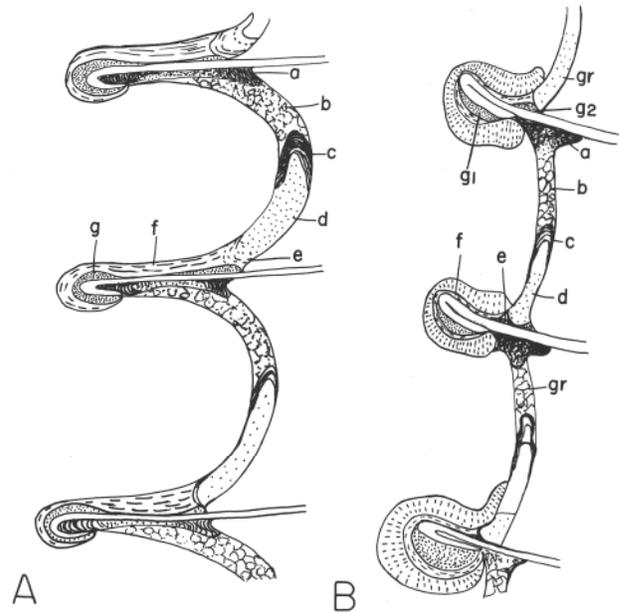


Figure 10

DIFFERENTIATION WITHIN THE DISCOSORID RING

A. *Ruedemannoceras*

B. *Westonoceras*

a—vinculum

b—granular zone

c, e—amorphous bands

d—chitinoid zone, bounded by the two amorphous bands

f—inner zone of the bullette

g—outer zone of the bullette

g₁—part of g, concentrated on the apical side of the neck

In *Westonoceras* (B) parietal annular deposits, fibralia, develop within the siphuncle.

and recrystallization. The extent of such variation and its phyletic significance has not yet been fully explored, largely because of the limitation of available material for the required study by thinsection. In particular, study of the Mandaloceratidae is needed to determine whether the "obstruction rings" are true bullettes which develop processes like the actinosiphonate deposits of the Oncoceratida, or whether they are a supplementary structure.

ONCOCERATIDA

Oddly, while in the Graciloceratidae, seemingly the archaic stock of the Oncoceratida, the rings are thin and seemingly homogeneous, in various lineages within the Oncoceratida the necks thicken and finally are produced into rays extending toward the siphuncle center. These structures, the actinosiphonate deposits of Hyatt (1900), are outgrowths of the connecting ring extending into the cavity of the siphuncle where, plainly, they develop independently in at least two lineages in the order. Form varies somewhat, but clearly the "deposits" represent thickenings of the ring developed in conformation with a previously established pattern of siphonal tissues. In details there is wide variation in form; probably our

present observations have not brought to light all such variations, but deposits may extend as rays which are simple or pectinate. Lobes may be homogeneous or may show differentiation of various regions. Apparently some rays seem to extend from one segment to the next, while others are segmentally repeated and may extend only short distances orad and apicad from a swelling of the ring at the septal foramen.

In the Ordovician, the Graciloceratidae, with small tubular siphuncles, and the Oncoceratidae, in which the siphuncles are expanded, are not known to have rays developed. However, the Valcouroceratidae represent a lineage in which rays are generally present, extending from the Chazyan through the Richmond, at the close of the Ordovician, continuing, though not many species are known, through the Silurian, and expressed as *Herhinteroceras* in the Lower Devonian of North America. *Jovellania*, confined to Europe, is a straight shell of triangular section, a derivative of this general lineage.

Flower (1943) found in *Valcouroceras* variation from (1) forms with slightly expanded siphuncle segments, the ring relatively thin, to (2) forms with more expanded segments, essentially scalariform in vertical section, with only slight thickening of the ring to (3) forms with more expanded, rounded segments, the ring thickened, and showing slight swelling at the tip to (4) more expanded segments in which the ring is extended as actinosiphonate lobes into the cavity of the siphuncle (see fig. 11A-E). Material was unfortunately very limited, and the above observations depend upon opaque

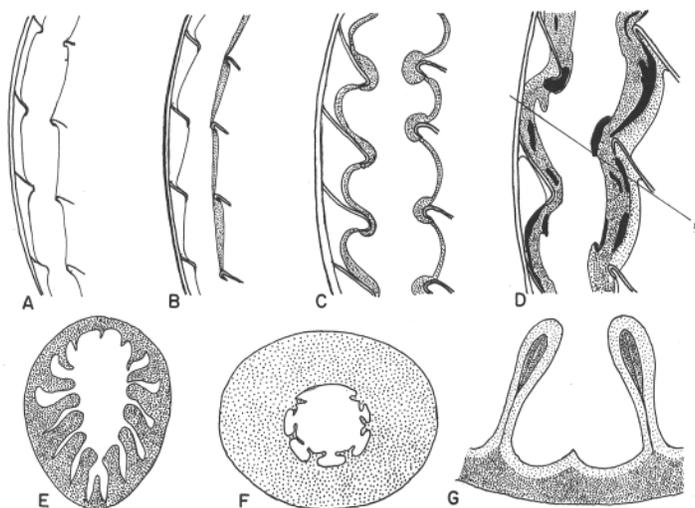


Figure 11

RAYS OF THE ONCOCEROID RINGS

A. Vertical section of siphuncle of *Valcouroceras*, early segments lacking expansion of the ring or any material expansion of the segment in the camerae. B. A more advanced condition from a later growth stage, showing the segment more widened, scalariform, with thickening of the ring apparent only dorsally. C. A later stage, showing rings widened, the outline curved, rings moderately thickened over most of their length, but greatly inflated apically. D. Longitudinal section of a later stage, showing widening of the ring, differentiation of materials within, and extensions as rays into the siphuncle. E. Cross section of the same form, showing symmetry of the lobes of the ring. F. Cross section of the siphuncle of *Brevicoceras pompeyense* at the septal foramen, showing section through the apical annular thickening of the ring, with short bifurcate extensions. G. Drawing of a portion of a cross section through the ring of *Archiacoceras*, showing differentiation of layers and axes of the rays.

sections.

At the same time, a study was presented involving a series of sections in *Archiacoceras* of the German Middle Devonian, in which rays are repeated segmentally but are so extended that those of adjacent segments fuse. In this genus, rays are club-shaped, rounded and widened distally, show concentric layering and an axial rod in cross section.

In the Brevicoceratidae of the Devonian, rings thicken over the septal foramen, and from this thickening short rays extend for a short distance toward the center, commonly bifurcating, and extend for slightly greater distances orad and apicad of the thickening (Flower, 1938, 1943).

Most forms showing actinosiphonate structure are rare, but a good suite of specimens of *Augustoceras*, in the Leipers formation of southern Kentucky, permitted a fairly extensive examination and thinsections were made through several siphuncles. From these sections, a reconstruction of the siphuncle was possible, as shown in Figure 12.

The lineage of the Valcouroceratidae, as developed in the Ordovician, is shown in Figure 13. The development of rays only in mature portions seems confined to *Valcouroceras* of the Chazyan, though *Minganoceras* is known from one specimen of one species, so we have no criterion as to whether it shows a similar ontogenetic progression. Clearly, in *Augustoceras* there is no evidence of early stages in which the rings

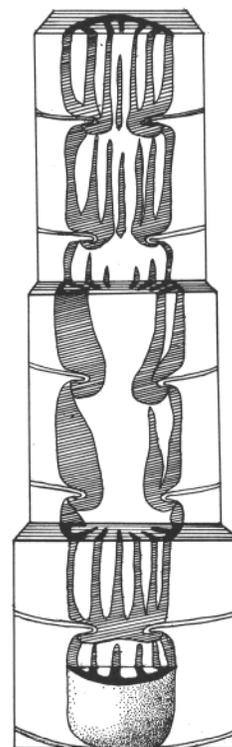


Figure 12

BLOCK DIAGRAM OF THE SIPHUNCLE OF *Augustoceras*

Showing exterior of the ring at the very base, but with sections at progressively deeper levels through the siphuncle above. The rays are shown here as segmental units, but with remarkably perfect fusion, and good alignment of the rays in successive segments.

remain thin, and while very earliest stages have been wanting, there is clearly no such marked ontogenetic progress here as there is in *Valcouroceras*. Though less material was available for those genera, specimens of *Kindleoceras* and *Manitoulinoceras* were available showing siphonal structure essentially similar to that of *Augustoceras*. Oddly, in a considerable suite of material of *Manitoulinoceras*, only two specimens were found showing good rays, suggesting that they were possibly delayed in appearance and that they then were developed

fairly rapidly throughout the length of the siphuncle only in essentially mature individuals.

Dechaseaux (1940) presented a study of the rays of *Jovellania*, but the results, disappointingly, did not involve the recognition of the identity of the rays with the rings; thin sections were not attempted.

Barrande's plates show numerous examples of rays in sec-

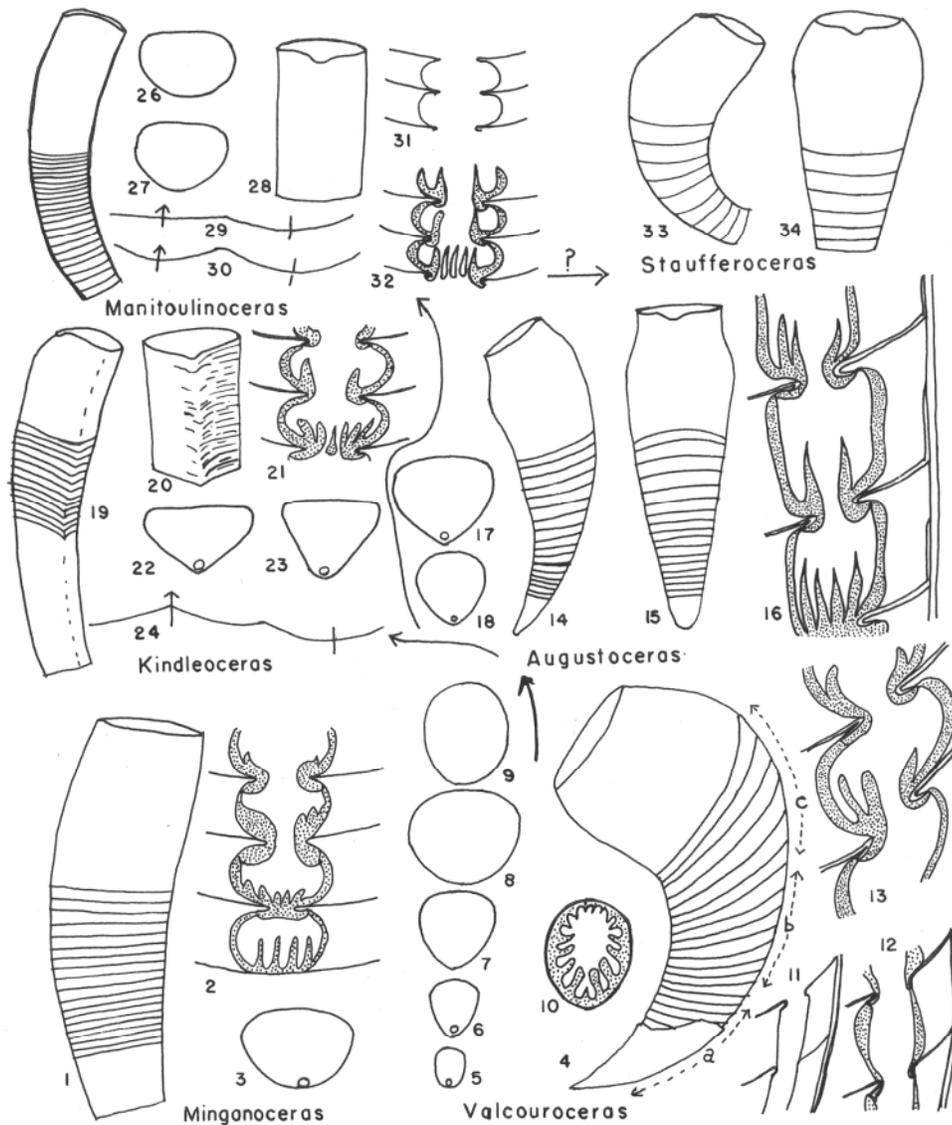


Figure 13

ORDOVICIAN VALCOUROCERATIDAE

Mingonoceras. 1. Lateral view; 2. horizontal section of siphuncle, ground from the venter near midlength of the type; 3. cross section.

Valcouroceras. 4. Lateral view of a moderate-sized species; 5-9. variations in cross section; 10. cross section of a mature siphuncle segment showing symmetrical development of rays; 11. early siphuncle segment, scarcely expanded, with thin rings; 12. a later stage, slightly expanded with ring moderately thickened; 13. mature segment, with thickening of ring extended as rays.

Augustoceras. 14. Lateral view, venter on right; 15. ventral view; 16. a vertical section through the siphuncle, showing rays as extensions of the rings; 17, 18. two cross sections showing variable widening and flattening of the dorsum.

Kindleoceras. 19. Lateral view, dorsum on right; 20. ventral view of a living chamber; 21. siphuncle, as seen from a section ground from the venter; 22, 23. cross sections, showing variation in proportions, but with the consistently triangular cross section; 24. projection of a suture

Manitoulinoceras. 25. Lateral view; 26, 27. cross sections, showing broadly rounded condition with variable dorsal flattening; 28. ventral view of a living chamber; 29, 30. variable development of dorsal and ventral lobes, shown in projection of the suture; 31. outline of siphuncle segments; 32. a siphuncle as seen from the ventral side with rings thickened.

Staufferoceras. 33. Lateral view, venter on left; 34. ventral view.

tion in various of the Silurian and Devonian Oncoceratida but are not enlarged sufficiently to show details. Teichert (1940) presented a study of some actinosiphonate brevicones from Australia and showed elaborate bipectinate rays in *Danaoceras subtrigonum*. Flower (1943) showed somewhat similar but more regular bipectinate rays in *Actinomorpha*.

Clearly much wider investigations of the rays in the Oncoceratida are needed in regard to variations in shape, particularly, and whether some rays are actually continuous or whether they are segmental units showing remarkably perfect fusion. Certainly fusion is demonstrable in the few forms in which investigations have been adequate, but with delay of thickening of the rings to late maturity, and subsequent rapid growth, what were originally segmental structures could become essentially continuous. Further, there is indication of differentiation of textural regions in the rings, a matter which has not been fully explored. However, the Oncoceratida clearly have no differentiation of regions in the ring comparable to that found in the Discosorida.

Oddly, Mutvei (1957), who fails to see the rays as other than a "deposit" and never considered their nature as outgrowth of the rings themselves, stated that nothing was known of the detailed structure of the "radial deposits."

THIN, APPARENTLY HOMOGENEOUS, RINGS

As indicated in Figure 6, at several points in the phylogeny of the Nautiloidea there is reduction of the primitively thick ring within which various regions can be differentiated to an apparently thin, homogeneous structure. Such rings may also be fragile, and in some material it is not uncommon to find the ring generally destroyed. Only in one genus, *Leurocycloceras* (Flower, 1941A) is the general absence of a well-calcified, ring apparently real. Thin and apparently homogeneous rings develop at the inception of the Michelinoceratida. As noted

above, there is a trend in the same direction within the Actinoceratida, apparently perfected in the Ormoceratidae, at least. The transition from the Tarphyceratida to the Barrandoceratida was drawn at the point at which the primitive thick rings give place to thin, homogeneous rings. The Oncoceratida present some perplexity in relation to the ring, for apparently thin, homogeneous rings develop in the Graciloceratidae, at the inception of the order, but secondary thickening takes place in more specialized members of the group. Such thickening is retained in the archaic genera of the Rutoceratidae, but in higher members of that family, and in derived Rutoceratida and Nautilida, no differentiation of structures within the ring has been observed in fossil material. Appelles (1892) sections of the shell of *Nautilus* show a ring with vertical pillars and some cavities, between two surface membranes, of which the inner one is the stronger and more prominent. Nothing of the sort has yet been reported in fossil material,* not even in sections of Cenozoic Nautilina. It must be noted that where the rings are thin and apparently homogeneous, there has not been a general effort made to examine the rings for fine structure, a situation which may in part account for the present anomaly. One might expect rings in the Nautilida and higher Rutoceratida to show an inner membrane at least, with fibrous structure on the outside, and perhaps even a trace of the finer outer membrane. Few of the siphundes of these younger coiled genera have been studied from thinsection. Oddly, one thinsection of *Buttsoceras* (Flower, 1952A, pl. i, fig. 9) shows a ring with a thin dark band prominent on the inner surface, and the outer part made up of crystalline material, and showing an irregular outer surface. Though suggestive of the condition of *Nautilus*, it is not certain that the outer irregular surface may not be adventitious.

*Except the primitive Actinoceratida which are remote from the ancestry of *Nautilus*.

The Siphon or Siphuncle

The strand which extends through the camerae of *Nautilus* was first termed the *siphon*. Two considerations were involved in the substitution for the term *siphuncle*: this was done, first, to explode the myth that *Nautilus* could alter the amount of gas in the camerae by means of this structure, and second, to remove possible confusion with the siphon of other molluscs. Actually, it is a rather far cry from the siphons developed in the Pelecypoda to the siphon, the hyponome, of *Nautilus*. The two structures are similar but not identical specializations, and similar restricted openings of the mantle cavity are not general in the gastropods and are undeveloped in the Monoplacophora and Polyplacophora, while in the Scaphopoda a very different respiratory arrangement has been made. While the term *siphuncle* is too entrenched in the English paleontological literature to be displaced, we can only look with envy upon the French, who, apparently able to see the lack of relationship between the siphuncle of *Nautilus* and the pelecypod siphons without becoming worried by the terminology, use the term *sipho* for the Cephalopod siphuncle. For brevity and euphony the writer has preferred to speak of *siphonal tissues* and the *siphonal strand*, as well as *siphonal deposits*, rather than to employ the long term *siphuncle*.

Some authors have used the terms *endosiphuncular* or *intrasiphuncular*. The use of such prefixes is cumbersome and pretentious and certainly is unnecessary unless *extrasiphuncular* structures are also spoken of. There is no need for such a term; structures outside of the siphuncle are more simply termed *cameral*.

Though it is essential to recognize that the neck and the ring, commonly thought of as the two essential parts of the siphuncle, are very distinct, it does not follow that the consideration of the siphuncle as an entity should be abandoned. The two structures may be so integrated as to form a tubular entity in which the neck and ring can be distinguished only by thinsection examination. Such complex siphuncles are largely but not completely confined to the order Endoceratida. The siphonal deposits are also a part of the siphuncle proper. They appear independently in the various orders, vary in form, composition, texture, and origin, and are discussed in a section by themselves. Ruedemann (1905) proposed the term *ectosiphuncle* for the siphuncle wall of necks and rings, and *endosiphuncle* for internal hard parts. The term *endosiphuncle* is convenient when applied to the inner parts of the siphuncle in the Endoceratida, where the parts, though they may be secreted periodically, show no segmentation in accord with that of the phragmocone, but it is less fortunate in its application to other cephalopods, where the structures are nonhomologous and usually fail to develop a single relatively so/id structure, except by fusion or segmental elements, each connected primitively with a siphuncle segment.

Developments of the siphuncle segments are best summarized in terms of the orders of the Nautiloidea.

Plectroceratina.—Here (see fig. 7) the siphuncle segment expands into siphuncular bulbs between the necks. In *Plectroceras*, necks are very short and the bulbs are prominent. In higher genera, the necks lengthen gradually with ontogeny, and elongation appears first and is always most advanced on the ventral side. With such lengthening the bulbs become restricted and finally lost.

Ellesmeroceratina.—In this suborder the siphuncle shows segments which are faintly concave to tubular in outline, composed in general of rather short necks, some, indeed, vestigial, and thick rings. In *Clelandoceras* (?) *rarum* and in the small family Apocrinoceratidae, the siphuncle segments are faintly expanded in the camerae.

Cyrtocerina.—This suborder is characterized by rings greatly extended into the cavity of the siphuncle. The lobes of the rings are relatively simple in *Eothinoceras* and *Cyrtocerina*, but are immensely projected forward in *Bat hnoceras*, extending for the length of more than one segment.

Endoceratida.—It is in this order that, with elongation of neck and ring, the two structures may become complexly integrated. Various types of structure are shown in Figure 9. It should be noted that with elongation of the necks, the anterior end of the ring which primitively begins at the tip of the neck may be extended forward between the necks. Elongation ordinarily involves the extension of the apical end of the ring to the tip of what was originally the next apical neck. In a few instances, however, rings may be extended beyond the necks, one lying on the next ring for some distance. Even with thinsections, rather well-preserved material is needed to determine the structure with certainty. Such material has not been available as yet for all genera. The preservation of many endoceroids as only siphuncles, usually endosiphuncles, with the necks and, commonly, the rings exfoliated, presents a bulk of material in which examination of relationships of necks and rings is simply impossible. Only two genera are known which depart from the usual tubular or concave profile of the segments. Segments are broadly rounded in *Tasmanoceras* Teichert and Glenister, and a genus yet undescribed from the Ordovician of Alaska shows segments short and strongly expanded, so that the siphuncle looks like the external shell of a cephalopod with closely spaced annuli.

Discosorida.—In this order siphuncle segments are expanded in various ways. *Ruedemannoceras* is the only genus known other than the Plectroceratina which shows in the young siphuncular bulbs.* In later stages expansion of the segment involves recurved necks, and the apical end of the ring may be broadly adnate to the apical septum outside of what was originally the point of contact, forming an area of adnation. Where necks are recumbent, the anterior end of the ring, the vinculum, is commonly broadly attached to what was originally part of the free part of the septum. There is some variation in degree of expansion and shape of segments in ontogeny. This is best exemplified in *Westonoceras*, in which early segments, though expanded at their ends, are straight over much of their length, and the segments are subquadrate in longitudinal section. However, in anterior segments the outline is much more broadly rounded. Form variations of segments has been shown by Flower and Teichert (1957).

Actinoceratida.—Here segments are again expanded and in

*Initial shell stages are not yet known for other genera of the order.

this order, the recumbent necks and areas of adnation are, if anything, more extremely developed than in the Discosorida. Segments are broad from the early portion of the shell. Some genera maintain a typical segment form to maturity but in others, particularly in *Actinoceras*, there is a gradual simplification of outline with ontogeny. It is now evident that *Leurothoceras* was erected on the basis of such simplified segments as are found in late growth stages of *Actinoceras* (Flower, 1957). In some genera, notably *Kochoceras*, *Lambeoceras*, and the Huroniidae, recumbent necks and broad areas of adnation develop so that broad areas of the free part of the septum are integrated into the siphuncle. Here, such parts of the septa may be curiously sinuate as seen in vertical section.

Michelinoceratida.—In this order segments are primitively tubular, but expansion develops in various orders and in *Offleyoceras* holochaoanitic necks are attained. Where siphuncle segments expand, various ontogenetic progressions of outline may develop. In the Proteoceratidae relatively early segments are broadly expanded, and there is a gradual adoral simplification of outline until mature segments may be tubular. The very earliest stages of these genera remain as yet unknown. In the Pseudorthoceratidae there is general adoral progression in expansion, with only the slightest simplification of outline at late maturity, here caused by progressive widening of the septal foramen while the maximum diameter of the segment is stable.

Ascoceratida.—Here the siphuncle shows a marked succession of three types of segments (Flower, 194 B). Planoconvex segments, slightly expanded ventrally, straight dorsally, characterize the earlier portion and continue to maturity in *Montyoceras*. In *Hebetoceras*, mature segments in the last few camerae are slender but biconvex. A third type, broadly expanded, the moniliform segment, appears in the latest camerae of *Probillingsites*. In younger forms the moniliform segment is associated with the ascoceroid sutures, and the ontogeny is accelerated. In some forms the camera at the base of the mature shell, from which the early slender portion is molted, show seemingly two or even three segments in outline. Thin-section examination is needed to determine whether such a camera involves originally several camerae, but with the septa suppressed.

Tarphyoceratida.—Here siphuncles are primitively very like those of the Ellesmeroceratida, of tubular to concave segments with thick rings. Only slight elongation of necks is known in the order.

Barrandoceratida.—This order is distinguished from the Tarphyoceratida by the development of thin, homogeneous rings. Primitively, siphuncle segments are tubular, but expanded segments develop in the Apsidoceratidae of the later Ordovician and again, in a different way, in the Silurian

genus *Uranoceras* and still again in the higher Rhadinoceratidae of the Devonian.

Ecdyceratida.—In this order, erected for the odd genus *Ecdyceras* (see Flower, 1962), the early siphuncle segments are tubular and thick-walled, even developing diaphragms. Later segments show a reduction to thin, homogeneous rings, and segments may be expanded slightly and faintly fusiform in outline.

Oncoceratida.—Here siphuncles are primitive tubular, but they remain so throughout the shell only in the archaic Graciloceratidae. Forms with expanded segments show gradual widening of the segments in ontogeny, best seen in Ghazyan Oncoceratidae and Valcouroceratidae; in younger forms, the early subtubular segments are more restricted apically, and such early stages are not evident in Silurian forms at all. In addition to broadly expanded segments, some members of this group, notably the Nothoceratidae and the Devonian endogastric genera *Bolloceras* and *Paracanthoceras*, as well as *Cyrtoceras*, develop concave segments. Transitions from the convex to the concave have not been noted.

Rutoceratida and *Nautilida*.—A few primitive members of the order Rutoceratida retain expanded segments, but for the most part siphuncles are tubular and simple in construction. The same condition holds, in the main, in the Nautilida. One should note, however, expansion developed in *Germanonauutilus* and the lengthening of the necks to a holochaoanitic condition in *Aturia* (Miller and Furnish, 1938); this last development parallels exactly the lengthening as noted in the Endoceratida, except that the rings are thinner and relatively simple.

It must be emphasized that the outline of the siphuncle segments may be very different dorsally and ventrally. The contrast is particularly marked in those forms in which the siphuncle passes through a steeply inclined part of the septum, instead of one which is relatively transverse. Where siphuncle segments are expanded, the necks in such instances may be most sharply recurved dorsally, most gently recurved ventrally; similarly, at the apical end of the segment, the area of adnation is marked ventrally, but vestigial or wanting dorsally. This condition applies similarly to the Oncoceratida, Actinoceratida, and some Michelinoceratida. Where marginal siphuncle segments are tubular, the contrast is less marked, but the initiation of lengthening of the neck on the venter in the Plectronoceratidae has already been noted.

Siphonal deposits are, of course, as integral a part of the siphuncle as the necks and rings. They are discussed separately below. Various types appear independently within various of the orders.

Siphonal Deposits

GENERAL RELATIONSHIPS

Under this heading are considered those structures within the siphuncle which are not obviously parts of the rings. Some structures, formerly considered as deposits, are parts of the rings, as the diaphragms of the older Ellesmeroceratida, the bullettes of the Discosorida, and the actinosiphonate deposits of the Oncoceratida, and are eliminated from the present discussion, having been treated above as parts of the rings themselves.

As noted in the *Introduction*, siphonal deposits similar in form appear independently at various points in the evolution of the Nautiloidea (*see* fig. 14), and these separate structures show specific characteristics of texture and habit, and, in part, in growth relationships with the shell as a whole. A better approach would be consideration of the deposits in terms of original composition, texture, and mode of secretion. However, while the evidence permits fairly safe conclusions on these matters for the deposits in some groups, it seems yet ambiguous for others. Habit shows the endoceroid endosiphuncle to have been dominantly aragonitic, with general loss of detail accompanying the general alteration to calcite. Structures within it are explicable only in terms of a structure deposited in the siphonal tissues. For structures characteristic of other groups, the evidence is much less conclusive. However, it should ultimately be possible to take these original differences into consideration.

Three possible modes of secretion must be considered: (1) derivation and differentiation from the connecting ring itself, (2) secretion within tissues of the siphonal strand, (3) secretion by specialized groups of secreting cells, a siphonal mantle, upon the surface of the siphonal tissues. Oddly, while the last mode of origin was generally postulated for the siphonal deposits (Flower, 1939), it is now the method which seems most suspect. Similarity of texture of the parietal deposits of the Discosorida with the cameral deposits suggests that both may be the result of mantle secretion, but there is as yet no real proof that a combination of growth lines and fine lamellae normal to the growing surface necessarily indicates such an origin. Also, if the ring is primitively secreted within the wall of a siphonal strand, the outer part of which becomes part of the cameral tissues, it is difficult to see how external epithelial secretions could occur within the ring. Indeed, on this basis the theory of the cameral mantle has been re-examined critically, but with evidence of vascular structures in *Leurocyloceras*, it cannot be abandoned.

In Figure 14 are shown the essential features of the siphonal deposits, and also of the rings, in relation to their position in the evolutionary scheme of the Nautiloidea. Where possible, the various form types are indicated diagrammatically. It will be seen at once that the relationships are intricate and that similar form types appear independently at a number of different points.

Hyatt (1900) recognized diaphragms in his Diphragmida, endocones in his Endoceratida, annuli or annulosiphonate deposits in the Annulosiphonata of the Cyrtocoanites, and also in part of his Orthoceratida—our present Michelinoceratida—and actinosiphonate deposits in his Actinosiphonata of

the Cyrtocoanites, which largely coincides with the present order Oncoceratida, though a few discosorid genera were included also. Mutvei (1957) presented a more pretentious classification of deposits on the basis of form and claimed that all of them were secreted as what are called here mantle deposits. He ignored differences in texture and habit and presented a purely topological classification which is oddly incomplete for a work presented in such authoritative terms. He recognizes annular deposits (annulosiphonate), radial deposits (actinosiphonate), conical deposits (endocones), and lobes, the latter being the structures of *Bathinoceras* which he claims are distinct from the rings. He overlooked linings, which may be segmental or nonsegmental, the rods of the higher Baltoceratidae, the diaphragms, and the odd oval structures found in some Ordovician Michelinoceratida (Teichert, 1933; Flower, 1952).

In the following sections the deposits are discussed in terms of the various orders in which they appear, with necessary brief reference to the condition of the rings and discussion of such evidence as exists on original composition, texture, and mode of secretion.

The term *siphonal deposits* is here preferred to *siphuncular deposits*, as shorter and more euphonious. There is no need for pretentious terms as intersiphuncular or endosiphuncular.

Several terms have been used for various types of annular deposits, based upon form. Strand (1933) distinguished the bullettes of the present Discosorida from the "lunnettes" of Actinoceratida and Michelinoceratida. This difference is fundamental, bullettes being parts of the rings. Flower (1939) distinguished parietal and pendant deposits, the latter primarily developed in the Actinoceratida. These terms, perhaps still useful in a descriptive sense, now appear of secondary importance in relation to a needed division involving consideration of structure, origin, and phylogeny.

ELLESMEROCERATIDA

This order is divided into three suborders defined as follows:

Plectronoceratina.—Rings thick but fragile, probably largely organic rather than calcareous, outlining siphuncular bulbs, expansions of the siphonal segments between the necks. Families Plectronoceratidae and Balkoceratidae.

Ellesmeroceratina.—Rings thick, well calcified, commonly preserved, commonly showing layered structure. Families Ellesmeroceratidae, Protocycloceratidae, Apocrinoceratidae, Baltoceratidae, Cyclostomiceratidae.

Cyrtocerinina.—Rings extended as lobes into the cavity of the siphuncle. Families Eothinoceratidae, Bathmoceratidae, and Cyrtocerinidae.

Thick rings prevail and have been already discussed. Diaphragms, extensions of the rings, prevail in the Ellesmeroceratidae and are indicated also for the ancestral Plectronoceratidae. They persist in higher families only in the Protocycloceratidae.

True deposits, apart from the rings, are known only in a group of genera within the Baltoceratidae and a few apparent

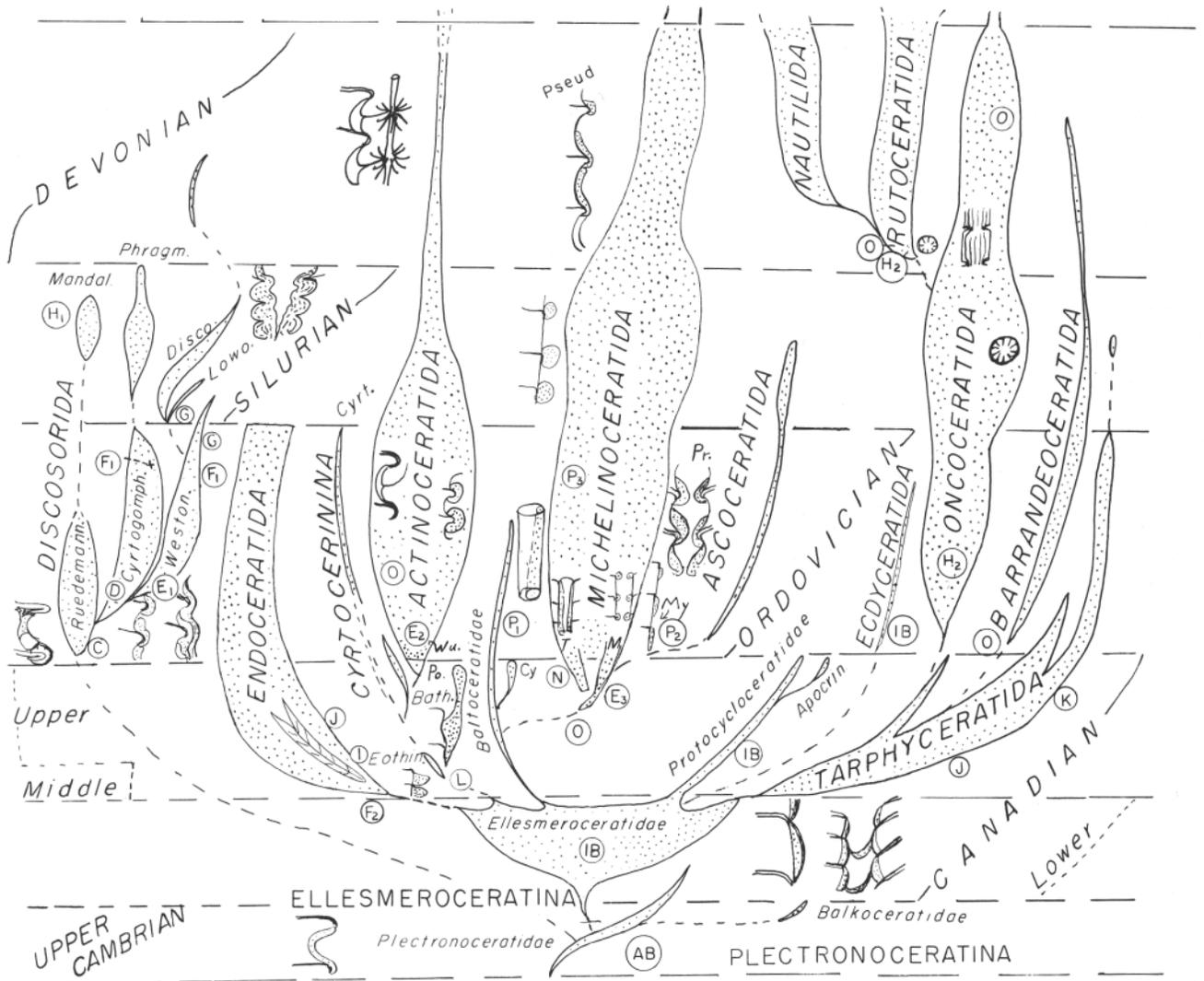


Figure 14

PHYLETIC DISTRIBUTION OF VARIOUS SIPHONAL DEPOSITS AND TYPES OF RINGS

Morphological changes are indicated by circled letters as follows:

- A. Siphuncular bulbs
- B. Diaphragms
- C. Discosorid type of ring
- D. Inflation of bullette
- E. Annular deposits:
 - E₁, discosorid type
 - E₂, actinoceroid type
 - E₃, michelinoceroid type
- F. Endocones:
 - F₁, discosorid type
 - F₂, endoceroid type
- G. Reduction of swelling of bullette
- H. Actinosiphonate or radial deposits:
 - H₁, "obstruction ring" in the Mandaloceratidae
 - H₂, rays in Oncoceratida and archaic Rutoceratida
- I. Ring thick, generally layered
- J. Dense amorphous portion of ring apically concentrated into the eyelet
- K. Rings extended outward along septa as apparent cameral deposits (Trocholitidae of Tarphyoceratida only)
- L. Ring extended as a thickened lobe into siphuncle cavity
- N. Nonsegmental lining in siphuncle
- O. Simplification of ring to a thin, apparently homogeneous, structure
- P. Other types of deposits:

P₁, rods, developed only in higher Baltoceratidae

P₂, segmental lining in *Mysterioceras*, appearing at adoral end of the ring and growing apical

P₃, oval structures in Ordovician Michelinoceratida

Taxonomic groups are abbreviated as follows:

ELLESMEROCERATIDA

Plectronoceratina: (none)

Ellesmeroceratina: Cy., Cyclostomiceratidae; Apocrin., Apocrinoceratidae

Cyrtoceratina: Eothin., Eothinoceratidae; Bath., Bathomoceratidae; Cyrt., Cyrtocerinidae

DISCOSORIDA

Ruedemann., Ruedemannoceratidae; Cyrtogomph., Cyrtogomphoceratidae; Mandal., Mandaloceratidae; Phragm., Phragmoceratidae; Weston., Westonoceratidae; Lowo., Lowoceratidae; Disco., Discosoridae

ACTINOCERATIDA

Po., Polydesmiidae; Wu., Wutinoceratidae. Higher families are not distinguished.

MICHELINOCERATIDA

M., Michelinoceratidae; T., Troedssonellidae; My., *Mysterioceras*; Pr., Proteoceratidae; Pseud., Pseudorthoceratidae

Protocycloceratidae. These forms develop rods within the siphuncles, always delayed considerably beyond the septa and siphuncle wall, pointed anteriorly, thickening gently apically, always lying against the ventral wall of the siphuncle, and, when fully developed, filling the siphuncle completely. Such rods are found in late Canadian and early Ordovician genera, including *Cyptendoceras*, *Rhabdiferoceras*, *Murrayoceras*, and *Cartersoceras*.

Thus far rods found in calcareous specimens show only coarse calcite crystals, lacking any trace of the original texture; this condition suggests an original composition of aragonite. Faint growth lines have been observed in a specimen in which the rod was silicified, probably early in its history of alteration, and evidently before calcite could replace the aragonite with the usual destruction of such textural details. There is no clear indication of origin, but secretion within tissues of the siphonal strand seems probable.*

DISCOSORIDA, THE FIBRALIA

The essential structural features of this order are discussed by Flower and Teichert (1957) and need only be summarized here with notes on some significant subsequent discoveries.

The archaic family Ruedemannoceratidae shows development of the discosorid ring, already discussed, with the bullette of two layers and uninflated. Oddly, *Madignaella* shows commonly, and *Ruedemannoceras* and *Westonoceras* show rarely, vestiges of a calcified central tube, probably the calcified wall of the central artery.

The derived Mandaloceratidae of the Silurian are as yet inadequately known internally; no suitably preserved material has been available for thinsection study of the structures. *Pseudogomphoceras* shows a siphuncle quite like that of the Ruedemannoceratidae, and Barrande's figure represents a central tube. Bullettes are uninflated. Higher Mandaloceratidae show two distinct trends: (1) in larger forms obstruction rings appear which are extended forward and backward as radially discrete processes, suggestive of the actinosiphonate deposits of the Oncoceratida. One may suggest that these represent specialized inflated bullettes, but thinsection study is required to demonstrate their nature; (2) in smaller forms the ring appears reduced in thickness and may become homogeneous. Again, needed material in limestone for thinsection has not been available.

In the Cyrtogomphoceratidae, bullettes are generally inflated and siphuncles are generally free from siphonal deposits. However, Sweet (1959A) has found in a *Cyrtogomphoceras* from Norway good endocones, and his genus *Konglungenoceras*; possesses similar endocones but shows the bullettes uninflated; presumably their suppression is secondary, as the genus is obviously specialized and not primitive.

The Phragmoceratidae show siphuncles with rings and their tips inflated into bullettes essentially as in the Cyrtogomphoceratidae, but no siphonal deposits are known. Siphonal deposits may be the explanation of the odd siphuncle figured by Barrande (see Flower and Teichert, pl. 38, fig. 5) for *Protophragmoceras beaumonti*, but the odd structure, observed in a single specimen only, remains without adequate explanation.

The Westonoceratidae show deposits which begin as annuli at the septal foramina. In most forms, these annuli grow forward and finally join to form a lining of segmental origin (fig. 15A). If, however, the growth of the deposit is modified

so that the deposit increases both adorally and adapically, endocones will result (fig. 5B), for the anterior growth of one deposit must cease when covered by the apical end of the next adoral deposit, but apically the end of one deposit grows over the preceding one, and apical growth is thus possible for the extent of several siphuncle segments, ceasing only when the siphuncle is so filled that a relatively small central tubular cavity remains.

*It may be argued, and with some merit, that these genera should be separated as a distinct family. Practical difficulties are involved,

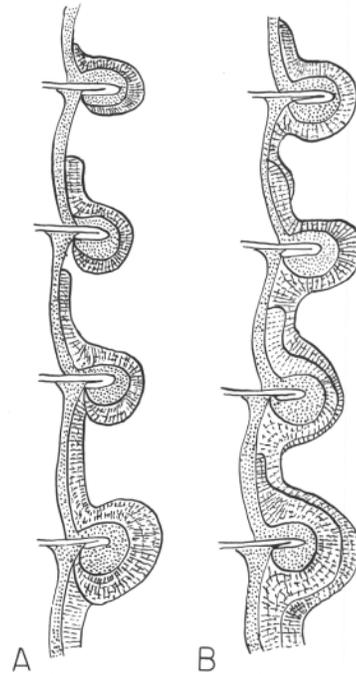


Figure 15
SIPHONAL DEPOSITS OF THE DISCOSORIDA

A. Deposits grow orad from their points of origin, finally fusing into a lining. Young stages are shown in the adoral segments.
B. Deposits grow both apical and orad from the point of origin. Adoral growth of one deposit is stopped when it is overgrown by another, but apical growth continues until the siphuncle is filled except for a small central tube. Parts of the rings are not shown.

stemming from the fragmental nature of the materials on which genera are based. It is certain that such rods are developed in *Cyptendoceras*, *Rhabdiferoceras*, *Murrayoceras*, and *Cartersoceras*, but the negative evidence of apparent absence in other genera is, necessarily, less conclusive. Oddly, Schindewolf (1942) has figured as an endocone a structure in *Baltoceras* which might possibly be such a rod, but if so, it is askew in the siphuncle, a condition not found in other genera. Additional material of the genus suggests such calcite to be only the complement of the filling of an incomplete internal mold. This conclusion seems correct from the material available to me, but should an organic rod be present in *Baltoceras*, the naming of the two families would be affected, the Baltoceratidae being used for forms with the rods, a new name being used for the simpler forms lacking a rod. The failure of material to show a rod in *Baltoceras* would suggest using Baltoceratidae for forms with empty siphuncles, proposing a new name for the forms with rods. Under the circumstances, the question is best avoided by the recognition of the rods as appearing in some specialized members of a group for which the family name Baltoceratidae is retained.

Deposits taking the form of endocones are known in the Westonoceratidae only in the holotype of *Winnipegoceras sinclairi* and in the younger Leipers species of *Faberocheras*; the older *Cynthiana*—*Catheys* species show annuli like those of *Westonoceras* and *Teichertoceras*.

In the Lowoceratidae endocones persist; they grow over rings with the bullettes inflated in the young stages but suppressed in the adult; in the Discosoridae the inflation of the bullette is completely lost. Sweet's (1959) discovery of endocones and unswollen bullettes in the Ordovician *Konglung-enoceras* presents an alternate possible origin of the Devonian endogastric genus *Alpenoceras*, instead of by the reversal of curvature of the Discosoridae. However, neither hypothesis seems proved; one may object to the reversal of curvature on one hand without evidence of transitional forms, but on the other, derivation from *Konglung-enoceras* involves a vexingly wider stratigraphic gap.

Tubes remaining where the endocones are well developed are simple tubes in *Faberocheras*. In some Discosorida the tubes show annular outlines, and in the Devonian *Alpenoceras* diaphragms crossing the tubes have been found.

The parietal deposits, whether annuli or endocones, show a general preservation of fibers normal to the surface, and such fibers are quite commonly preserved; growth lines are also apparent, but they are less common and, in general, less prominent. The general retention of texture suggests a structure which was originally high in calcite, if not completely of calcite, rather than aragonite, for experience has shown that purely aragonitic structures commonly lose their textures in alteration to calcite in fossil material.*

Quite clearly one sort of deposit takes the form either of annuli growing forward to join in a lining, as in the Pseudorthoceratidae, or in the form of endocones. Quite clearly also, such deposits develop in the Westonoceratidae and are inherited in higher families, but also appear independently in a few specialized genera of the Cyrtogomphoceratidae which, from general features and their relatively young age, can hardly lie in the immediate ancestry of the Westonoceratidae.

A term is convenient for these deposits, which are uniform in texture but so variable in form. The term *Praha* is proposed, from the dominant preservation of fibers vertical to the inner surface.

THE ENDOCEROID ENDOSIPHUNCLE

The endosiphuncle is peculiar to the Endoceratida and is a solid filling of the apical part of the siphuncle, pierced by a slender tube, and having the anterior end conically excavated. The first Endoceratida resemble their ancestors in the Ellesmeroceratidae in general aspect, in the siphuncle wall, and in the nature of early stages, and are distinguished primarily by the development of the solid endosiphuncle instead of relatively thin, widely spaced diaphragms. Indeed, some slender, straight Ellesmeroceratidae are so like the simpler Endoceratida in general aspect that the endosiphuncle remains as the main criterion for separation.^f

As noted above, Ruedemann (1905) proposed the term *endosiphuncle* for any structures within the ectosiphuncle, defining the latter as the siphuncle wall of necks and rings; this distinction seems unnecessary and, in the light of subsequent findings, particularly the recognition that "actinosiphonate" deposits are properly parts of the rings, even misleading. Further, structures grouped under the term are non-

homologous. It has seemed better to restrict the term *endosiphuncle* to the structures found in the Endoceratida than to drop the term completely and propose a new one.

Commonly in the Endoceratidae of the Ordovician proper, the endosiphuncle is made up of increments of growth of varied but usually appreciable thickness, the *endocones*, separated by thin dark bands, evidently representing resting stages in growth, the *endosiphosheaths* (Ruedemann, 1905). It has been generally accepted that all endosiphuncles are formed in this way and that loss of evident sheaths distinguishing individual endocones is due to conditions of preservation. However, the study of considerable suites of material suggests that in many Canadian endoceroids, largely of the Proterocameroceratidae and also the Allotrioceratidae, such resting stages may be largely wanting because growth of the endosiphuncle was essentially continuous. Further, it seems probable that in early growth stages where the appearance of endocones would require a revision in hydrostatic relationships, such growth was normally continuous and quite possibly fairly rapid, to shorten a critical and possibly vulnerable stage in the life history.

Some confusion has developed concerning the terminology of cones and sheaths which stems in part from Ruedemann's (1905) suggestion that sheaths were well developed only in late growth stages, for if the term *sheath* is thus confined, there is no proper term for the vestiges of sheaths when they are found in younger stages. It is this situation which is responsible in a very large part for some misstatements found in descriptions such as "endocones distant" instead of "wide" or "thick." It is such misstatements that are the apparent basis for Mutvei's (1959) claim that most students of the Endoceratida have regarded endocones as thin distant structures, with only inorganic calcite between them. Certainly, neither Dr. Ruedemann nor I have entertained any such belief, and I know of no serious student of the group who has.

Several problems still surround the extent of the division of the endosiphuncles into discrete endocones separated by endosiphosheaths. In a large part, certainly, the absence of sheaths is so general in well-preserved material that it must be original, but certainly inorganic factors do play a significant role in the obliteration of the sheaths. Ruedemann regarded the sheaths as clearly developed only in late growth stages of *Proterocameroceras brainerdi*, and the same generalization can be reasonably applied to other forms. However, I have found that the anterior part of the endosiphuncle may commonly show sheaths in individuals so different in size that maturity alone cannot be the explanation; rather, it seems that the exposed anterior end of the endosiphuncle was commonly subject to gentle replacement which preserved these structures, while the earlier portion was not.

Probable growth relationships and variations in the pattern of the endosiphuncle are shown in Figure 16. In Figure 16A is shown the theoretical early aseptate stage of the shell; this has not been found, but neither have similar stages of other

*Dr. Ming-Shan Sun has tested a bit of the deposit of a *Faberocheras* with X-ray diffraction and found it calcite in its present state.

^f*Pachendoceras* was, indeed, described as an endoceroid, and in gross aspect is close to *Proendoceras*; likewise, gross features of the phragmocones of the ellesmerocoid *Ellesmeroceras* and the endoceroid *Cotteroceras* could be confused, though shells of the genus *Cotteroceras* are generally somewhat larger in size.

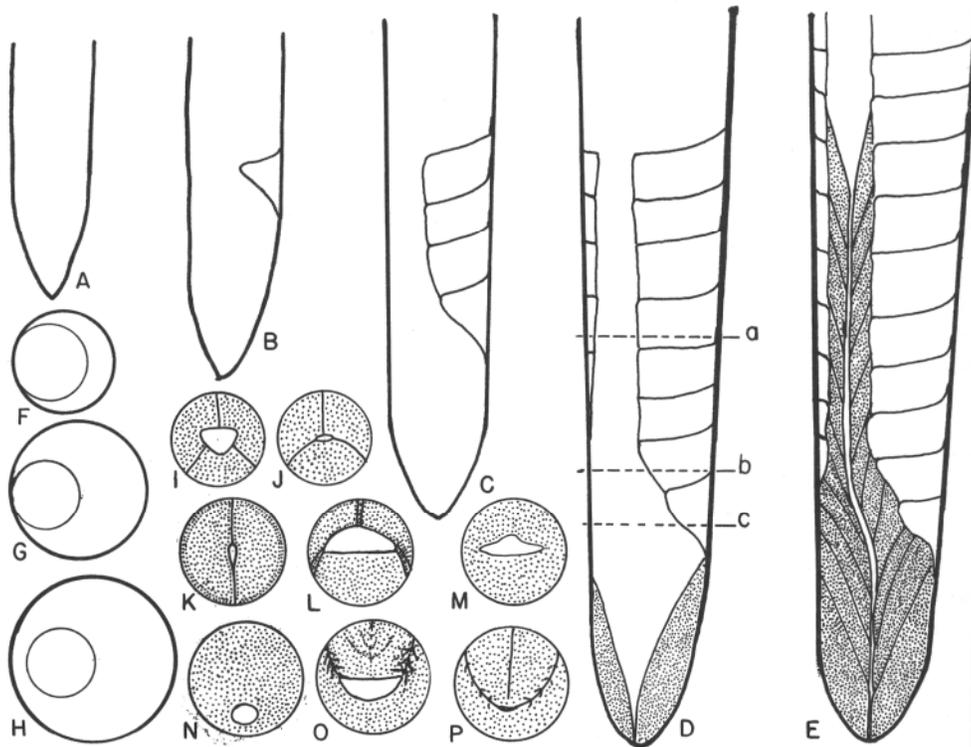


Figure 16

GENERAL MORPHOLOGY OF THE ENDOCERATIDA

A. A theoretical early aseptate portion of a shell. B. A later growth stage, showing formation of the first septum of a form with a *Nanno* type of early stage. C. Further growth with development of additional septa. D. Further growth, with the first layers of the siphuncle formed apically. E. Further growth, the anterior end wanting, with appreciable development of the endosiphuncle. F. Early cross section as at *c* in fig. D. G. Later cross section, as at *b* in fig. D; H. Later cross section, as at *a* of fig. D, showing removal of siphuncle from the venter, a condition not universal in the order. I-P. show cross sections of siphuncles, exhibiting various patterns of endosiphuncle, tube and blades. I. Endosiphuncle triangular, the apex ventral, with three blades. J. A depressed tube and three blades, as commonly found in typical Trenton *Endoceras*. K. Compressed tube and vertical blades of *Vaginoceras*, *sensu stricto*. L. Semicircular endosiphuncle as in *Coreanoceras*. M. Subtriangular tip of endosiphuncle, pointed above. N. A round cone terminating close to the venter, as in some *Endoceras*. O. Inverted crescentic cone of *Meniscoceras* (Flower, 1941). P. Later growth stage, showing the endosiphontube and blades of the same genus. (From Flower, 1957).

nautiloids. Figure 16B, also unobserved, shows the formation of the first camera and 16C shows several camerae, still with no development of the endosiphuncle. These stages are also theoretical; no specimens have been found with so few camerae and no endocones; it may be that actually a small endosiphuncle develops at such a stage as 16C; certainly, endocones are useful at such an early growth stage to establish the stability of the organism in a horizontal position. In 16D, with a longer series of camerae, the endosiphuncle is developed, but retarded beyond the development of septa; typical material of *Nanno aulema* Clarke is comparable to this figure. In 16E with further growth, the living chamber and some anterior camerae lie outside the limits of the figure, and the endosiphuncle is increased. These drawings are based upon Ordovician forms with a *Nanno* type of apex; such species range from the Chazy to the Richmond; their absence in Canadian strata is an indication that the *Nanno* type of apex is derived and not primitive. Figures 16F through H are cross sections, showing reduction of the size of the siphuncle and, finally, its slight removal from the ventral wall of the shell.

Variations in the pattern of the endosiphuncles exist which supply useful taxonomic criteria. The simplest form is one with an endosiphuncle smooth, conical, round in cross section, terminating in a small, simple, central tube, but there

are extensive deviations from this simple pattern. The anterior end of the endosiphuncle may be prolonged ventrally or dorsally; in *Lamottoceras* Flower (1955C) the anterior limit of the endosiphuncle shows pronounced lobation. The endosiphuncle may be long or short; it may terminate in an endosiphontube which is central or close to either the dorsum or the venter; *Dideroceras holmi* (pl. 3, fig. 5) shows an endosiphuncle in which the tube is ventral in the young and later central. *Dideroceras ventrale* shows an endosiphuncle which terminates very close to the venter in a tube which remains ventral throughout the known length of the species. Endosiphuncles are commonly smooth, but some are known to show low annuli or longitudinal striation or fluting; some undescribed piloceroids show marked striations confined to late growth stages, and others are known in which the endosiphuncle becomes shallow and wrinkled at maturity. The tube may vary in cross section as well as in position, being round, triangular (pl. 5, fig. 8-10), quadrangular, oval, semicircular or crescentic. Ruedemann (1905) regarded *Proterocameroceras brainerdi* as having the endosiphuncle terminating in a flat tube, called the *endosiphocoleon*, which later had additional material deposited along the sides, leaving only a small, round

tube apically. Additional material has failed to show such a development to be general, and quite probably the tube is originally small and circular in the young, later becoming horizontally flattened. In *Rosoceras* (pl. 4, fig. 2, 13-22), the tube is commonly transverse with the edges downcurved.

Diaphragms may develop within the tube, but such structures are far from universal in the Endoceratida and are generally wanting in the Endoceratidae. *Narthecoceras crassiphonatum* (Whiteaves) is one of the few Ordovician endoceroids with such diaphragms well developed, but they are more common in Canadian types, both of the Proterocameroceratina and of the Piloceratidae. In the Ellesmeroceratida, diaphragms are commonly confined to apical parts of the siphuncles. It was generally supposed that there was a similar growth relationship in the Endoceratida, but some new material shows diaphragms not only through the endosiphontube but penetrating the endosiphococone. Diaphragms in the tube of *Bisonoceras corniforme* are shown on Plate 5, figure 12. In an undescribed *Bisonoceras*, one with a tube which is considerably higher (pl. 5, fig. 14), the diaphragms are evident only near the anterior end of the tube. The extreme adoral part of this section passes away from the center and shows only endocones and endosiphosheaths, lying outside the plane of the anterior end of the tube. *Dartonoceras* (pl. 5, fig. 15-19) has a relatively slender siphuncle with an unusually large compressed tube, in which diaphragms are exceptionally well shown and unusually closely spaced. Plate 4, figures 10 and 12, shows sections from two slender endoceroid siphuncles from the first piloceroid zone of the El Paso limestone, in which the diaphragms extend for some distance into the endosiphococone. These forms show that the diaphragms continue to develop after growth of the endosiphuncle proper has stopped. Indeed, it may be that the development of diaphragms is a phenomenon which is delayed until close to maturity, and then secretion is relatively rapid throughout the length of the endosiphontube and endosiphococone.

Cross sections of the endosiphuncles will commonly show a number of radial bands extending from the cone or tube to the periphery of the siphuncle. These are the *endosiphoblades*, and together with the varied features of the cone and tube supply criteria of potential taxonomic value, for the patterns are characteristic of species and of genera. Such patterns may involve ontogenetic changes. Some blade patterns, along with variations in section of the cone and tube, are shown in Figure 16I-P. A characteristic pattern was shown for *Proterocameroceras* by Ruedemann (1905). Kobayashi found characteristic patterns also for *Manchuroceras* (1935) and some varied patterns among different species of *Coreanoceras* (1936A). Flower (1941) found a distinctive pattern for *Mensisoceras*, and later for other genera, including *Emmonsoceras* (*Hudsonoceras*, Flower, 1955), *Allotrioceras*, and *Mirabiloceras*, and later for a group of slender endoceroids from the Canadian (Flower, 1956) and also for some Ordovician genera (Flower, 1958).

Work in progress has brought to light some very distinctive patterns in additional forms, largely on the basis of material from the El Paso group, a few of which are shown in the present work. *Bisonoceras*, a genus allied to true *Piloceras*, has characteristically a pair of curved blades, the convex sides directed laterad, on the dorsum (pl. 5, fig. 2-4, 8-10), the ends of which may appear on etched or weathered surfaces as narrow, incised grooves (pl. 5, fig. 13). Oddly, in the young, these

curved blades are wanting; instead there is a pair of straight, rather strongly divergent, dorsolateral blades (pl. 5, fig. 5, 6) which disappear when traced orad. The curved dorsal blades are not derived from them but are completely new structures, wanting in the early stages. In addition, mature *Bisonoceras* shows a ventral blade which bifurcates a number of times before attaining the siphuncle margin (pl. 5, fig. 8-ro), and there are present stubs of lateral blades, the distal parts of which are almost never preserved, shown on Plate 5, figure 9, as stubs; some are preserved partially or, rarely, over almost their entire length (pl. 5, figs. 2 and 3).

Perhaps the most remarkable blades so far observed are those characteristic of the genus *Rosoceras*, described below and shown on Plate 4, figures 2, 13-22. From a tube which is transverse, though commonly with the edges slightly downturned at the sides, as on Plate 4, figures 2 and 17, there are numerous fine blades which bifurcate extensively as they are traced to the margin. Relatively strong bases may involve a prominent dorsal blade and two pairs of lateral blades, one pair downcurved, the other straight and horizontal (pl. 4, fig. 14-16) or directed obliquely upward slightly (pl. 4, fig. 2, 17). The blades become finer toward the periphery of the siphuncle. Where coarse calcite is formed in replacement, the blades may be lost, but one series of specimens represented by two sections, shown on Plate 4, figures 18 and 19, shows carbonaceous material at the periphery aligned with the three main basal blades, and duplicates rather closely the pattern of simple trifid blades characteristic of a number of more primitive forms; however, here the apparent blades become widened and their boundaries become more obscure, as traced to the edge of the siphuncle.

The habit of the endosiphuncle is such as to permit the drawing of very definite conclusions as to its original condition and mode of secretion (Flower, 1955). It is evident that the endosiphuncle was originally dominantly of aragonite, with variable amounts of organic matter, and that alteration to calcite, a general condition, is attended by a general loss of fine textures and poor preservation or complete loss of such structures as the blades. The blades themselves cannot be interpreted as vascular structures; they are, with rare exceptions to be discussed later, not segmentally repeated radial structures but are tabular and longitudinally continuous. The complex integration of septal necks and rings in the siphuncle wall is of such a nature in higher members of the order as to preclude any except the most indirect and devious connection between the siphonal tissues and the camerae. Instead, it appears that the blades are to be interpreted as the differentiation of areas of supporting tissue, probably designed to hold the endosiphontube, or its forerunner in tissue, in place and were thus essentially ligamental. Their retention in the endosiphuncle was originally developed as very delicate crystal arrangement, with probable concentration of organic materials. Blades are never apparent upon the anterior faces of the endosiphococones. Their preservation in the endosiphuncle can be explained only by the hypothesis that the endosiphuncle was calcification within the tissue of the siphonal strand.

In an endosiphuncle of a material as susceptible to replacement as is aragonite, the various structures are variously expressed under different histories of alteration and replacement. Fortunately, enough material showing varied modes of

replacement permits some generalizations. Purely calcitic replacement, though it may retain endosiphosheaths in the anterior part of endosiphuncles, may show the blades only as shadows, faintly differentiated in color, or may destroy them completely. The clearest blades, those which appear as thin bands with light centers and dark borders, are certainly to be found in specimens which were subjected to very gentle incipient silicification which evidently occurred before alteration of the aragonite to calcite. With later alteration of the main part of the endosiphuncle to calcite, the blades remain expressed as thin dark bands with quite definite walls, even though other parts of the siphuncle may show extremely coarse crystals of calcite.

Without such early silicification, it would appear that in many siphuncles aragonite was dissolved and replaced by calcite, and the calcite forms an essentially geoidal pattern, like that filling an empty cavity. In such instances, fibers of crystals form bands lining the exterior of the endosiphuncle and also extending along the surfaces of the blades, but with more advanced replacement, the blades themselves lose their original boundaries, and we have instead broad "shadow blades," with the surfaces poorly defined, surrounding areas of, commonly, coarse calcite crystals.

In advanced replacement, in which probably secondary silicification is involved, acting upon specimens retaining either the original blades or their shadows, there are apparent volumetric changes, shrinkage or expansion; it is hard to say which and it does not matter greatly, but such volumetric changes produce cracks which may follow blades to some extent but may pass from one blade to another, like lightning jumping from one post to another, and such specimens may show superimposed upon a more or less perfectly preserved blade pattern other bands which are completely adventitious.

Blades or their shadows may show poor color differentiation or none; sometimes slight silicification permits accentuation of the blade pattern by etching. Weathering may also accentuate it. Specimens have been found which are partially exposed, and the exposed surfaces have accumulated a dark stain, largely limonitic. Sections of such specimens have shown that not uncommonly either blades or their shadows are regions of permeability along which the staining may extend well into the interior of the endosiphuncle, though rarely to the deeper buried side.

It is necessary to approach the blades with the realization that they represent original organic structures, originally reflected when the endosiphuncle was secreted as regions differentiated by delicate types of crystal structure and concentration of organic materials. They are variously altered under varied modes of preservation. It is as though one were required to reconstruct tissues from sections variously prepared, fixed, and stained, some methods preserving much of the pattern, others destroying large parts of the original structure, and that one is set the problem of reconstructing the original pattern without knowledge of the varied modes of treatment of the tissue. The susceptibility of blade patterns to alteration requires that they be studied from considerable suites of specimens, and even then much caution is needed and considerable experience is helpful.

All bladelike structures may not be uniform. In *Emmonsoceras* (= *Hudsonoceras* Flower, 1955) it was noted that the siphuncle in longitudinal section shows rhythmically repeated transverse bands of calcite darker than the rest. It is in cross

sections taken through such areas that one finds "secondary blades," which supplement "primary blades" which are continuous longitudinally. Presumably, the secondary blades are rhythmically repeated structures which may well be, like the primary blades, reflection of ligamental bands in the tissues of the siphonal strand.

Possibly allied are the *funicles* or *endosiphofunicles* which Ruedemann (1905) first noted in the siphuncles of *Cassinoceras explanator*. These are bladelike structures which appear to be short and seemed confined, in that form, to the region between two endosiphosheaths, as seen in cross sections. Somewhat similar structures are shown on Plate 4, figures 8 and 9, in a cross section of an undescribed piloceroid, which shows no sheaths, a new genus which is closely allied to true *Piloceras*. Here, in enlargement, the siphuncle reveals short, radial structures which tend to bifurcate distally. Some, as those in the lower right of Plate 4, figure 9, are closely bound up with the continuous blades, while others, as those in the upper center of the same figure, are found where no blades are preserved. These funicles may well be vestiges of linear radial structures, which are normal, not to the plane of a cross section, but to the endosiphococone surface; thus any normal cross section, particularly where the angle of the cone is wide, will show only an extremely limited portion of the whole pattern. Fibers in such an arrangement are suggested by a number of longitudinal sections, as that of *Vaningoceras styliforme* Flower (1958, pl. 61, fig.). While preserved funicles suggest such a pattern, one might hope that other modes or preservation might show it more completely. A remarkably preserved piloceroid, described below as *Disphenoceras conicum* (pl. i, fig. 1-5), shows a weathered siphuncle which preserves a pattern of fibers, which was first gently silicified, then altered to calcite and later weathered, the weathering bringing out a pattern of transverse and longitudinal fibers in addition to the radial fibers sloping normal to the endocone surfaces. The specimen shows also weathering-out of small round pits. From other specimens, these pits are spherules of calcite, a rather common effect developed in replacement and not representing original organic textures.

Ruedemann found in cross sections of *Proterocameroceras* that the trifid blades, which in that material are the broad bands here called shadow blades, run from the endosiphontube to similar bands lining the margin of the endosiphuncle. This material he interpreted as an endosiphonolining, a lining developed in the siphuncle prior to the deposition of endocones, and presumably extending slightly orad of the anterior margin of the endocones. Extensive observations have led to the conclusion that this apparent lining does not extend orad of the endocones and that it is a replacement phenomenon in the endosiphuncles, and a very common one, particularly in material showing rather advanced alteration. Such a lining is shown in a *Rossoceras* showing advanced alteration on Plate 4, figures 8-19. In other preservation phases, it may be wanting. Oddly, the development of a lining which is secreted organically, and within which endocones are later deposited, is known in some specialized Endoceratida, but as yet has been recognized with certainty only in the remarkable and highly specialized family Allotrioceratidae. The features of *Allotrioceras* and *Mirabiloceras* are shown in Text Figure 17.

Allotrioceras shows in the adoral part of the endosiphuncle

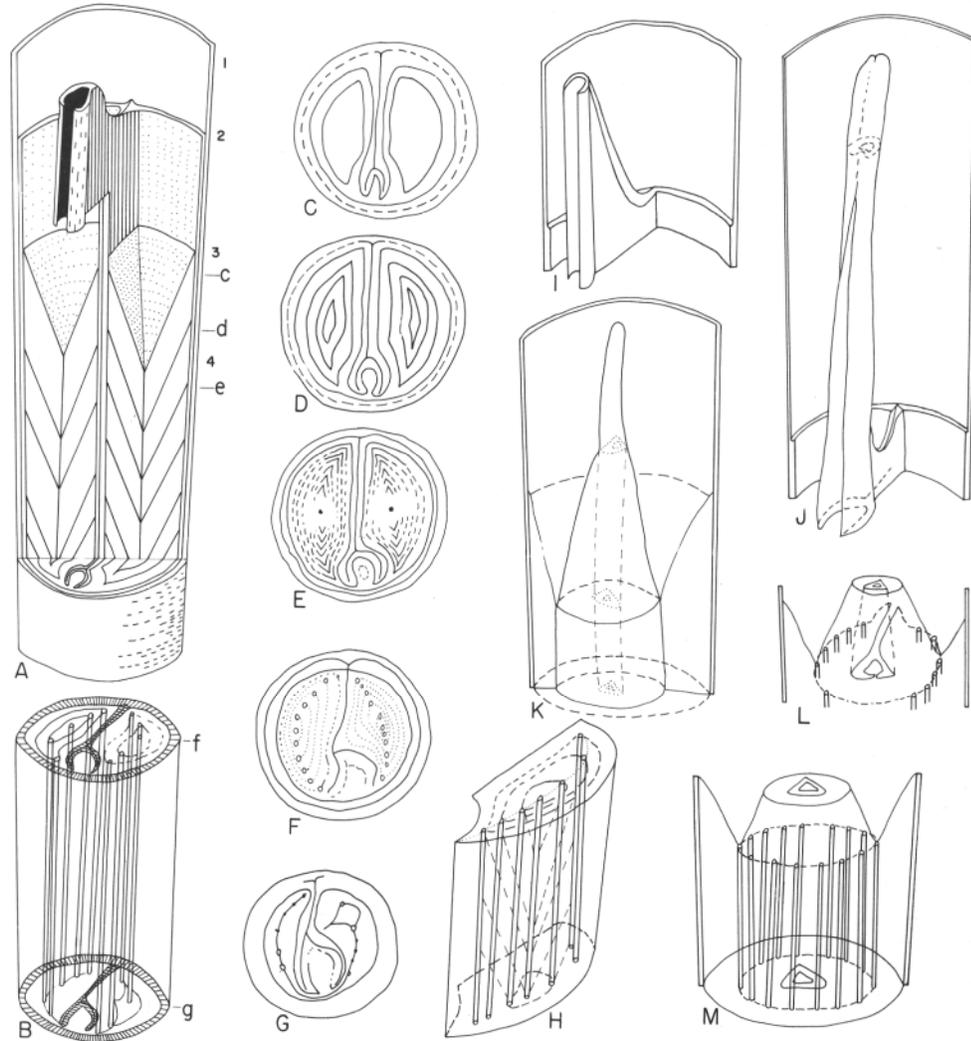


Figure 17

ENDOSIPHUNCLES OF THE HIGHER ALLOTRIOCERATIDAE

A-H. *Allotrioceras*. A. shows the anterior part of the endosiphuncle in dissection showing the median partition, bifurcate at its tip, with simple endocones, each terminating in a single tube, in the two sides of the siphuncle. B. shows an earlier condition in which the pair of cones is still evident, but several tubes are present in each half. C-G. show a series of cross sections; the positions of C-E are indicated in Figure A by lower-case letters. F. and G. are from more apical parts showing a transition from the anterior paired cones to a condition in which the shorter partition shows the tubes connected by a blade passing beneath it, as oriented in G. Subsequent work has shown the partition to be ventral rather than dorsal, and the condition here is essentially that of the adult of *Williamsoceras*. H. is a diagrammatic transparency of the relation of the multiple tube to the cones in one half of the siphuncle, which is here divided completely by the partition as in F.

I-M. *Mirabiloceras*. I. theoretical origin of the central pillar, as a forward extension of the partition of *Allotrioceras*, with the base suppressed, being developed only apically. J. shows a fuller forward extension of the tip of the process. In K., endocones are secreted around the central pillar. L. shows the tubes extending apicad from the endosiphuncle, a condition shown more completely in M.

a lining from which there extends a median process, the tip of which is forked, the two forks approaching each other at their tips. In the large cavities on either side of the process are developed endocones, in which the longitudinal section shows faint, closely spaced growth lines. In the apical part of the endosiphuncle, however, the median process is shortened. There one finds not two tubes, as would be expected from the condition of the anterior portion, but an arc of tubes passing around the median partition. Similar multiple tubes were found forming a circle around a median pillar in *Mirabiloceras*, in which the endocones form a V-shaped trough completely surrounding the pillar. A logical explanation of this form is that the central pillar represents the tip of the forked

process of *Allotrioceras*, which is here immensely prolonged forward, while its base is retarded and, indeed, unknown. The main part of the lining, however, does persist.

A third form, here described as *Williamsoceras* (pl. 2, fig. 1-7), from the Whiterock of Nevada, shows an endosiphuncle in which there is no lining, but instead a vertical, narrow, ventral process. Cones are draped around this process, and they become increasingly crescentic in cross section as one approaches their apices. Oddly, the apex of the endosiphuncle is attained first ventrally, and the dorsal termination is always found farther apical, so that the tip of the cone slopes mark-

edly ventrorad. Near its tip the cone comes to be traversed by buttresses, the cavities between the buttresses are narrowed to small round tubes which extend for the known length of the siphuncle, known parts of which certainly reach close to its original apex.

The *infula* is a term proposed for a dark band, seen in cross sections, which is not radial like the blades but instead connects the multiple tubes of the Allotrioceratidae. It marks also the position in the cross section of the apical termination of the endosiphuncle. It may or may not attain the periphery of the endosiphuncle, depending on the position of the arc connecting the tubes. It reaches the siphuncle edge in *Williamsoceras adnatum*, but in another undescribed species of the genus it does not; it is present, removed from the wall, in *Mirabiloceras* and in the young of *Allotrioceras*; in later stages of this genus, all but two of the tubes disappear, and the infula is wanting there.

Disphenoceras conicum shows in the anterior end of the endosiphuncle two longitudinally continuous structures, wedge-shaped in cross section. To these structures the name *endosiphonewedge* was applied. Obviously the wedge of this form, the ventral process of *Williamsoceras*, the lining and median process of *Allotrioceras*, and the lining and pillar of *Mirabiloceras* are all similar in that they appear to be texturally distinct from the endocones which are formed later, and which are modified in accordance with the pattern of those structures. The origin of such structures is yet obscure. It has been shown that the endocones themselves are cenogenetic structures, but within the tubes and, at maturity, even the endosiphuncle, diaphragms, a heritage from the ancestral Ellesmeroceratidae, may be developed. It is, then, easy to visualize the lining, processes, or wedges as similar cenogenetic structures, with the endocones developing later and modified according to these previously formed structures. It is not, however, certain that these odd processes may not have developed first as wrinkling in the endocones, only later becoming distinct in texture and showing to varying extents good surfaces between them and the endocones.

Probably no odder series of specializations are found in any part of the cephalopod than those observed so far in the endoceroid endosiphuncles. They supply criteria of taxonomic value. It is well that this is so, for many endoceroids, particularly in the Canadian, are known from abundant endosiphuncles only; phragmocones, living chambers, and even siphuncle walls remain, unknown. Plainly these parts, which were more delicate, were destroyed by abrasion prior to burial of the endosiphuncles, which alone remain because of their solid construction.

The essential features of the endosiphuncle have been outlined long ago, in part by Holm (1885) and in part by Ruedemann (1905). However, these structures, until quite recently have received inadequate attention. Regrettably, the treatment of the Canadian Endoceratida (Ulrich, Foerste, Miller, and Unklesbay, 1944) ignored the blades completely and assumed that a series of endosiphuncles shown as fillings, to which the term "speiss" has been applied, showing wide variation in form and surface features, pertained to a single species. Mutvei (1957) has claimed that all "conical deposits" are secreted on the exterior of the tissues of the siphuncle and has denied the organic nature of the endosiphonblades, dismissing them as cracks and breaks in the endosiphuncles. Our present observations have supported the validity of the often elaborate and complex blade patterns. Mutvei's authorita-

tively worded statement must be dismissed as a combination of inexperience and overconfidence.

The endosiphuncle of the Endoceratida shows remarkable and bizarre variations upon a relatively simple primitive structure; quite probably our present observations have only begun to explore some of the specializations and variations which evolved within the group, and fuller attention to these structures is to be urged. Problems remain which require fuller examination, as, for example, whether apparent absence of blades in some of the older and simpler Endoceratida is real or whether they are lost in alteration, and whether wedges, linings, and other accessory structures are derived from modified endocones.

ACTINOCERATIDA

Deposits in the actinoceroid siphuncle are always annuli, beginning at the septal foramen, growing until they practically fill the siphuncle in adapical segments, diminishing in the adoral part as one progresses through younger segments, and with the usual adoral region in which the deposits are not developed at all. Such a region persists in mature specimens as shown by Flower (1957) from mature, relatively complete, specimens of *Actinoceras*. As the siphonal annuli grow (fig. 8), they bypass and surround a siphonal vascular system which consists of a central canal, a series of radial canals in each segment which pass from the central canal to a narrow open space on the inside of the free part of the ring, termed the *perispantium*. As cameral deposits grow abutting on the outside of the ring, the growth of perispantium deposits, black carbonaceous deposits commonly showing growth lamellae, may reduce the perispantium correspondingly.

The original nature of the annuli is somewhat problematical. Most commonly, the annuli are coarsely and extensively replaced with coarse crystals of calcite. Under the best of conditions, growth lines are evident, but lamellae normal to the surface of secretion are not demonstrable.

Origin of the deposits is bound up with the question of the origin of the Actinoceratida. Teichert (1933) presented two disparate suggestions; one, the uniting of the Endoceratida and Actinoceratida in the Euryisiphonata—cephalopods with large broad siphuncles, and two, a possible origin in those older genera, the Plectronoceratidae, with expanded siphuncles. Today neither explanation can be accepted. Oddly, the siphuncular bulbs of the Plectronoceratida are recapitulated in the young of *Ruedemannoceras*, the oldest of the genera of the Discosorida, and the only advances required are a bending of the necks, specialization within the ring, and the development of cameral deposits. Derivation of the Actinoceratida from the same source is unsupported by any ontogenetic evidence, not a final objection, to be sure, but a significant one when the Discosorida show such evidence. Similarities with the Endoceratida rest upon the relatively broad siphuncles and the moderately long necks of some Actinoceratida. It is now evident, however, that such endoceroids as approach the actinoceroids most closely are the specialized Endoceratidae and that the similarity is not shared by the archaic Proterocameroceratidae which have very short necks. Further, the specialized rings of the primitive Actinoceratida are completely unlike those developed in the Endoceratida. Flower (1941, 1946) suggested that a transition might

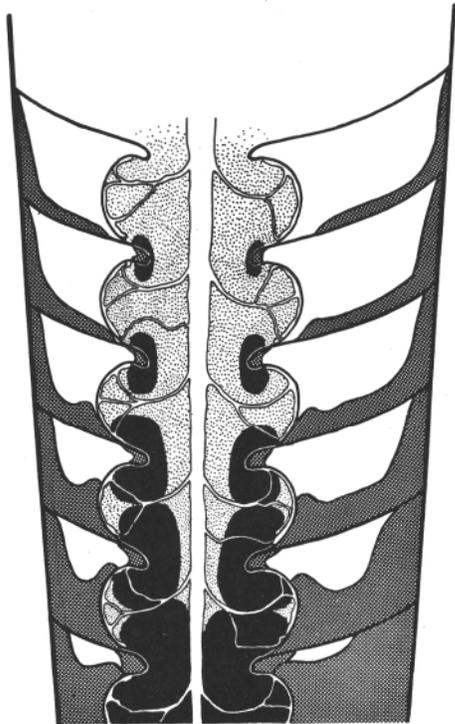


Figure 18

Section through the phragmocone of *Actinoceras* showing gradual apical increase in both cameral and siphonal deposits, the siphonal vascular system in the siphonal tissues, which is surrounded by the annular deposits as they grow. (After Teichert, 1933, 1935.)

exist between the genus *Bathmoceras*, in which the rings are extended far forward as lobes into the cavity of the siphuncle, and the rather similar deposits of *Polydesmia*, the oldest of the actinoceroids. Such a change implies (a) retardation of the development of the lobed portion from the essentially linear or cylindrical portion and (b) differentiation of this part from the primary part of the ring in texture. Oddly, if Mutvei is correct in stating that the lobes of *Bathmoceras* are distinct from the ring, this transition is made easier and is better substantiated, and the differentiation of the lobe from the primary part of the ring must exist farther back than was previously thought.

As the annuli develop, they enclose the siphonal vascular system. The number and arrangement of the radial canals, particularly, varies in the Actinoceratida. Logically, one would expect a trend beginning with numerous, irregular, fine branching tubes to one of fewer, larger, and more regular tubes with the development of the perispantium. In the ancient *Polydesmia*, the tubes are numerous, fine, and branch as they approach the perispantium. In the *Wutinoceratidae*, a reticular pattern develops, a step toward the development of fewer and more regular tubes. In the *Armenoceratidae*, in part, there is a series of double arcs, in other *Armenoceratidae* and in all of the *Actinoceratidae* only a single series of arcs, and in the *Ormoceratidae* the radial canals are essentially horizontal, leaving the central canal at right angles.

MICHELINOCERATIDA

Annuli or annulosiphonate deposits are the prevalent type of siphonal deposit in this order, which contains the bulk of the generalized "*Orthoceras*" in the sense of orthocones with

slender or secondarily expanded siphuncle segments. However, there are some other types which present some perplexity in relationship and interpretation.

Our knowledge of texture and composition of the annuli is yet inadequate. Certainly, however, they differ widely in habit from those of the Actinoceratida, for while the actinoceroid annuli are generally extensively replaced with coarse-grained calcite, even obscuring growth lines, the deposit in the Michelinoceratida is commonly granular, rather fine-grained, and may be black, in whole or in part, indicating the original incorporation of considerable organic matter. Material is commonly finely granular in thinsection, with growth lines obscure or wanting, but thus far only a few Michelinoceratidae and Pseudorthoceratidae have been thus examined.

The annuli in their simplest form appear as small round structures, as seen in section, originating apparently from and certainly attached to the apical end of the ring. They are, of course, doughnut-shaped structures, extending within the siphuncle circumference, though they may tend to appear first on the venter and may be uniformly slightly more advanced in growth there than on the dorsum. In Figure 19A the annuli remain fairly symmetrical and may grow over the free part of the ring where cameral deposits impinge upon its outer surface, a condition found in the Silurian *Geisonoceras* and indicated also for some Ordovician material.

In Figure 19B is shown the general condition found in the Silurian genus *Virgoceras*, where the annuli lie always close to the ring, grow adorally but never adapically, and eventually fuse to form a continuous lining with the siphuncle. In Figure 19C is shown the condition found in *Dolorthoceras* of the Pseudorthoceratidae, which is much as in Figure 18B, except that the siphuncle segments are expanded, and the rings remain uniform in thickness and their original annular condition is not obvious where they are fully grown and have formed a fused lining. Differentiation extends further. In the Pseudorthoceratinae (see Flower, 1939) the rings show marked ventral concentration, so much so that they may fuse and form a continuous lining on the venter while, in the same segment, there is scarcely more than a small annulus developed on the dorsum. With further growth, material is added to the lateral edges, which grow around and meet, though apparently never closing completely, on the dorsum. In the Cayutoceratinae there are two parts of the ring differentiated in color and texture, but present material has not permitted investigation by thinsections, and the original nature of the parts is not yet understood properly. In the Macroloxoceratinae (Flower, 1957A) shown in Figure 19E, the deposits are curiously thickened in the apical half of the segment, are thin adorally, and are clearly traversed by a simple series of radial canals. This development is known only from a small group of genera of late Devonian and Mississippian age.

In *Harrisoceras*, a genus of the Middle Silurian (fig. 19F), the annuli tend to be large, though fairly symmetrical. There is some variation in form when they are enlarged; in some forms they are only narrowly attached to the ring and tend to be inflated in the siphuncle; in others, largely in Bohemian species, they show some similar inflation, but are extended also for appreciable distances apicad and orad of their point

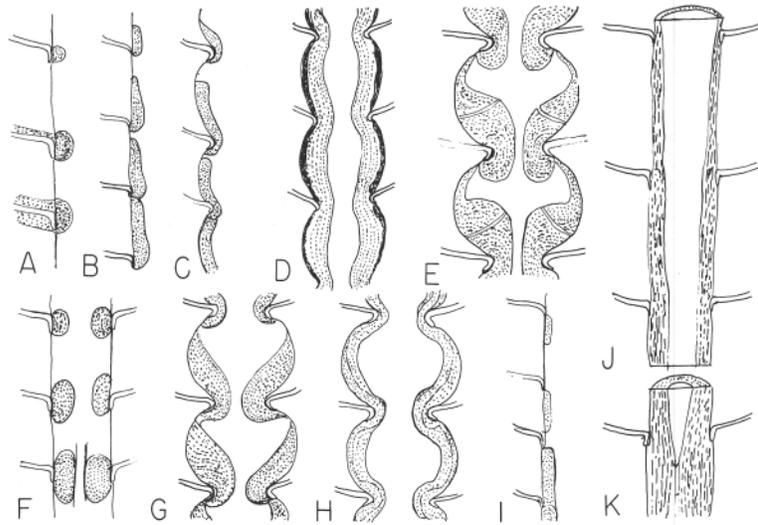


Figure 19

ANNULAR SIPHONAL DEPOSITS AND LININGS IN THE MICHELINOCERATIDA

- A. Small annuli of the Michelinoceratidae, which are shown here in the apical part extending over the rings only where cameral deposits lie against the outside of the ring, as in *Geisonoceras*.
- B. Annuli grow forward, fusing to form a lining of segmental elements in a tubular siphuncle, from *Virgoceras*.
- C. Structures essentially as in B, but showing more uniform thickness, and in an expanded siphuncle, supplying the pattern of the simpler Pseudorthoceratidae; from *Dolorthoceras*.
- D. A siphuncle with slightly expanded segments, and a lining of apparently continuous lamellar material, separated from the rings by either a thin outer layer of matrix or of darker organic material. *Stereoplasmodocerina*, from Kobayashi, 1936.
- E. Siphuncle of *Macroloxoceras* of the Pseudorthoceratidae, showing characteristic deposits, thick apically, thin adorally in each segment, the thick part traversed by radial canals. Characteristic of the Macroloxoceratinae. From Flower, 1957A.
- F. Siphuncle of *Harrisoceras*, showing large inflated annuli, which, apically, support part of a free tube.
- G. Siphuncle from an early portion of *Proteoceras*, showing characteristic form of the annular deposits.
- H. Siphuncle of *Striatoceras striatum*, (after Teichert, 1934) showing a lining of apparently irregular lamellar elements.
- I. Siphuncle wall of *Mysterioceras*, showing siphonal deposits appearing at the anterior end of the ring, growing apicad, deposits finally fusing to a segmental lining.
- J. *Buttsoceras*, from the anterior portion of a well grown shell, showing gradual apical thickening of the lining and faint suggestions of lamellae curving out more strongly just orad of the septal necks, a faint suggestion of origin in annual deposits.
- K. Apical portion, representing an earlier growth stage; the lining thickens apicad more rapidly and terminates in a narrow tube traversed by diaphragms. Both specimens figured by Flower, 1962.

of inception along the free part of the ring. Where growth is advanced, the rings may support a calcified central tube, as shown in the lower part of the figure.

In early stages of *Proteoceras* (Flower, 1955C) are found annuli in expanded siphuncle segments (fig. 9G), and such a development has been confused with that of the Devonian Pseudorthoceratidae. *Proteoceras* shows a deposit which is thickened at the septal foramen, thins adorally rapidly, so that the surface of the deposit, as seen in section, shows oblique, nearly flat, surfaces diverging adorally. Unlike the Pseudorthoceratidae, these deposits grow somewhat apicad as well as orad from their point of inception, and deposits may meet somewhere in the middle of the segments rather than at the point at which the two rings are in contact. Such apical development is better shown in some other genera, and such conditions have been illustrated by Teichert and Glenister (1953). It is apparent that this sort of development characterizes the family Proteoceratidae, dominantly Ordovician, with some specialized Silurian representatives, notably *Cyrtactinoceras*. Apparently also, this family and the Pseudorthoceratidae of the Devonian are independent developments, though there is an odd parallelism between the condition of the Chazyan *Proteoceras* and the late Devonian *Macroloxoceras*, as can be seen here by comparison of figures 19E and G.

In contrast to the annuli, which may or may not fuse to form linings, is a continuous lining made up of thin, fine layers, developed in the Troedssonellidae, a family thus far known from the late Canadian *Buttsoceras* and the early Ordovician *Troedssonella* (Flower, 1962A). The anterior portion, Figure 19J, shows a lining which thickens gently apicad, but leaves a definite cavity in the center of the siphuncle. With further growth than is shown here, the cavity becomes tubular and rather irregular in form, but lacks diaphragms or any canals passing to the siphuncle wall. In a fragment showing a young growth stage, however, it was found that the cavity decreases in size adapically more rapidly, as shown in Figure 19K, and terminates in a narrow tube across which diaphragms may be built (Flower, 1962A).

There is some suggestion in growth lamellae that curve outward orad of the septal necks that this lining is possibly a modification of simple annuli, and the idea finds further support from the fact that *Michelinoceras* with simple annuli is known in beds slightly older than those containing *Buttsoceras* with linings. However, the morphological evidence is not conclusive, and further finds may alter the now apparent stratigraphic sequence of the genera.

Mysterioceras (see Teichert and Glenister, 1953), known only from beds of Ordovician age of Tasmania, shows a deposit which begins at the anterior instead of the posterior end of the ring (fig. 191), grows apicad, joining the next adapical deposit, and a lining of segmental units is built up. With later growth, the lining thickens, but it is not altogether clear from the figures whether this is a simple thickening of segmental linings or whether one lining grows over another. It is suggested that *Mysterioceras* may be allied to the Troedssonellidae (Flower, 1962A).

A puzzle not yet solved is provided by several Ordovician forms which appear to have nonsegmental linings. Kobayashi (1936) shows for *Stereoplasmocerina* a thick light lining, apparently nonsegmental, composed of fine, longitudinal lamellae. Dark material of variable thickness separates this lining from the wall of the siphuncle, and it is thickest in the expanded parts of the segments. Kobayashi regarded this as matrix. An alternate possible explanation is a continuous lining with an outer dark and an inner light layer. Sweet (1958) has illustrated as a *Stereoplasmocerina* an orthocone with similar expanded segments, and has shown a lining which is apparently continuous and homogeneous; a similar lining is illustrated for *Ctenoceras*.

Another puzzling form is found in *Striatoceras striatum* (Troedsson, 1926) of the Cape Calhoun beds of Greenland. This is an orthocone with a subcentral siphuncle of broadly rounded segments. Teichert (1954) has presented an illustration of the siphuncle showing a lining within it made up of lamellar layers of considerable thickness. Is such a lining related to that of the Troedssonellidae? It is possible that derivatives of the Troedssonellidae might develop expanded siphuncle segments and Kobayashi's *Stereoplasmocerina* and this *Striatoceras* might represent such a lineage. It is also possible that the lining of *Striatoceras* might be developed from annular structures, as are the endocones of the Discosorida. Teichert's figure fails to suggest such regular growth as is consistent with segmental origin, but more material might alter the present interpretation. Unfortunately, there is at present no more material to be had of *S. striatum* other than the type material, and the same appears to be true for *Stereoplasmocerina tofangoense*.

Two other very odd structures have been found in siphuncles of the Michelinoceratida, which are as yet not understood, but they seem to show no relationship to the structures discussed above. Some unnamed small orthocones from concretions of the Canajoharie shale of New York show in specimens in which there has been considerable marcasite replacement, odd marcasite bands outlining oval bodies on either side of the siphuncle interior as seen in section. Are these replacements of originally solid deposits or are they essentially sheetlike structures enclosing a marginal cavity and separating it from a central cavity? Present evidence is insufficient to answer this question. Teichert (1933) has figured this form, and an interpretation is shown in Figure 20B.

Flower (1952) found equally odd but quite different structures in the siphuncle of a small *Kionoceras* from the Chazyan of the Champlain Valley shown in Figure 20A. The siphuncle is tubular, but within it are oval bodies seemingly calcareous, the outer walls sharp, the inner surface more obscure, but the inner surface shows evidence that the cavity within is wide adorally, narrow apically, rather like the cavity left

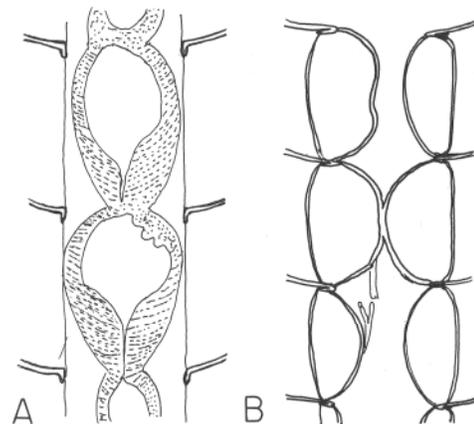


Figure 20

ANOMALOUS STRUCTURES IN THE MICHELINOCERATIDA

A. Siphuncle of a Chazyan *Kionoceras* (from Flower, 1952) with odd oval bodies in the siphuncle. B. Siphuncle from an unnamed orthocone from the Canajoharie shale of Florida, N. Y. (from Teichert, 1933), showing dark bands separating a central and peripheral regions.

in the deposits of *Proteoceras*. As yet, no comparable structure has been observed elsewhere, and no suggestions as to the nature and origin of the structure have been made. The bodies are in part somewhat displaced, and the interpretation that they are foreign objects washed into the siphuncle is not impossible. Such an explanation, however, offers no better solution to their nature and is opposed by the fact that in length the bodies are essentially equal to the segments of the siphuncle which they occupy.

In general the siphonal deposits appear first some distance from the base of the living chamber and grow gradually, so that the ontogeny may be found by tracing deposits apicad in a series of camerae. There appear to be Michelinoceratida in which no siphonal deposits are developed, but specimens are incomplete apically and the possibility always exists that siphonal deposits are greatly retarded rather than absent, as is suggested by the specimen which Barrande figured (pl. 387) as *Orthoceras rivale* and which shows siphonal deposits, but only in extreme apical camerae. In *Orthoceros regularis* (Schlotheim) it is evident that no siphonal deposits are developed in the anterior 40 camerae, more of the phragmocone than is known for many species. It is evident also that in both this form and in *Sinoceras chinensis* (Foord), from the illustrations of Yü (1930), there is a similar absence of siphonal deposits in the known portion of the phragmocone. Apparently the same condition holds for some Chazyan forms with tubular siphuncles, for, though specimens are more fragmentary, they show a uniform absence of demonstrable organic siphonal deposits. Possibly the excessive retardation or complete loss of siphonal deposits may prove of taxonomic significance, but as yet too little is known of the relationships in the Michelinoceratida with tubular siphuncles to attempt the definition of groups on such a basis.

OTHER ORDERS

In the remaining orders, Ascoceratida, Ecdyceratida, Tarphyceratida, Barrandeoceratida, Oncoceratida, Rutoceratida, and Nautilida, no true siphonal deposits are known. As the

"actinosiphonate deposits" of the Oncoceratida are parts of the rings, they are discussed under that heading. It is worth noting that the actinosiphonate rings develop within the Oncoceratida and are retained in primitive members of the derived Rutoceratida but lost in more advanced forms.

Cameral Deposits

The subject of cameral deposits has been covered in another work (Flower, 1955B) and need only be summarized here, with some notice of subsequent discoveries and views.

Deposits in the camerae present a puzzle from their apical concentration. Barrande (1855, 1877) thought that they were formed only in young individuals, being laid down on septa which were then the base of the living chamber, a view also stated by Miller, Dunbar, and Condra (1933) who also suggested resorption of the anterior ends of mural deposits prior to the formation of the next septum, but inspection of any series of specimens of a species will show that this is untrue; regardless of the growth stage, there is a specific adoral interval of vacant camerae behind the living chamber (see fig. 21), then a series in which cameral deposits show apical progress in thickness and maturity, and apically there may be a region in which such further apical thickening is absent or difficult to discern, owing to the apically diminishing size of the camerae. Teichert (1933) pointed out that the hyposeptal deposits showed the deposits to be formed in close camerae. Flower (1939) elaborated the spatial relationships more fully, having earlier (1936) found evidence of the uniform adoral empty camerae in a good suite of *Striacoceras typos*. He proposed a tissue in the camerae, the cameral mantle, by which the cameral deposits were secreted and which originated in part from tissue left behind on the adoral face of the septum, and in part from tissue left outside the connecting ring when it was secreted in the siphonal strand.

Two matters are involved in the form of the cameral deposits, their longitudinal distribution, as seen in longitudinal sections of the shells, and their radial distribution. Teichert (1933) proposed the terms *episeptal* and *hyposeptal*, *episeptal* for deposits formed on the upper face of the septum, as shells are conventionally oriented with the aperture up, and *hypo-*

septal for those formed on the under surface, with reference to the same conventional orientation. In incipient phases of growth, where both hyposeptal and episeptal deposits appear, they may be discrete, but where their growth is advanced they may be joined for a considerable distance along a line called the *pseudoseptum*; some early workers regarded the pseudoseptum as an organic membrane rather than the junction of two solid surfaces. Flower proposed the term *mural deposits* for those formed primarily against the mural part of the septum or conch as the case may be. Such deposits grade to some degree into episeptal deposits, as in Figure 22D, but with maturity grow as in 22E, being seemingly truncated by the anterior septal face. More extremely mural deposits are shown in Figure 22C, where the deposits scarcely extend along the free septa. A strictly ventral section of the same form would probably show a boss. Where the neck is recurved, a circulus, "stutzring," or supporting ring may develop; this is essentially an actinoceroid feature. A deposit peculiar and known thus far only in the Discosorida is mainly mural but extends as a continuous mass over both apical and anterior septal faces; for this type, the term *holoseptal* is proposed (fig. 22F).

Schmidt (1956) pointed out that episeptal and hyposeptal were named in reference to the conventional orientation of the orthocone for illustration, with the aperture directed upward, and proposed to call episeptal and mural deposits *distal*, and the hyposeptal deposits *proximal*, both terms having reference to the body mass of the animal. Unfortunately, it seems that such terms might lead to some confusion, as an equally logical point of reference is the apex of the shell, and perhaps anterior and posterior would be better. However, it seems

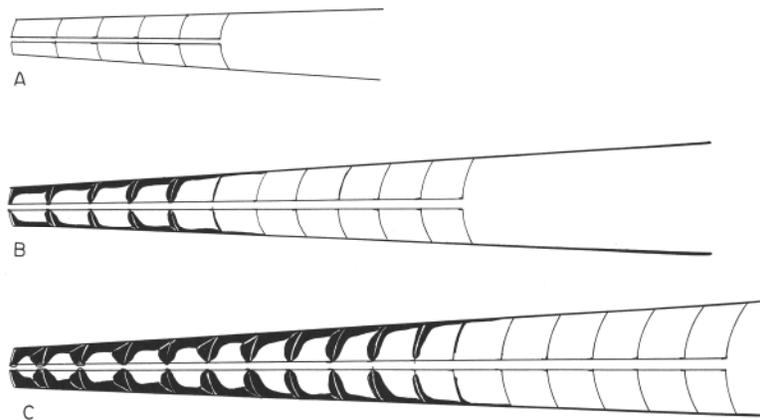


Figure 21

TYPICAL GROWTH RELATIONSHIPS OF CAMERAL DEPOSITS

Three stages of growth of a single shell are shown, the camerae at the left being identical, with further apical parts not shown. In A, the illustrated camerae are vacant; in B, and in A, the anterior six camerae are vacant, but they are subsequently developed camerae, and deposits are present in those shown in A. In C, the base of the living chamber is at the extreme right of the figure, followed by six vacant camerae, then a series in which the deposit thickens progressively apicad, grading into a series in which further apical increase in the mass of cameral deposits is not perceptible.

questionable whether the change from the now fairly familiar episepal and hyosepal would be a real advantage. Probably chance sections through lobes of the deposit partially embracing the siphuncle are responsible for Schmidt's perisiphonal deposits.

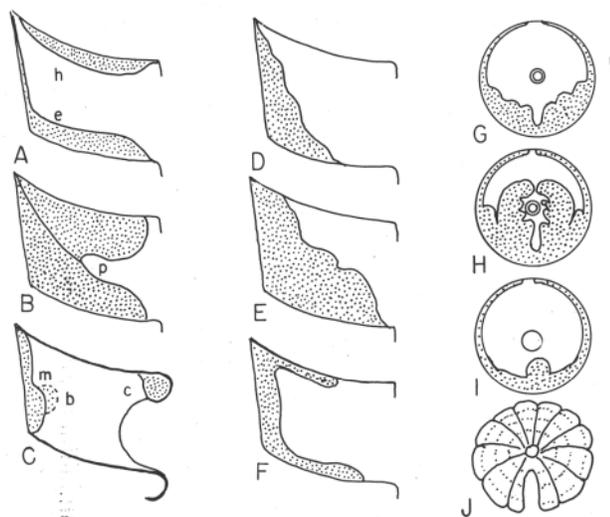


Figure 22
CAMERAL DEPOSITS

- A. A camera showing episepal (e) and hyosepal (h) deposits moderately developed.
 B. A camera showing similar deposits in advanced growth, united along a pseudoseptum.
 C. A camera containing mural deposits (m), which in midventral section may show a midventral boss (b); also a circulus supporting the recurved septal neck. The two deposits would not be found together in the same cephalopod.
 D. A more common type of mural deposit, which, thickening apically, grades to some extent into the episepal deposit.
 E. An advanced growth stage of the same deposit, showing its growth so that it appears truncated by the next adoral septum.
 F. The holosepal deposit, thus far definitely known only in some Discosorida.
 G. Cross section of the cameral deposits in a young stage of *Pseudorthoceras*.
 H. A more advanced growth stage of the deposits of the same genus, showing the ventrolateral masses extended into lobes partially surrounding the siphuncle.
 I. Cross section of "*Orthoceras*" *ludlowense*, showing the development of a midventral boss.
 J. Sketch of the internal mold of the cameral deposits of *Leurocyloceras*, showing the ventral process outlined, and radial and concentric markings.

Cameral deposits may develop complex surface patterns (pl. 1, fig. 13, 14); further, such patterns may vary with the ontogeny of the individual deposit. In the Pseudorthoceratidae the deposit shows a narrow middorsal hiatus (fig. 22G), thin dorsolateral bands, which may show striated surfaces, thicker ventrolateral masses, which may show striated or botryoidal surfaces, and a ventral sinus. These deposits are mural, and their apparent thickness in cross section will vary, depending on the point at which the section cuts the camera, being thin adorally, thick adapically. With further growth (fig. 22H) the ventrolateral masses are greatly increased and produce lobes which may partially surround the siphuncle. Sections through such lobes may produce isolated bits of deposit in longitudinal section close to the siphuncle, which is

probably the explanation for what Schmidt (1956) called perisiphonal deposits.

Quite a different pattern is shown by cross sections of "*Orthoceras*" *ludlowense* Miller* (fig. 22I) in which deposits are wanting again middorsally, thin dorsolaterally, thicker ventrolaterally, but are extended into a midventral boss in the middle of each camera. A similar pattern has been found characteristic of *Pleurorthoceras* (Flower, 1962B).

The information which cross sections supply is limited, unless one is prepared to grind progressively and assimilate the results as was done by Störmer for trilobite appendages. The real surface pattern is apparent only under rather exceptional conditions of preservation. It is apparent commonly in *Striacoceras typus* (Saemann) (see Flower, 1936), where cameral deposits are commonly exfoliated with the conch and the mural part of the septum, leaving on the apparent internal mold an impression of the deposits (pl. I, fig. 13, 14). Again, in specimens of *Leurocyloceras niagarensis*, internal molds of dolomite, from which calcitic shell parts have been dissolved, may retain the surface pattern with great fidelity; in this form both episepal and hyosepal deposits are developed, and they show a pattern of radial and concentric markings with also a midventral process comparable to that of "*Orthoceras*" *ludlowense*. The same genus has shown impressions which can only be caused by blood tubes in the cameral tissues (see Flower, 1941A).

Again, specimens in which the shell is silicified and then leached from the matrix may show cameral deposits; this condition has been found in *Buttsoceras adamsi*, as noted by Ulrich and Foerste (1936) and shown by Flower (1962A).

Quite one of the most singular deposits is that found in the genera *Arthrophyllum* Beyrich and *Lamellorthoceras* Termier and Termier, where the deposit extends as thin, fine, radial bands from the periphery toward the siphuncle. Teichert (1961) has presented additional illustrations and descriptions of this type of structure. Here shell parts may weather away leaving internal molds showing the finely sculptured pattern, very much as in *Leurocyloceras*, only much more elaborate, and with much higher relief.

In both the Discosorida and Oncoceratida, deposits are commonly exfoliated with the other shell parts, leaving a series of faint linear impressions on the steinkerns of phragmocones. Generally apical portions of such shells where deposits are thicker and may show more elaborate patterns are unknown, but in an early portion of a *Westonoceras* (see Miller, Youngquist, and Cullison, 1954, pl. 44, fig. 2) there are holosepal deposits which thicken midventrally, showing as their impression on the internal mold a pattern which suggests an actinosiphonate siphuncle as that of *Augustoceras*, exposed and partly eaten into by weathering. The form is, however, a true *Westonoceras*, and the apparent siphuncle segments are false, though the deposit there thickens and partially surrounds the siphuncle but remains some distance from the actual siphuncle wall.

Quite probably our present knowledge of varied patterns of cameral deposits is still incomplete.

Cameral deposits appear at several points independently in the evolution of the Nautiloidea. They are wanting in the older Ellesmeroceratida and are known in advanced but not

*Probably this species is allied to *Pleurorthoceras*.

primitive members of the Baltoceratidae and also in the Protocycloceratidae. They are generally developed in the older Discosorida but are suppressed or vestigial in the Lowoceratidae and Discosoridae, where siphuncles become large and heavy, though it must be noted that few specimens of these families are known showing much more than the endocone-filled heavy siphuncles.

In the Actinoceratida, deposits are generally developed, and though they show ventral concentration and a bilateral pattern in cross section (Flower, 1957) and may be mural or episeptal and hyposeptal, with the circulus commonly developed, the full variation of surface patterns has not yet been explored.

It is in the Michelinoceratida that the cameral deposits show their fullest development, and also their widest variation in pattern. Here belong the Pseudorthoceratidae, *Pleurorthoceras*, *Lamellorthoceras*, *Leurocycloceras* and, indeed, most of the radial patterns discussed above. True cameral deposits in the Endoceratida are not as yet known. Careful examination leads to the conclusion that such linings of calcite in the camerae as are observed in that order are inorganic. No cameral deposits are known in the Ascoceratida. Perhaps the most remarkable development of cameral deposits anywhere in the Nautiloidea is that found in *Ecdyceras* (see Flower, 1962) where such deposits leave only small central cavities in the centers of the camerae, except in adoral camerae where, as usual, deposits thin and disappear when traced orad in the phragmocone. As noted above, deposits persist in general in the Oncoceratida, but commonly remain thin, and are seen as faint linear impressions on internal molds of phragmocones. Rather thicker deposits are only rarely developed; a startling case is in the gyroconic genus *Stereotoceras*, which shows a rather characteristic surface pattern of deposits unlike that of most Oncoceratida (see Flower, 1950).

The wide variation in surface pattern, growth relationships, and occurrence make cameral deposits tools of potential value to the taxonomist. Interestingly, before the nature of these deposits was understood, they were noted and used taxonomically, though not always correctly. The radial lamellae of *Art hrophylum* led to the early recognition of that genus, and it was suggested that these cephalopods developed something in the camerae comparable to the septa of corals. *Orthoceras selkirkense* Whiteaves seemed to be an annulated cephalopod, and was referred by Foerste to *Cycloceras*, but the apparent annuli prove to result from exfoliation of cameral deposits with the conch. Oddly, in *Michelinoceras michelini* and a group of allied species, cameral deposits are either so greatly retarded that they are confined to apical camerae, where they have not yet been observed, or are wanting altogether. They are developed, though they may be apically concentrated to an extreme degree, in many of the smaller orthoconic species, and can be found even in *Protobactrites*, *Plagiostomoceras* of the Silurian, *Arkonoceras* and the Bacritidae of the Devonian, and are apparent, though very thin, in the Mississippian belemnites, though definitely observed only in *Eobelemnites* and *Pseudobactrites* (Flower, 1945; Flower and Gordon, 1959).

Coiled orders lack cameral deposits in general. The Trocholitidae alone show deposits, but they appear to be outgrowths of the connecting ring rather than true cameral deposits. Rather extensive deposits are developed, however, in the Lituitidae (Holm, 1885; Sweet, 1958).

Apical concentration of cameral deposits varies widely.

Teichert (1961) has shown a figure of an *Arthrophyllum* showing such deposits extending essentially throughout the phragmocone, though thinning and immature in the adoral camerae. Generally there are from 5 to 12 adoral camerae without any trace of deposits, the condition within a species being uniform for the growth stage and fairly uniform in neanic and epebic stages. In *Orthoceros regularis*, the most adoral trace of cameral deposits is found 32 camerae from the living chamber in a mature individual. Though this seems extreme, and certainly is extreme in relation to most Michelinoceratida, the shell continued apically for another 80 to 100 mm and must have contained at least fifteen more camerae in which deposits should show a progressive apical increase in thickness and maturity.

The development of cameral deposits in (1) the Discosorida, (2) the higher Baltoceratidae and derived Michelinoceratida, (3) in the Protocycloceratidae, (4) in the Actinoceratida, (5) in the Lituitidae, and (6) in the Oncoceratida is the result of the beginning of secretion of the cameral mantle in these various points in the evolution of the Nautiloidea, and suggests that the cameral tissue responsible for this secretion was probably an archaic feature of the cephalopods, common to these stocks and their common ancestor, to be found in the archaic Plectronoceratidae.

Teichert (1933) has presented some figures showing the materially great weight of a relatively thin cameral deposit around the periphery of the shell in contrast to a seemingly more massive deposit in the actinoceroid siphuncle. One cannot estimate the hydrostatic relationships much more closely; indeed, even these figures are approximations, for they do not take into account the general ventral thickening of the deposits nor the elaborate sculpture of their surface patterns as developed in the various groups. It is, however, quite evident that it is these deposits, together with the siphuncle with its various deposits, which so weigh the shell apex as to locate the center of gravity of the organism at essentially midlength of the shell, thus permitting the orthoconic forms to assume the horizontal mode of life which is indicated by the color bands known for such shells. Furthermore, the general ventral concentration facilitates stabilization with the venter beneath. Cameral deposits are the main agent in balancing the shells of the Michelinoceratida; in the Actinoceratida they are still of great importance, but the larger siphuncles, apically filled with annular deposits are also to be considered. Only in the Endoceratida are siphuncle fillings the sole agent in adjusting the shell to a horizontal mode of life. In view of Teichert's estimates, one may conclude that the slender endoceroids, even with large siphuncles, must have had relatively light shells, and it would require exceptionally large siphuncles to produce necessarily heavy shells which would require a benthonic mode of life.

With the extensive studies now available of cameral deposits, understanding of their function in the balance of the shell and the adjustment permitting the orthocones to swim, while maintaining a horizontal shell position with the venter down, it is hardly necessary to defend the reality of these organic structures. Mutvei (1956) has asserted that all these structures are inorganic, and that a cameral mantle is impossible, presumably because none is found in *Spirula* or *Natal-*

lus. One wonders where similar reasoning would lead if it were applied to other groups. The study of a living holothurian and a stellaroid might cause one to reject completely the pore-rhombs of cystids, and might lead to the conclusion that the carpoids as a group are fossil hallucinations, and serve as a fitting prelude to a return to the views of Berringer's time.

Mutvei, in rejecting the organic nature of the cameral deposits and the cameral mantle, has developed upon himself the responsibility of finding some alternate explanation for the following phenomena:

1. Cameral deposits exhibit specific and often elaborate bilaterally symmetrical surface patterns. Symmetry is consistent with the bilateral symmetry of the shell.

2. Cameral deposits exhibit marked ventral concentration.

3. Cameral deposits are independent of orientation of the shell in the sediments. Commonly, however, the weight of the deposits causes the shell to come to rest with the venter beneath.

4. Cameral deposits are apically concentrated, but their growth pattern is consistent with the growth of the shell as a whole, which can be commonly expressed in terms of a number of vacant camerae, a number of camerae showing marked apical progress in ontogeny of the deposits, and an apical region in which such further progress is not perceptible; the first two of these may be constant or may be a number varying gradually with ontogeny; they may be expected to vary slightly as the third interval increases regularly with growth.

5. Ventral concentration of deposits is general, and independent of the ventral, central, or even dorsal position of the siphuncle.

6. As in the Actinoceratida, the perispatium permits the development of a system of few large blood vessels from a primitive pattern of numerous finer ones, in *Leurocycloceras*; where the ring is not calcified, a similar development is possible in the cameral tissues. Impressions of such vessels have been found in the cameral deposits. Obviously rejection of the organic cameral deposits and tissues requires another explanation for these regular tubular structures.

7. *Leurocycloceras* has shown two types of cavities in the cameral deposits formed apparently by organisms living in the camerae, parasitic in the broad sense (Flower, 1941A). One such cavity is short and conical and its development does not affect the growth of the cameral deposits perceptibly. The other, an irregular vermicular cavity, is found in a camera where growth of the deposits has been markedly retarded. While by some stretch of the imagination one could explain the first as some organism, which, like *Pholas*, may burrow into rock or, in this case, inorganically deposited calcium carbonate, though some tall explaining is necessary to produce

such characteristic cavities thus far found only in cameral deposits of cephalopods, it will take some greater ingenuity to explain the vermicular cavity as developed here in calcium carbonate and at the same time retarding its deposition.

8. Some other explanation must be found for the calcite areas reported in *Rayonoceras*, representing materials, since destroyed and replaced, which originally blocked invading sediments partially penetrating the camerae. These are easily explained as remnants of cameral tissue.

9. Without the cameral and siphonal deposits, no observable mechanism exists to so weigh the shell apex as to permit a horizontal mode of life of the straight cephalopod, while at the same time the buoyant effect of gas is sufficient to permit facile swimming. One must return to one of several unsatisfactory assumptions: (1) That gas was not present in the camerae, which is highly improbable. If the long phragmocones were not of some use such as gas would impart, it is hard to see how the orthocones could have been such a successful group in the Paleozoic. (2) That apical camerae were filled with liquid. This is not impossible, but of course cannot be proved or disproved from the hard parts which are all that are available as fossil evidence.

10. Examples of orthocones are known showing cameral deposits surrounded by invading matrix; the most striking such instances show the conch largely lost, but the free parts of the septa are preserved surrounding the siphuncle; their preservation was materially aided by the additional support of cameral deposits. This condition has been found in a number of examples, but is perhaps most strikingly displayed in published material by some of the specimens of *Butsoceras* recently figured (Flower, 1962A). Some other explanation must be found for such calcareous structures, formed with bilaterally symmetrical patterns prior to breakage and burial of the shell.

Further observations on surface patterns of cameral deposits are badly needed. So far, the preservation conditions under which they are best seen have been found in relatively few species mostly from specialized associations. Until more observations can be made, the relationship or variation of pattern with taxonomic groups cannot be evaluated. As yet, while cameral deposits show characteristic patterns in some lineages, observations are too scattered geographically and stratigraphically to serve as more than suggestions as to general patterns in broad, taxonomic groups. There is, however, indication that the pattern of these deposits will be found to be of particular value in the tracing of lineages in the Michelinoceratida.

Orientation

From the inception of the Platyhelminthes on in the animal kingdom, symmetry is fundamentally bilateral. In the evolution of the various groups there may be odd modifications, the superficial pentaradial symmetry developed in the Echinodermata is one type, but there are others which involve primarily twisting in the vertical plane. Except in the Echinodermata and some sessile types, there is always an obvious anterior end and a posterior end, also a top and bottom, which serve as a basis of reference, and it is in relation to these that the terms *dorsal*, *ventral*, *anterior*, and *posterior* are oriented. It is evident, however, that there are some strange modifications which give rise to different interpretations as to homologies of surfaces. Mutvei (1957) has been impressed by one aspect of this situation and has presented a revised series of terms for the orientation of the cephalopod. They are based on the premise that the mantle and shell are fundamentally dorsal, and from this he concludes that the aperture, and the part of the cephalopod protruding from it are ventral, and that the septal surface is fundamentally dorsal; thus, the dorsal surface of general usage is anterior, the ventral surface posterior. He finds support for this premise in the embryology (known only in the specialized Coleoidea) and emphasizes that the foot, which is primitively ventral, involves the cephalopod "head."* This is no news to anyone. However, one may well wonder what results in orientation the application of similar principles might have when applied to the Brachiopoda, Echinodermata, Bryozoa, Ascidia, Cirripedia, to cite only a few groups where there are odd modifications affecting or obscuring the general orientation and bilateral symmetry. The proposal is the more curious in view of the favor with which some paleontologists view the idea that early ontogenetic stages have no phyletic significance. It also bypasses neatly the problem posed by some phases of embryological development, as, for example, the gymnastics by which some embryos turn around completely in the egg in their development. Should these premises prove valid, a general re-examination of orientation of adults would be pertinent throughout the animal kingdom, and one could query anew whether the closing of the embryos on the apparent dorsum and venter respectively in the arthropod and the chordate lineages represent a real homology, and if so, in which instance the terminology of orientation should be reversed.

However, it may be questioned whether the reasoning which is here applied to the Cephalopoda is necessarily valid. One can visualize an organism with fundamental dorsal, ventral, lateral, anterior, and posterior regions remaining stable while the organs and their apertures to the exterior twist and revolve variously within, but there is another viewpoint which is equally valid and will lead to different and equally odd results. The fundamental pattern of the mollusc is that of a crawler, with a foot protruding from the shell, but at the anterior end of the foot there is a mouth and eyes of some sort, while at the posterior end there is an anal opening and a gill chamber. We think, generally, of the mouth as anterior, but there are numerous forms where this is not strictly true, as the Nemertine worms, which have a proboscis anterior to the mouth, tentacles anterior to the mouth in several groups, or, as in the commoner gastropods, where the mouth is to be

found well within the anterior crawling surface of the foot. In the interpretation of the cephalopods, more than one viewpoint expressed by Mutvei is possible. It would be equally valid to argue that the whole surface covered by the mantle is dorsal, and that the dorsal surface has been extended, while, with migration of the primitively posterior gill chamber and anal opening, which are rotated first down and then around forward, the dorsal surface is immensely increased, and the ventral surface is all but obliterated. In the sagittal plane, the venter is reduced to the area between the mouth and the gill chamber. Meanwhile, what of the "foot"? The solution here is not obvious, but the vestiges of tentacles in *Loligo*, which are primitively on the under side and surround the juncture of the embryo with the yolk sac, migrate so that they finally surround the mouth; thus the primitive foot involves the small area between the mouth and the gill chamber but is spread laterally, migrating forward around the mouth to a point at which it loses its real identity, and its recognition rests upon the general definition that, as it has to do with locomotion and seizing food, it must be represented by the tentacles.

There are, of course, still further complications in orientation supplied by the fact that the relationship of the main body mass of the mollusc and its shell are plastic to a degree, most marked in the gastropods where spatial relationships are very different when the animal is expanded and when it is contracted.

Obviously, with two possible interpretations of symmetry and the relationships of the fundamental ventral and dorsal regions, it is far better to admit that in spite of torsion of the gill chamber, which has migrated ventrad and then turned adorally, a revolution of essentially half a circle, the body mass of the cephalopod, whether nautiloid or coleoid, has a fundamental anterior region with mouth, eyes, and sense organs which makes a good head, clear dorsal and ventral differentiation, with the posterior end primitively having the siphonal strand as an extension, and lying against the septum of the primitive chambered shell.

Some note should be taken of directional terms which are widely used, in particular by Miller and the writer, in description of cephalopod shells. Dorsum is the upper side, dorsal is the adjectival form, and dorsad is adverbial, indicating toward the dorsum. Venter, ventral, and ventrad are similar terms. Oral pertains properly to the mouth, and caudal to the posterior end. However, the term apertural referring to the aperture of the shell, has been used for shell structures, and oral or orad in the shell is figurative, pertaining to the mouth of the shell. Apical and apicad have been preferred to caudad in view of the obvious twisting of internal organs, and the fact that while shelled cephalopods have no obvious tail (though that term could be applied to the caudal fins of the squids) there is always a definite apex to the shell. Such terms have been in quite general use in cephalopod descriptions for the fifteen or twenty years of the more recent work, and many of

*As the late humorist, Will Cuppy, put it, "The foot which is mostly head is divided into arms; if that's clear."

them were used earlier by Foerste and by Hyatt. Oddly, correspondence relating to the Treatise of Paleontology revealed the astonishing opinion on the part of some that this writer had made up these terms himself. It was even more amazing to find in the work of the Discosorida (Flower and Teichert, 1957) that these terms were removed by the editor and other and more cumbersome terms substituted without the author's knowledge, and correction was denied through two sets of proofs. The matter is worth noting as thus far at least, it is only in that work that such more unwieldy terms as "adventrally" for ventrad are to be found. For the benefit of others whose background in zoology may be insecure, it may be stated that these and similar terms are of general use among zoologists; the writer first met them in the laboratory of a course in elementary zoology, circa 1931, and they may be found in such laboratory guides to elementary zoology as Reid and Young (1930). They are also noted by Shrock and Twenhofel,

1953, P. 443.

It should be noted with approval that Gordon (1957) has introduced further terms such as "dorsorad" or "ventrorad" for structures sloping or extending toward the mouth on the venter or dorsum respectively. Such terms save space.

The terms distal, distad, proximal, and proximad are confusing in relation to cephalopod shells, owing to variation in their use in relation to a point of reference. Schmidt (1956) suggested applying such terms to cameral deposits with reference to the body mass of the animal, but they have been and, indeed, may be used with equal validity with reference to the beginning of the shell or the apex, as it is more commonly known. More properly, distal and proximal are employed with reference to bodies or appendages having a definite free end and a definite point of attachment.

Glossary

Here are arranged alphabetically morphological terms and a few taxonomic terms commonly found in descriptions of the Nautiloidea. Some terms, connected with ornament or cross section of the whorl, have not been mentioned in the above discussion. An effort has been made to include those terms in general use, though occasionally with indication of preference, even when they are synonymous, and to include various past usages, which are variable and even loose in some instances. Two short-lived proposals are not indicated: First, the terminology which Grabau (1929) proposed on the theory that the endoceroid siphuncle was homologous with the conch of other nautiloids, and second, the novel and rather cumbersome terminology proposed by Mutvei (1957, 1957A) for which simpler terms have long been in use.

In general, adjectival and adverbial derivatives of nouns are included under the nouns, though this was not possible in some instances, and would have been confusing where prefixes bring such terms into widely different parts of the glossary.

ABDOMEN.—synonymous with the venter (Hyatt, 1894).

ABDOMINAL.—(adj. form) from abdomen.

ABDOMINAL ANGLE.—a sharp angle separating ventral and lateral faces in some nautiloids. Largely used in connection with coiled forms.

ABDOMINAL FACE.—the ventral face, or flattened ventral surface of the shell.

ABDOMINAL SHOULDER.—a strongly rounded zone separating relatively flat ventral and lateral faces in some nautiloids.

ACHOANITIC.—a term substituted for aneuchoanitic (Teichert and Glenister, 1954) for septal necks which are so short as to be scarcely developed.

ACTINOSIPHONATA.—Hyatt's (1900) subdivision of his Cyrt-
ochoanites, in the specialized members of which actinosiphonate deposits are developed. Now abandoned, as it included the present Oncoceratida, a few Discosorida, and *Eremoceras* and *Cyclostomoceras* of the Ellesmeroceratida.

ACTINOSIPHONATE.—a descriptive term applied to supposed deposits in the siphuncle, now evident as true extensions of the connecting rings, in which rays extend from the siphuncle toward the siphuncle axis, but do not meet there; also, rays may extend forward and apicad from swellings at the tips of the septal necks.

ACTINOCEROID.—a descriptive term applied to the Actinoceroidea of Teichert, the present order Actinoceratida, characterized by straight shells with expanded siphuncle segments in which annuli leave unfilled a siphonal vascular system of central canal, radial canals in each segment, leading to a perispantium.

ADAPERTURAL.—a descriptive term meaning toward the aperture (adv.—adaperturally); adoral is preferred as shorter.

ADAPICAL.—toward the apex (also adv.—adapically).

ADNATION, area of.—the region in expanded siphuncles in which the connecting ring lies in contact with the septum outside of the septal neck.

ADORAL.—pertaining to the mouth; in this instance, to the mouth of the shell (also adv.—adorally); preferred to adapertural.

AIR CHAMBER.—the space set off by septa in the phragmo-

cone; in view of doubt as to whether the older fossil cephalopods had air in the "air chambers," the term *camera* was proposed, and is in general use.

AMORPHOUS BANDS.—narrow parenthesis-like bands of amorphous material in the connecting rings of the Discosorida, bounding the chitinoïd zone.

ANEUCHOANITIC.—a term proposed for septal necks so short as to be scarcely developed (Ulrich and Foerste, 1933, 1936). Teichert and Glenister proposed the shorter synonymous *achoanitic*.

ANNULAR ELEVATION.—a term applied to the thickening of shell at the base of the living chamber involving muscle scars (Mutvei, 1957; Sweet, 1959), but also involving the aponeurotic bands.

ANNULAR LOBES.—a small secondary lobe in the middorsal region of many coiled shells, often a small deep lobe in the center of a broader, shallower lobe across the whole dorsum.

ANNULI.—rings or ringlike structures used (1) for markings on the shell surface and (2) for annular deposits, actually appearing first as hollow doughnutlike rings, in the siphuncle at the region of the septal foramen.

ANNULOSIPHONATA.—a division of Hyatt's (1900) Cyrt-
ochoanites in which annuli or annulosiphonate deposits developed. Now abandoned, as it originally contained the Actinoceratida and several families now assigned to the Michelinoceratida, Barrandeoceratida, and Discosorida.

ANNULOSIPHONATE.—a descriptive term applied to annular or doughnutlike deposits in the siphuncle, or to cephalopods having such deposits. Annulosiphonate deposits are a form classification for several structures discrete phyletically and differing in composition.

ANNULUS.—(1) the simplest type of ringlike deposit in the siphuncle; (2) the muscle scar at the base of the living chamber, the annular elevation of Mutvei.

APERTURE.—the anterior opening of the conch; also termed the mouth of the shell.

APICAD.—(adv.) toward the apex of the shell.

APONEUROTIC BANDS.—bands of fibrous tissue in Nautilus, leaving impressions on the shell interior. One band extends between the main shell muscles on the dorsum; two, one anterior and one posterior, traverse the venter. They combine with the lateral shell muscles in the "annular elevation" of Mutvei, and actually, muscles other than the main shell retractor muscle are involved.

ASCOCEROID.—a descriptive term for shells of the Ascoceratida, in which the early slender portion is molted, the anterior pear-shaped portion develops septa which swing forward into distinct dorsal saddles.

BASAL ZONE.—a region at the base of the mature living chamber, best developed in breviconic forms, where the shell is thickened, leaving a narrow concave band on the internal mold. Involved in this are certainly gerontic incipient septa, closely spaced and thin or wanting except at the margins, cameral deposits, and muscle impressions.

BICONVEX SEGMENT.—in general, a siphuncle segment slightly convex on both dorsum and venter; specifically, seg-

ments of this type which occupy the second ontogenetic stage in the Ascoceratida, best seen in the primitive forms.

BLADE.—a shortened and generally used form of endosiphoblade; blades are tabular, longitudinal structures, longitudinally continuous, in the endoceroid endosiphuncles, extending most commonly from the central tube to the siphuncle margin, but where multiple tubes exist, may form a band connecting such tubes. This last is here given the new name *infula*.

BREVICONE.—a cephalopod shell which is short, generally rapidly expanding, which may or may not be contracted at the mature aperture (also adj.—breviconic).

BRIM.—the portion of the neck which is recurved, in cephalopods with expanded siphuncle segments. In practice, with relative measurements of brim and neck, the two (the one the recurved part, the other the linear extent) overlap.

BULB.—see *siphuncular bulb*.

SULLETTE.—a term proposed by Strand (1933) for annuli in the siphuncle which are actually swellings of the apical end of the septal neck. Also, in the Discosorida (Flower and Teichert, 1933) similar regions of two distinct layers at the apical end of the ring commonly but not always swollen in this way.

CAECUM.—see *siphonal caecum*.

CAMERAE.—(singular, camera) the spaces between septa, formerly called air chambers (adj.—cameral, pertaining to camerae).

CAMERAL DEPOSIT.—a calcareous deposit formed in the camera (equivalent to and preferred to intracameral deposit).

CAMERAL GAS.—gas secreted in the camerae. In *Nautilus* it is essentially dissolved air resecreted from the blood; as nitrogen shows increased solubility under such pressure as deep water provides, the gas in *Nautilus*, which inhabits relatively deep water, shows a high nitrogen content. Presumably cameral gas was present in most if not all fossil forms, appearing certainly very early, though not certainly in the very oldest cephalopods.

CAMERAL MANTLE.—the tissue in the camerae which secreted the cameral deposits (Flower, 1939), vestiges or impressions of which are occasionally found.

CAMERAL TISSUE.—synonymous essentially with the cameral mantle.

CENTRAD.—(adv.) toward the center, in cephalopods, commonly the axis of the shell or siphuncle.

CENTRAL CANAL.—a canal developed in tissues of the siphonal strand of the Actinoceratida, consisting of one or more continuous linear tubes, from which radial canals extend; it is commonly outlined by annulosiphonate deposits, and very rarely, may show an independent calcified wall of its own.

CIRRVIN ZONE.—a region in the discosorid connecting ring of clear, yellowish material suggesting chitin, occupying commonly the apical half of the free part of the ring, and bounded by the two amorphous bands.

CICAMIX.—the scar at the apical end of some nautiloid shells marking the supposed point of contact of an original uncalcified protoconch which is commonly lost. Formerly regarded as general for the Nautiloidea, it now appears highly doubtful for the primitive orders.

CIRCULUS.—a cameral deposit formed around the recurved septal neck, the stutzring of Teichert (1933).

CONNECTING RING.—a segmentally repeated structure, dominantly of calcite and organic matter, secreted primitively within the wall of the siphonal strand or, secondarily, upon

its surface. Primitively, segments of the rings may outline the siphuncle, but secondarily rings and necks may become intricately involved, overlapping one another. Primitively thick, the ring may show regions differentiated in texture and composition.

CONCAVE SIPHUNCLE.—a descriptive term (Foerste, 1924) for siphuncle segments of strongly concave outline. First applied to specialized Oncoceratida, the term is also applicable to some Ellesmeroceratida and Endoceratida.

CONCH.—properly the shell wall, as distinct from the subsequently added septa, rings, and siphonal and cameral deposits. It has also been used for the entire shell.

CONCHIAL FURROW.—a shallow, longitudinally continuous furrow on the interior of the midventral part of the shell (Flower, 1931). In rare instances, two supplementary ventrolateral furrows may develop.

CONCHIOLIN.—a chitinlike, brownish substance forming, in *Nautilus*, the apical initial layer of the septum. Also, in a broader sense, similar substance developed elsewhere, but not definitely recognizable in fossil Nautiloidea.

CREST.—a portion of the aperture or growth lines swinging forward, as opposed to the sinus, which swings apicad.

CYRTO.—prefix indicating gentle curvature.

CYRTOCERACONE.—a nautiloid shell which is a cyrtocone at maturity, curved, describing from one-fifth to three-fifths of a revolution (adj.—cyrtoceratonic).

CYRTOCHOANITES.—in Hyatt's (1900) classification one of the major divisions of the Nautiloidea, characterized by recurved septal necks and expanded siphuncle segments. The group, since found to be polyphyletic, is now abandoned.

CYRTOCHOANITE.—descriptive term for septal necks which are recurved so that their tips point outward from the siphuncle axis.

CYRTOCONE.—a gently curved shell or part of a shell, whether mature or immature (also adj.—cyrtoceran, cyrtoconic).

DIAPHRAGMS.—transverse partitions, usually concave anteriorly. Two sorts are known: (1) diaphragms crossing the siphuncle in generalized Ellesmeroceratida and (2) diaphragms crossing the endosiphonate and rarely extending into the endosiphonate in the Endoceratida, and rarely, in the *Discosorida* and *Michelinoceratida*.

DISC.—a conventional term for measurement across the coil of a coiled nautiloid shell.

DISTAD.—(adv.) toward the extremity of an attached body or process.

DISTAL.—(adj.) pertaining to the free end of an attached process or body. Application to cephalopod shells has not been uniform in usage, the distal end being sometimes considered the anterior growing end, with the aperture, again, the apex, as the part farthest from the vital body parts of the animal.

DISTAL DEPOSIT.—a term for hyposeptal deposits (Schmidt, 1956).

DORSAD.—(adv.) toward the dorsum, a general zoological term.

DORSAL.—(adj.) pertaining to the dorsum.

DORSAL HIATUS.—in cross sections of camerae, a narrow dorsal area lacking cameral deposits.

DORSAL FURROW.—an earlier term for the septal furrow; not now in general use.

DORSOLATERAL BANDS.—dorsolateral areas of cameral deposits which are relatively thin in contrast to the thicker ventrolateral masses (Flower, 1939) commonly with faint striation or pitting.

DORSORAD.—a term (Gordon, 1957) for a structure sloping orad on the dorsum.

DORSUM.—the upper surface of a bilaterally symmetrical animal, as opposed to the under surface, the venter.

ECTOSIPHUNCLE.—the part of the siphuncle forming the siphuncle wall; that is, rings and necks, as opposed to supplementary internal structures (Ruedemann, 1905). Not in general use, as some apparent endosiphuncles are segmental and parts of rings or derived from rings.

ELLESROCEROID.—(1) a descriptive term for shells of the Ellesmeroceratida and (2) more specifically, shells with ventral siphuncles, thick rings, and diaphragms.

ENDOCEROID.—(1) a member of the Endoceratida, characterized by endocones in the siphuncle and (2) slender straight Endoceratida as opposed to rapidly expanding and commonly curved forms, the pilocerooids.

ENDOCONE.—(1) a unit of deposition in a siphuncle, conical, pointing apically, of some appreciable thickness, separated from its fellows by dark growth lines or endosiphoblades, and (2) an endosiphuncle with the anterior end a conical cavity as above, but without clear evidence of individual conical units of growth.

ENDOGASTRIC.—a shell curved with the venter internal, concave, the dorsum external and convex.

ENDOSIPHON.—a prefix pertaining to structures within the primary siphuncle of septal neck and connecting ring (Ruedemann, 1905) now confined largely to structures in the Endoceratida.

ENDOSIPHOCOLEON.—proposed by Ruedemann (1905) for a flat tube found in adoral parts of some Endoceratida, connecting apices of endocones. It was then believed to be filled in laterally after formation, resulting in an apical round cavity, the endosiphotube. More recent work suggests that the tube, circular in young stages, may become flat or variously modified later in ontogeny, and the endosiphocoleon is not recognized as a distinct entity.

ENDOSIPHOLINING.—defined originally as a lining in the endoceroid siphuncle developed prior to endocones, and within which the endocones are secreted (Ruedemann, 1905). Subsequent work has indicated that the apparent lining, commonly seen in cross sections of endosiphuncles, is adventitious, bands of calcite deposited in the periphery of the structure in replacement, and the lining is not general. It is, however, developed in the higher Allotrioceratidae (Flower, 1957).

ENDOSIPHOCONE.—the conical cavity found at the anterior end of the endoceroid endosiphuncle (Ruedemann, 1905). Also speiss.

ENDOSIPHOCYLINDER.—the cylindrical cavity in the anterior end of the endoceroid siphuncle, anterior to the endosiphuncle and the endosiphocone. Not in general use.

ENDOSIPHOSHEATH.—thin, dark band between two adjacent endocones, regarded as marking a resting stage in the growth of the endosiphuncle.

ENDOSIPHOTUBE.—the tube connecting apices of endocones, also, without individual endocones, the tube extending to the

tip of the conical apex of the endoceroid endosiphuncle. It may vary widely in cross section and may or may not appear to have a definite wall of its own.

ENDOSIPHOWEDGE.—a process, wedge-shaped in cross section in the endoceroid endosiphuncle modifying the section of the endosiphocone; it may be continuous with the endocones, or seemingly distinct from them; it may interrupt cones or they may grow over the wedge.

ENDOSIPHUNCLE.—(1) as originally proposed (Ruedemann, 1905) applicable to any solid structure within the ectosiphuncle; (2) now generally specifically applied to the endoconal structure developed in the Endoceratida.

EPHEBIC.—a general zoological term for maturity.

EURYSIPHONATA.—a group of cephalopods characterized by relatively large siphuncles (Teichert, 1933) including the Endoceratida, Actinoceratida, and the poorly defined Cyrtoceroidea. Now obsolete.

EURYSIPHONATE.—applying to the Euryisiphonata; having a siphuncle of relatively large diameter (obsolete).

EVOLUTE.—(adj.) a condition of loose coiling; commonly applied to anterior parts of coiled shells in which coiling becomes looser than in the early part.

EXOGASTRIC.—a shell curved or coiled with the venter external and convex, the dorsum concave or internal.

EYELET.—an apical region of the connecting ring, largely confined to the Endoceratida, in which the ring, as seen in longitudinal section, shows an elliptical region of dense, amorphous material, commonly more or less completely surrounded by lighter, more coarsely granular material making up the generalized part of the ring (Flower, 1941). Oddly, the eyelet may retain its identity where recrystallization obscures identity of the remainder of the ring from septa and inorganic calcite.

FIBRALIA.—a term proposed for the siphonal deposits of the Discosorida which, whether they take the form of annuli or of endocones, show commonly preservation of fine vertical fibers, which are commonly more prominent than the growth lines.

FORAMEN, SEPTAL.—the opening in the septum for the passage of the siphuncle.

FREE PART OF SEPTUM.—the part of the septum which traverses the conch, passing from the suture, its junction with the free mural part of the septum and the conch, to the bending of the septal neck. Part of it may be incorporated secondarily in siphuncles with broadly expanded segments and areas of adnation.

FUNNEL.—a term now generally abandoned and rather loosely used in earlier paleontological works. Hyatt (1883-1900) employed it for the septal necks, but it has been used on occasion for the entire siphuncle wall and also for endoceroid endocones. Mutvei (1957) has revived it for the siphuncle wall in general. It was also used for the hyponome of the soft parts.

GERONTIC.—a general zoological term for individuals showing old age phenomena. In some instances, correctness of application to some nautiloid shell features developed at maturity is debatable.

GOMPHOCEROID.—descriptive term applied to breviconic shells in which the aperture of the mature living chamber is appreciably contracted.

GROWTH LINES.—surface markings of the conch reflecting the shape of the aperture at earlier growth stages.

GYROCERACONE.—a shell which at maturity describes a loose spiral (also adj.—gyroceraconic).

GYROCONE.—a shell which describes a loose spiral, regardless of maturity (also adj.—gyroceran, gyroconic).

HEMICHANOANITIC.—a term describing septal necks which are essentially parallel to the siphuncle axis and extend for about half the length of a segment; as opposed to orthochoanitic, which is shorter, holochanoanitic, where the neck is the length of the segment or nearly so, and loxochanoanitic, in which necks slant apicad and centrad (Teichert and Glenister, 1954).

HOLOCHOANITES.—an order in Hyatt's (1900) classification characterized by large tubular siphuncles with long septal necks, believed at that time to lack connecting rings; it included the Diphragmida, essentially the present Ellesmeroceratida, and the Endoceratida, essentially the present order of that name. It is now abandoned, as the holochanoanitic condition is secondary and is not generally developed in the Ellesmeroceratida and is not even universal in the Endoceratida.

HoLocrioANinc.—a descriptive term for septal necks which extend for the length of one siphuncle segment. Formerly, still longer necks were included, which are now separated as macrochoanitic (Teichert and Glenister, 1954).

HOLOSEPTAL DEPOSITS.—cameral deposits which are mainly formed against the outer wall of the camera, but extend without a break onto both apical and adoral septal surfaces. Primarily known from the Westonoceratidae of the Discosorida.

HYPONOMIC SINUS.—a ventral sinus commonly present in nautiloid apertures which facilitated protrusion of the hypopome for swimming, and probably also facilitated respiration when the animal was retracted within the shell.

HYPONOME.—the funnel, the anterior tubular opening of the gill chamber, in the tissues of living Cephalopoda.

HYPOSEPTAL DEPOSITS.—cameral deposits formed on the under surface of the septum, as the shell is commonly oriented for purposes of illustration; that is, on the anterior wall of the camera.

INFULA.—a dark longitudinally continuous band connecting multiple tubes in endosiphuncles of specialized Endoceratida. Formerly included with the endosiphoblades.

INTRACAMERAL.—a descriptive term applied to structures, mainly deposits, in the camerae. See *cameral deposits*. The prefix *intra-* is superfluous.

iNvoLuTE.—a descriptive term for coiled shells in which the outer whorls more or less completely embrace the inner whorls.

IMPRESSED ZONE.—the concave area on the dorsum of the outer whorl of a coiled cephalopod, excavated for the reception of the venter at least of the preceding whorl.

LATERAD.—(adv.) toward the side or lateral portion.

LATERAL.—pertaining to the side portion.

LATERAL ANGLE.—(1) an angle seen in cross sections of shells where only dorsal and ventral faces are developed; (2) the angle separating the generalized ventral portion of the ascoceroid sigmoid suture from the dorsal sigmoid saddle.

LATERAL FACE.—a flattened lateral region of a shell.

LATERAL SINUS.—a re-entrant or sinus in aperture or growth lines.

LIGNE NORMALE.—the term introduced by Barrande for what is now called the septal furrow.

LINING.—applied to siphonal deposits where a true lining is

developed; such linings are continuous in some forms as in the Troedssonellidae, and are formed in other instances of fusion of segmental elements.

LIRAE.—raised lines on the surface of the conch, properly, either longitudinal or transverse, the term has been used less properly as confined to longitudinal elements only.

LITUMCONE.—a shell of the general aspect of *Lituites*, with the early part coiled, the coil giving way abruptly to an anterior straight portion.

LIVING CHAMBER.—the anterior aseptate part of the cephalopod shell occupied by the main body mass of the animal, in contrast to the phragmocone.

LOBE.—a portion of the suture which swings apicad.

LOXOCHOANMC.—a term applied to septal necks of moderate length differing from the orthochoanitic or hemichoanitic in that they point obliquely back and also in toward the center of the siphuncle.

LUNETTE.—a term applied to an annulosiphonate deposit which is distinct from the connecting ring, in contrast to a bullette which is part of the ring. Lunettes are polyphyletic, and the term no longer seems particularly useful.

MACROCHOANITIC.—descriptive term for septal necks which extend for more than a single segment, typically extending for from one and a half to two segments (Teichert and Glenister, 1954). Formerly such necks were included in *holochanoanitic*.

MURAL DEPOSITS.—cameral deposits formed primarily against the mural wall of the camera; in some instances the deposit is thickened apically, and thus these deposits grade into episeptal deposits, but in advanced growth stages, they grow centrad so that the anterior septum seems to truncate the deposits.

MURAL PART OF SEPTUM.—the part of the septum which extends forward from the suture, at which the free part joins the conch; it may vary in length, being sometimes commensurate with the length of the camera, sometimes very short.

MUSCLE SCARS.—scars, actually thickening of the interior of the shell at the base of the living chamber, marking the point of attachment of the muscle.

NAUTILICONE.—a coiled nautiloid shell with some appreciable degree of involution, in contrast to a tarphyceratcone, in which involution is slight or wanting (also adj.—nautilan, nautiliconic).

NEANIC.—a term applied to the growth stage between the nepionic and the adult.

NECic.—(1) a useful abbreviation for the septal neck, the apical projection of the septum around the siphonal strand; (2) also, the necklike produced anterior end of the living chamber in some Ascoceratida.

NEPIONIC.—a term applied to the earliest postembryonic growth stages in organisms in general. Hyatt (1894) made subdivisions, such as anepionic, etc., but general need for such refinements has not been found by other students of the Nautiloidea.

NEPIONIC LINE.—a constricted line found commonly in the young of Paleozoic Ammonoidea, but rarely as well marked in Nautiloidea, marking the end of the nepionic stage; commonly at or near the end of the first whorl.

ONCOCEROID.—a general descriptive term for shells resembling *Oncoceras*, in general, slightly exogastric brevicones

with the mature aperture moderately contracted. Also, a member of the Oncoceratida.

ORAD.—toward the aperture or the mouth of the shell.

ORTHO CERACONE.—a mature nautiloid shell which is straight throughout (also adj.—orthoceraconic, orthoceran).

ORTHOCHOANITES.—in Hyatt's (1900) classification, the order of cephalopods with dominantly tubular siphuncles, the septal neck parallel to the siphuncle axis. It is now abandoned, and the straight shells, the Michelinoceratida, prove to be phylogenetically distinct from the exogastric curved and coiled orders which are, in a more general sense, loosely united in the ancestral Tarphyceratidae, though the coiled Rutoceratida and Nautilida are separated from the older coiled Tarphyceratida and Barrandeoceratida, being derived through the Oncoceratida, which Hyatt put in his Cyrtchoanites.

ORTHOCHOANITIC.—septal necks bent so as to be parallel to the siphuncle axis and moderately short.

ORTHO CONE.—an immature shell or a portion of a shell which is straight (also adj.—orthoceran, orthoconic).

PARIETAL DEPOSITS.—siphonal deposits beginning at the septal foramen as annuli, which extend longitudinally in growth, lying against the ring.

PENDANT DEPOSITS.—siphonal deposits beginning as annuli which are inflated with further growth, but remain hanging in the siphuncle attached to the wall only at the narrow point of inception at the region of the septal foramen.

PERISPATIAL DEPOSITS.—deposits formed in the perispantium, appearing first at the ends, and generally confined to the region where cameral deposits abut on the outside of the ring; deposits are carbonaceous and show growth lamellae.

PERISPATIUM.—in the Actinoceratida, the perispantium is a space on the inside of the free part of the connecting ring, never filled with annulosiphonate deposits, part of the siphonal vascular system; a space for blood, permitting exchange of metabolic materials through the ring with the cameral tissues.

PHRAGMOCEROID.—shells resembling *Phragmoceras* in the broad sense, endogastric brevicones with markedly contracted apertures. Usage has varied with the concept of *Phragmoceras*, but the present concept involves further shells of strongly compressed section, a narrow aperture with a small main aperture and a very long hyponomic sinus.

PHRAGMOCONE.—the part of the shell traversed by septa, in contrast to the adoral living chamber.

PILOCEROID.—a rather loose term for an endoceroid shell (some are known only from siphuncles) which is short, rapidly expanding, and commonly endogastric; in contrast to the straight, slender endoceroid.

PLANOCONVEX SEGMENT.—a siphuncle segment faintly convex on one side (the venter), straight on the other; a special term for such segments in the Ascoceratida, where the pianoconvex segment represents the oldest of three successive types, the other being the biconvex and the moniliform segments.

PLEURONK.—a rhythmically repeated lateral swelling of the conch, not involving increased thickening of the shell, as opposed to nodes, which have a real thickness, and costae which show some considerable continuity around the shell (Flower in Flower and Kummel, 1950).

PROBULLETTE.—the apical end of the discosorid ring, of two layers, prior to its swelling into a readily recognizable annular structure, the bullette.

puoTocoNcx.—the inflated bulbous apical part of the shell

developed generally in the Ammonoidea and known in a few Nautiloidea.

PROXIMAn.—toward the base of an attached body or process.

PROXIMAL.—adjectival form.

PROXIMAL DEPOSIT.—hyPOSEPTAL deposit, one formed on the proximal end of the camera with reference to the living chamber (Schmidt, 1956).

RADIAL CANAL.—one of a series of tubes found primarily in the Actinoceratida, extending in each siphuncle segment from the central canal to the perispantium. Patterns (Flower, 1957) may be dendritic, reticular, horizontal, or may comprise a system either of double or of single arcs. Also applied to tubular passages through the deposits from the siphuncle center to the periphery in the Macroloxoceratidae of the Pseudorthoceratidae.

RECUMBENT NECK.—a septal neck so strongly recurved that its recurved portion is in contact with the free part of the septum.

RODS.—siphonal deposits, known only in the higher Pal-toceratidae and some Protocycloceratidae, round rods lying against the ventral wall of the siphuncle, pointed anteriorly, thickening apicad, and eventually filling the apical part of the siphuncle completely.

SADDLE.—a portion of the suture which swings forward.

SEPTAL FURROW.—a middorsal linear region on the phragmocone where the mural part of the septum is wanting. The *ligne normale* of Barrande, the dorsal furrow or carina of Flower (1936).

SEPTAL NECK.—the portion of the septum which is bent apicad around the siphonal strand at the septal foramen, ordinarily considered a part of the siphuncle. The funnel of Hyatt (1883-1900) is largely synonymous.

SEPTUM.—one of a series of partitions dividing the phragmocone into camerae, generally divisible into a mural part, a free part, and a septal neck.

SEPTUM OF TRUNCATION.—a septum apicad of which the earlier part of the shell is commonly voided in life; known only in the Ascoceratida, Ecdyceratida, and in the Sphooceratidae of the Michelinoceratida.

SHEATH.—a shortened form of endosiphosheath; a thin dark layer separating individual endocones and regarded as a resting stage in the growth of the endosiphuncle; also developed in the Discosorid endocones.

SHELL.—the entire hard external part of the mollusc, including in the Nautiloidea the conch, septa, rings, and siphonal and cameral deposits.

SICMOIN SUTURE.—the adoral sutures of the Ascoceratida (Miller, 1932) in which the dorsal saddle, or sigmoid outline, is sharply set off by a lateral angle from the simpler ventral portion.

SIPHON.—(1) properly the strand of tissue and involved hard parts extending through the phragmocone. Siphuncle is synonymous; (2) the term is occasionally used for the tissues to the exclusion of the hard parts, as siphonal strand; (3) in older works the term was applied to the aperture of the gill chamber, now generally called the hyponome. *Siphuncle* was proposed because (1) the idea that this tube could alter proportions of water and gas in the camerae was erroneous, and (2) siphon had also been used for the hyponome of the soft parts.

SIPHONAL CAECUM.—the apical closure of the siphuncle in

the apical chamber of the Nautiloidea, or in the protoconch of the Ammonoidea.

SIPHONAL DEPOSITS.—calcareous or at least hard and preservable deposits within the siphon or siphuncle. Formerly some parts of the connecting rings have been included under this category.

SIPHONAL MANTLE.—the theoretical tissue, a part of the epithelium of the siphonal strand specialized for secreting shell material on its surface, responsible for the siphonal deposits (Flower, 1939). It now appears that many such deposits are formed within tissues, and the siphonal mantle as a source of deposits outside the tissue is possible in some instances, but it is not adequately demonstrable at present.

SIPHONAL STRAND.—the strand of tissue extending through the phragmocone. It was held (Flower, 1939) that the ring was secreted within rather than on its surface primitively, the outer part thus becoming part of the beginning of the cameral tissue.

SIPHONAL TISSUE.—the tissue remaining essentially within the connecting rings.

SIPHONAL VASCULAR SYSTEM.—the vascular or blood system in the siphonal tissue, commonly preserved only in the Actinoceratida, in connection with which this term was first proposed (Teichert, 1933), where growth of annulosiphonate deposits fills the siphuncle segments apically except for this system of central canal, radial canals, and perispantium. Indications of similar systems are less complete in other groups.

SIPHUNCLE.—(1) the strand of tissue extending through the camerae, with attendant hard parts; (2) has been sometimes used for the hard parts alone. *Siphon* is synonymous with the broader usage; in the narrower usage, *siphon* has been restricted to the tissues. The broader usage is preferable, with *siphon* synonymous.

SIPHUNCULAR BULB.—a term introduced by Kobayashi for the expansion of that part of the segment outlined by the connecting ring alone and known only in the Plectronoceratina and in early ontogeny of *Ruedemannoceras* of the Discosorida.

STENOSIPHONATA.—a group proposed by Teichert for cephalopods with small siphuncles; not well defined and now obsolete.

STENOSIPHONATE.—cephalopods attributed to the Stenosiphonata, having siphuncles of relatively small diameter.

STRIAE.—properly linear incised or excavated markings, in contrast to lirae, which are raised linear markings. The term has been improperly applied to fine, transverse markings in general.

SUBORTHOCHOANITIC.—septal necks which point only very slightly outward and are intermediate between the true orthochoanitic and the definitely cyrtchoanitic.

SUTURE.—the line, prominent on internal molds, marking the juncture of the free part of the septum with the conch; the mural part of the septum extends forward from the suture in contact with the conch.

TARPHYCERACONE.—a mature shell coiled but with the impressed zone shallow or wanting (adj.—tarphyceraconic).

TARPHYCONE.—similar, but not confined to mature complete shells; also adj.—tarphyceran, tarphyconic.

TEST.—has been used for shell or conch; not in general use in the Cephalopoda; a test, as opposed to a shell, is a structure not necessarily completely composed of organic materials, as

in the Protozoa, where some tests are of cemented sand grains, though homologous structures may be purely organic.

TROCHOCEROID.—a coiled shell of the Nautiloidea in which the coil departs from the plane of symmetry; spires are described artificially, as sinistral or dextral in relation to the orientation applied to gastropods.

TORTICONE.—synonymous with trochoceroid, which has been more widely used in the Nautiloidea.

TRUNCATION.—the natural removal of the apical part of the shell in life in the Nautiloidea, known definitely only in the Sphooceratidae of the Michelinoceratida in the Ecdyceratida, and the order Actinoceratida.

TUBE.—(1) a shortened form of endosiphontube, convenient in descriptions pertaining to the Endoceratida; (2) a central tube free in the siphuncle; see *central tube*.

UMBILICAL ANGLE.—an umbilical or dorsolateral shoulder of the shell which is sharply angled as seen in cross section.

UMBILICAL CALLUS.—a thickening of the shell, as developed in mature *Nautilus*, covering earlier whorls in the center of the coil.

UMBILICAL SEAM.—in cephalopods with an impressed zone, the point of contact of two successive whorls as seen externally.

UMBILICAL SHOULDER.—a strongly rounded dorsolateral region separating flatter lateral and dorsal regions.

UMBILICAL PERFORATION.—a cavity in the center of the coil of a tarphyceracone or nautilicone; it is present, except where covered secondarily by the umbilical callus, in the coiled Nautiloidea and is found in some Devonian Ammonoidea; in higher Ammonoidea, the bulbous protoconch fills the umbilical perforation completely.

UMBILICUS.—the center of a coiled shell; in one sense, the cavity of an outer whorl through which earlier whorls and the umbilical perforation may be seen.

VACUOSIPHONATE.—a descriptive term for siphuncles empty of deposits.

VENTRAD.—(adv.) toward the venter.

VENTRAL.—(adj.) the under side of a bilaterally symmetrical organism, commonly the crawling surface; also ventrad, adv.—toward the venter.

VENTRAL SINUS.—(1) properly applied to the midventral excavation commonly developed in cameral deposits; (2) the term has also been applied to the ventral sinus of the shell aperture more properly and more widely known as the hyponomic sinus.

VENTROLATERAL MASSES.—ventrolateral regions in cameral deposits, separated by the ventral sinus and bounded laterally by the relatively thin dorsolateral bands. Commonly the ventrolateral masses are thick, the surface may be elaborately sculptured and with advanced growth may be extended as lobes partially surrounding the siphuncle; such lobes, as seen in section, may appear discrete and are probably the basis of the perisiphonal deposit.

VENTRORAD.—(adv.) sloping forward on the ventral side (Gordon, 1957).

VLUTION.—a part of a coiled shell describing a complete revolution.

WHORL.—synonymous with volution.

Supplementary Notes

It was originally intended that only line-drawing text figures would illustrate the present work, and the proposals of new taxa would be eliminated. To further both ends, the publication of this work was delayed until after completion of the revision of the order Ellesmeroceratida, contained in our Memoir 12. This work included definition of three new sub-orders, some new genera, and photographic illustration of some critical structures, notably, some siphuncle walls, one of the rare examples of preservation of layers in the conch in Early Paleozoic materials, diaphragms, and the ventral rods.

However, it was felt desirable to add photographic illustrations of some other structures. Most of these are discussed adequately in the main part of the text, but additional discussion of the siphuncle of *Protocycloceras affine* is included below.

It was also necessary to mention structures best displayed by material which is at present in manuscript in other works, still in the process of completion, and it seemed that confusion would be avoided by mentioning these forms by name, and including in the following pages such descriptions as would eliminate the appearance of *nomina nuda*. Illustrations of such forms are, for the most part, supplemented to show the gross aspect of the species, but fuller illustration and description will appear in these works which, it is hoped, will be published within a year. The works involved are (1) descriptions of Endoceratida of the El Paso group, (2) descriptions of cephalopods from the Garden City and Pogonip successions of Utah and Nevada, (3) El Paso and other Tarphyceratida.

Protocycloceras affine Ulrich, Foerste, Miller, and Unklesbay
PE 4, fig. 37

Protocycloceras affine Ulrich, Foerste, Miller, and Unklesbay, 1944.
Geol. Soc. Amer., Special Papers, no. 58, p. 81, pl. 41, fig. 913,
pl. 42, fig. r o.

---- Flower, 1953, Mem. 12, N. Mex. Inst. Min. and Tech., State
Bur. Mines and Mineral Res., p. 126, text fig. 44•

The perplexities attending interpretation of this species, particularly in relation to its internal morphology, have been discussed previously, but the critical material came too late to be incorporated in the plates. The Protocycloceratidae are possibly a polyphyletic group, treated at present as a family, because no clear separation is possible. It is, however, demonstrable that in this family there are (1) forms with small apparently empty siphuncles (2) forms with diaphragms crossing the siphuncle and (3) forms with a ventral rod in the siphuncle, possibly supplemented by diaphragms. Conceivably, the small empty siphuncles and the larger ones with internal structures might belong to a single lineage; considerable evidence suggests that diaphragms may be greatly delayed or completely suppressed in forms with small slender siphuncles, though a correlation between size of the siphuncle and the development of diaphragms is certainly not perfect nor universal, as is shown by *Ectenolites Primus*.

One specimen, shown in Plate 4, figures 3.5, and Text Figure 23 C-E, shows a siphuncle in which there is apparently an anteriorly thinning ventral rod, shown on the left; the cavity remaining apparently develops diaphragms. At the anterior end, the matrix, confined to the dorsal side, shows a crescentic

cavity such as normally supplements a ventral rod, and a ves-

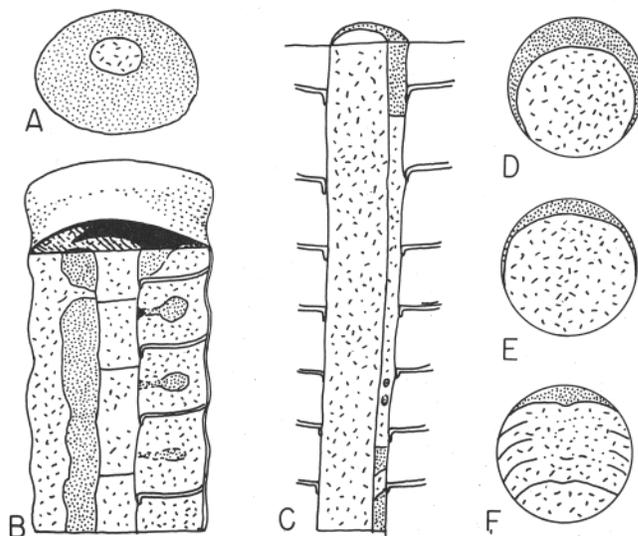


Figure 23

STRUCTURE OF *Protocycloceras affine* U. F. M. & U.

A. section at the anterior end of the specimen shown in B, showing the small subcentral siphuncle. B. Outline drawing of Pl. 4, fig. 6, with the anterior unsectioned end shortened for simplicity, showing on the left, septa and camerae, largely filled with deposits, next the small siphuncle, traversed by several narrow sharply defined transverse bands, evidently diaphragms, next an area of irregular calcite, dark matrix, and light and dark material, calcite, possibly in part representing cameral deposits apparently matrix, at the extreme left; the last two zones represent phragmocone. Dark material at the extreme left is matrix outside of the shell. Based upon USNM no. 109517. C. diagrammatic section through the siphuncle of Pl. 4, fig. 6, showing a ventral rod at the left, the supposed venter, the remaining cavity filled with calcite imperfectly, with sharp transverse bands, evidently representing diaphragms. D. Cross section at the anterior end of C, after Pl. 4, fig. 4. E. Cross section at apical end of C, from Pl. 4, fig. 5. F. Cross section from another specimen, showing an apparent ventral rod with a median excavation. USNM no. 109518, from a suite of unfigured paratypes. From the St. Armand limestone, Phillipsburg, Quebec.

tige of the same general pattern is seen in the section at the apical end in Plate 4, Figure 5. The specimen shown in Plate 4, figures 6 and 7, and in Text Figure 23 A and B is that which Ulrich, Foerste, Miller, and Unklesbay (their pl. 42, fig. 10) illustrated and described as containing a lining in the siphuncle; they also oriented the specimen in the other direction, regarding the anterior unsectioned part as apical. A rough cross section at the apical end shows some slight crushing, but is adequate to demonstrate that the siphuncle is subcentral and relatively small, and that its continuation in the longitudinally sectioned part is confined to what those authors considered one side of the lining in the siphuncle. More astonishing is the presence of several fine transverse bands which, from comparable material, are interpreted as diaphragms. To the right of the siphuncle several septa are seen, and though their curvature is, as usual in *Protocycloceras*,

very shallow, there can be no question as to the orientation of the shell for they are slightly concave adorally; also septal necks can be made out quite clearly. The left side of the specimen shows a band of calcite near to and including the shell wall, and between it and the siphuncle is an irregular band of matrix. Septa are not evident here, and were probably destroyed; it is uncertain to what extent the calcite at the left is adventitious, and to what extent it may include cameral deposits. On the right side, presumably ventral or nearly so, the camarae are largely filled with cameral deposits, leaving small round cavities in the camarae narrowly connected with the siphuncle by thin dark bands, a condition quite general on the ventral side of *Protocycloceras*.

These specimens are the only ones so far known which suggest that after development of a ventral rod, the remainder of the cavity may be traversed by diaphragms, yet such a development should not be surprising when one recalls that the tubes and even the endosiphocoones of some endoceroids may show a quite similar development. As shown earlier (Flower, 1963B) *Protocycloceras whit fieldi* is known to show good series of diaphragms, but ventral rods are not certainly known, though Ruedemann (1906) figured one specimen, assigned to *P. lamarcki*, which may contain a real ventral rod; the two forms, *P. whit fieldi* and the specimen assigned to *P. lamarcki*, are both from the Fort Cassin beds of New York.

DIAPHRAGMS IN THE ENDOCERATIDA

Diaphragms have long been known to occupy the tubes of some Endoceratida, as noted by Ruedemann (1905) but the condition is certainly far from universal, and such structures are generally wanting in the Endoceratidae. Kobayashi (1936) figured them for *Manchuroceras*, and Ulrich, Foerste, and Miller (1943, p. 37, fig. 2) indicate diaphragms crossing the tube of *Cassinoceras amplum*. Diaphragms crossing the tube of *Bisonoceras corniforme* are shown here in Plate 5, figure 12, in *Bisonoceras* sp., a form with a larger endosiphotube, in Plate 5, figure 14. At the extreme anterior end the illustrated section passes tangentially through the endosiphotube wall, and anterior endocones rather than diaphragms are shown. *Dartonoceras* (pl. 5, fig. 16-19) is a small slender form with an unusually large tube in which diaphragms are developed with unusual frequency and clarity. More astonishing is indication in two specimens, both slender "endoceroid" siphuncles, as yet of uncertain position, shown in Plate 4, figures 10 and 12; in both specimens diaphragms have not only developed in the endosiphotube, but penetrate the endosiphocoone. Such specimens suggest most strongly that the diaphragms continue growth in mature individuals in which the growth of endocones has ceased; possibly even their appearance is a feature of late rather than young ontogenetic stages in the Endoceratida.

DIDEROCE R AS Flower

Genotype: *Endoceras wahlenbergi* Foord

Dideroceras Flower, 1950, Jour. Paleontology, vol. 24, p. 609.

---- Flower, 1955, *Ibid.*, vol. 29, p. 368.

---- Flower, 1958, *Ibid.*, vol. 32, p. 440.

---- Sweet, 1958, Norsk Geol. Tidsskr., bd. 38, h. 1, p. 33-35.

Dideroceras is a slender endoceroid of the Endoceratidae characterized by extremely long "macrochoanitic" necks, which range from one and a half to two camerae in length.

The siphuncle is close to the venter, but becomes narrowly

separated from the venter in late growth stages. Evidence of Holm's figures suggests that apical portions are of the *Nanno* type, and such apices include *Nanno belmmitiforme* Holm. The material here figured shows (1) thinsections of the siphuncle wall, not previously illustrated except by line drawings, (2) variation in the pattern of the endosiphocoone, which varies from short to very slender, in most forms the cone terminates centrally in the adult, but in *D. ventrale* it is ventral throughout, and in *D. holmi* it is ventral in young stages only. There is also indication of variation in cross section of the endosiphocoone, which may be simple and round, or may be flattened dorsally and obscurely pointed ventrally.

I have had, for some years, these several specimens, showing in addition to these differences, different proportions in the spacing of septa and some considerable variation in the curvature of the septum, as seen in vertical section. Plainly a number of species are involved. They are briefly described and named below, thus removing the confusion of supposed variation in what was regarded as a single species, *Dideroceras wahlenbergi* (Foord). Regrettably, the specimens are accompanied only by approximate stratigraphic data, and I had waited for some ten years in the hope that this work might be done more adequately by someone more familiar with the sections, and based upon material of more precisely known stratigraphic origin.

Dideroceras is known from the Orthoceras limestone sequence of Sweden; Sweet (1958) has figured material from Norway, and YU has figured and described as several species of *Vaginoceras* (it must be remembered that Hyatt's definition of *Vaginoceras* involved the long septal necks which are properly confined to *Dideroceras*) from central China. *Chisiloceras* Gortani from the Chisil Pass is allied, differing in that the siphuncle is subcentral in position.

The present material has failed to show blade patterns at all clearly; the absence is certainly due largely to calcitic replacement of the endosiphuncles. Holm, however (1895, pl. 22, fig. 6), has figured a cross section of a siphuncle with an endosiphocoone rather like our Plate 3, figure 3, but with one ventral blade and what is obviously one of a pair of dorsolateral blades preserved.

Dideroceras -wahlenbergi (Foord)

Pl. 3, fig. 2-4

This form is similar in proportions to the form figured by Foord (188, Catalogue Fossil Cephalopoda of the British Museum, vol. I). Our present specimen is a portion of phragmocone 10.5 mm long, containing 12 camerae of nearly uniform length, 9 mm, with the siphuncle increasing from ix to 13 mm in diameter; there are four camerae in a length equal to the adoral shell diameter apically, five in a similar length adorally. A characteristic of this species is the curvature of the septa, which attain their greatest depth at the shell center, and slope faintly orad from the center to the dorsal margin of the siphuncle. This is not clearly shown in our section, which is oblique, but more nearly horizontal than vertical. The siphuncle wall, shown enlarged in Plate 3, figure 4, has necks rather difficult to trace, as their apical parts have been darkened, and are thus difficult to distinguish from the matrix and the rings, but they can be seen extending for nearly one and a half segments; between the bending of the septal neck

and the extension of the next adoral septum can be seen the anterior limit of the connecting ring. The apical end of the ring is found terminating at the same point at which the septal neck terminates. The eyelet is not clearly developed, but is suggested by dark amorphous material in the apical part of the ring, largely developed on its outer surface, which is in contact with the septal neck, and is confined to the region in which the ring and neck overlap into the next apical siphuncle segment from that to which they properly pertain.

Figured specimen. Collection of the writer, No. 291, from the Red Orthoceras limestone, Westergotha, Sweden.

Dideroceras magnum Flower, n. sp.

Pl. 3, fig. 1, 6; pl. 4, fig. it

This is a large species, with the curvature of the septa similar to that of *D. wahlenbergi*, but the shell becomes much larger, and the camerae are proportionately deeper. The holotype, shown complete, though reduced to the length of the plate, is shown in Plate 3, figure 1, and a partial cross section at the base in figure 6. The specimen has a complete length of 435 mm, of which both dorsum and venter are preserved for the basal 340 mm. Only one side of the shell is preserved; in Plate 3, figure 1, the venter is at the left. At the very base the shell is 44 mm across, the siphuncle 15.5 mm, and 1.5 mm from the venter. In 120 mm the shell has become 57 mm across, the siphuncle 18 mm, and is barely separated from the ventral wall of the shell. The intervening part was sectioned vertically and is shown on Plate 4, figure I I; camerae vary erratically in length from 23 to 25 mm. The septum, strongly curved dorsally, becomes transverse in the middle, and sloped slightly forward to the siphuncle. Here the depth of the septum is three-fourths the length of the camera, and about one-third the shell diameter. Although the siphuncle wall is obscure in our figure, it shows under the microscope wall structure like that of *Dideroceras wahlenbergi*. The cross section at the extreme base (pl. 3, fig. 6) is inverted in relation to the position of the shell in the sediment. Marginally, a band of calcite represents a cross section through the anterior end of the endosiphococone. The cavity within was filled with gray-green sediment, shown above in the figure, while the other half is filled with inorganic calcite, some now dissolved.

The camerae are spaced 2.5 in a length equal to the adoral shell diameter apically, with three camerae in this length adorally. *D. wahlenbergi* shows adoral shortening of camerae in relation to shell diameter. If that species attained the large diameters shown by *D. magnum*, the septa would be twice as closely spaced as are those of this species.

Holotype. American Museum of Natural History, No. 22353, evidently from the Upper Red Orthoceras limestone, Skärloff, Oeland, Sweden.

Dideroceras gracile Flower, n. sp.

Pl. 3, fig. 7

This species is known from a portion of phragmocone 195 mm long, in which the shell is circular in section and expands from 19 to 24 mm, while the siphuncle, circular and barely tangent to the ventral wall, increases from 9.5 mm to 12 mm. Septa slope apicad from the dorsum to the siphuncle quite strongly, are gently curved, but still strongly oblique where they join the siphuncle. The depth of the septum as thus seen is three-fourths the length of the camera and not quite one-third the height of the shell. Camerae increase gently in

length from 8.5 to 11 mm but are slightly shortened adorally, four and half occupying a length equal to the adoral shell height; but there are only two camerae in that length where there are the longest, but nearly three at the extreme adoral end. The endosiphococone, not quite all of which is shown, is 78 mm long, unusually slender, and is centrally terminated. An unfigured anterior 90 mm of the siphuncle is empty.

Discussion. The very slender camerae, obliquity of the septa where they join the siphuncle on the dorsal side, and the very long slender endosiphococone distinguish this species. A thin section from the anterior part of the siphuncle shows a wall structure identical with that of *D. wahlenbergi*.

Type and occurrence. Holotype, from the Orthoceras limestone of Oland, No. 922; collection of the writer.

Dideroceras holmi Flower, n. sp.

Pl. 3, fig. 5

This species has the septa becoming transverse on the dorsal side of the siphuncle. The type increases from a circular shell of 22 mm with a ventral circular siphuncle of 9 mm to a shell of 31 mm and a siphuncle of 11 mm in 99 mm; in this length, the basal eight camerae occupy 47 mm, the adoral eight 52 mm, there being 16 in all. Apically, four and adorally five camerae occupy a length equal to the adoral shell height. In vertical section the septa are more strongly curved between the dorsum and the siphuncle than in most species; they are transverse, even pointing slightly forward, where they join the siphuncle here, whereas in most other species of comparable dimensions, the septa slope obliquely apicad from the dorsum to the siphuncle with less pronounced curvature.

The specimen shows an endosiphococone 53 mm long, terminating in a central tube. In the apical 10 mm of the specimen, however, the tube becomes sinuate, moving halfway from the center to the venter.

Type and occurrence. Holotype, No. 923, Orthoceras limestone, "transition beds" (from upper red to upper gray?), Kinnekulle Mountain, Sweden; collection of the writer.

Dideroceras ventrale Flower, n. sp.

Pl. 4, fig.

This species is known from a specimen a little over 195 mm long, in which the shell is circular, the siphuncle ventral. The shell increases from 21 mm and a siphuncle of 9 mm at the apex to a siphuncle of 11 mm and a shell width (the height seems to have been equal and the section circular of 26 mm. The camerae increase only gradually in length, from 9 to 11 mm in the length of the specimen; the apical ten camerae occupy 95 mm; the next ten occupy 96 mm. The siphuncle shows the endosiphuncle material extending far forward dorsally, scarcely developed ventrally, and the endosiphococone, 98 mm long, terminates 1.5 mm from the venter. Apically the endosiphuncle is of recrystallized calcite and fails to show original details.

Type and occurrence. No. 924, Orthoceras limestone, Deland; collection of the writer.

Genus BISONOCERAS Flower, n. gen.

Bisonoceras was a manuscript name originally proposed for piloceroids, known mainly but not completely from siphuncles more curved and more rapidly expanding than those of

Piloceras, and more rapidly expanding than those of the materially younger genus *Cyrtendoceras*. With further investigation it became evident that insofar as shape is concerned, such siphuncles could not be separated clearly from associated species of the aspect of *Piloceras*. No similar problem attends distinction from *Cyrtendoceras*, but the reasons are practical; *Cyrtendoceras* is known from only a few specimens, and the endosiphuncle is incompletely known both as to form and as to details of structure; also, the species are materially younger, occurring in the Ordovician proper, while the known *Bisonoceras* are thus far confined to the Middle Canadian. The form of the apical part of the endosiphuncle of *Cyrtendoceras* is unknown; the section of the endosiphuncle is known only for its extreme anterior part; the tube and blades have not been observed.

In both *Piloceras* and *Bisonoceras* the endosiphuncle is smooth, moderate in length, and terminates in a centrally located tube. However, profound differences were found in the pattern of the tubes and blades. In true *Piloceras*, the tube is so strongly compressed that it is difficult to say where the dorsal and ventral margins give way to prominent dorsal and lateral blades; these blades are characteristic, and bifurcate, each one once, about half way to the siphuncle margin. In *Bisonoceras*, however, the tube is a compressed triangle, with one attenuated point ventral, and two sharp dorsolateral points. From the dorsolateral points are derived two prominent blades, curved, convexity directed laterad, and their dorsal edges are narrowly separated on the dorsal margin of the endosiphuncle, where a median blade is represented only by a short stub which has never been found to extend to the tube. The ventral blade has a strong base, but its tip is always obscure; abundant material suggests that this blade bifurcates several, perhaps many, times as it approaches the venter. Stubs of lateral blades have been found, which may also bifurcate. Astonishingly, in young stages the ventral blade is apparently simple, and there is a pair of straight dorsolateral blades. It was thought that these dorsolateral blades were the same as those which are curved in later portions of the siphuncle, but a number of sections have shown this assumption to be untrue; adorally, these blades disappear, but in sections in which they are most anteriorly continued, the curved dorsal blades, here joined at their bases, can also be seen, so it is evident that two distinct structures are involved.

Several specimens are known retaining the phragmocone. The siphuncle wall is, as in *Piloceras* and *Piloceratae* in general, holochanitic. The cross section of the phragmocone is strongly compressed. Specimens showing the length of the anterior part of the siphuncle lacking the endosiphuncle have been fragmentary, but are adequate to show that such an extension was appreciable, and that, with the addition of the living chamber, the whole shell must have been a gyrocone. Endosiphuncles up to 30 mm in height are known, and the phragmocone at such a point must have been 60-80 mm in height. Indications are that complete shells must have attained whorls of imposing size, probably up to two feet across.

Although only the genotype is described at the present time, *Bisonoceras* is known from a variety of species varying widely in rate of expansion and curvature of the endosiphuncle, and grading into the dominantly cyrtoconic *Piloceras* in both respects. The pattern of the cross section of the tube and the blades fails to show similar gradation, and thus supplies the only logical basis for a clear separation of the genera. *Bisonoceras*, *Piloceras*, and several allied undescribed genera are par-

ticularly characteristic of the first piloceroid zone of the El Paso group, the Victorio formation of the Demingian. As yet, *Bisonoceras* has not been recognized from any other region, or from higher horizons.

The generic name *Bisonoceras* has appeared in several general discussions of the El Paso limestone and its faunal succession, by the writer, but there has been no formal description, and no species have been described; it has been, then, only a *namen nudism*.

Bisonoceras corniforme Flower, n. sp.

Pl. 5, fig. 1-3, 5, 11, 12

This is a large compressed shell, evidently gyroconic when complete, both shell and siphuncle compressed and fairly rapidly expanding in the greater part of the known portion, though possibly both siphuncle and shell were more slender in the poorly known anterior portion. The specimens known are largely endosiphuncles, and indicate that the endosiphuncle alone described a revolution of 120 degrees, forming a whorl roughly 20 mm across, and attaining an adoral height of 55 mm. Whole shells were, of course, much larger, our material indicates that where the siphuncle was 35 mm high, the shell was 55 mm high, and that the phragmocone probably continued orad of the endosiphuncle for a curving dorsal length of 80 mm, orad of which was a living chamber of probably 100 mm in length; quite possibly these estimates are extremely conservative.

Surface markings are unknown; such shell fragments as have been observed are essentially smooth. Sutures slope forward from venter to dorsum, but the septal ridges on the siphuncle are essentially transverse. Siphuncle walls are holochanitic. The cone is simple, the tube small, compressed, and persistent curved dorsal blades, the convexity directed outward, are characteristic; other blades are rarely seen, but a ventrolateral pair is shown on Plate 5, figures 2 and 3. Apically, a pair of straight dorsolateral blades is found instead of the curved dorsal pair of mature endosiphuncles.

The holotype is an endosiphuncle 95 mm long, increasing from 11 and 13 mm at the base, to an adoral height of 40 mm and an estimated width of 26 mm. Septal ridges are transverse, ranging in spacing from 4.5 basally to 6 mm adorally. Though generally gyroconic, the siphuncle shows variations in expansion and curvature with growth showing the venter nearly straight, the dorsum diverging and convex apically, both dorsum and venter curved adorally; a missing apical part shows quite rapid expansion; it is known from other specimens. The radius of curvature for the dorsum ranges from 50 mm apically, then 40 mm, curvature decreasing to a radius of 60 mm adorally.

Types and occurrence. Holotype, No. 851, from the Victorio Mountains, paratypes Nos. 639, 770, 765, 767, 774 from various other localities in New Mexico; the species is widespread in the first piloceroid zone, Victorio formation, of the El Paso group.

A paratype, No. 767, is figured in longitudinal section; the tube is shown traversed by several diaphragms. Though essentially mature, anterior endosiphuncles are not clearly preserved.

Bisonoceras spp.

Pl. 5, fig. 4, 6-io, 13, 14

These figured specimens represent species of *Bisonoceras* now in manuscript, which will be fully described and more extensively illustrated later, and are here figured to show some significant morphological features. Plate 5, figure 4 is an enlargement from a section similar to Plate 5, figures 2 and 3, but shows the distal parts of the dorsal blades more clearly, exhibiting sharp dark boundaries, with a lighter center, and feathering of the edges, the impingement of growth lines on the blades, similar to the condition which Ruedemann (1905) reported for *Proterocameroceras brainerdi*. Figure 6, an apical section through the same specimen, shows the straight divergent dorsolateral blades clearly; they are only faintly indicated in figure 5, the holotype of *B. corniforme*. Figure 7 is a section through the early stage of another specimen in which the calcite pattern is adventitious; the tube is preserved, but the original blade pattern is lost, but apparently the dorsal and ventral blades did, in the beginning, influence the development of calcite in two lateral regions. Figure 13, a dorsal view of the same specimen as figures 4 and 6, is presented to show the not uncommon development of faint incisions on the surface of an etched endosiphuncle, marking the termination of the curved dorsal blades. Figures 8-10 are through another form, a specimen in which the curved dorsal blades are clearly shown—they are marked externally by grooves as on Plate 5, figure 13; the tube is considerably larger than in *B. corniforme*, and the bifurcating ventral blade is quite well preserved, but only stubs of lateral blades are present, and they are clear only in figure 9. Plate 5, figure 14 is a longitudinal section of a *Bisonoceras*, a form with a rather large tube, showing diaphragms near the anterior end of the tube. At the extreme anterior end, the plane of the section passes tangentially through the wall of the tube, and some endocones cross the center of the section in the region of the tube. The clarity of individual cones and sheaths at the anterior end is in part a replacement phenomenon, as it is found in immature specimens as well as in mature endosiphuncles, but this form is apparently mature or nearly so, and possibly organic factors are also involved.

Figured specimens. All forms are from the first piloceroid zone, the Victorio formation, of the El Paso group; numbered specimens and specific localities are indicated in the explanation of the plates.

DISPHENOCERAS Flower, n. gen.

Genotype: *Disphenoceras conicum* Flower, n. sp.

This is a piloceroid known only from the siphuncle which is conical, moderately slender for a piloceroid, faintly endogastric, compressed, characterized by the development of two wedges modifying the endocones, one dorsal, and one ventral. The cone is centrally terminated; the wedges are large apically, nearly touching, and the dorsal wedge, and probably the ventral one also, seems composed of essentially concentric layers.

Discussion. This remarkable piloceroid, yet known from a single siphuncle, is distinctive in the dorsal and ventral wedges. The type shows in addition traces of fenestrate fibers in the endosiphuncle which are probably a matter of propitious preservation, rather than a feature peculiar to this form.

Disphenoceras conicum Flower, n. sp.

Pl. 1, fig. 1-5

This is a slender conical siphuncle, faintly endogastric. The type is a portion of an endosiphuncle 52 mm long, expanding in height from 15 to 19 mm in a dorsal length of 29 mm. The venter is nearly straight, very faintly endogastric, the dorsum is convex, somewhat more strongly curved, suggesting a siphuncle in which there is a marked adoral decrease in rate of expansion. The anterior end of the endosiphuncle is markedly oblique, strongly extended forward on the venter, and the preserved part, nearly transverse at the base, is 50 mm long ventrally and 30 mm dorsally. The anterior surface shows the endosiphuncle thinning, and quite narrow except where modified by the dorsal and ventral wedges. Matrix fills the endosiphococone, but the tube is apparently central. The weathered basal surface shows the wedges nearly meeting in the center of the siphuncle; the dorsal wedge is larger than that of the venter; it is weathered, and shows layers which are concentric on the ventral and lateral surfaces and seem to surround a central axis largely if not completely; the extreme dorsal surface is lost by weathering.

This form is unique in that the main part of the endosiphuncle shows, on a weathered surface, traces of a lattice or fenestrated pattern of fibers; horizontal and vertical fibers are clear, oriented, not in a plane, but apparently normal to the endosiphococone surface; less clearly evident is a third series, radial, but normal also to the cone surface, and thus extended orad from the margin to the center. In addition, the surface shows irregularly distributed round cavities, but as in secondary replacement spheres of calcite commonly develop which have no organic significance in other Endoceratida, it is unlikely that they have any organic significance in this form. Blade patterns and the presence or absence of diaphragms in the endosiphotube are unknown.

Endosiphuncle texture. This specimen was evidently subject to silicification which was slow and gentle, and occurred early in the history of preservation of the specimen, before alteration to calcite could destroy textures, and was then accentuated by weathering. As noted already, the most significant feature is the development of longitudinal and transverse fibers by weathering, with, less clearly, indication of a third series normal to the cone surfaces, extending from the center to the endosiphococone or tube. Such radial fibers have been observed elsewhere, notably in the figured section of *Vaningoceras styliforme* (Flower, 1958, pl. 61, fig. 1). Likewise, such structures seem allied to the endosiphofunicles (Ruedemann, 1905), made known first in relationship to *Cassinoceras explanator*, but present in other forms, and shown here, though only local traces are preserved, for an undescribed genus related both to *Piloceras* and *Bisonoceras*.

However, longitudinal and transverse elements in the fibers have not been shown by previous material, in part because of the rarity of the preservation of any of these structures, but certainly also in a large part because transverse and longitudinal sections, from which most such structures have been observed, are not adapted to showing these matters.

Type and occurrence. From the second piloceroid zone, of essentially Jefferson City age, Hembrillo Canyon, San Andres Mountains, New Mexico.

DARTONOCERAS Flower, n. gen.

Genotype: *Dartonoceras gracile*

This endoceroid genus is known only from endosiphuncles, which are moderately slender, gently curved apically, straight adorally, compressed in section. The cone is simple, terminates in an unusually large endosiphon tube which is traversed by close and conspicuous diaphragms. The blade pattern is not as yet known except in the most general way; it is evident that there are (1) a dorsolateral pair, (2) a lateral pair, (3) a ventrolateral pair of blades.

Dartonoceras gracile Flower, n. sp.

Pl. 5, fig. 15, 16

The holotype is a portion of a siphuncle, evidently compressed in section, but weathered from one side. It expands from 6 to 12 mm in height in the basal 20 mm, in the apical part of which the ventral profile is slightly but definitely concave; beyond, the shell is more nearly straight and less rapidly expanding, increasing in height in the next 35 mm to 17 mm; in all, the specimen is 70 mm long, but adorally the complete height is not shown, due to weathering. The anterior 38 mm represents the endosiphon cone; endocone material extends farther forward dorsally than ventrally, and dorsally the cone is about 42 mm in length. The tube is central, evidently compressed, 2 mm high where the siphuncle is 14 mm high, and 1.5 mm high near the apex where the siphuncle is 7 mm high. Diaphragms in the tube are close and prominent, curved forward at the edges, the curvature slight basally, more pronounced adorally. Septal ridges slope ventrorad, and are 4 mm apart basally, 5 mm apart adorally.

Holotype. No. 660, from beds above the oolite, Demingian, El Paso limestone, Mud Springs Mountain, New Mexico.

Dartonoceras cf. gracile

Pl. 5, fig. 17-19

Under this name is figured a second specimen of *Dartonoceras* representing a somewhat later growth stage than the genotype. It may possibly be conspecific, but shows some differences, mainly an indication of a shorter endosiphon cone and the siphuncle appears to be straight and somewhat more slender. Such differences may possibly be developed at a later growth stage, but at present, without more material, a decision at the specific level is not possible. The specimen is figured here as it shows traces of the blade patterns, and again shows the large compressed tube with prominent diaphragms. The section shown on Plate 5, figure 17 is 30 mm from the extreme anterior end of the endosiphuncle, which is extended farther forward dorsally than ventrally. The section shows the siphuncle 17 mm wide and 20 mm high, with a cavity, which must mark essentially the anterior end of the endosiphon tube, 4 mm high and 3 mm wide. Traces of blades are mainly peripheral, but indicate a dorsolateral pair, a horizontal lateral pair, and a ventrolateral pair. A vertical section through the apical part shows the tube containing numerous diaphragms in the apical 20 mm; the adoral 6 mm shows the tube filled with dark material, evidently matrix. This specimen, No. 919, is from the first piloceroid zone, from the east side of the Florida Mountains, New Mexico.

ROSSOCERAS Flower, n. gen.

Genotype: *Rossoceras lamelliferum* Flower, n. sp.

Rossoceras is a straight slender endoceroid, nondescript externally, with a ventral siphuncle, with hemichoanitic necks but rings extending for one and one-half segments. The endosiphon cone is flattened ventrally, terminates in a transverse tube, the edges slightly downcurved. Cross sections show the endosiphuncle penetrated by numerous blades which bifurcate, and may be extremely numerous. Commonly the base of one dorsal blade is prominent, and there may be two bases of lateral blades, one pair downcurved, the other pointing obliquely dorsolaterally. The blades are continuous longitudinally, and longitudinal sections show them as continuous narrow dark bands.

This genus, which will be described more fully in a work now awaiting publication, dealing with Garden City and Pogonip cephalopods, is here illustrated to show the unique development of the numerous blades. The species are of Whiterock age, occurring in the highest Garden City limestone, zone L, probably in the Swan Peak quartzite, zone M, and represented in zones L, M, and N in the Pogonip group of western Utah and Nevada. At present, only the genotype is described, several other species are known to the writer, which remain for the present in manuscript.

Rossoceras lamelliferum Flower, n. sp.

Pl. 4, fig. 2, 13-22

This species is known largely from isolated siphuncles, but the shell is a straight slender endoceroid with transverse sutures and a ventral tubular siphuncle, the segments only most faintly concave between the septal ridges. Ordinarily siphuncles show slight flattening, but it is evident that some distortion is involved in some of the specimens; the venter commonly shows slight flattening where it is in contact with the ventral wall of the shell. Endosiphuncles are known ranging from 7 and 10.5 mm to 26 and 34 mm, which would encompass a length of about 550 mm.

Plate 4, figures 13, 14, show two cross sections, 30 mm apart through the endosiphon cone of a syntype, No. 364, showing traces of bases of three primary blades, and the numerous fine branches are particularly well shown dorsally, but are partially lost by recrystallization ventrally. Plate 4, figures 15 and 16 show two sections, slightly less than X 1, from another syntype, No. 361; figure 15 shows accentuation of two horizontal blades, probably strengthened by alteration, while the dorsal blade is obscure; numerous fine blades are clear peripherally, but in the central part are lost by recrystallization. Figure 16, 15 mm orad of 15, shows strengthened horizontal blades, an eccentric dorsal blade, and again fine branches are evident only peripherally. Figures 2 and 17 are sections, 40 mm apart, X 2, of syntype No. 359, slightly silicified; figure 2 shows the two pairs of main branches of the horizontal blades and a clear dorsal blade; in figure 17 the same pattern is shown, but the bases are more obscure and the finer branches are more clearly preserved. Figures 20 and 21 are two sections 40 mm apart through an endosiphon cone showing a rather irregular cone surface; in figure 22, the dorsal part is shown enlarged, showing details of the fine branches of the blades. Under advanced recrystallization, the branching of the blades may be obscured; such a condition is represented

on Plate 4, figures T 8 and 19, representing an undescribed species of *Rossoceras* (USNM No. 140155), from Ikes Canyon, Toquima Range, Nevada. The two sections are from two siphuncles as seen on the same surface; close examination will show irregularity of the terminal parts of the blades, and a suggestion of branching, but the general aspect is that of a trifold blade pattern, such as is shown commonly by Canadian Endoceratida which have never exhibited the branching of *Rossoceras*; in treating such material, good series of specimens showing varied modes of replacement are needed, and without some caution and some experience, this form would certainly be considered a distinct genus.

The syntypes of *R. lamelliferum*, Nos. 357-365, in the collection of the writer, are from the highest 20 feet of the Garden City formation, from Green Canyon, on the northern edge of Logan, Utah.

WILLIAM SOCERAS Flower, n. gen.

Genotype: *Williamsoceras adnatum* Flower, n. sp.

This is a straight, slender endoceroid, the conch and suture pattern not yet certainly known, but evidently quite generalized. The siphuncle wall is holochonitic. The siphuncle is slender and generalized in aspect externally, but the endosiphuncle is unique; first appears a high rather narrow ventral process; cones are draped about this process, and as they are traced apicad, they leave an endosiphococone of strongly crescentic cross section. The cone is terminated ventrally considerably orad of its dorsal termination. Near its oblique apex it is first traversed by a series of buttresses, the buttresses widen apically as the endosiphuncle thickens, and finally all that is seen is an arc, usually evident as a prominent dark band, the infula, connecting a series of tubes which extend to the siphuncle apex.

At present only the genotype is described, though several allied species are known. *Tallinoceras* Balashov is possibly allied, but shows only two small lateral tubes narrowly separated from a large central tube; apparently no arclike series of numerous tubes is developed. The necks are macrochoanitic and, unlike *Williamsoceras*, the tubes are traversed by diaphragms.

Williamsoceras is certainly to be assigned to the Allotrioceratidae, and is regarded as the ancestor of *Allotrioceras* and *Mirabiloceras*; it suggests further, a connection not with *Meniscoceras*, which was first believed to be the origin of the family, but with *Coreanoceras*.

Williamsoceras adnatum Flower, n. sp.

Pl. 2, figs. 1-7

This species may be distinguished at the present from all previously known forms by the characters of the genus. The holotype, the only form here illustrated, is a portion of a siphuncle 150 mm long, increasing from 15 and 16 mm to 28 and 32 mm, being slightly depressed. A section at the anterior end (pl. 2, fig. 1) shows the ventral process, which continues slightly laterad on the lower left, marking the anterior end of the endococones; a dark axial line in the process is evident. Plate 2, figure 2 shows a section 45 mm farther apicad; here the ventral process fails to show evident boundaries, though its axis, widened distally, is clear. Endococones have partially filled the remaining cavity, and below, on either side of the process, but clearest on the right, are several dark conical areas, formed by vestiges of endosiphosheaths drawn out into triangular areas, but surrounding small round tubes; dorsally, the remainder of the endosiphococone appears as a prominent crescentic cavity filled with dark matrix; at the upper right, one buttress crosses it. In figure 3, 12 mm farther apicad, the crescentic endosiphococone is narrower, its lower limbs are more restricted, and several additional buttresses appear. Further restriction of the endosiphococone is shown on Plate 2, figure 4, which lies only 4 mm apicad of figure 3; the cone is here so narrow, except on the middle left, that it is difficult to say whether the cavities should be interpreted as cone or tubes. The next illustrated section, 43 mm farther apicad, shows a series of tubes, some large and round, but the ventral ones smaller, connected by a dark infula which appears adnate ventrally on the endosiphuncle surface. The axis of the ventral process is still clear. Figure 6 is a longitudinal vertical section cutting a lateral series of tubes; it lies 35-58 mm apicad of figure 5. Though displaced by a joint in the middle, the section shows tubes quite clearly, and indicates that they lack diaphragms. Figure 7, taken at the apical end of the region shown in figure 5, is a relatively apical section, but shows no significant departures from the structure found in figure 5.

This species is represented by a series of specimens, all from the highest 20 feet of the Garden City formation, zone L, from Green Canyon, at the northern edge of Logan, Utah. The holotype, No. 342, and paratypes, Nos. 343-345, are in the collection of the writer. The species will be more fully described and illustrated in another work, now awaiting its turn at publication.

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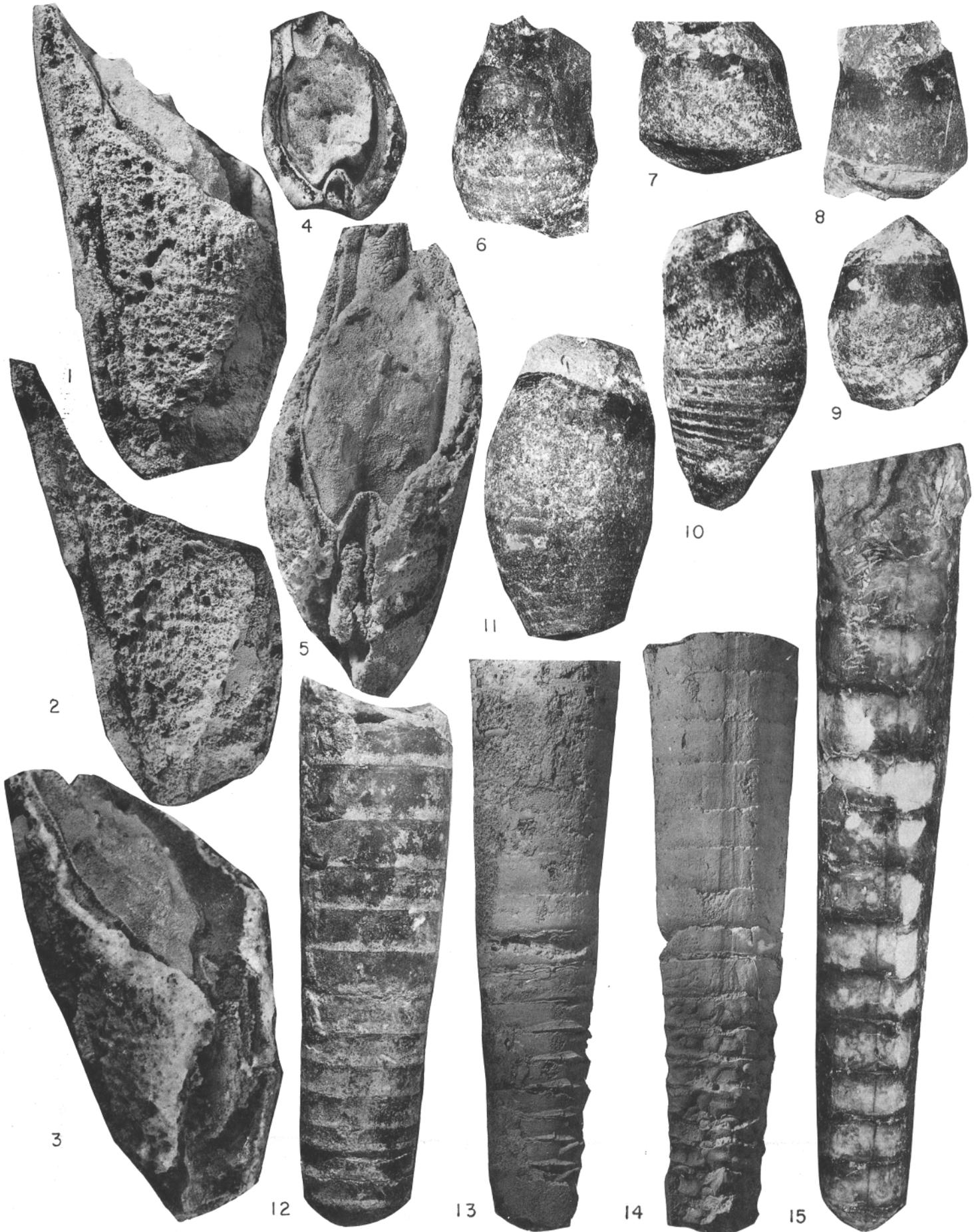
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PLATES 1-6

WITH EXPLANATIONS

PLATE 1

Figures	Page
1 - 5 . <i>Disphenoceras conicum</i> Flower, n. sp.	5 8
1, 2. lateral views, with varied lighting, showing the traces of fenestrate texture brought out by weathering; the small round pits probably represent spherules of inorganic calcite which have been dissolved in weathering. 3. dorsolateral view, photographed unwhitened, all x 2, 4. Adoral view, X 1.5, 5. specimen viewed directly upon the oblique adoral surface, showing the texture of material in the dorsal wedge. No. 408, from the second piloceroid zone of the El Paso, Mckelligon formation, from Hembrillo Canyon, San Andres Mountains, New Mexico.	
6-11. A series of oncoceroids from the middle Trenton, Fairy River, near Montmorenci, Quebec, photographed unwhitened and showing carbonaceous material concentrated in a zone just prior to the mature aperture. All X i .	10
1 2 . <i>Striacoceras typus</i> (Saemann)	1 5
A portion of a phragmocone in which weathering has produced light bands representing large portions of the mural parts of the septa. No. 405, Cherry Valley Limestone, Stockbridge Falls, New York.	
1 3 - 1 4 . <i>Striacoceras typus</i> (Saemann)	I I
Two views of a portion of phragmocone showing cameral deposits exfoliated. Not illustrated are four adoral camerae, 40 mm long and a living chamber of 100 mm in length; 13. lateral view, venter on right; 14. ventral view, showing cameral deposits and, adorally, the three conchial furrows. Same locality and horizon, No. 406.	
1 5 . <i>Leurocycloceras bucheri</i> Flower	1 5
A portion of a phragmocone, X 1, viewed dorsally, photographed unwhitened, showing the septal furrows represented by thin dark bands and imperfectly aligned in successive camerae. No. 407, from the Laurel limestone, from about two miles east of Westport, Indiana.	



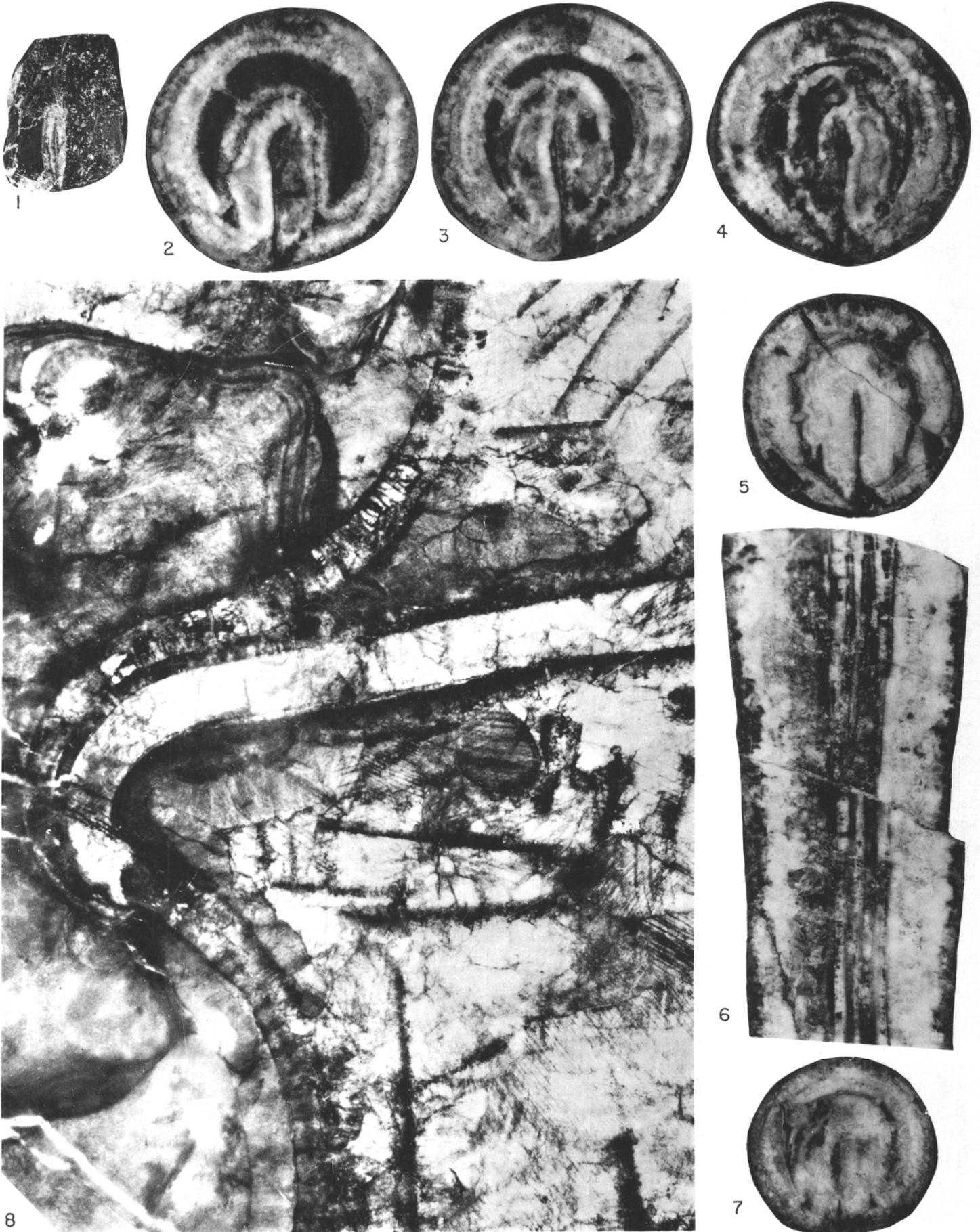
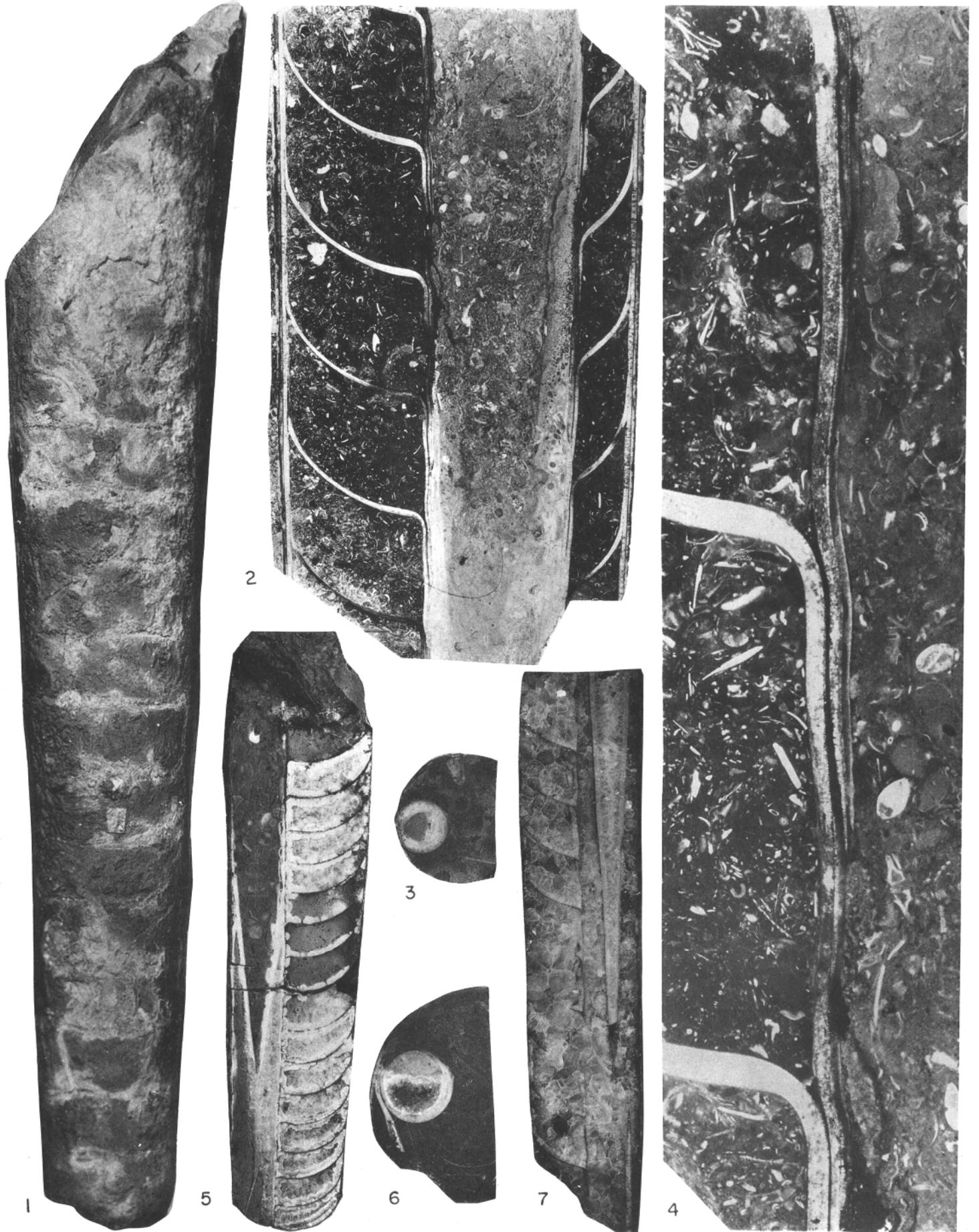


PLATE 2

Figures	<i>Page</i>
17	60
<p><i>Williamsoceras adnatum</i> Flower, n. sp.</p> <p>1. Anterior end of the siphuncle, showing only the ventral process developed, without endocones, X 1. 2. Cross section, X 2, 43 mm apicad of figure 1, showing a section in which the crescentic endosiphococone is largely open dorsally, though at the ventrolateral extremities it has terminated, leaving several small tubes, outlined in black triangular areas; the axis of the ventral process is a prominent black band; dorsolaterally, in the upper left, one buttress traverses the endosiphococone. 3. A section, x 2, 6 mm apicad of figure 2; here the endosiphococone is more restricted at its ends, where more tubes are apparent, and the development of buttresses across the wider dorsal portion is more advanced. 4. Section, x 2, 4 mm farther apicad, showing still further restriction of the endosiphococone, now more strongly divided, and the areas between the buttresses are merging into the endosiphotubes. 5. Cross section, x 2, 45 mm farther apicad, showing a ring of tubes connected by a dark infula and the axis of the ventral process. 6. longitudinal section, 20-55 mm apicad of figure 5, showing continuity of the tubes and absence of diaphragms, slightly displaced by a joint. 7. Cross section at the apical end of figure 6, showing tubes connected by an infula as in figure 5. All from the holotype, No. 342.</p> <p>From the upper zo feet of the Garden City formation, Green Canyon, Logan, Utah, No. 342.</p>	
8	14, 22
<p><i>Adamsoceras</i> cf. <i>isabellae</i> Flower</p> <p>Portion of a thinsection, a longitudinal section through the siphuncle, showing layers of the septum represented in Text Figure 5, and differentiated regions of the connecting ring. From the <i>Rysotrophia</i> zone of the Whiterock beds, Ikes Canyon, Toquima Range, Nevada.</p>	

PLATE 3

Figures	<i>Page</i>
6. <i>Dideroceras magnum</i> Flower, n. sp.	56
<p>I. The holotype, reduced from a length of 428 mm, venter on right, showing space of septa. 6. Part of a cross section, x 1, taken from the base of the type, showing the size and position of the siphuncle. The section cuts the anterior end of the endosiphuncle. The cavity within contains matrix in the upper half, is filled in the lower half with inorganic calcite. This section, with the venter on the left, is upside down in relation to the position in which the shell was buried. American Museum of Natural History. No. 22353, Skarlaf, Oeland, Sweden.</p>	
24. <i>Dideroceras wahlenbergi</i> (Foord)	55
<p>2. a longitudinal section, oblique to the vertical axis, showing mural parts of septa and siphuncle wall. Full length of the necks is not evident, the apical portions of the necks being darkened. About X 3. 4. Enlargement of portion of the siphuncle wall from the same section, showing necks extending for one and a half camerae, rings beginning at juncture of necks and extending apicad on the siphonal side of each neck. X 12. 3. Cross section at the base of the specimen, X I, showing anterior end of endosiphuncle, with an endosiphococone which is faintly pointed ventrally and strongly flattened dorsally.</p>	
5. <i>Dideroceras holmi</i> Flower, n. sp.	56
<p>Holotype, vertical section, X 1, "Transition limestone," Kinnekulle Mt., Sweden, No. 923, showing a centrally terminating cone, but with the tube ventral in the earliest observed stage.</p>	
7. <i>Dideroceras gracile</i> Flower, n. sp.	56
<p>Holotype, vertical section, x 1, showing an exceptionally long, centrally terminating endosiphococone. Upper gray, Orthoceras limestone, Oeland.</p>	



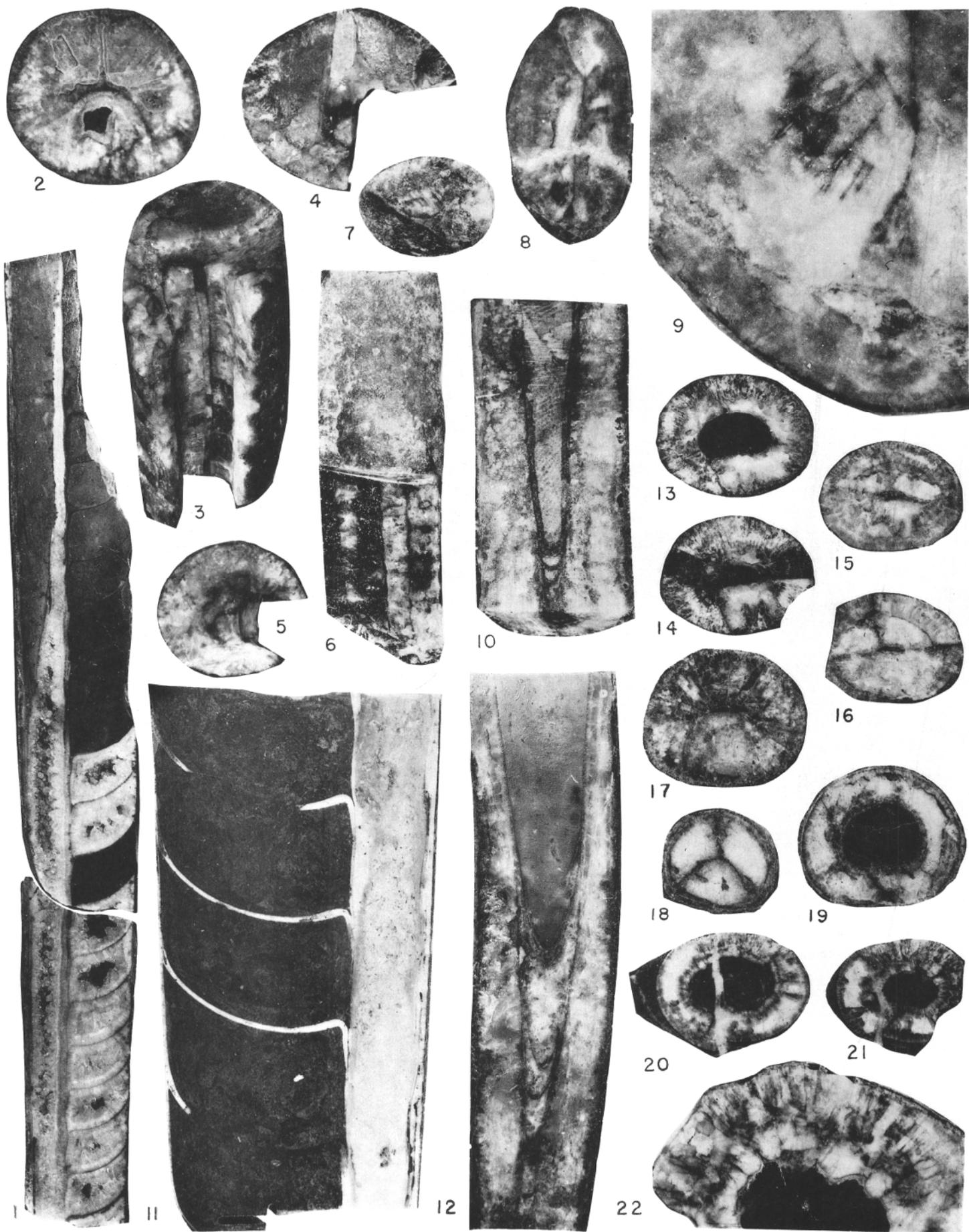
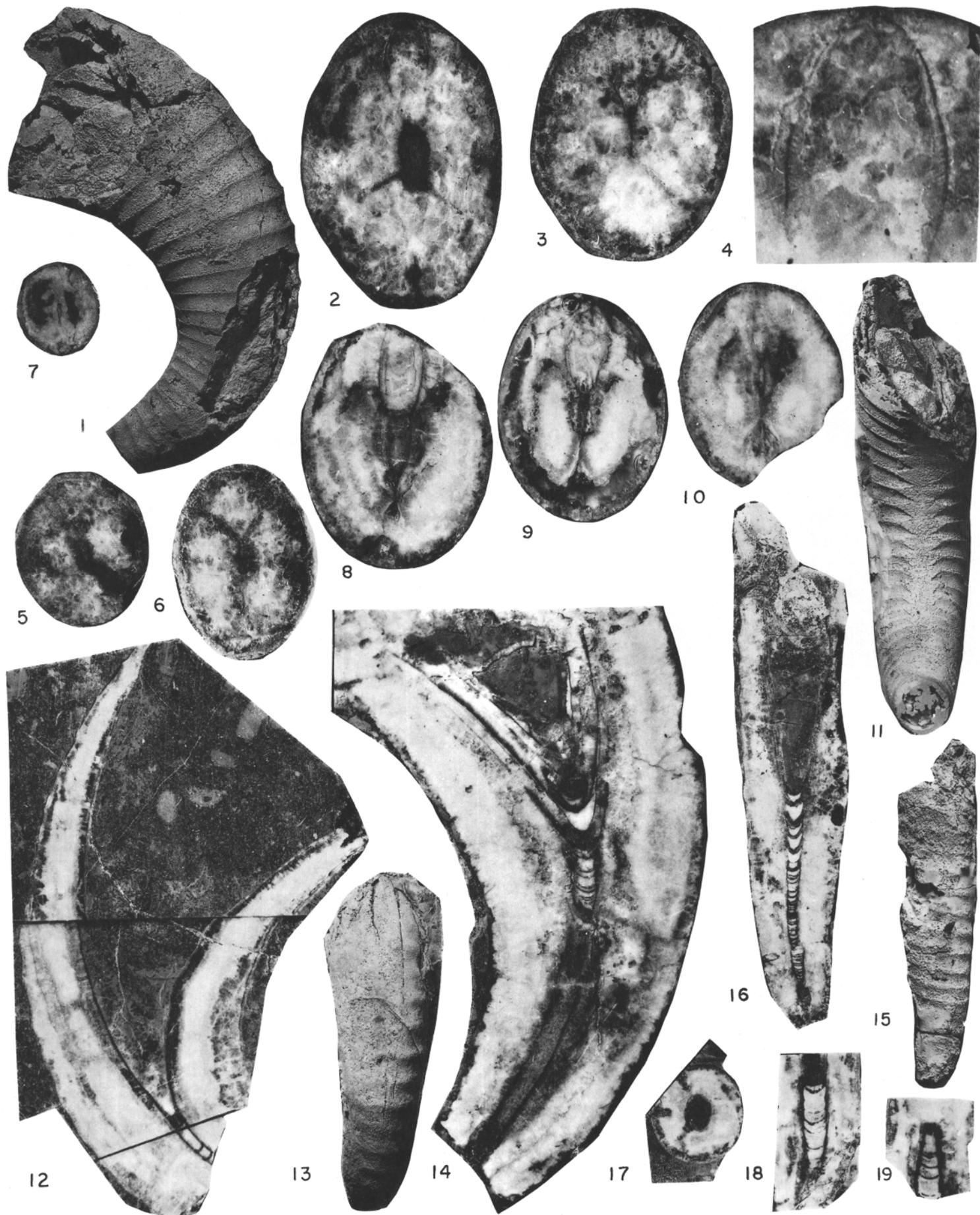


PLATE 4

Figures	Page
1. <i>Dideroceras ventrale</i> Flower, n. sp.	56
Vertical section of the holotype, showing the ventrally terminating endosiphococone. Orthoceras limestone, Skär-11öff, Oland, Sweden. Collection of the writer. No. 924.	
2. <i>Rossoceras lamelliferum</i> Flower, n. sp.	59
A cross section, X 2, from a paratype (No. 359) showing slight silicification, and general retention of the numerous blades, though with some possibly artificial accentuation of dorsal and downcurved lateral blades. Highest 20 feet of the Garden City formation, Green Canyon, at the northern edge of Logan, Utah.	
35. <i>Protocycloceras affine</i> Ulrich, Foerste, Miller, and Unklesbay	54
A previously unfigured paratype, USNM, No. 109518. In fig. 3, the specimen has been ground down to the siphuncle, only in the middle. On the ventral side of the siphuncle, to the left of the figure, there is apparently a ventral rod, thinning slightly adorally; to the right is space in which alternating calcite and matrix are separated by sharp horizontal lines, suggesting diaphragms filling the supplementary cavity. Fig. 4 shows the anterior end, fig. 5, the apical end. All are about X 2.5.	
67. <i>Protocycloceras affine</i> Ulrich, Foerste, Miller, and Unklesbay	54
Fig. 6 shows, in longitudinal view, the specimen regarded by Ulrich, Foerste, Miller, and Unklesbay as having a lining within the siphuncle. To the lower right, are seen camerae with the septa nearly transverse. Next is the true siphuncle, filled with calcite, and showing faint transverse bands suggesting diaphragms; to the left, both the dark band and the marginal band of light calcite represent the phragmocone. Fig. 7, an anterior view of the same, shows the relatively small subcentral siphuncle, which, under the previous interpretation would be necessarily large and marginal. USNM, No. 109517. A paratype.	
89. Undescribed genus and species of piloceroid	55
8. cross section through the endosiphuncle, showing vertical very narrow tube, and vertical blades bifurcating rather irregularly. 9. enlargement of the lower left portion of the same, showing part of the ventral blade, with traces of endosiphofunicles in the upper center, apparently free of other blade structures, and again, less clearly, in the bifurcating ventral blade in the lower right. No. 763, from the first piloceroid zone of the El Paso group.	
10. Longitudinal section of an undescribed slender endoceroid siphuncle showing clear endosiphococone, with diaphragms extending well up into the cone. No. 895, first piloceroid zone, Victorio Mountains, New Mexico.	55
11. <i>Dideroceras magnum</i> Flower, n. sp.	56
Vertical section, venter at right, from the base of the holotype, AMNH, No. 22353. Upper Red Orthoceras limestone, Skär-11öff, Sweden. Natural size.	
12. Anterior portion of endosiphuncle of an undescribed slender endoceroid from the first piloceroid zone of the El Paso, showing a second example of diaphragms penetrating the endosiphococone. No. 906.	55
13-22. <i>Rossoceras</i> , sections showing multiple blades	51
A series of cross sections showing varied aspects of the cone, tube, and blades. Except for fig. 18-19, these represent <i>Rossoceras lamelliferum</i> ; 18-19 is not specifically determined. 13-14. Two cross sections, x 1, showing two sections, 13, anterior, through the endosiphococone, with numerous fine blades preserved, 14, section through apical part of endosiphococone, showing bases of trifold blades, branching and less distinct distally. 15-16. Two cross sections of another paratype, No. 361, showing numerous fine blades partly preserved, but with accentuation of dorsal and lateral blades, largely by alteration. 17. Cross section, x 2, from a more apical portion of the same specimen represented by fig. 2, showing numerous branching blades, with divergent lateral blades prominent. 18-19. <i>Rossoceras</i> sp. USNM, No. 140155, from Ikes Canyon, Toquima Range, Nevada, two cross sections in which replacement has strengthened dorsal and down curved lateral blades, resulting in a trifold pattern, more like that of many simpler Endoceratida. The two sections are from two specimens, shown on a single surface. 20-22. <i>R. lamelliferum</i> . (No. 357) 20 and 21 are two sections through the endosiphococone, which here shows unusual irregularities of the surface, possibly a gerontic phenomenon. Fig. 22 is an enlargement showing the blades in more detail.	
All except figs. 18-19 are in the collection of the writer, and from Green Canyon, Logan, Utah, from the upper 20 feet of the Garden City limestone.	

PLATE 5

Figures	Page
1-3, 5, 11. <i>Bisonoceras corniforme</i> Flower, n. sp.	57
Holotype, r, l r. lateral and ventral views, X r. 2. anterior cross section, X z, cutting the endosiphococone, showing the paired dorsal curved blades, and two ventrolateral stubs of blades, possibly, from their position, belonging to different pairs. 3. a more apical section, passing through the endosiphotube, showing curved dorsal blades and one ventrolateral blade preserved. 5. an apical section, X 2, showing shadows of divergent dorsal blades of the young stage, and a stronger ventrolateral shadow blade. No. 851, from the first piloceroid zone, Victorio formation, from the Victorio Mountains, New Mexico.	
4, 6, 13. <i>Bisonoceras</i> sp.	58
4. Cross section, enlarged about X 7, showing clear dorsal portions of the curved dorsal blades, with light centers, sharp dark edges, extended as feathering, the extensions representing impingement of sheaths on the blades. 6. Cross section from an apical portion, showing more clearly than in fig. 5, the straight dorsolateral blades of the young stages of <i>Bisonoceras</i> . 13. Dorsal view of the siphuncle, X r, showing expression of the termination of the dorsal blades of the adult upon an etched siphuncle surface. No. 852, first piloceroid zone, Victorio Mountains.	
7. <i>Bisonoceras</i> sp.	58
A cross section, X r, from the base of an endosiphuncle, in which calcitic replacement has taken place, as though filling two lateral cavities. Presumably the dorsal and ventral blades controlled solution and replacement resulting in these cavities, but all blades are now lost, and the pattern is largely adventitious. No. 772, from the first piloceroid zone of the Cooks Range, New Mexico.	
8-10. <i>Bisonoceras</i> sp.	58
Three sections from a form showing clear dorsal blades, the branching ventral blade, and stubs of lateral blades, all X 2. Fig. 8 cuts the specimen close to the apex of the endosiphococone; the other two cut the endosiphotube, which is higher and more prominent than in <i>B. corniforme</i> . The dorsal blades are closer together in the apical region, fig. 10, than anteriorly, in fig. 9; fig. 9 is the only one showing at all clearly stubs of additional lateral blades. No. 848, from the first piloceroid zone of the Cooks Range, New Mexico.	
12. <i>Bisonoceras corniforme</i> Flower, n. sp.	57
A paratype, shown in a longitudinal section; several parts were sectioned separately, and the surfaces shown vary slightly as to depth into the specimen. Endosiphosheaths are obscure throughout, even though the siphuncle is, from its size, essentially mature; the small tube shows several diaphragms. No. 767, from the first piloceroid zone of the Cooks Range, New Mexico.	
4. <i>Bisonoceras</i> sp.	58
A longitudinal section, showing the tube with diaphragms closely spaced near the anterior end; at the extreme anterior end the section passes centrally through the wall of the tube, and it is difficult to differentiate diaphragms from the endosiphosheaths which here cross the center of the sectioned surface. No. 920, X 2, from the first piloceroid zone, from the east side of the Florida Mountains, New Mexico.	
15, 16. <i>Dartonoceras gracile</i> Flower, n. sp.	59
15. Interior of the holotype siphuncle, X r, with the septal ridges sloping forward on the left, the ventral side. 16. Opposite side of the specimen, sectioned, showing the deep endosiphococone, the unusually large tube, and abundant and prominent diaphragms; the specimen was weathered, and the extreme base shows a weathered surface of the siphuncle, with closely spaced diaphragms, somewhat offset from the sectioned surface. From beds above the oolite, El Paso group, Mud Springs Mountain, New Mexico.	
17-19. <i>Dartonoceras</i> cf. <i>gracile</i>	59
17. a cross section, X 2, oriented with the venter beneath, showing a section essentially at the junction of the cone and tube, with traces of blades, suggesting a lateral pair, a dorsolateral pair, and a slightly more divergent ventral pair. 18, 19. opposite sides of a longitudinal section, X 3, taken at the base of fig. 17, showing the large tube with abundant diaphragms. From the first piloceroid zone of the El Paso, from the east side of the Florida Mountains, No. 919.	



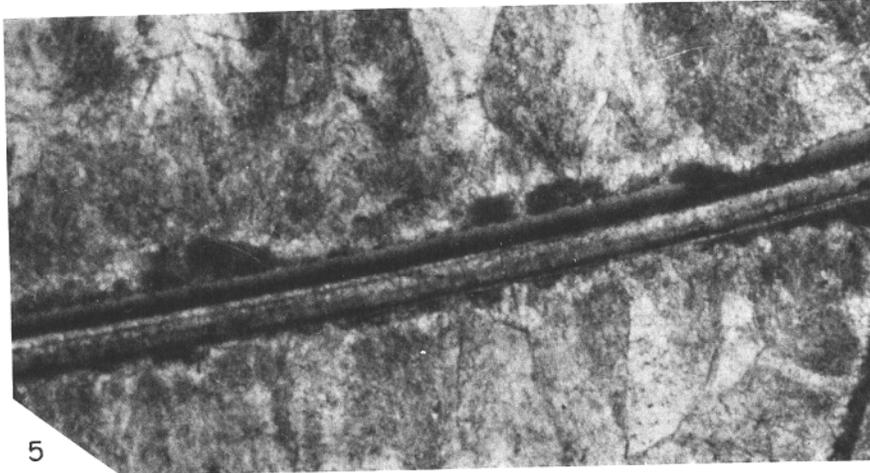
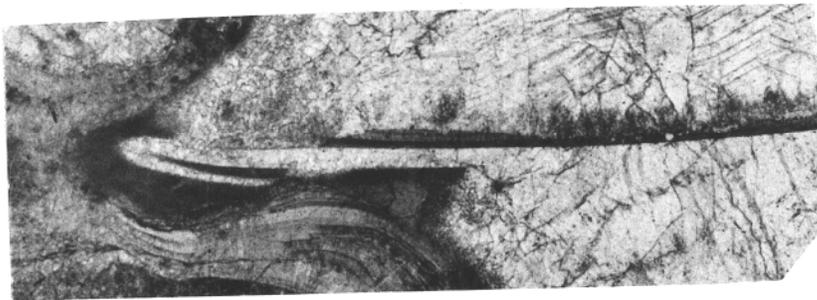
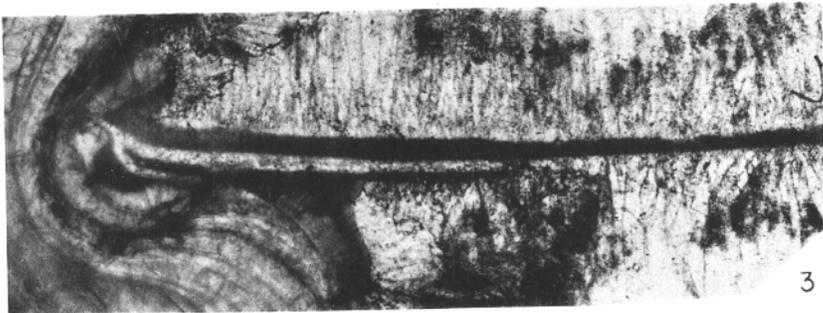
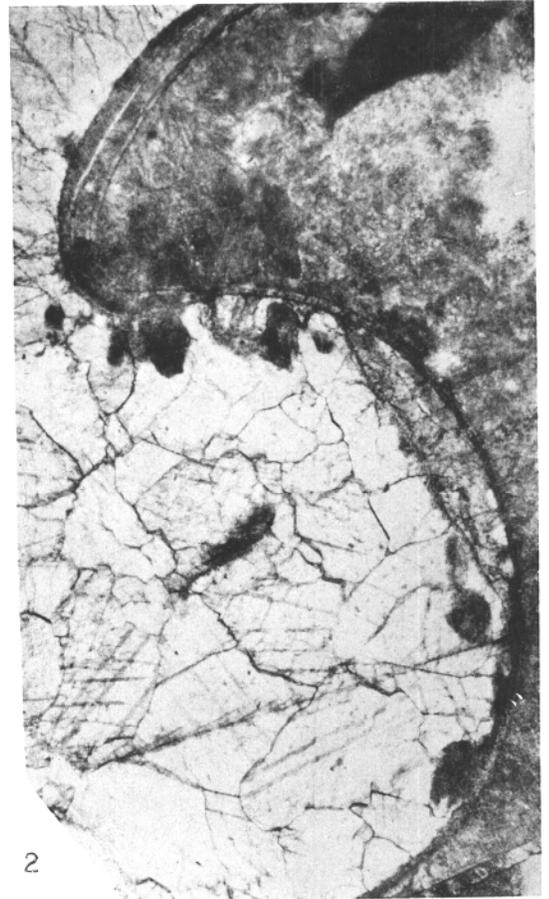
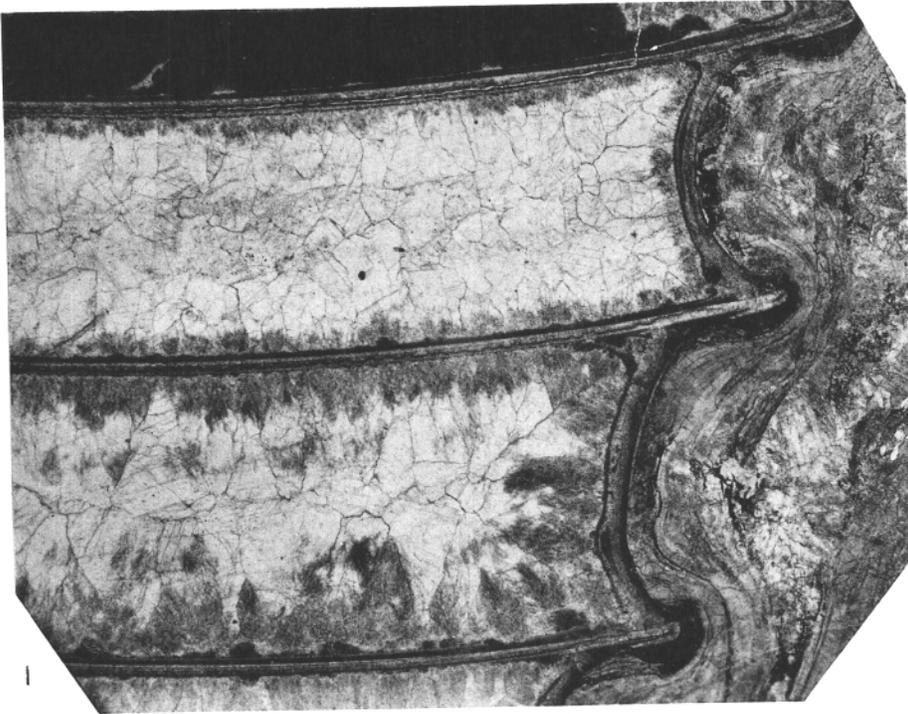


PLATE 6

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|--|------|
| 1 , 5 . <i>F a b e r o c e r a s</i> , s p . | 1 4 |
| <p>A thinsection, showing parts of the septa and siphuncle wall, showing some variation in layers of septa and rings. Fig. 1 is X 9; Fig. 5 is a further enlargement of the apical sep turn of Fig. 1, X 34, showing the anterior layer of the septum in which two layers of different hues are evident, and which merges into the ring at the right; a very narrow clear band separates it from the main mass of the septum, which shows only irregular calcite crystals; apically a thin clear layer is evident, but it is clear only on the right half of the figure and continues within the recumbent neck. The dark knotlike body in the ring, shown in the anterior part of Fig. 5, has been observed only in this section.</p> | |
| 2 . <i>A c t i n o c e r a s r u e d e m a n n i</i> F o e r s t e and T e i c h e r t | 2 2 |
| <p>A thinsection, X 12, of one of the very few <i>Actinoceras</i> showing fine transverse structures in the free part of the ring comparable to those of <i>Adamsoceras</i>, shown in Pl. 2, fig. 8; here the ring is very much thinner. The apical part of the ring seems generalized and granular in structure, shown above; there is no homologue here of the dark region at the anterior end of the ring of <i>Adamsoceras</i>.</p> | |
| 3 , 4 . <i>F a b e r o c e r a s</i> , s p . | 1 4 |
| <p>Thinsections (No. 79, showing structure of septal layers and rings. Fig. 3, X 16, shows the main part of the septum composed of irregular calcite crystals; to the right the septum seemingly merges with calcite of the camera below; the recumbent neck shows a spur, not noted elsewhere. The anterior layer is thick and dark; near the siphuncle a dark layer on the apical side of the septum separates the vinculum from the main crystalline part of the septum. Fig. 4, X 18, shows calcitic septum again with the boundaries separating it from inorganic calcite lost in places; the anterior layer is damaged, showing irregularities in thickness and breaks in distribution, but shows a lighter anterior and a darker posterior layer; apically, dark material separates the vinculum from the crystalline part of the septum and is surrounded by the recurved neck.</p> <p>All from thinsections in the collection of the writer; No. 2 is from the Chaumont limestone, near Watertown, New York; the others are from the Leipers formation of the Cumberland River near Rowena, Kentucky.</p> | |

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Numbers in boldface indicate main references

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