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THE CEPHALOPOD ORDER DISCOSORIDA

By ROUSSEAU H. FLOWER and CURT TEICHERT



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THE CEPHALOPOD ORDER DISCOSORIDA

By ROUSSEAU H. FLOWER¹ and CURT TEICHERT²

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ABSTRACT

The Order Discosorida is revised and expanded to include 7 families and 40 genera. Additional groups, not as thoroughly investigated morphologically, notably the Trimeroceratidae and Dies-toceratidae, may prove to stem from the discosorids rather than from the oncoceroids.

Unity of morphological structures, notably those within the primitively thick connecting rings, demonstrates the unity of the order, and indicates that resemblance of many genera to those of other stocks, notably the Oncoceratida, is homeomorphic.

Morphology is discussed in detail, and supplies a clue to phylogeny. The siphuncular bulbs of young *Ruedemannoceras* suggest an origin of the order in the Plectronoceratidae, independent of all other cephalopod stocks. Primitive forms have thick rings the tips uninflated in endogastric shells (Ruedemannoceratidae). They gave rise to the straight breviconic Mandaloceratidae with little internal modification at first, and on the other hand to the endogastric Cyrtogomphoceratidae in which the bullettes are swollen. The Phragmoceratidae develop from the Cyrtogomphoceratidae with only minor internal changes. The Westonoceratidae are derived from the same source by reversal to exogastric curvature, development of deposits in the siphuncle which are at first discrete and later grow over one another to form endocones. The

Lowoceratidae are slender shells, showing structural similarity to the Westonoceratidae in the young, but in the adult have broadly expanded siphuncles in which bullettes are uninflated, a condition found throughout life in the Discosoridae.

Distribution of genera is reviewed; our present knowledge of the stock is incomplete, owing to insufficient knowledge of the boreal faunas to which the main groups are confined. Nevertheless, the main trends of evolution can be traced.

The ecology of the various genera is discussed and it is concluded that most of them must have been benthonic and epibenthonic crawlers, while some were probably restricted swimmers. Genera with visored apertures, such as *Phragmoceras*, present special problems.

Systematic treatment is complete only down to the generic level. Some species are only listed, with notes on distribution and peculiar features, others are described where new information adds to the concept of the genus, and some new ones are described and illustrated. Restudy has resulted in the change of generic position of a number of species. Some are removed to genera outside of the order Discosorida. Such forms, mainly belonging to the new family Apocrinoceratidae, genera of the Oncoceratida, and the new genus *Cliftonoceras* referred to the Uranoceratidae, are discussed in an appendix.

Part 1. GENERAL DISCUSSION

By ROUSSEAU H. FLOWER and CURT TEICHERT

INTRODUCTION

The order Discosorida constitutes a group of cephalopods characterized primitively by siphuncles with broadly expanded segments and unusually thick, complex connecting rings containing specialized structures described in detail below. Most significant and most prevalent is the development of two layers in the tip of the ring, the bullette. In primitive stocks it is not thickened, but in more advanced ones it is swollen and mimics deceptively the annular deposits of the Michelinoceratida and some Actinoceratida. Also, in advanced forms parietal deposits similar to those in the Pseudorthoceratidae, and finally endocones resembling the endocones of the Endoceratida are developed in the siphuncle. But in specialized types the connecting ring can become thin and homogeneous.

In spite of this morphological variety, the order represents a phyletic lineage relatively isolated from its contemporaries (Fig. 1.). It is regarded as stemming from the archaic Plectronoceratidae of the Ellesmeroceratida.

As now interpreted, the two orders Discosorida and Oncoceratida include almost all cyrtocoines and brevicoines with expanded siphuncles from the Chazyan to the extinction of such forms in the late Paleozoic. For a long time most of these forms were united in HUTTON'S order Cyrtocoanites, and discosorids, when first recognized as cephalopods, were believed to be aberrant genera of the Actinoceratidae. The old order Cyrtocoanites is

now divided essentially into three orders: Actinoceratida, Oncoceratida, and Discosorida (FLOWER, *in* FLOWER & KUMMEL, 1950). The discosorids agree with the actinoceratids and differ from the oncoceratids in having the siphuncle segments broadly expanded from the earliest growth stages. The older oncoceratids show in the young (and even more rarely in the adult) segments which are tubular or nearly so, which is taken to be an indication of their ancestry in exogastric Canadian cyrtocoines with tubular siphuncles, the Bassleroceratidae. The actinoceroids differ from the discosorids in their large blunt apical ends, and in the presence from their inception of siphuncles with annulosiphonate deposits and an elaborate canal system.

There is so much external resemblance between many oncoceroid and discosorid genera that the possibility of an oncoceroid origin of the discosorids had to be investigated. It also seemed possible that the discosorids could be an artificial group in which were assembled specialized forms of oncoceratid derivation. Late Ordovician Westonoceratidae (*Winnipegoceras*, *Westonoceras*) resemble contemporaneous Oncoceratidae in form, though not in internal structure. In the Silurian, there is again a striking and, indeed, a confusing convergence between *Sthenoceras* of the Phragmoceratidae, and *Danoceras* of the Oncoceratidae. Again, the Mandaloceratidae of the Silurian show discosorid affinities, on one hand, and similarities

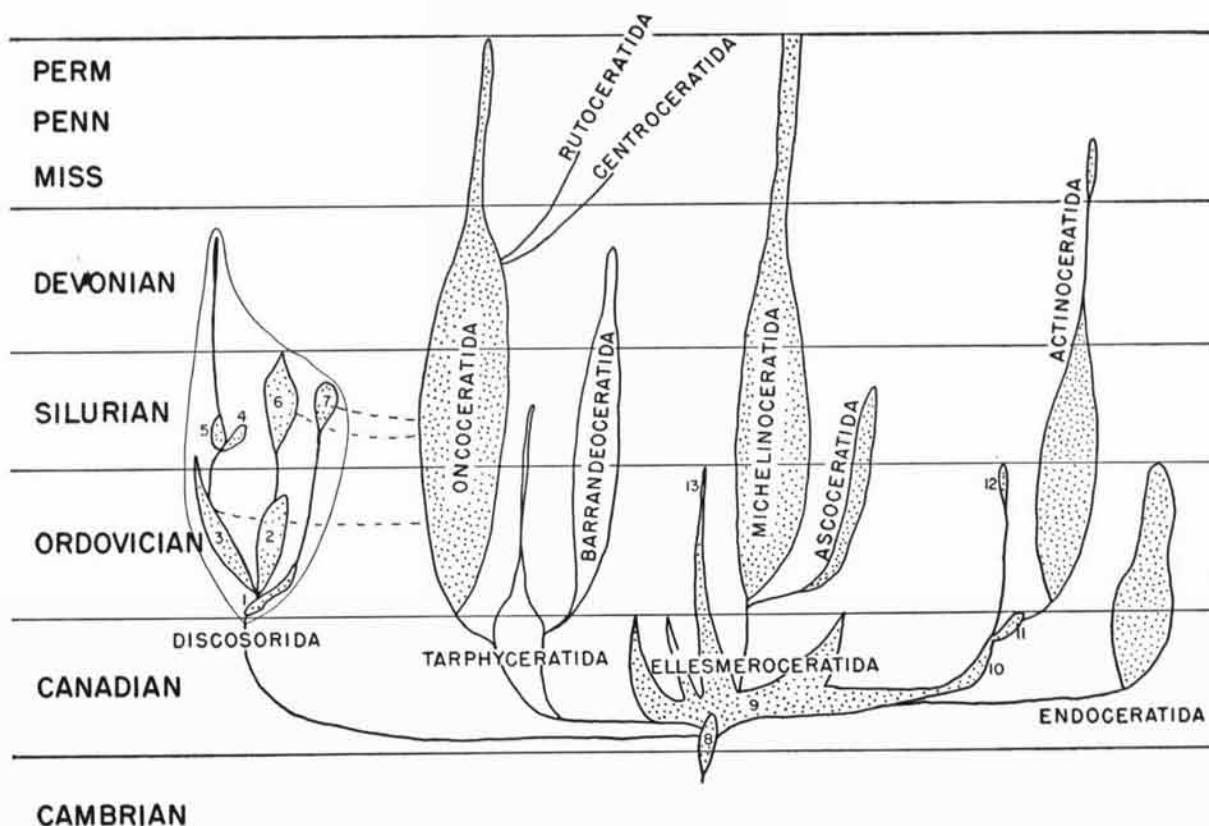


FIGURE 1. Phylogeny of the older Nautiloidea, showing the orders, and emphasizing the isolated position of the Discosorida.

Families of the Discosorida and a few of those of the Ellesmeroceratida are indicated by numbers as follows:

DISCOSORIDA.—(1) Ruedemannoceratidae.—(2) Cyrtogomphoceratidae.—(3) Westonoceratidae.—(4) Lowoceratidae.—(5) Discosoridae.—(6) Phragmoceratidae.—(7) Mandaloceratidae.

ELLESMERO-CERATIDA.—(8) Plectronoceratidae.—(9) Ellesmero-

ceratidae.—(10) Eothinoceratidae.—(11) Bathmoceratidae.—(12) Cyrtoceratidae.—(13) Baltoceratidae.

Dotted lines connecting the Discosorida and Oncoceratida indicate the three occurrences of contemporaneously convergent homeomorphs, between the Westonoceratidae and Oncoceratida in the Ordovician, between *Sthenoceras* and *Danaoceras* and between the Mandaloceratidae and the Hemiphragmoceratidae in the Silurian.

with contemporaneous forms (Hemiphragmoceratidae, Trimeroceratidae), on the other, to such an extent that it is still not certain, because of lack of good material, whether some oncoceroids may not be incorrectly included in the Mandaloceratidae. *Glyptodendron* shows remarkable homeomorphy with slightly younger genera derived from the Barrandeoceratida. It became evident, however, that it was among specialized and not primitive discosorids that these resemblances with other stocks were found. Restudy showed that the structures within the connecting ring, previously unknown, supported the unity of the order Discosorida as a group, and that we were concerned with many cases of convergence with other stocks.

In the process of the present investigations, the Discosorida grew from 4 to 7 families, and from 12 to 40 genera. Instead of being a minor group, it came to be one of appreciable dimensions. It is still small in comparison with the Oncoceratida, which includes more than 150 genera, but it is by no means insignificant. Strangely, the rarity of the known forms is a reflection of a very interesting and significant fact, namely, that in its major

evolutionary development (in the Ruedemannoceratidae, Cyrtogomphoceratidae, Westonoceratidae, Lowoceratidae and Discosoridae) the stock is mainly confined to North American boreal faunas of Ordovician, Silurian and Devonian age. Scarcity of the stock is perhaps largely a reflection of the fact that the faunas in which the stock developed occur for the most part in places either relatively inaccessible or at least outside the common collecting grounds. In contrast, the Phragmoceratidae and Mandaloceratidae are recognized as elements in Middle Silurian faunas throughout much of Europe and North America, though their greatest development seems to have been in the prolific cephalopod faunas of Étage E₂ of the Bohemian basin.

The present treatment of the group is very uneven. It was originally intended to present a summary of the order down to generic level. Species were only to be listed. This course is maintained for those species for which reproduction of figures and descriptions would be a pointless duplication of work already done. However, some species were reinvestigated, supplying new information on the internal structure of the genera. Such forms re-

quired illustration and careful description. In the process of some ten years of investigation, species had come to light which called for description. They add to knowledge of stratigraphic range of genera and some of them contribute to understanding of morphology. In some genera homeomorphy with oncoceroids is such that, without knowledge of internal structure, the two orders are almost bound to be confused, and therefore critical analysis was required of the evidence available. Species removed from genera of the Discosorida are only listed under those genera to which they were previously assigned. To clarify their position now rather than to leave their discussion for a later work, these forms are assembled at the end of the systematic discussion in the appendix.

ACKNOWLEDGMENTS

It would not have been possible to bring this study to its present degree of completion without the generous loan of much material for study. Often also, permission to make sections of type and other material has been requested, and granted. A collection of Discosoridae, and also material of *Alpenoceras* from the Winnipegosis dolomite, was loaned by the Geological Survey of Canada through the kindness of Dr. W. A. BELL. Specimens of *Glyptodendron*, *Cyrtogomphoceras* and several other crucial genera similarly were loaned by the U. S. National Museum through the

kindness of Dr. G. A. COOPER. Dr. TRYGVE STRAND and the Paleontologisk Museum of Oslo loaned several important specimens, notably of the genus *Kiaeroceras*, and supplied photographs, here reproduced, of thin sections of that genus. The Natural History Museum of Stockholm and Mr. HARRY MUTVEI loaned material of *Phragmoceras* from Gotland, including several specimens from which thin sections were made. Dr. BERNHARD KUMMEL, then of the University of Illinois, loaned material from the unique genus *Tuyloceras*, and later additional material was borrowed from the Savage collection, now at the Illinois Geological Survey, through the kindness of Dr. C. W. COLLINSON. Dr. G. M. EHLERS and the University of Michigan loaned material of *Alpenoceras* and the genotype of *Teichertoceras*. Mr. W. H. SCHEVILL and the Harvard Museum of Comparative Zoology loaned material of *Protophragmoceras*. Dr. G. WINSTON SINCLAIR has submitted for study an important collection of cephalopods from the Trenton of Quebec, which contained a number of new species. R. H. FLOWER's own collection has formed the basis for a significant part of the study, largely because he felt perfectly free to use it for thin sections. All type materials from this source are to be deposited in the collection of the New Mexico Bureau of Mines in grateful acknowledgment of the support in time, materials and assistance given to this investigation.

Dr. BRIAN GLENISTER, of the University of Western Australia, has contributed photographs and information, and has loaned specimens of the Australian genus *Madiganella*.

A number of the thin sections were mounted and prepared with the help of Miss HELEN DUNCAN.

HISTORY OF INVESTIGATION AND DEVELOPMENT OF PRESENT CONCEPT OF THE DISCOSORIDA

The first discosorids were described by BIGSBY (1828) as "columns composed of circular discs" from Thessalon Island, Lake Huron. He regarded these fossils as problematical and did not name them. HALL (1851, 1852) described very similar fossils from the Silurian of New York and Michigan as *Discosorus conoideus*, but he too did not venture an opinion as to the systematic affinities of this "peculiar fossil body." It was BARRANDE, in 1866, who first suggested that *Discosorus* might be a cephalopod, but further studies of these fossils only tended to revive the doubts which he expressed in 1874 (p. 752). It remained for WHITFIELD (1882) to demonstrate beyond doubt that the "discs" described by BIGSBY, HALL, and BARRANDE were cephalopod siphuncles, because he found parts of septa attached to them. Consequently, HYATT (1883) listed *Discosorus* as a subgenus of *Actinoceras*, "with siphons apparently inseparable from the siphons of *Actinoceras*, but having some doubtful characteristics." FOORD (1888) was the first to regard *Discosorus* without qualifications as a member of the Actinoceratidae and, therefore, a true cephalopod. He was followed by HYATT in 1900.

No further contributions to the knowledge of discosorids were made until 1924 when FOERSTE redescribed *Discosorus*, established a closely allied genus *Stokesoceras*, and also described the genus *Westonoceras*, whose affinities to *Discosorus* were not recognized until much later. FOERSTE & TEICHERT (1930) included all three genera in the actinoceroid family Armenoceratidae TROEDSSON be-

cause of their extremely short ("armenoceroid") septal necks and their much inflated siphuncle segments. However, a year later, TEICHERT (1931) restudied *Discosorus* and some allied genera and established the family Discosoridae for *Discosorus*, *Stokesoceras*, and a new genus named *Endodiscosorus*. This family he removed from the actinoceroids and stated that it was "impossible to decide to what order of cephalopods it may belong." Slightly later TEICHERT (1933) studied the internal structure, especially connecting ring and cameral deposits, of *Westonoceras* and established for it the new family Westonoceratidae, because he recognized that the structure of the genus was fundamentally different from that of all other actinoceroids. In 1935, TEICHERT added to this family *Teichertoceras* FOERSTE, and also, more doubtfully, *Calhounoceras* TROEDSSON.

In the meantime, STRAND (1933) had called attention to small annular deposits in the vicinity of the septal necks of Ordovician species which he assigned to *Protophragmoceras* and *Danoceras*. He named these structures *bullettes*, in contrast to the "lunettes" of actinoceroids, and referred the two genera in which he had observed them to the Phragmoceratidae and Oncoceratidae, respectively. In a note at the end of his paper, taking cognizance of TEICHERT's work, he pointed out that the *Westonoceras* specimens described by TEICHERT showed very similar structures, and he suggested, correctly, that in all probability *Westonoceras* was not an actinoceroid, but was instead allied to other genera possessing *bullettes*

which he retained in the "Actinosiphonata." Concurring, TEICHERT (1937) transferred the Westonoceratidae to his order Gomphoceroidea which is more or less identical with FLOWER's Oncoceratida (in FLOWER & KUMMEL, 1950).

In the 1930's FOERSTE described many new cephalopod genera among which there were several brevicones and stout cyrtocoines with large nummuloidal siphuncles whose affinities remained uncertain, but were generally believed to be with the oncoceroids.

FLOWER (1940) proposed the Discosorida as a superfamily, and presented the following classification in abstract: Family Ruedemannoceratidae (*nov.*), *Ruedemannoceras* (*nov.*); Family Westonoceratidae TEICHERT, *Westonoceras*, *Teichertoceras*, *Wilsonoceras* (an error for *Winnipegoceras*); Family Cyrtogomphoceratidae (*nov.*), *Cyrtogomphoceras*, *Landeroceras*; Family Discosoridae TEICHERT, *Discosorus*, *Stokesoceras*, *Endodiscorus*, *Kayoceras*; and Family Lowoceratidae (*nov.*), *Lowoceras*, *Tuyloceras*. The group was recognized as ranging from Chazyan into Middle Silurian, and possibly extending into the Devonian, a conclusion later confirmed, and based upon forms now assigned to *Alpenoceras*.

At that time it was recognized that although cyrtocoenic cephalopods appeared abruptly in the Chazyan, there were several distinct stocks. Most of the forms, now assigned to the Oncoceratida and the Michelinoceratida, show siphuncles which either approach closely to or actually attain simple tubular segments. There remained two groups, however, which have broadly expanded siphuncles from the earliest growth stage then known. One group was the Actinoceroidea, dominantly orthocoines, with annular deposits and a complex canal system. The other group is made up of cyrtocoines and brevicones. The siphuncles are empty in primitive forms, later developing annular deposits, and still later endocoines. Primitively the connecting rings are thick, and this group, obviously distinct from the actinoceroids at the time when both groups appeared, was the Discosoroidea.

A fuller description of the group (FLOWER, 1946) accompanied the description of the Cincinnatian cephalopods. Here the morphology was discussed in greater detail, and it was noted that the annular constriction of the cavity of the siphuncle at the septal foramen is, when developed, partly due to parietal annular deposits, and partly to a swelling of the connecting ring itself. ENDO's little known *Yabeites* was tentatively assigned to the Ruedemannoceratidae, a conclusion which has since been found to be incorrect. TEICHERT has restudied the type material and confirmed KOBAYASHI's (1941) earlier conclusion that the genus is an actinoceroid. The new genus *Strandoceras* was proposed for Ordovician species previously assigned to *Protophragmoceras* (TEICHERT, 1930; STRAND, 1933); *Glyptodendron* and *Kiaeroceras* were added to the order; and the new genera *Faberoceras* and *Clarkesvillia* were described. *Faberoceras* was particularly significant, showing a transition between the annular deposits of the siphuncles of many Ordovician genera and the endocoines of the Silurian Discosoridae. The suggestion was made that the Phragmoceratidae might prove to belong to the discosorid line. A diagram of the phylogeny was presented.

SCHINDEWOLF (1942), in a work which came into our hands only after the publication of the one noted above, presented a description of some discosorids from the Eifel Devonian. He proposed subgenera *Discosorus* and *Stokesoceras* of the exogastric *Discosorus*, and *Endodiscosorus* and *Endostokesoceras* as subgenera of *Endodiscosorus*. Unfortunately, his concept of *Discosorus* and *Endodiscosorus* as genera which are exogastric and endogastric respectively was erroneous, and the Devonian forms which he described are proper members of the genus *Alpenoceras*.

FLOWER (in FLOWER & KUMMEL, 1950) raised the entire group to ordinal rank, proposing for it the name of Discosorida. In accordance with practices recommended in memoranda circulated in connection with the *Treatise on Invertebrate Paleontology*, the ordinal groups were given -ida endings throughout.

TEICHERT & GLENISTER (1952) added two very significant genera from the Ordovician of Australia, *Madiganella* and *Hecatoceras*. *Madiganella*, originally assigned to the Cyrtogomphoceratidae, proves to be allied instead to *Ruedemannoceras*. Further, *Hecatoceras*, though apparently endogastric, shows structures very close to those of the more advanced species of *Faberoceras* in which endocoines develop.

Later TEICHERT & GLENISTER (1954) assigned to the Westonoceratidae the new genus *Apocrinoceras*, from the upper Canadian of Australia. This form, which we at first welcomed as the first and only pre-Chazyan member of the order known thus far, is here removed to the family Apocrinoceratidae, and is now regarded as a group stemming from the annulated Protocycloceratidae in which the siphuncle becomes slightly expanded within the camerae.

Some years ago the writers were asked to undertake the description of a part of the Nautiloidea for the *Treatise on Invertebrate Paleontology*. It was patently absurd to try to trace the range of genera when the largest nautiloid assemblages described, those of the Silurian and Devonian of Bohemia, had largely escaped any further assignment than the old form-genera in vogue in the days of BARRANDE. True, some new genera had since been based on these species, but only rarely had more than the type species been assigned to them. More than nine tenths of the species remained unassigned. Though limitations of material and of the illustrations and descriptions published by BARRANDE left many species inadequately known, the results of restudy were more successful than were at first believed possible. Work on *Nautilus*, *Gyroceras*, *Trochoceras*, *Cyrtoceras* was largely completed, and considerable progress was made on the form-genus *Orthoceras*. The work of both of us, however, was interrupted by moves to other locations and the intervention of other duties.

At first most brevicones and cyrtocoines, with exception of the Phragmoceratidae, were regarded as belonging to the Oncoceratida. A few of the generic groups seemed anomalous in that their connection with other oncoceroids was not well fixed. *Apocrinoceras* could be a fore-runner of the Westonoceratidae, with which it agrees in the thick rings and subquadrate outline of the segments of the siphuncle. However, it shows so little in common

with *Ruedemannoceras*, that if *Apocrinoceras* is a primitive discosorid, *Ruedemannoceras* must be considered an unrelated form or the product of a very early offshoot.

Meanwhile, homologies of structure, particularly in the connecting ring, reaffirmed the relationship of *Westonoceras* and *Ruedemannoceras*. Further, the simplicity of the connecting rings, the absence of deposits within the siphuncle, and its greater age, suggested that *Ruedemannoceras* is primitive and quite possibly the archaic stock of the Discosorida. The early stages of *Ruedemannoceras* show siphuncular bulbs similar to those of the Pletronoceratidae, and suggest an origin of the discosorids in that family, independent of all other cephalopods. Curiously, the authors had previously concluded that the thick rings of the discosorids must indicate origin in some part of the Ellesmeroceratida. Here was the first clue to a definite origin within this rather large and diverse order.

GENERAL MORPHOLOGY

It is superfluous here to review the general morphological features of cephalopod shells. Though there have been marked advances in the understanding of these structures, largely since 1930 (TEICHERT, 1933; FLOWER, 1939), they have been well summarized in recent works (FLOWER, 1946; FISCHER, in MOORE, LALICKER & FISCHER, 1952). It remains to note those features peculiar to or strikingly developed in the Discosorida.

Probably the shell wall and septa were dominantly aragonitic, as in most cephalopods. Replacement by calcite and loss of fine structural details in the process has destroyed any indication of shell layers that may have been present. Septa of the discosorids show one peculiarity, in that a septal furrow has never been observed in the group. A possible reason for its absence may be that the mural part of the septum is generally, and probably uniformly very short, extending less than half the distance forward from the suture to the next septum. That the conchial furrow has not been observed may be less significant. The structure is commonly faint and very well-preserved internal molds must be examined if one hopes to see it. Almost uniformly, surfaces of internal molds of specimens in this order are rather poor. Absence of the conchial furrow may be more apparent than real.

It is structures within the siphuncle which particularly characterize the Discosorida. The essential features are shown in the accompanying Figure 2. Structures are variable within the order, and the distribution of the various features is shown in relation to the phylogeny in Figure 3.

Primitively, the discosorids are characterized by broadly expanded siphuncles with thick connecting rings. No annular deposits are found within the siphuncle (Fig. 2A). This feature persists in the Ruedemannoceratidae, and their descendants the Mandaloceratidae. In *Ruedemannoceras*, adult segments (but never the young ones) show differentiation in the connecting ring, here indicated in general terms. Further details will be discussed in the following section. Beyond the tip of the

neck there is a broad area, extending slightly along the surface of the anterior septum, its apical surface typically concave and holding the next region within it. This is termed the *vinculum*. It consists of dense, locally amorphous calcite (*h* in Fig. 2A). The anterior half of the ring, made of coarse granular material (*granular zone*) follows. The apical half of the free part of the ring contains a zone of fine-grained clear yellowish material, as seen in thin section, so suggestive of chitin that it is termed the *chitinoid zone*. It lies typically between two narrow bands, curved with the concave sides facing the chitinoid zone like two parentheses. These are termed the first and second *amorphous bands*. The tip of the ring which curves around the cytochoanitic septal neck, is divided into a zone of dense amorphous material and on the side facing the cavity of the siphuncle, a band showing lamellae paralleling the curving surface of the ring. Properly, the amorphous band lies outside the lamellar one, but expansion of the siphuncle, and curvature of these structures around a strongly recurved septal neck, gives them the aspect of concentric structures, with the amorphous band, morphologically on the outside, the innermost of the two. As there are already two amorphous bands, confusion is eliminated by referring to these two layers as the inner and outer zones of the bullette, adopting the obvious pattern of these as concentric structures and abandoning the strict morphological application. Paradoxically, it is the inner band which is, by strict morphology the outer one, but to all practical purposes, the structure has been turned inside out. It is these two layers which together become inflated in more specialized discosorids. STRAND (1931) applied the term *bullette* to such swellings, and it seems proper to retain his term. True *bullettes* are confined to the discosorids, and are structures always showing these two layers. Analogous swellings occur in the oncoceroids where actinosiphonate deposits are either incipient or degenerate, but they are never layered, and nothing comparable to the zones of the connecting ring noted here, have been found in that order.

The *Cyrtogomphoceratidae* exhibit the next step in advance. The rings are essentially similar, except that the bullette here for the first time is swollen into an annular structure. Commonly, the inner zone is concentrated into one large mass on the apical side of the recurved septal neck, and another small mass on the an-

terior side, close to the second amorphous band. The vinculum is clearly developed at the anterior end of the ring (Fig. 2B). Good material for proper study by thin sections has been lacking. Opaque sections and a few published figures suggest some differentiation within the free part of the ring, but are not sufficient to show a gen-

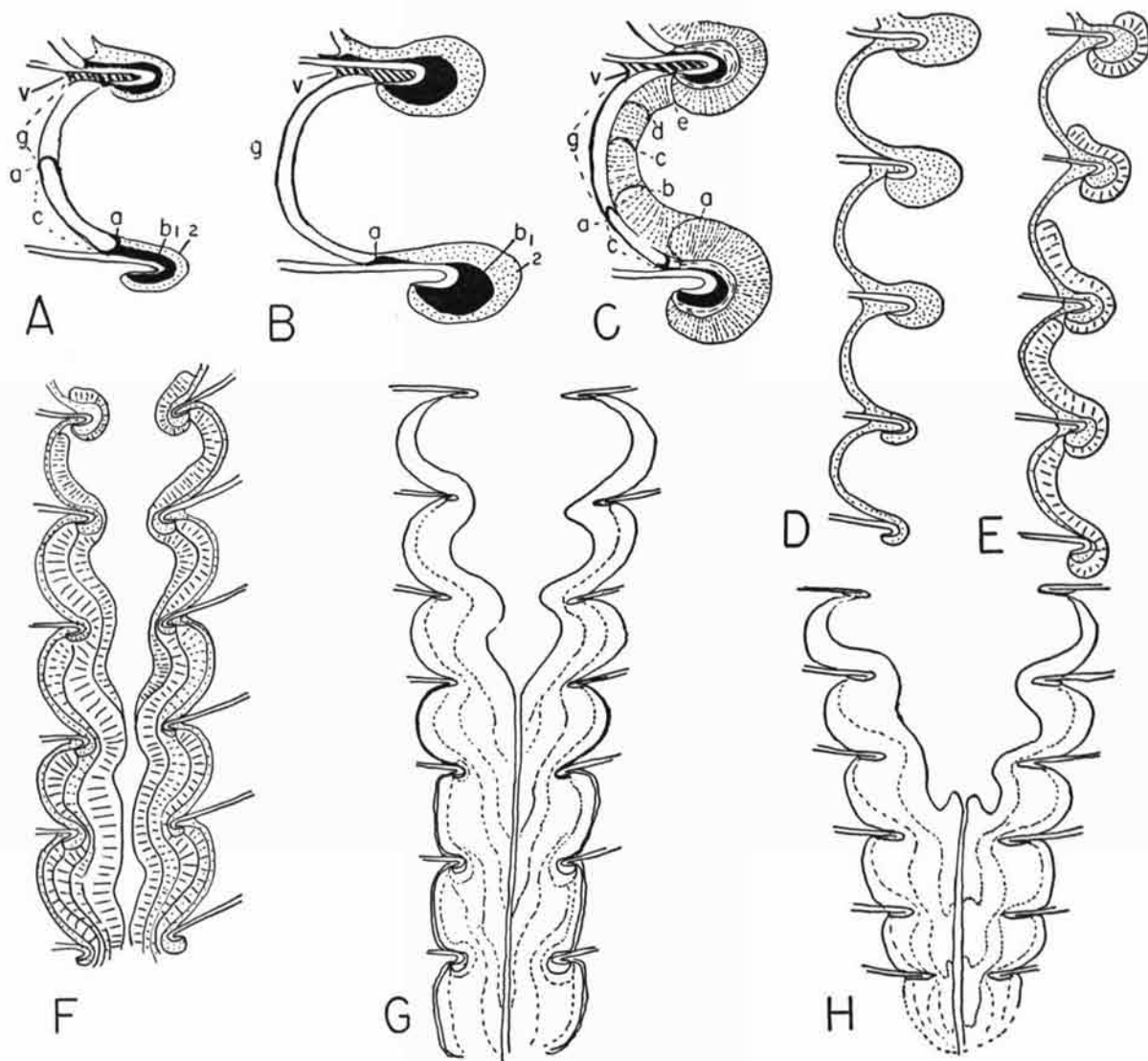


FIGURE 2. General morphology of discosorid siphuncles.

A. Segment of siphuncle of *Ruedemannoceras* showing thick ring with (*v*) vinculum, (*g*) granular zone, (*a*) amorphous bands, (*c*) chitinoid zone, (*b*) bullette with (1) inner and (2) outer layers.

B. Segment of siphuncle of *Cyrtogomphoceras*, showing (*v*) vinculum, (*g*) granular zone, (*a*) second amorphous band, (*b*) bullette, swollen, with (1) inner zone divided, and (2) outer zone thick and uniform. Absence of first amorphous band and chitinoid zone may be more apparent than real.

C. Generalized segment for the simpler Westonoceratidae, showing same part of the connecting ring as in A, with bullettes slightly swollen. Within, parietal deposits form first at the septal foramen, and grow gradually forward, successive stages being indicated by letters *a* to *e*, inclusive.

D. Generalized series of connecting rings showing typical adoral increases in size of the bullettes.

E. Growth pattern of Westonoceratidae, combining bullettes which increase in size adorally, with parietal deposits progressing from young to mature as traced adapically.

F. Growth pattern for advanced species of *Faberoceras*, with thick rings, bullettes, and parietal deposits extended into endocoines.

G. Ontogenetic succession of *Tuyloceras*, somewhat abbreviated and generalized, showing early segments similar to those of F, with succeeding segments broader, losing the swollen bullettes and developing thinner and apparently more homogeneous rings.

H. *Discosorus* siphuncle, showing a series of broadly rounded segments, rapidly increasing in size (rings apparently simple and homogeneous), and endocoines. The condition found in the anterior part of *Tuyloceras* here dominates the entire siphuncle.

eral pattern. Although only the granular zone is indicated in the accompanying figure, it is believed that the chitinoid zone and first amorphous band are present (Fig. 2B).

In the Westonoceratidae annular deposits appear superimposed upon a connecting ring with vinculum, bullettes, and some indication of the granular and chitinoid zones and the two amorphous bands. The deposits form around the bullettes, and each one grows forward, various progressive stages for an individual ring being indicated by *a* through *e* in Figure 2C. Primitively, each of these deposits (properly, parietal annulosiphonate deposits) are limited by the surfaces of the individual connecting rings.

Bullettes in the Westonoceratidae increase in size as they are traced from apical to adoral segments. The same may be true of the Cyrtogomphoceratidae. Probably it is less apparent there because scarcely any good sections showing considerable intervals of the phragmocones have been available for study. The condition found in the

Westonoceratidae, best developed in *Faberoceras* and *Clarkesvillia*, is shown in Figure 2D. It is also illustrated by the sections on Plates 17-19 and 21. Parietal deposits grow in the discosorids very much as they do in the Pseudorthoceratidae (FLOWER, 1939). They grow individually, adding material at their adoral ends until growth is completed. Their development is delayed somewhat after the secretion of the septa and connecting rings. Consequently, in a series of segments of the siphuncle in the Westonoceratidae (Fig. 2E) one will find the bullettes increasing in size and prominence adorally, while the parietal deposits will be complete apically, but individually increasingly immature as segments located farther adorally are inspected, and absent in a series of anterior segments.

Glyptodendron shows an interesting variation on this pattern. Parietal deposits are suppressed. They are either completely absent or so confined to apical segments that they have not been observed. Bullettes are nearly suppressed, but show a reversed ontogenetic relationship.

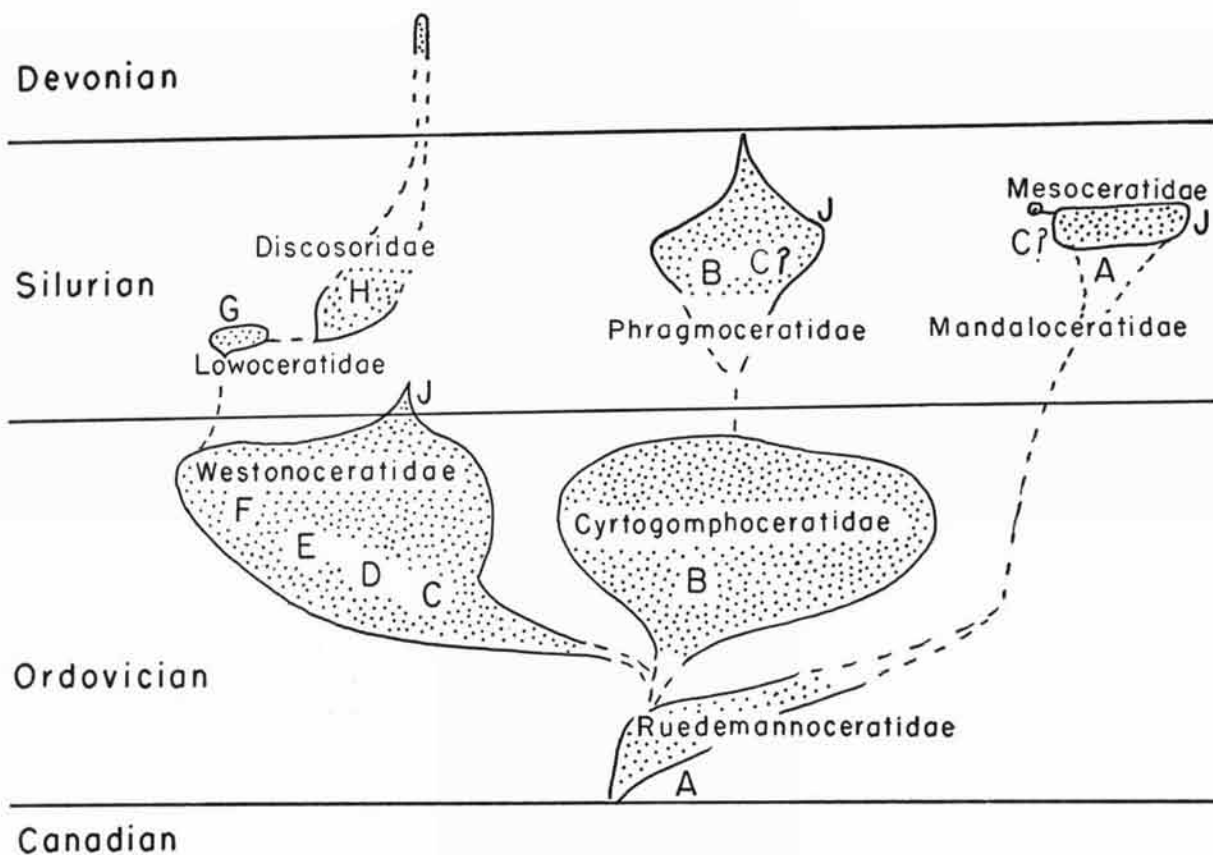


FIGURE 3. Diagram of phylogeny of the Discosorida, showing relationship and range of families.

Letters indicate the distribution of the morphological features, largely corresponding to the features shown in Figure 2.

- A. Thick rings, bullettes unswollen, no annular deposits.
- B. Thick rings, bullettes swollen, no annular deposits.
- C. Parietal annulosiphonate deposits added to the pattern of B.
- D. Bullettes markedly enlarged in adoral siphuncle segments.
- E. Typical growth pattern of bullettes and parietal deposits clearly developed.

F. Annular deposits extended in growth through a series of segments, forming endocones.

G. Young as in F, adoral segments with apparently thin homogeneous connecting rings.

H. Thin rings, no evident bullettes, and simple endocones throughout ontogeny.

J. Simplification of internal structure by reduction of bullettes, and thinning of rings, essentially similar to G and H, but without the adjunct of endocones.

They are wanting in the earlier segments of the siphuncle, but still remain as vestigial structures in the anterior segments, which resemble closely the lower three segments of Figure 2D.

In more advanced species of *Fabroceras*, the parietal deposits grow to excess. They are no longer confined to individual segments but grow over one another and the end result is a series of endocones, as shown in Figure 2F, superimposed upon thick rings with bullettes.

Tuyloceras, of the Silurian Lowoceratidae, shows early portions of siphuncles which are almost identical with the adult of *Fabroceras* (Fig. 2G), with thick rings small bullettes, and endocones which quite obviously begin as parietal deposits. Anterior segments, however, lose the bullettes, the ring is not obviously thickened, and within it are only normal endocones.

The Discosoridae (Fig. 2H) show siphuncles in which the simple rings and cones persist throughout life. Obviously, the early stages of *Tuyloceras* which recapitulate features of the Ordovician Westonoceratidae, are here pushed back and lost tachygenetically. Thinning of rings here may be a preservation phenomenon and more apparent than real. Such an interpretation is suggested by the retention of rather thick rings, though void of swollen bullettes, in the best preserved material of *Alpenoceras*, the last survivor of the stock in the Devonian.

The Phragmoceratidae stem from the Cyrtogomphoceratidae, and in general, show an apparent simplification of the ring. Bullettes are still developed, and composed of two layers, and set off from the rest of the ring by the second amorphous band. The anterior part of the ring appears to be undifferentiated, even the vinculum ap-

pearing to be uniform with the rest of the ring. As noted in discussion of the family, some published figures suggest accessory deposits within the siphuncles. No material has been available to study the structures at first hand. They appear to be analogous to the parietal deposits and endocones (which are not distinct structures) of the Westonoceratidae. Necessarily, their appearance in the Phragmoceratidae must be independent of that in the Westonoceratidae, and the structures seem to have some peculiarities of their own.

The Mandaloceratidae are a Silurian family derived from the Ruedemannoceratidae independent of other stocks (Fig. 3). Clearly, *Pseudogomphoceras* shares the thick rings and central canal of the Ordovician *Madiganella*. More advanced forms show at first similar broad segments with thick rings, but lack the central tube. Again, no material was available to study the structures directly, but BARRANDE's illustrations show two interesting modifications. First, in some forms the siphuncles become smaller, simpler in outline, and the rings appear to become thin and perhaps homogeneous. Second, in *Mandaloceras* and some allied forms, there are "obstruction rings" which have the position of inflated bullettes and possibly that is what they are. They show irregular projections on the surfaces in some specimens, and thereby suggest actinosiphonate deposits. It must remain for those having access to adequate material to study these structures by thin sections, and to determine whether they are modified discosorid bullettes, or whether they are actually allied to actinosiphonate deposits. If they are, the Mandaloceratidae as here delimited, are a polyphyletic group of remarkable contemporaneously convergent homeomorphs.

STRUCTURE OF THE CONNECTING RING

It was recognized at an early stage in the study of this group that a striking peculiarity was the unusual thickness of the **connecting ring**. Thick rings, in which various structures may be differentiated, are characteristic of primitive cephalopods, but become reduced to thin homogeneous structures in most specialized stocks. Thick rings characterize the Ellesmeroceratida, most (probably all) of the Endoceratida and the Tarphyceratida, with which the Bassleroceratidae are now united. They are lost in the Oncoceratida, though secondary thickening may appear there which develops into actinosiphonate deposits, in the Michelinoceratida, Ascoceratida, and largely if not completely in the Actinoceratida. The "Kontaktschicht" of TEICHERT (1933) may be a structure of the ring in the actinoceroids; otherwise their rings are thin and homogeneous. The discosorids are the only group in which the thick ring is retained in segments which are strongly expanded within the camerae. They are likewise the only major post-Canadian group of cephalopods which retain thick rings. Other post-Canadian elements with thick rings are found in the Endoceratida, a group already well differentiated in the Canadian, and such remnants of the Canadian Ellesmeroceratida as *Baltoceras* and *Cyrtoceras*, and the Trocholitidae

of the dominantly Canadian Tarphyceratida (Fig. 1; also FLOWER 1952, fig. 7, p. 35).

Thickness of the ring indicates that the discosorids are a natural group, but thickness alone could possibly be achieved by homeomorphy. Study of the rings in greater detail and higher enlargement shows differentiations of various parts not previously suspected. These structures are well displayed only in exceptionally well-preserved material and ordinarily thin sections are required for their study. Unfortunately, most of the discosorids are rather rare, and material adequate for study of the structures by thin section has been difficult to obtain. Happily the genera represented by adequate material typify several of the families, and comprise a reasonable series of samples within the order. In the light of thin sections, it has been possible to interpret a number of opaque sections in which the bullette and its two layers and the vinculum can sometimes be differentiated from the rest of the ring, though structures in the free part of the ring cannot usually be interpreted with certainty. Of such importance are these structures that they are discussed in detail here in direct relationship to the genera and species where they have been observed.

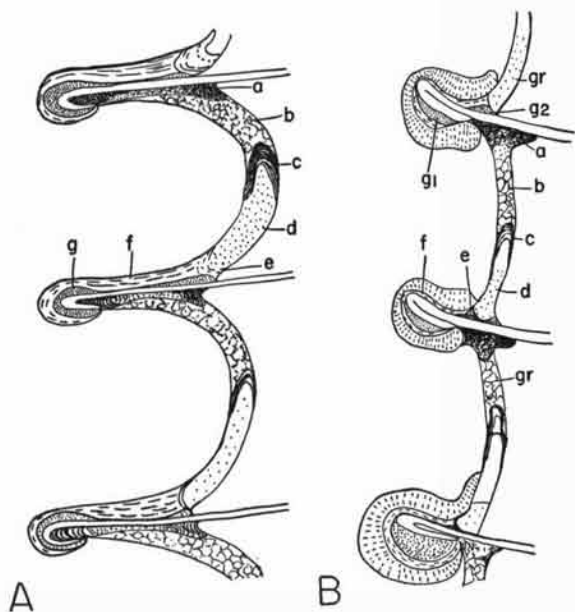


FIGURE 4. Dorsal wall of siphuncle of *Ruedemannoceras boycii* (A) and *Westonoceras* sp. (B), showing differentiation of structures within the connecting ring somewhat diagrammatically.

Explanation.—*a*, vinculum; *b*, granular zone; *c*, first amorphous band; *d*, chitinoid zone; *e*, second amorphous band; *f*, outer zone of bullette; *g*, inner zone of bullette, united in *Ruedemannoceras*, divided into two parts (*g1* and *g2*) in *Westonoceras*; *gr*, granular zone.

CONNECTING-RING STRUCTURES IN RUEDEMANNOCERAS BOYCII

Pl. 1; Pl. 5; fig. 7; text-figs. 4A, 5, 7A

Two thin sections are available for study. The first, through the apical portion of a fairly large individual, discussed in detail under description of the species, is worthy of note here for only two features. First, toward the shell apex the siphuncle segments approach and actually attain the form of siphuncular bulbs, previously known only in the Plectronoceratidae (FLOWER, 1952). Second, the connecting rings are thick but fail to show any differentiation of structure; even the bullette is not differentiated and faint traces of lamellae parallel to surfaces of the rings are the only features evident here (Pl. 2, figs. 9, 10; and text-figs. 12, 13).

The adult stage (Pl. 1; Pl. 5, Fig. 7; text-figs. 4A, 5, 7A) can be studied from a thin section with a mean height of 21 mm. near mid-length. It includes 12 segments of the siphuncle, those at the ends being somewhat incomplete. Segments average 2 mm. long, and increase in height from 3 to 3.8 mm. at the septal foramen and from 5 to 6 mm. at the point of greatest expansion in the camerae. Expansion of the segment in the camerae is always somewhat more pronounced on the dorsum than on the venter, and dorsally the apical end of the ring is very broadly adnate to the free part of the septum. The ring is also markedly thicker on the dorsal than on the ventral side, and it is there that its structures are most sharply differentiated.

The septal necks are strongly recurved, the brim

slightly more than twice the length of the neck, narrowly free, and nowhere in contact with the transverse part of the septum. The thickness of the ring causes its outer side to lie broadly in contact with the adapical side of the septum beyond the tip of the neck, and its adapical end is adnate on the anterior side of the next adapical septum for a distance slightly greater than the brim ventrally, and 2.5 times the brim dorsally.

It is on the dorsal side that the necks are thickest and their structure is best exhibited. Beyond the tip of the septal neck lies the vinculum. Its inner and outer corners are most readily seen, consisting of conspicuous dense, medium gray amorphous calcareous material, recalling that of the eyelet in the endoceroids. The region between shows very fine granular material, relatively translucent in thin section. This grades into the outer amorphous spots, clearly without a natural boundary between them. The apical side of the vinculum is faintly concave, receiving the free part of the connecting ring. Material of the vinculum penetrates the cavity between the recurved brim and the free part of the septum.

Slightly less than half of the free part of the connecting ring belongs to the granular zone. This consists of definitely granular material, probably calcite, which is relatively light in thin section, as it transmits light more readily than any other part. Just anterior to the middle of the segment, the granular zone gives way to the first amorphous band, composed of material like that in the two extremities of the vinculum. The band is curved as seen in section, the anterior side strongly convex, the adapical side strongly concave. The remainder of the ring is composed of translucent yellowish material, containing scattered dark granules which may be different material, or might originally have been fine punctae. The whole appearance of the material here is so reminiscent of chitin that it is named the chitinoid zone. The temptation to identify the material as chitin is strong, but in view of the replacement which has affected even the best specimens, this is regarded as unsafe. In this connection it is interesting to note that TEICHERT (1933, p. 124,) suspected chitinous composition for the connecting rings of actinoceroids, in which *Westonoceras* was then included.

At the point where the adapical end of the ring first comes to join the anterior surface of the next adapical septum, the chitinoid zone is terminated by a second amorphous band. It is curved, like the first, but in the opposite direction, so that the two bands surround the chitinoid zone like two parentheses.

The ring continues along the septum to the very tip of the brim. It is differentiated into an inner zone (actually, as noted above, morphologically the outer zone, but here forming the inner of two concentric structures) of dense amorphous material. On the dorsum, the inner zone is fairly uniform in thickness around the recurved neck, but thins along the anterior side of the septum, thickening again slightly as the second amorphous band is approached.

The two adapical zones together compose the bullette. STRAND (1933) first proposed this term for inflations, consisting supposedly of annular deposits within the siph-

uncle. True swelling of this part of the connecting ring is not apparent in *Ruedemannoceras*, but is developed uniformly in the Cyrtogomphoceratidae, Phragmoceratidae, and Westonoceratidae. Homologies are evident, so much so that it seems proper to apply the term bullettes to these two apical layers of the connecting ring throughout the discosorids, whether they are swollen or not.

On the ventral side the ring is thinner and expansion of the siphuncle segment is less marked. The bullettes are evident here, though they are thinner as they are traced around the recurved septal neck. The anterior end of the bullette is swollen into a buttress-like structure, where the free part of the ring joins the anterior surface of the septum.

The free part of the ring shows poor differentiation, and indeed, is differentiated from calcite within the camerae only with difficulty. The simplicity here has probably been increased by replacement of original structures, but similar simplicity in *Westonoceras* suggests that it is real and original to a very considerable extent. The anterior end of the ring is developed into a vinculum, though one smaller and less easily discerned than that on the dorsum.

The section shows considerable variation of the features described above from segment to segment. To a very large extent this is due to the thickness of the section. At the anterior end the section is thinner than at the apical end. The features of the connecting ring tend to be obscured and may disappear entirely beyond a certain critical thickness. Organic structures tend to become faint in sections that are too thin, and instead, details of crystallization, quite obviously secondary, tend to appear. The same critical thickness applies to many other organic structures. We have found that it applies also to the rings of endoceroids; a section of *Actinoceras* showing fine perispatial deposits (TEICHERT, 1933) failed to show the structure at all when ground slightly thinner.

As the structures are traced from segment to segment, it becomes evident that replacement has played some role in the variable expression of the structures. The two layers of the bullette are usually well differentiated but there is wider variation in expression and clarity of the structures in the free part of the ring (granular zone, chitinoid zone, and two amorphous bands). The second amorphous band remains more distinct than the others, forming the anterior boundary of the bullette. It is believed that preservation phenomena are not altogether adequate to explain the variations in other structures. In part, there may be ontogenetic progression from one segment to another, as is evidently true of the structures in *Faberoceras*, as shown in the following pages. However, it is strongly suspected that radial differentiation in the connecting ring exists, though the present thin sections, few in number and consisting largely of vertical or nearly vertical sections, are insufficient to show its details. Where the pattern differs from that described above, the first amorphous band and the chitinoid zone may be faint, unrecognizable, or different in proportions. It may be that if the ring could be etched out and its surface studied that one would find the chit-

inoid zone to be a special region on its surface which is surrounded by a ring of amorphous material. Where it is most fully developed, a section through it will show that it is bounded at either end by amorphous bands, which might tend to join where the section is tangential. If the chitinoid zone is, then, a lenslike structure in a setting of amorphous material, a section too far toward either side would fail to show the structure at all. Probably the pattern is not as simple as this. Clearly, there is radial differentiation of structures in the free part of the ring. Only with more numerous thin sections of well-preserved specimens can the details of variable distribution be explained properly. TEICHERT & GLENISTER (1953, pl. 6, fig. 11,) figure a linear median structure of the siphuncle of *Hecatoceras longiquum*, which also suggests radial differentiation of the connecting ring.

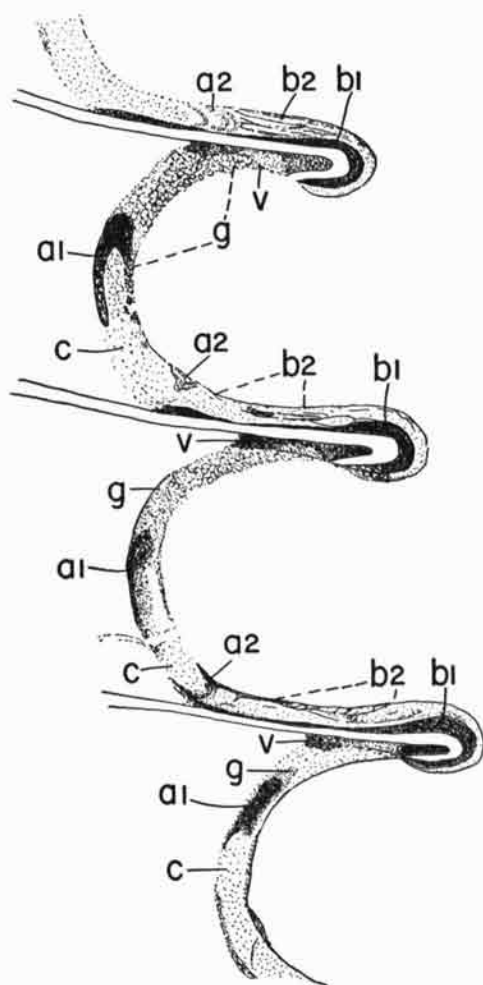


FIGURE 5. *Ruedemannoceras boycii*, dorsal wall of siphuncle showing variation of extent and expression of the various parts.

Explanation.—Based on the basal portion of the section shown in Pl. 1. *v*, vinculum; *g*, granular zone; *a1*, first amorphous band; *c*, chitinoid zone; *a2*, second amorphous band; *b1*, inner zone of bullette; *b2*, outer zone of bullette.

CONNECTING-RING STRUCTURES IN WESTONOCERAS

Pl. 10, fig. 5; Pl. 11, fig. 1; Pl. 12, text-fig. 4A, 6

The following observations are based on a single section of *Westonoceras* sp., consisting of a small portion of phragmocone from Baffin Island. The origin is not known more precisely. The specimen is one of a handful apparently picked up loose on the shore, as the surface shows evidence of being water-worn. The entire section contains 7 segments of the siphuncle in a length of 19 mm.; they are subquadrate in vertical section and quite typical of the genus in form. Necks are short, recumbent, and the brim is twice as long on the dorsum as on the venter. On the ventral side parietal deposits are complete and their outer margin between the septa appears as a thin definite line which was at first mistaken for the whole of the connecting ring. Closer study shows that the ring is thicker, of granular calcite, and its outer surface can be differentiated from inorganic calcite in the camerae only with difficulty. Fine textural differences exist, which in this section can be seen slightly more clearly when the specimen is examined while being rotated in polarized light. The vinculum is not differentiated. The bullette is inflated, and its inner and outer layers can be distinguished. There is not the usual sharp change in texture from the outer layer of the bullette to the remainder of the ring.

The anterior part of the section shows a central tube lying free within the matrix of the siphuncle. The dorsal wall shows much thicker rings. The vinculum and the two layers of the bullette are clear throughout, and the second amorphous zone is generally present and clearly differentiated. Differentiation within the free part of the ring is variable. The bullettes are surrounded by parietal deposits more extensive adapically than adorally, as usual. In one segment, an isolated mass of such deposit in the middle of the connecting ring suggests that deposits grow more laterally from the ventral side than anteriorly from their inception at the foramen on the dorsum as in the *Pseudorthoceratinae* (FLOWER, 1939).

Details of the ring (Pl. 11, fig. 1; Pl. 12; and text-fig. 6) are variable. The basal segment shows a small but well-defined vinculum, on the adapical side of which the granular zone extends for about half the length of the segment. There follows a zone of yellow and white calcite, the white apparently being coarser calcite replacing the original structure which is regarded as representing the first amorphous band. Apical of it there is yellowish calcite, less fine-grained than the typical chitinoid zone, of which it is suggestive in color and position. The apex of the ring and bullette are missing.

The second segment shows clearly a vinculum, the dense opaque material darkest at the inner edge and near the outer ends, the whole contrasting very sharply with the light coarse granular calcite which makes up most of the free part of the segment. Material is darker on the outer (cameral) surface, and there it is darkest near its apical end. A short distance before meeting the apical septum, the granular zone gives way to some yellowish calcite which may represent the chitinoid zone, from which the second amorphous band can be distinguished, though not as clearly as usual. The bullette shows the inner band on the apical surface of the brim, the outer band continues from over its surface around the bent neck to its anterior side, and only the thinnest trace of the anterior division of the inner band is seen near the second amorphous band. Outside the ring on the anterior face of the first complete septum is a mass of botryoidal yellow calcite with radial and fainter concentric structure. Over it is dark calcite, apparently containing inorganic impurities and contrasting with the clearer calcite making up most of the cavity of the camera. Whether this mass (and there are commonly similar ones in this position throughout the phragmocone, though decreasing in size as traced adorally through a series of camerae) is organic or not is uncertain. In texture they resemble cameral deposits, and their tendency to enlarge in apical camerae again suggests this interpretation.

The third ring shows a vinculum with inner and outer corners darkest and densest, the middle made up of a mass of fine-grained yellow calcite, its structure obscurely botryoidal, and the surface extends adapically convexly. Usually this surface of the vinculum is concave. Beyond this mass is a clear granular zone which is rather short, terminated adapically by light yellow calcite, the rounded surfaces and traces of radial and concentric structure of which suggest botryoidal growth. As traced adapically, it gives way to material similar in color but of coarser texture, and is followed by yellow material with small dark granules typical of the chitinoid zone. The second amorphous band is obscure. The bullette shows the usual clear differentiation of the main mass of the inner layer and a small isolated portion on the anterior side. The outer band is lamellar and fairly uniform in thickness.

The next ring shows the vinculum with dark opaque gray material at its inner corner, with similar but less distinct material at its outer corner, the middle of fine-grained yellow calcite with curving concentric and faint radial lines suggesting botryoidal growth. This material extends adapically for some distance except for a small thin band of granular material close to the inner (siphonal) surface of the ring. Both give way to a structure showing curved growth surfaces of alternate light yellow

EXPLANATION OF PLATE 1

RUEDEMANNOCERATIDAE—*Ruedemannoceras*

Ruedemannoceras boycii (WHITFIELD), from *Maclurites* ledges, middle Chazyan (Ordovician), at type section of Chazyan southwest of Chazy, N.Y.; specimen in collection of the writer. (Same specimen as illustrated on Pl. 5, fig. 7).—Portion of a vertical longitudinal thin section, dorsum at left showing detailed structure of siphuncle, $\times 25$. The lower three segments on the dorsum show differentiation of vinculum, granular and

chitinoid zones, two amorphous bands, and the two layers of the bullette, and are unretouched. The venter, ground below the critical thickness, shows the structures rather poorly, and they have been slightly retouched. Note greater expansion of segments on dorsum, greater thickness of ring, longer area of adnation and brims.



FLOWER & TEICHERT—Order Discosorida (Cephalopoda)



and opaque dark gray material, suggesting the texture of the first amorphous band. Beyond it is a short area of white coarse granular calcite. It gives way with a sharp contact to yellow material containing fine dark granules, evidently the chitinous zone. The second amorphous band is again faint, and the two layers of the bullette are similar to those described in preceding discussion.

The last connecting ring, only the apical part of which is shown in Figure 6, shows a normal development of the bullette. There is prominent dark gray opaque material, the second amorphous band, bounding its anterior end. The remainder of the ring, not shown, is of rather coarse-grained white calcite, evidently rather coarsely replaced. Such calcite continues into all of the receptacle except the dense fine-grained inner corner.

These variations in structure are described in detail, and illustrated in Figure 6, as photography fails to show the color differences, and the results in general are not as clear as may be desired. The variation found here from segment to segment supports the suggestion that these structures both suffer from phenomena of replacement, and also show some individual variation, suggesting that these regions are structures varying in distribution around the periphery of the dorsal side of the ring in manner not yet understood.

CONNECTING-RING STRUCTURES IN FABEROCERAS

Pl. 11, fig. 2; Pl. 16-23; text-fig. 7C-K, 8, 9

The following observations are based upon a suite of specimens collected by R. H. FLOWER, all from the Leipers beds (Upper Ordovician) of the Cumberland River valley near Rowena, Kentucky, at localities now covered by the waters impounded by the Wolf Creek dam. Several species of *Faberoceras* are clearly involved. Most sections were made from relatively small portions of phragmocones and for the most part no attempt was made to identify the material specifically prior to making thin sections. Because several species are involved, and because the long slender phragmocones supply a series of segments showing considerable ontogenetic variation, these sections show more variation in structure than is exhibited by the more restricted material on which the observations of previously discussed genera were based.

Likewise, there is also greater variation in phenomena of replacement among the *Faberoceras* sections. As in *Ruedemannoceras* and *Westonoceras*, radial variation is a possible explanation of some of the variations exhibited.

Comparison with *Ruedemannoceras* and *Westonoceras*, and some of the variations noted in *Faberoceras*, are shown in Figure 7. The more significant features of *Faberoceras* may be summarized as follows.

The marked distal thickening of the ring on the dorsal side of the siphuncle and clearest differentiation there of parts of the ring do not apply to *Faberoceras*. Commonly, the ring is slightly thicker ventrally than dorsally. The vinculum is broad on both dorsum and venter, ranging from a condition in which it is continuous but shallow and strongly concave for reception of the free part of the ring to one in which it is divided into separate inner and outer portions. In general, the anterior end of the ring is more broadly attached to the septum on the dorsum than on the venter. At the adapical end of the ring is more broadly adnate to the adapical septum on the venter than dorsum. On the dorsum the anterior extension of the bullette is short, in many specimens extremely short (Fig. 7C), but on the venter its extension may be appreciable along the anterior face of the septum. The condition of the inner zone of the bullette is particularly different; it is scarcely developed on the anterior side of the septum on the dorsum, but may be well extended along it on the venter. Further, it may extend out from the siphuncle along the anterior face of the septum for some distance, to such an extent that its identity with the connecting ring is not at once apparent. Such progressive growth of the inner layer of the bullette is progressive during ontogeny, and is seen as a progressive development from early to late stages wherever any appreciable series of segments can be studied from a single thin section (Pl. 21, 22). It is evident also that a similar progressive increase of the anterior extension of the bullette reaches forward on the dorsal side, but the condition on the dorsum in any one segment is one which would be approached on the venter only in a segment from a much earlier part of the siphuncle. It is a curious fact that the greater thickness of the ring on the venter and the greater development of the anterior extension of the bullette are characteristic of this genus. That both trends are progressive with ontogeny indicates that the

EXPLANATION OF PLATE 2

RUEDEMANNOCERATIDAE—*Ruedemannoceras*

FIGURE

1. *Ruedemannoceras boycii* (WHITFIELD), specimen from *Mac-lurites* ledges, middle Chazyan (Ordovician), at type section southwest of Chazy, N.Y. Nearly vertical section, slightly oblique to longitudinal median plane, showing cameral deposits as white calcite against black matrix, $\times 1$.
- 2-4, 9, 10. *Ruedemannoceras boycii* (WHITFIELD), phragmocone from same horizon and locality as Fig. 1.—2, Ventral view, $\times 2$.—3, Vertical section from adoral part of specimen, $\times 2$, opposing anterior five camerae of Fig. 4.—4, Lateral view, venter at left, $\times 2$.—9, Siphuncle from same section, showing details of septal necks and thick but essentially homogeneous rings, $\times 15$.—10, Thin section, venter at left, adjoining Figs. 2 and 4 at adapical end, showing siphuncle from the probable second segment and transition from siphuncular

bulbs to normal cyrtocoanitic segments with thick flattened septa at transition, $\times 10$.

- 5-7. *Ruedemannoceras boycii* (WHITFIELD), an immature specimen from the upper Chazyan reef beds near Little Monty Bay, Lake Champlain, N.Y.—5, Ventral view, $\times 1.5$.—6, Septum at base of living chamber, $\times 1.5$.—7, Oblique lateral view, phragmocone sectioned exposing siphuncle, $\times 1.5$ (shown in greater enlargement on Pl. 3, fig. 4).
8. *Ruedemannoceras boycii* (WHITFIELD), portion of phragmocone, ground in two slightly intersecting planes, showing typical ephelic outline of siphuncle segments in opaque section, $\times 2$. A thin section (Pl. 1; Pl. 5, fig. 7) fits directly on the anterior end of this fragment.

All specimens in collection of the writer.

specialization of the ring is more advanced on the venter than the dorsum. Barring such differences as are directly related to the oblique position of the septa in relation to the axis of the siphuncle, the dorsal side shows features approaching those on the venter at a much earlier growth

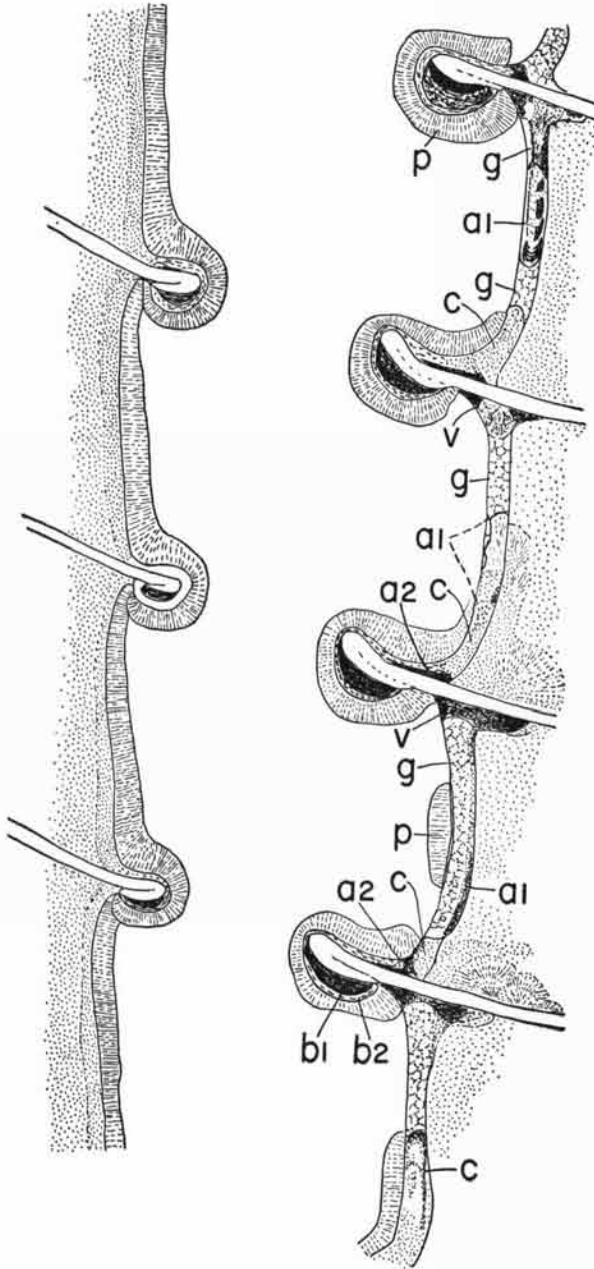


FIGURE 6. Siphuncle of *Westonoceras* sp., dorsum on right.

On the venter parietal deposits are mature, the rings are thick but show differentiation of only two layers of the bullette. On the dorsum, the differentiation within the ring is clear, but somewhat variable from segment to segment; parietal deposits are much less advanced.

EXPLANATION: *v*, vinculum; *g*, granular; *a1*, first amorphous band; *a2*, second amorphous band; *c*, chitinoid zone; *b1*, inner layer of bullette, here divided; *b2*, outer layer of bullette; *p*, parietal deposits.

stage. As practical difficulties attend the preparation of thin sections representing any appreciable length of the phragmocone, this evident fact permits one to use the dorsal side of the siphuncle as a basis for deductions as to the nature of the earlier stages on the venter. This has been found useful and reliable in tracing the progression of modification of the vinculum and bullette. It is less reliable for the structures within the free part of the ring, in which, as noted under discussion of *Ruedemannoceras*, there is reason to suspect more complex radial relationships. FLOWER (1939) has pointed out the curious reversal of ontogenetic stages found between the fixed and alterable parts in cephalopods. The alterable parts, exemplified by cameral and siphonal deposits, range from immature to mature when traced backward from the youngest to oldest camerae. The reverse is true of the fixed parts, which are structures of the septa and connecting ring. It has already been noted that the bullettes attain their largest size in late camerae and may, indeed, be vestigial in the earliest stages. It is not surprising to find increased specialization of structures within the ring behaving in the same general way. However, it is an inevitable conclusion from present observations that the ring shows a more advanced condition on the venter than the dorsum in *Faberocheras*. This is an amazing fact, for which no explanation can be offered at present. It is the more surprising when one considers that all indications suggest that *Ruedemannoceras* and *Westonoceras* show a directly reversed relationship; the ring in these genera being simple ventrally and specialized dorsally. The logical explanation, namely, a reversal of curvature and misinterpretation of the dorsum and venter in these forms, lacks support from any of the other structures on which criteria of orientation can be based, e.g., hyponomic sinus of the aperture and cameral deposits.

Figure 7C shows a relatively generalized condition of *Faberocheras*, as observed on the dorsal side of the siphuncle, which, as previously noted, is typically more primitive than the condition found on the venter in the same segment. Certainly it is here more comparable with the conditions observed in *Ruedemannoceras* and *Westonoceras* than those found commonly in later growth stages on the dorsum or the same growth stage on the venter. The vinculum is broad and shallow, but still a single structure as seen in thin section. The granular zone and the first amorphous band separating it from a chitinoid zone are also fairly typical. As in other genera, these three structures are variable in clarity and expression, details of which are discussed later. The bullette is here small and the inner zone confined exclusively to the apical surface of the recurved brim.

Figures 7D, 7E and 7F show variations in the vinculum, 7D showing a condition in which the vinculum is apparently greatly extended adapically along the free part of the ring, based upon the apical segment shown in Figure 8. That material here consists of masses of tiny acicular crystals arranged in imperfectly concentric structures, evidently botryoidal growths, suggests that this phenomenon may be one of replacement rather than an original structure.

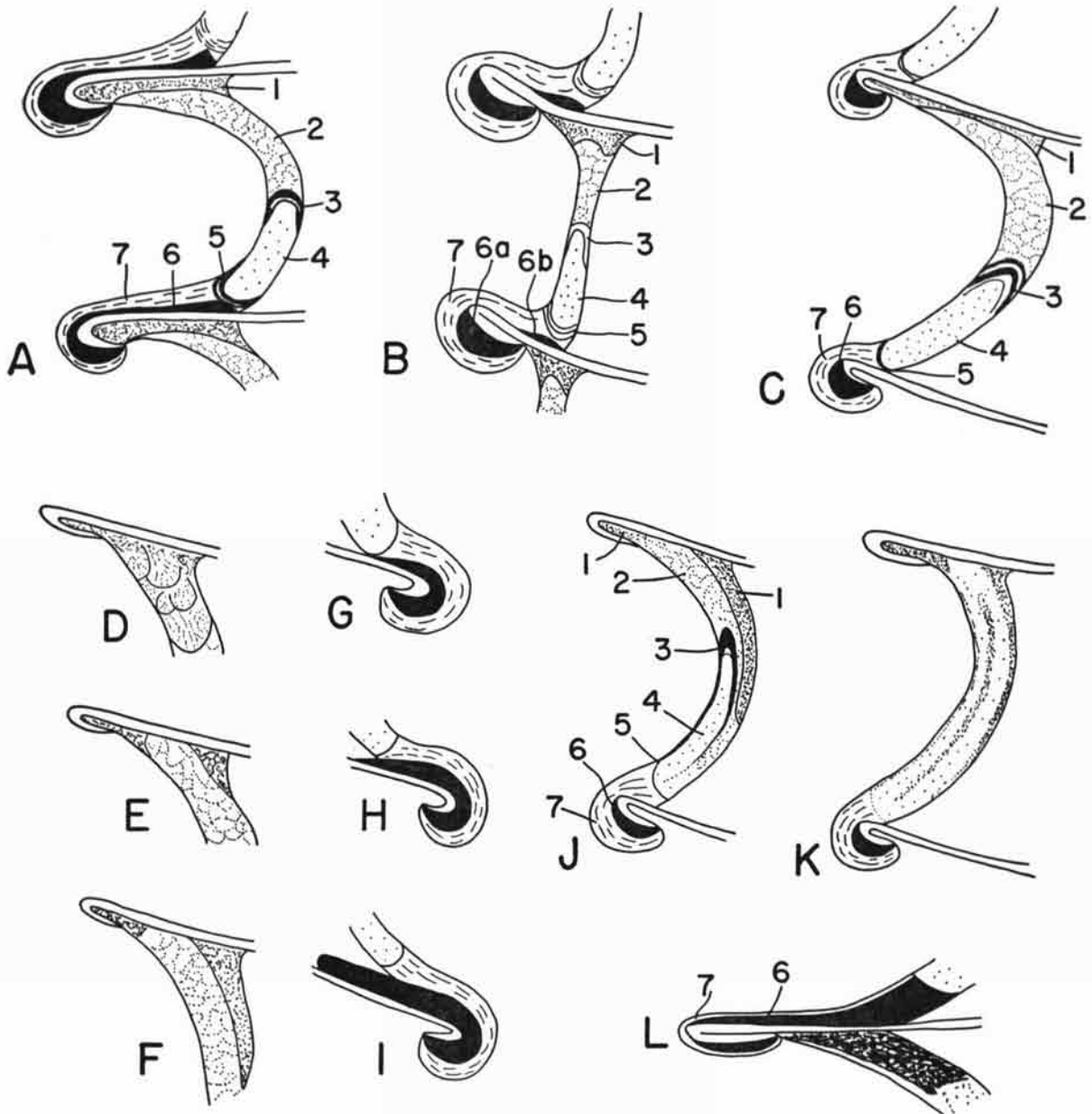


FIGURE 7. Structures within discosorid connecting rings.

A. Ruedemannoceras boycii, showing regular zonation of (1) vinculum, (2) granular zone, (3) first amorphous band, (4) chitinous zone, (5) second amorphous band, (6) inner, and (7) outer layer of bullette.

B. Westonoceras sp., showing same features as in *A*, the essential modifications being inflation of the bullette and differentiation of the inner layer into (6a) small anterior portion and (6b) large apical portion.

C. Faberoceras sp. Generalization of dorsal wall of siphuncle in relatively early stage, showing small shallow vinculum, zonation of free part of ring comparable to that in *A* and *B*, short area of adnation and small bullette, with inner zone confined to the apical part.

D-F. Variations in the vinculum of *Faberoceras*. *D*. Probable replacement of vinculum and part of granular zone, in which fibrous crystalline material extends appreciably adapically. *E*. Complete division of vinculum into inner and outer parts by the granular zone. *F*. Prolongation of outer part of vinculum along length of granular zone.

G-I. Variation in bullette on ventral side of *Faberoceras*. *G*. Inner zone of bullette prolonged over anterior surface of septum. *H*. More marked development of anterior extending over inner zone of bullette. *I*. Inner zone markedly thickened, and extending along anterior face of septum outside of the remainder of connecting ring.

J. Diagrammatic representation of section showing outer part of vinculum extending along the outside of ring with first amorphous band extended as a dark line or band on inside of ring, and a second band in its center.

K. Banded condition of connecting ring, observed in late stages of *Faberoceras* and in *Alpenoceras*. The inner and central dark bands are derived from the first amorphous band, its middle portion suppressed; outer band derived from further prolongation of the outer part of the vinculum. The bullette retains its identity.

L. Recumbent septal neck and portion of connecting ring from *Discosorus*, in which inner and outer parts of bullette are recognizably differentiated from free part of ring and with indications of the vinculum.

Figure 7E shows the granular zone of the ring in contact with the septum, and as a result, the vinculum is divided into inner and outer parts. In Figure 7F these parts have become somewhat specialized, the inner part remaining small, the outer part being extended appreciably apicad along the outside of the granular zone. Figures 7E and 7F show two progressive stages of a series which is logically initiated by the conditions shown in the anterior end of Figure 7C.

Again, Figure 7C shows the beginning of a series exemplifying the progressive advance of the inner layer of the bullette. In 7C this structure is confined to the adapical side of the septal neck, a condition that is common on the dorsum. In Figure 7G the inner layer is shown to have progressed so that it is found on the anterior surface of the septum, though its extent there is small. This figure is taken from a section through the ventral side of the siphuncle, but it is approached closely also in sections of the dorsal wall taken at extremely late growth stages. In Figure 7I the anterior end of the whole bullette is slightly more extended forward, but growth of the inner layer has outstripped that of the outer layer, and it extends very slightly along the septum beyond the point at which the main part of the ring curves forward and becomes free. Figure 7H shows the extreme development of this trend, observable in the anterior end of the section shown on Plate 22 and (though less strikingly) on Plate 21. It is shown clearly also in the anterior end of the specimen illustrated in Plate 11, figure 2. Here the inner layer of the bullette forms a thick band which extends some distance along the anterior face of the septum, so that it appears at a casual glance to be a structure quite apart from the connecting ring proper.

Many sections of *Faberocheras* show little or nothing of the structure of the free part of the ring, though the ends (vinculum and two layers of the bullette) are almost invariably differentiated clearly. Such a condition is shown in Plate 20, figure 2. Again, opaque sections and some thin sections as well, show alternating light and dark bands parallel to the curved surfaces of the ring. It is evident that they are a modification of zones already noted in *Ruedemannoceras* and *Westonoceras*, and shown also, though only rarely, in *Faberocheras*. One way in which this banding may have been developed is suggested by Figures 7J and 7K. In Figure 7J, based on a section shown less diagrammatically in Figure 8, the outer part of the vinculum is extended along the outside of the granular zone, which in turn, is extended along the outside of a structure terminated adorally by the obvious homologue of the first amorphous band, and apparently including also the chitinoid zone. The bullette is typical, short, because it is here seen on the dorsal side of the siphuncle. Its anterior margin is sharp, representing the second amorphous band, but this band here has no appreciable thickness, as in sections discussed previously. The extension of this development (Figure 7K) shows a dark outer band on the ring, a possible ultimate extension of the outer part of the vinculum. The middle and inner dark bands appear to be derived from the two linear extensions of the first amorphous band, the median part of which is suppressed. As in the preceding section, the bullette is simple and terminated anteriorly by a sharp curved band which apparently represents the second amorphous band.

The interpretation just given is presented in tentative terms because another ontogenetic succession shown in Figure 9, suggests an alternate method of development in which the chitinoid zone becomes reduced to a short section close to the juncture of the ring with the anterior face of the adapical septum; dense dark bands on the outer and inner surfaces of the ring may involve in part structures of the first amorphous band, but are so continuous with the inner and outer parts of the vinculum that an origin from that structure is suggested. It may well be that the amorphous materials comprising the vinculum and two amorphous bands are more closely interrelated than observation of previous sections would lead one to believe.

The variation of the individual sections of *Faberocheras* here illustrated, is best discussed in terms of the actual figures and sections. Plate 20, figure 2, shows a series of segments in which the septal necks are well differentiated and replaced with coarse calcite, which is relatively transparent in thin sections. The brims are narrowly free, being long dorsally and short ventrally. The dark bands seen on the anterior sides of the septa are composed of fine-grained yellowish material rather suggestive of the chitinoid zone. The vinculum is distinct and divided completely by the free part of the ring even on the dorsal side. The bullette on the dorsum is sharply terminated anteriorly and the inner layer is confined to the adapical surface of the recurved brim. On the venter the differentiation of the two layers is less evident and the anterior extension of the whole bullette is appreciably greater. The section is off center at the anterior end and becomes progressively more excentric when traced to its apical end. The free part of the ring is uniformly represented by coarse relatively transparent calcite; evidently this effect is the result of replacement.

A considerable series of segments from one continuous section is shown in Plate 21. The section is divided into two photographs which adjoin, the anterior end of the section being shown on the right. This section is exceptional in that the bullettes are markedly larger on the dorsum than on the venter, but they are typical in showing the anterior extension of the inner layer of the bullette developed only on the venter and clearly advanced in this respect only in the extreme anterior end of the section. The vinculum and bullettes are well differentiated from the remainder of the segment, but differentiation within the remainder of the ring is not indicated at all in the early segments and is variable and somewhat obscure in the anterior ones. Anterior segments suggest prolongation of the outer part of the vinculum along the outside of the ring on the dorsal side of the siphuncle. In the extreme lower right a suggestion of the amorphous band is seen and the second segment above shows a relatively clear short chitinoid zone on the venter, terminated anteriorly by amorphous material. This ring is broken in the middle, the anterior part representing the granular zone. The penultimate ring on the dorsal side shows indication of irregular and rather reticular amorphous material occupying the greater part of the length of the free part of the ring. The one before it shows a short granular zone (the amorphous band) and a rather long chitinoid zone, in the median part of which there appears to be a faint dark band. Possibly the structure here is analogous to that shown in Figure 7J.

One section, of which only a small part is reproduced (Pl. 19, figs. 2, 3), is unique in that within the bullette the tail of a tiny trilobite is embedded. The section is well off center with reference to the axis of the siphuncle, so that the bullette here is seen crossing the cavity of the siphuncle. Inner and outer zones are poorly differentiated. The tail lies close to the recurved inner portion of the ventral septal neck, shown on the left of the figure. It should be noted that the bullette is here covered completely by a parietal deposit, slightly yellowish in thin section, showing the usual vertical lamellae and fainter lines parallel to its surface. Clarity of these structures was sacrificed in the photographs, developed to show the trilobite pygidium in the ring with maximum clarity. The presence of parietal deposits surrounding the bullettes is a significant indication that the occurrence is a natural one, rather than denoting introduction of the tail into a cavity in the cephalopod structures. Plainly, the trilobite fragment must have been embedded in the bullette at the time when the whole of the connecting ring was secreted, essentially contemporaneous with the secretion of the septum at its anterior end. It is not evident whether the tail was isolated, as it now appears to be, or whether the trilobite was complete, the remainder being lost because it lay outside the plane of the present section. Ordinarily parasitic organisms (particularly those having hard parts) may wander into any part of the host and the eggs of some Nematelminthes are provided with spines which facilitate this circuitous and involuntary travel. The idea that the trilobite might be a parasite of the cephalopod must probably be abandoned. Probably the trilobite tail entered the tissue through some perforation of the alimentary canal, wandered about, and finally was embedded in the bullette. It is tempting to conclude that the bullettes (for which no good function has been proposed) might have served to imbed and eliminate from the tissues such foreign objects as this; no other sections have shown similar bodies, however, and therefore the occurrence here described is probably exceptional and fortuitous.

The apical part of the same section (not illustrated by a photograph) exhibits some zonation in the free part of the ring and other features worthy of special note. The section is shown in Figure 8, which depicts the dorsal side only of three successive segments.

Septa are represented by light calcite throughout. A remarkable feature is the presence of bands of conchiolinous or chitinous material on the anterior faces of the septa. On the first septum, this band terminates near a spurlike development at the bend of the neck and then swings forward a short distance along the outside of the ring. A similar band on the second septum terminates before reaching the connecting ring. On the third segment the band reaches the ring and extends forward in a swollen bulbous process along its outer side. This structure may be an incipient cameral deposit. It can hardly be the homologue of the layer of conchiolin reported in *Nautilus*, which lies on the opposite side of the septum.

The apical ring shows a normal bullette in which replacement has obscured the two original layers. Its anterior termination is sharp; possibly replacement of the bullette, but not of the rest of the ring, has increased the sharpness of the distinction here. Before it lies a short

chitinous zone, terminated by a rather thick first amorphous band. In front of it, and continuing adapically a little way on its outer side, is the granular zone. The vinculum shows typical inner and outer parts but in the central portion are some fine masses of acicular crystals; while the vinculum appears to be of unusual length, it may be that part of the granular zone is replaced, as suggested in Figure 7D.

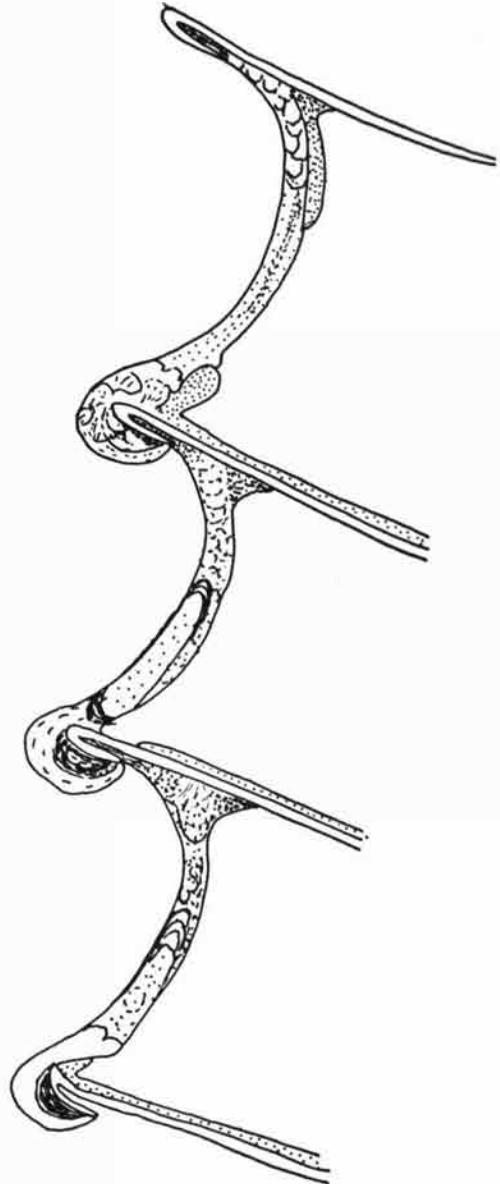


FIGURE 8. Portion of dorsal wall of three segments of the siphuncle of *Faberoceeras* sp.

The drawing shows the apical part of a section, the adoral portion of which is shown in Plate 19, figure 2. Parts of the ring are identifiable here with unusual clarity. Segments appear to show a progression adorally from a typical development of the granular zone, first amorphous band, and chitinous zone to a banded structure. Chitinous material on the anterior faces of the septa is an exceptional feature, revealed poorly or not at all in other sections.

The second segment shows the two layers of the bullette, the inner one being developed only on the adapical surface of the brim. The second amorphous band is clear, with a chitinoid zone in front of it unusually long for *Faberoceras*. Adorally it is terminated by the first amorphous band, which has the inner limb extended along the inner surface of the ring apparently to the second amorphous band. Its outer limb is nearly as long, and separates the chitinoid zone within from an extension of the granular zone on the outer side of the ring. The granular zone occupies the whole width of the



FIGURE 9. Portion of ventral siphuncle wall of five segments of *Faberoceras* sp.

The illustrated wall is the same as that shown in Plate 19, figure 1, and Plate 18, figure 2. Here the progression suggests an alternate derivation of the banded condition involving possible extension of both the inner and outer part of the vinculum, joining the modified first and second amorphous bands.

ring in front of the first amorphous band. Its anterior end is obscured by fine acicular material in imperfectly radial masses, evidently a botryoidal structure possibly due to replacement. The fine dark inner and outer parts of the vinculum are distinct, the inner one very small and the outer one larger and extended along the face of the septum into a small buttress. The third segment shows extensive replacement in the bullette, the second amorphous band being lost. The main part of the ring displays a banded structure, with a thin sharp dark inner surface and a median dark band separating two lighter areas on either side. Possibly, as suggested in Figures 7J-7K, the banding has developed here by suppression of the median part of the first amorphous band; if so, the inner light zone mainly represents the chitinoid zone and the outer one the extension of the granular zone seen in the preceding segment.

The anterior end of the ring shows no fine structure, because it was ground below the critical thickness. There is a suggestion there of a considerable extension of the vinculum, but this structure may be due to replacement such as is suggested in Figure 7D. The inner part of the vinculum is composed of relatively opaque amorphous material, which is practically confined to the region that is nearly enclosed by the very long brim and free part of the septum. The outer part, similar texturally, is prolonged along the outer side of the free part of the ring, extending about one-third of the distance toward the preceding septum.

This section is of particular significance, as it suggests one way in which the banded type of ring could develop from the type of structure which characterizes the older and more primitive *Ruedemannoceras* and *Westonoceras*, the nature of this change being shown diagrammatically in Figures 7J and 7K. As is indicated in discussion of the next section, which suggests a slightly different mode of development, neither explanation seems to be conclusive.

Another section (Pl. 19, fig. 1; adapical part enlarged, Pl. 18, fig. 2) shows somewhat dissimilar differentiation within the ring. This is apparent only in the basal part of the section and only on the ventral side. The structures are indicated more clearly in Figure 9. The apical connecting ring is incomplete apically, the bullette and the second amorphous band being lost. Its apical part shows a clear band which is evidently the chitinoid zone. It is short, and directly anterior to it are two short dark bands on the inner and outer sides of the ring, which suggest the linear extensions of the first amorphous band, the curved central part of which is not evident. Material between the dark bands is uniform with that of the granular zone, which here occupies most of the length of the ring. The inner dark band becomes thin as it is traced forward, but appears to continue and join the very small inner part of the vinculum. The second segment also shows a very short chitinoid zone (without definite boundary between it and the granular zone) in the middle of the ring. On the outer and inner surfaces are dense opaque bands with granular material between them. They are thick adapically and thin adorally. The inner band is definitely continued forward to join the inner part of the vinculum. The outer band seems also to join the outer part of the vinculum, but is rather ir-

regular and the connection is less definite. The outer part of the vinculum is thickened into a buttress-like structure, different in composition from the remainder. It is believed that the textural difference is a replacement phenomenon. The third segment shows a thin second amorphous band and very short chitinous zone, which is sharply set off from the material in adoral adjacent parts. In front of it the ring is banded, showing a thick dark inner band which continues to the inner part of the vinculum, a dark median band which does not extend to the extreme anterior end, and a thinner band which continues to the outer part of the vinculum. Granular material lies between these dark bands. The fourth segment shows a thicker and more prominent second amorphous band, the chitinous zone being gone and the free part of the ring composed mainly of granular material. There is a thick dark inner band which continues to the inner part of the vinculum but no median band. The outer part of the ring is irregular and evidently incomplete. No clear outer band is evident. The outer part of the vinculum is small. The last segment, only part of which is shown in the figure, shows a sharp anterior termination of the bullette and a very thin second amorphous band. Farther forward, the ring shows a median dark band and thinner ones on the outer and inner surfaces. The bullettes seen in this section are typical of the genus, showing (from apical to adoral ends of the section) a progressive development of the inner zone of the bullette forward and out along the surface of the septum, such as has been shown diagrammatically in Figures 7G-7I.

Plate 11, figure 2, is of particular interest in that its apical end shows an essentially tangential section of the bullette, which is here marked by several dark longitudinal bands. It supplies additional evidence of radial differentiation of the structures of the ring already suspected from other evidence. Anterior segments show a remarkable and indeed exceptional thickening of the ring on the ventral side, with obscure banding and some mottling which varies from segment to segment along the length. The dark portions represent fine-grained amorphous material and the lighter ones coarser calcite of more granular texture. This section shows strikingly the forward and outward development of the inner zone of the bullette, but on the dorsum the inner zone is shorter, appearing to develop a buttress-like structure in the anterior segment, similar to that shown on Plate 21.

Opaque sections (Pl. 17, fig. 1-3; pl. 18, fig. 1) of specimens from the Leipers formation are notable in that the bullettes are typically represented by white calcite that contrasts strikingly with the gray material of the rest of the ring. Curiously, *Faberocheras elegans* of the Corryville beds shows no such differentiation (Pl. 23), although a suggestion of differentiation of inner and outer zones of the bullette is seen, variable and evidently altered somewhat by replacement.

CONNECTING-RING STRUCTURES IN DISCOSORUS

Pl. 29, fig. 1; Pl. 29, fig. 1; text-fig. 7L.

Specimens of *Discosorus* proved rather unsatisfactory for a detailed study of the connecting ring. All available material consisted of isolated siphuncles. Abrasion prior

to burial had removed substance of the connecting ring except parts protected by invagination of the siphuncle in the region of the septa. Secondly, the material was largely silicified, and silicification tends generally to obscure original structures of the connecting ring. One section (Pl. 29, fig. 1), though slightly off center, shows quite clearly the extremely long brims which are recurved and in contact with the free part of the septum, although, under the circumstances, it is hardly free. Beyond the tip of the brim there is a slight thickening of the ring, which appears in section as a dark wedge-shaped mass, that in texture recalls the inner part of the vinculum. Where the apical end of the ring approaches the septum, it appears as a thin translucent band, and between it and the septum is another dark wedge-shaped mass of amorphous material (Fig. 7L) that suggests the much extended anterior end of the inner layer of the bullette in *Faberocheras*. Around the strongly recurved part of the neck, the light area (probably representing the outer zone of the bullette) is present alone but on the adapical surface of the brim it is narrowly separated from the brim by amorphous dark material (probably the remainder of the inner part of the bullette). One segment shows inconclusive suggestion of an adapical termination of the vinculum in a part of the ring which is finely and rather irregularly granular.

The section suggests strongly that the vinculum and the two original layers of the bullette still exist in *Discosorus*, though the bullette is so thin that it can be recognized only by study of thin sections under rather high magnification. Also, the thickness of the ring is plainly much reduced in contrast to that shown by genera previously discussed.

Comparison with the opaque section of *Alpenoceras ulrichi* (Pl. 31, fig. 1) indicates that the rings are rather thick, at least in the early growth stages of that species. The thick rings, within which traces of longitudinal banding can be seen, are somewhat reminiscent of the banded rings noted in more advanced growth stages of *Faberocheras*. This is particularly evident in the two lower segments of the figure, but no inflation of the tip of the ring into a swollen bullette occurs. The anterior ends of the rings are extended outward into buttress-like structures with dark inner and outer tips lacking such banding as appears in the free part of the ring. The adapical ends of the rings differ slightly and variably in color from the free banded portion and are suggestive of the two layers of the bullettes, as in *Discosorus*. Particularly suggestive of the bullette is the top of the ring shown in the anterior segment on the ventral side (upper left of the figure). Since structures of the ring are commonly not evident in opaque sections, such faint indications as are found here seem the more significant and lead to the conclusion that *Alpenoceras* probably has the vinculum and bullette differentiated and the free part of the ring banded as in more advanced stages of *Faberocheras*. Of course, conclusive proof of knowledge of further details must await material available for study by thin sections.

SCHINDEWOLF (1942, pl. 36, fig. 1) has illustrated a thin section of *Alpenoceras eifelense* (SCHINDEWOLF) showing clear septal necks; the connecting rings can be seen also though only on the ventral side. His section is

illustrated at too low magnification to show structures of the rings, but there is a suggestion of a differentiated apical part of the ring, the bullette, where it is traced around the recurved septal neck.

CONNECTING-RING STRUCTURES IN PHRAGMOCERAS

Plates 42 and 43

Three thin sections made from specifically undetermined phragmocones of three specimens of *Phragmoceras* from the Silurian of Gotland, show camerae and siphuncle filled with calcite, alteration of original structures being variable but generally pronounced. The sections show septal necks generally recumbent with long brims, segments broadly subquadrate to obscurely heart-shaped in vertical section, and thick rings terminating in bullettes, which exhibit only faint indication of the inner and outer layers. The thick rings fail to show differentiation of structures in the free portion and their anterior end reveals no clear differentiation of the vinculum.

Section no. 1 (Pl. 42, figs. 1, 2) is from a relatively early portion of a phragmocone with five segments (fig. 2) occupying a length of 8 mm. They increase in size rapidly across the septal foramen and are broadly expanded in the camerae; the ring is broadly adnate at its anterior end on the dorsum and at its adapical end on the venter. Brims are much longer dorsally than ventrally. At high magnification (Pl. 42, fig. 1) the bullettes show indication of the original two layers, which partly have been lost through alteration. On the dorsum the free part of the ring is thick, the outer zone being bounded by dark material and the inner surface marked by a dense, still darker band, that is comparable to the interior of the ring of *Fabroceras*. The vinculum cannot be distinguished. On the venter differentiation of the two layers of the bullette is wanting. The bullette extends over the adoral surface of the septum, and can be seen to terminate in a sharply defined curve, concave adorally. This is similar in conformation to the second amorphous band observed in other genera, but it is here not sharply set off from the remainder of the bullette. The anterior part of the ring is evidently considerably replaced by rather coarse calcite similar to that in the camerae and

cavity of the siphuncle. Some difference is noted between the anterior and apical ends, the apical part having a narrow dark band that marks its inner surface. Otherwise no differentiation regarded as original and organic can be detected. The vinculum cannot be recognized. A septal neck from the anterior part of the section (Pl. 42, fig. 5) shows dark material of the neck outlined with white inorganic calcite, the form here being somewhat clearer than elsewhere.

Section no. 2 (Pl. 42, figs. 3, 4) shows segments much larger in proportion, from a relatively late part of the phragmocone. Three segments occur in a length of 14 mm. on the venter; the adoral segment expands from 6.5 (measured between septal necks rather than bullettes) to 10 mm. Inorganic calcite lines the camerae and lies against the outer wall of the siphuncle. Within the siphuncle there is irregular vesicular calcite, apparently inorganic. Plate 42, figure 3, shows the outline of the segments, thickness of the rings, and the bullettes, which are inflated only on the dorsal side. Plate 42, figure 4, is a further enlargement of the anterior septal neck on the dorsal side, showing the recumbent neck, the bullette, in which differentiation of inner and outer layers is still evident, and the anterior part of the ring below the septum. The free part of the ring anterior to the bullette is destroyed. In this section the free part of the ring exhibits a fainter lamellar structure parallel to its surface. At the anterior end calcite simulates the vinculum in form, but the structure is so replaced that it is impossible to say with certainty that the structure is organic and original.

A third section (Pl. 42, fig. 6; Pl. 43) shows a longer series of segments, of which the second has a maximum height of 4 mm., in the plane of the septum, and the last complete segment a height of 9.6 mm. Preservation is quite different here. The dorsal wall shows large bullettes almost completely confined to the adapical side of the recumbent brim. They merge anteriorly into the remainder of the ring without sharp differentiation of materials. The free part of the ring reveals obscure layering, and a thin dark band on its inner surface. Though the ring thickens slightly as it joins the anterior septum, no differentiation of the vinculum is visible. On the venter the brims are shorter and the bullette is inflated on adoral and adapical sides of the septum, showing faintly differen-

EXPLANATION OF PLATE 3

RUEDEMANNOCERATIDAE—*Ruedemannoceras*, *Franklinoceras*

FIGURES

1,2,4,6. *Ruedemannoceras boycii* (WHITFIELD).—1, specimen from middle Chazyan (Ordovician), from type section west of Chazy, N.Y. Horizontal section through a late growth stage, showing relatively narrow siphuncle segments with faint traces of bullettes, $\times 2.3$.—2, Details of siphuncle ($\times 6$) from section shown in Pl. 2, fig. 3.—4, Section from basal part of specimen shown in Pl. 2, fig. 7, illustrating preservation phase in which calcite fills the camerae and obscures the original rings, at left, showing early stages with flattening and thickening of septa, apical siphuncle segments approaching but not attaining the condition of siphuncular bulbs (apical end slightly retouched), $\times 4$.—6, Apical part of specimen shown in

Fig. 5 (retouched) indicating details of siphuncle and septa more clearly. Specimens illustrated in Figs. 4-6 are from reefs of the upper Chazyan, near Little Monty Bay, Lake Champlain, New York.

3,7. *Franklinoceras elongatum* FLOWER, n. sp., holotype, from middle Chazyan beds (Ordovician) at type section of Chazy, southwest of Chazy, N.Y.—3, Exterior of internal mold, lateral view, venter at right, $\times 1$.—7, Reverse side of same specimen showing outline of siphuncle, incompletely preserved and poorly differentiated in color (slightly retouched), $\times 1.2$.

All specimens in collection of the writer.



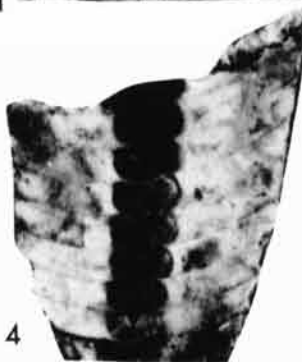
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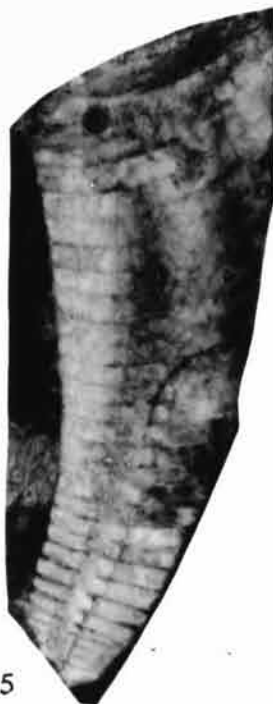
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7



tiated inner and outer zones. The free part of the ring here is straighter and thicker, with layering somewhat more clearly shown than on the dorsal side, and the innermost side bears a thin very dark band. Where the apical end of the ring joins the anterior face of the septum on the venter, a buttress of dense dark amorphous material is observed.

In general, these sections show clear evidence of the

bullettes which are variable in preservation but originally composed of two layers. The free part of the ring shows lamellar structure and is obscurely layered parallel to its length. The vinculum cannot be recognized, being either not differentiated or actually reduced and lost completely. The bullettes, their structure, and the layering of the ring are features adequate to show the affinities between *Phragmoceras* and other discosorids.

PARIETAL DEPOSITS AND ENDOCONES

As previously noted, organic deposits distinct from the materials of the connecting ring are unknown in the Ruedemannoceratidae and Cyrtogomphoceratidae, though originally, the swollen bullette of the Cyrtogomphoceratidae was regarded as such a deposit and not recognized as a primary structure of the connecting ring.

Deposits in the siphuncle appear first within the family Westonoceratidae (TEICHERT, 1933) and persist through the younger families Lowoceratidae and Discosoridae. They vary in form. The oldest and simplest genera show annulosiphonate parietal deposits (FLOWER, 1939) hereafter referred to simply as parietal deposits. In their habit of growth they are very similar to those found in the Pseudorthoceratidae, particularly in the subfamily Pseudorthoceratinae (FLOWER, 1939). The deposit appears first at the tip of the connecting ring on the ventral side and grows gradually forward until it joins the next anterior deposit. Similar material is apparent on the dorsum isolated from the initial part at the septal foramen. This indicates clearly that the deposit develops on the dorsum as much by lateral growth around the interior of the ring from the venter as from simple forward growth on the dorsal side.

Endocones (TEICHERT, 1931) develop from annular deposits when the individual deposit is no longer confined to the inner surface of an individual connecting ring. Instead, one deposit grows over the preceding one and the whole mass becomes thickened into a pattern of endocones leaving an annulated or straight central tube. In the Westonoceratidae the endocones are known in some of the Covington species of *Fabroceras*, but not in the oldest species of late Trenton (Cathys and Cynthia) age. They are encountered again in the section of the one known specimen of *Winniepegoceras sinclairi*.

It is evident that the endocones are nothing more than parietal deposits with a different pattern of growth. The two structures are identical in texture and composition and in many sections of *Fabroceras* they cannot be distinguished. It was at first believed that parietal deposits always precede endocones, and that cones, continuous through a series of segments, lie within a layer of discrete segmental annular deposits. Examination of much additional material has shown that commonly this is not true. What may begin as an annular deposit, growing forward from the septal foramen to the anterior end of the ring, may grow apically also and cover all previous deposits. Indeed, there is much in the appearance of the sections to support the interpretation that an individual cone develops simultaneously throughout its entire length (Pl. 17, figs. 1, 2; Pl. 18, fig. 2). Rather amazingly, the endocones may occupy the apical part of a siphuncle, while the anterior segments may show discrete parietal deposits, which by their variation from segment to segment show all evidence of growing forward in the segment like the deposit of *Westonoceras*. This is shown clearly in the rather extensive section illustrated in two portions on Plate 21. The rather rough section of the early portion of *Tuyloceras* (Pl. 27, fig. 2) shows a suggestion of discrete annular deposits preceding endocones. Endocones alone persist into its later stages, and occur alone throughout ontogeny of the Discosoridae (Fig. 2G, H).

It is evident that discosorid parietal deposits and endocones are homologous and that endocones are only a modification of the parietal deposits. In thin sections both commonly show a pattern of growth lines normal to the curving surfaces of the structures and fine lines normal to the surface. These are well shown in numerous thin and

EXPLANATION OF PLATE 4

RUEDEMANNOCERATIDAE—*Madiganella*; WESTONOCERATIDAE—*Lavaloceras*

FIGURE

1-6. *Madiganella* sp., specimen from Ordovician at Maree Bluffs, Western Macdonnell Ranges, central Australia; Univ. Adelaide collections.——1, Ventral view, $\times 1$.——2, Septal view, venter beneath, $\times 1$.——3, Lateral view, venter at left, $\times 1$.——4, Vertical section, $\times 1$ (an enlargement of the siphuncle is shown on Pl. 5, fig. 8).——5, Ventrolateral view (whitened) showing course of sutures, $\times 1$.——6, Ventrolateral view (same as Fig. 5, natural color) showing apparent growth lines which mimic septa and suggest deep ventral lobes, $\times 1$.

7. *Madiganella magna* TEICHERT & GLENISTER, holotype from Ordovician on Ellery Creek, Heavitree Ridge, about 50 miles west of Alice Springs, central Australia; Univ. Adelaide, Dept. Geol., no. NTO-10. Part of siphuncle, showing portion of central tube, $\times 2$ (photograph from Dr. TEICHERT).

8-9. *Lavaloceras cartierense* FLOWER, n. sp. holotype, from Terrebonne or Tetreauville beds, upper Trenton (Middle Ordovician), at dam on Jacques Cartier River, Quebec; collection of the writer.——8, Ventral view, $\times 1$.——9, Lateral view, venter at left, $\times 1$.

some opaque sections illustrated in this paper (Pls. 11, 12, 18, 21; Pl. 27, fig. 4, 5; Pl. 28, fig. 2-4; Pl. 29, fig. 1, 2). SCHINDEWOLF (1942) has presented excellent illustrations of the structures in *Alpenoceras eifelense*.

It is evident that these deposits within the siphuncle are absent in older Discosorida. They appear first in the Westonoceratidae, though they have not been observed in all genera and may be absent in some, and continue into the Lowoceratidae and Discosoridae. Similar annular deposits in other stocks have originated independently and differ in lacking evidence of the prominent radial lamellae which are so uniform in the Discosorida. This is certainly true of the deposits developed in the Michelinoceratida. Replacement and coarse recrystallization is common in actinoceroid siphuncles and for this reason statements concerning their original structure are tentative. It is, however, certainly true of the small deposits in the common Cincinnati forms where alteration and replacement are at a minimum.

Likewise the endocones have developed several times independently. In the discosorids they are modified parietal deposits. In the Endoceratida, where the structures are best known, they are primary structures in the siphuncle, without forerunners of any known sort. There, the fine structure uniformly fails to show fibrous lamellae normal to the cone surfaces and this together with other evidence, has led to the conclusion that these endocones are deposited within the tissues of the siphon (FLOWER, 1954). Endocones are again developed, probably from annular deposits, in the remarkable Baltic Ordovician genus, *Troedssonella* KOBAYASHI (type species, *Polygrammoceras endoceroides* TROEDSSON, 1932), and in *Striatoceras* SHIMIZU & OBATA (based on *Sactoceras striatum* TROEDSSON, 1926) (TEICHERT, 1934; FLOWER, 1939, 1939b). Apparently these Ordovician genera are not closely related to one another or to the discosorids. *Troedssonella* seems to be a specialization from early Ordovician Michelinoceratidae with tubular siphuncles, whereas *Striatoceras* is clearly a specialization in the Ordovician family Stereoplasmoceratidae.

The lamellae normal to growth lines and surfaces of the deposits are without counterparts in either the annular or endocone deposits of any of the types discussed above. The pattern is of a type generally associated with true shell secretion, that is, secretion of calcareous material upon the surface of a specialized tissue, a functional mantle. FLOWER (1939) had previously proposed that this was the origin of all annulosiphonate deposits, whereas TEICHERT (1933, 1934) had suggested that in actinoceroids, at least, annular deposits developed through calcification of tissues. For some years FLOWER has looked upon his earlier views as too broad a generalization. The annular deposits in the Michelinoceratida differ in texture and composition from the cameral deposits. They lack lamellae normal to the surface. Such lamellae are typical of cameral deposits, though they may of course be lost where secondary replacement alters the fine structure and the cameral deposits must certainly have been secreted by a cameral mantle (FLOWER, 1939, 1955). The different composition of the siphonal deposits here suggests a different origin, though this is not actually required.

Lamellae normal to the surface are characteristic of many, indeed most, Recent molluscan shells, where they are prisms commonly of aragonite and less commonly of calcite. In nearly all fossil material, replacement, commonly of aragonite by calcite, has obscured or completely destroyed the prismatic structure. We have not observed it in the shell wall or septa of any Paleozoic nautiloids, but it is a common phenomenon of cameral deposits, where replacement is either at a minimum, or where it is fine and slow, essentially representing histometabasis. Further support of the secretion of cameral deposits by a cameral mantle has been discussed elsewhere (FLOWER, 1939, 1943, 1955).

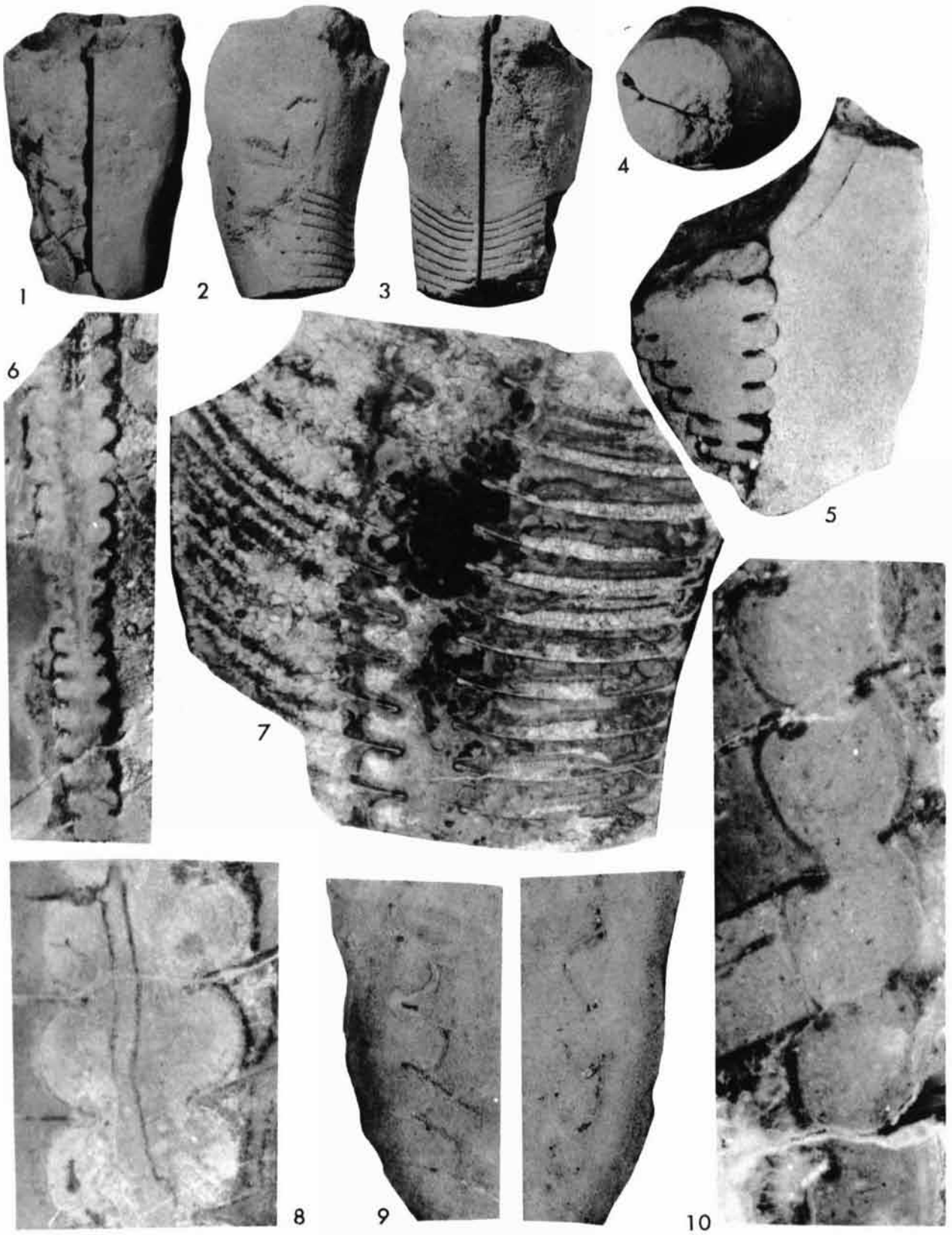
The fine structure of the deposits within the Discosorida suggests that, quite apart from the origin of annular deposits and endocones in other cephalopod groups, they were here secreted upon the surface of a functional mantle surface. If so, the tissues of the siphonal strand

EXPLANATION OF PLATE 5

RUEDEMANNOCERATIDAE—Ruedemannoceras, Madiganella; CYRTOGOMPHOCERATIDAE—Ulrichoceras, Cyrtogomphoceras, Landeroceras; WESTONOCERATIDAE—Teichertoceras, Hecatoceras

FIGURE

- 1-4. *Ulrichoceras beloitense* FOERSTE, holotype, from upper buff member of Platteville limestone (Middle Ordovician), Beloit, Wis.; U. S. Natl. Mus., no. 25302.—1, Dorsal view, $\times 1$.—2, Lateral view, venter at right, $\times 1$.—3, Ventral view, $\times 1$.—4, Septal view, venter at right, $\times 1$. (See also Pl. 9, fig. 3.)
5. *Cyrtogomphoceras* sp. cf. *C. rotundum* FOERSTE & SAVAGE, from Lander sandstone member of Bighorn dolomite (Ordovician), near Lander, Wyo.; U. S. Natl. Mus. no. 2050. Vertical section through phragmocone showing outline of siphuncle segments, $\times 1$, all original calcareous material removed by solution.
6. *Hecatoceras longiquum* TEICHERT & GLENISTER, holotype, from Ordovician, Mystery Creek Quarry, Ida Bay, southeastern Tasmania; Univ. Tasmania, Dept. Geol., no. 20826. Vertical section of siphuncle, $\times 1$.
7. *Ruedemannoceras boycii* (WHITFIELD), from middle Chazy (Ordovician) at type section southwest of Chazy, N.Y.; collection of the writer. Entire thin section (illustrated in part on Pl. 1) showing siphuncle segments and cameral deposits on the concave ventral side, venter at right, $\times 4$.
8. *Madiganella* sp., Ordovician, central Australia. Enlargement of portion of section illustrated on Pl. 4, fig. 4, showing details of central tube, $\times 4$.
9. *Landeroceras prolatum* (MILLER), from Lander sandstone member of Bighorn dolomite (Ordovician), near Lander, Wyo. Two opposing sections from specimen illustrated on Pl. 8, showing structure of siphuncle, $\times 1$.
10. *Teichertoceras sinclairi* FLOWER, n. sp., holotype, from Simard limestone (Ordovician), Ste. Anne de Chicoutimi, Que.; collection of the writer. Vertical section of anterior end of siphuncle, venter at right, showing form of segments and small bullettes, $\times 4.5$. (Same specimen as shown on Pl. 9, fig. 1, 2.)





must have been resorbed in order to retreat before the advancing calcareous deposit. Probably the central artery remained as a remnant and the central tube of the endocones was developed to accommodate it. Its function of supplying blood to parts of the siphuncle must have ceased and it is then not surprising to find the tube of some specimens traversed by diaphragms. SCHINDEWOLF has figured diaphragms in the siphuncle of *Alpenoceras eifelense*. They are found also in *Winnipegoceras sinclairi* (Pl. 15, fig. 5) and in one section of *Faberoceras* sp. (Pl. 17, fig. 2) but are clearly not a commonly developed feature, being definitely absent in many other forms where good endocones are known.

If this origin of the siphuncle deposits is correct, and admittedly the matter requires further investigation, the mantle must have originated from buds of epithelial tissue which formed a part of the siphonal strand from its inception. These buds must have been located at the tips of the connecting rings. Possibly they originated from such a tissue at the tip of the septal neck, being pushed

inward and thus becoming a part of the siphonal strand when the connecting rings were laid down. Such buds remain dormant for a time while normal growth of other parts of the shell progresses, and then must develop into rather rapidly growing mantle surfaces. The eventual result of such growth is that the original surface of the siphuncle tissue comes to be separated from the connecting rings which it had secreted some time before. The idea, though seemingly radical to paleontologists, is paralleled by many structural changes in ontogeny (in particular, embryology) of numerous organisms. It is considerably less remarkable than morphological changes among insects, such as occurs between the nymph and adult of the Odonata and it is downright conservative when compared to changes taking place in pupation of the Holometabola. Separation of the connecting ring from the surface of the siphuncle strand which formed it is analogous to the periodic molting characteristic of the Arthropoda, where the chitinous exoskeleton is periodically removed from the hypodermis which secreted it.

CENTRAL TUBE

Several of the discosorids show a central tube within the siphuncle. Its wall was evidently calcareous originally, and the structure is found completely surrounded by matrix and unattached to other hard parts. The invasion of sediment into the siphuncle evidently often destroyed the tube and accordingly such parts as are observed are fragmentary and commonly somewhat distorted. TEICHERT & GLENISTER (1952) noted that such a tube is very characteristic of *Madiganella* but their figures (pl. 105, figs 1, 2) show only a small portion of the tube in one segment of the siphuncle. Examples of better-preserved tubes are illustrated in the present paper (Pl. 4, figs. 4, 7; Pl. 5, fig. 8). In view of invasion of the siphuncle by matrix, the fragmentary nature of the tube is less remarkable than the fact that such a structure should be preserved at all. It is found also in *Pseudogomphoceras* (Pl. 34, fig. 15, 16), which is remarkably like *Madiganella* internally and for this reason is regarded as its descendant. Remnants of a similar tube are shown in a section of *Westonoceras* (Pl. 10, fig. 5; and Pl. 11, fig. 1). MILLER, YOUNGQUIST & COLLINSON (1954, p. 94, fig. 12) have presented a line drawing of a section of *Westonoceras* showing what appears to be a similar but much more perfect tube.

Similar free tubes are rare in nautiloids but are known in a few other specimens. TEICHERT (1933, pl. 14, fig.

48) figured a section of *Diestoceras scalare* showing a portion of a tube. FLOWER (1939a) figured a similar free tube in the Silurian genus *Harrisoceras* of the Michelinoceratidae. TEICHERT & GLENISTER (1952) remarked in commenting upon the general disparity of structures between *Harrisoceras* and *Madiganella*: "It thus seems to us that the endosiphuncular tube does not possess the taxonomic significance attributed to it by FLOWER, and that it may be a feature developed independently in many families." This statement denotes a misunderstanding of FLOWER's views. *Harrisoceras* commonly exhibits such a tube, but species of the genus have been recognized in which the tube has not been seen. The idea that all cephalopods with such a free central tube are genetically related was never entertained by FLOWER.

TEICHERT (1933, p. 153, fig. 20) observed a tube which was partially free in an incompletely calcified siphuncle of *Huroniella persiphonata* (BILLINGS).

Another example, isolated taxonomically from all others is the late Canadian genus *Buttsoceras*. The tube is remarkably persistent in this genus, which belongs to the Ellesmeroceratida, and is almost as singular as would be a spondylium in a linguloid shell. Because of the disparate structure, in contrast to that of other members of the Ellesmeroceratida, the tube has been considered of sufficient significance to warrant setting this

EXPLANATION OF PLATE 6

CYRTOGOMPHOCERATIDAE—*Cyrtogomphoceras*

FIGURE

- 1-2. *Cyrtogomphoceras* sp., from Mt. Silliman beds (Ordovician), of Baffin Island; U. S. Natl. Mus. collections.—1, Vertical section showing detail of necks, thick rings, and bullettes, $\times 4$.
—2, Vertical section of entire specimen, $\times 1$.
3,4. *Cyrtogomphoceras nutatum* (FOERSTE & SAVAGE), holotype, Illinois Geol. Survey.—3, Vertical section of early portion of siphuncle, $\times 2$.—4, Basal siphuncle segment showing

styloitic walls where solution has removed original structure leaving tip of the septal neck and trace of the bullette, $\times 6$. See Pl. 7, fig. 1-3 for entire specimen.

- 5,6. *Cyrtogomphoceras dowlingi* (FOERSTE), hypotype, from Dog Head member of Red River series (Ordovician) at Little Tamerack Island, Lake Winnipeg, Manitoba; collection of the writer.—5, Vertical section from early part of shell, $\times 1$.
—6, Lateral view of entire specimen, $\times 1$.

genus apart in a family of its own, *Buttsoceratidae* (FLOWER & KUMMEL, 1950).

In all probability, the central tube is the calcified wall of a central artery such as *Nautilus* possesses for carrying blood adapically throughout the length of the siphuncle. It returns through a haemocoel in parenchymous tissue within the siphonal strand. This cavity surrounds the artery.

Quite another aspect is presented by the tube found passing through the center of the endocones in the more specialized *Westonoceratidae* and persisting throughout the *Lowoceratidae* and *Discosoridae*. This has been discussed in the preceding section dealing with deposits within the siphuncle. It seems logical that here the cavity of the siphuncle is filled with solid calcareous material

except for the central artery, and if so, this tubular cavity within the endocones is essentially homologous with the free central tube discussed above.

Unlike the central canal of the actinoceroids, the free central tube of the discosorids and that found as a cavity in the endocones as well seem to be simple and they do not produce radial canals running to the wall of the siphuncle. The tube enclosed by the endocones is annulated and slightly expanded within the middle of each segment. The expansion, however, is plainly not a feature of the tube itself but rather the result of conformation of the endocones with the broadly expanded siphuncle segments in which they were formed. Diaphragms crossing the tubes found enclosed by endocones have already been discussed.

CAMERAL DEPOSITS

Cameral deposits are developed in many of the Ordovician *Discosorida* and persist in the Silurian *Mandaloceratidae* and *Phragmoceratidae*. They are apparently lost in the Silurian *Lowoceratidae* and *Discosoridae*. It is in those families that the siphuncle becomes extremely large and the deposits of endocones greatly developed. Thus the siphuncles alone may provide enough weight to take over the hydrostatic function of cameral deposits completely.

Deposits in *Ruedemannoceras* are first episeptal, and formed primarily along the free part of the septum. They are peculiar in being thicker near the siphuncle than toward the wall of the shell. With further growth they extended along the outer wall of the camerae where the mural part of the septum is extremely short and finally they may extend some distance along the anterior septum. Such material is hyposeptal in position but not comparable to true hyposeptal deposits. They are structures quite distinct from the true hyposeptal deposits in the *Actinoceratida* and *Michelinoceratida*. Deposits are thick ventrally and thin dorsally. Our sections suggest a definite radial pattern but no exfoliated specimens are known showing its details and sections now available are insufficient to show more than a suggestion of a bilaterally symmetrical pattern, details of which may be rather complex. Probably deposits are present in *Madiganella* but the known specimens are all relatively late portions of phragmocones, too close to the living chamber for these deposits to appear in them.

In the *Cyrtogomphoceratidae*, *Phragmoceratidae*, and *Mandaloceratidae*, massive deposits similar to those of *Ruedemannoceras* are not known. However, cameral deposits are commonly manifest in these families as relatively shallow longitudinal thickenings along the outer wall of the phragmocone. They are commonly detected from their impressions on internal molds of the phragmocones from which the deposits have been exfoliated, appearing as alternating ridges and grooves which are quite regular in spacing around the circumference of the specimen. That no thicker deposits are known is partly due to

a reduction of these structures, as is evident in the *Phragmoceratidae* and probable in the *Mandaloceratidae*. It may be more apparent than real in the *Cyrtogomphoceratidae*, for apical portions of phragmocones are practically unknown in this family.

Westonoceras and the *Westonoceratidae* in general show similar ridges and grooves on the internal molds of phragmocones, their origin being attributed to incipient cameral deposits. However, adapical portions of phragmocones of *Westonoceras* are known in which the deposits are thicker. It is evident that they are thicker ventrally than dorsally and exhibit a bilaterally symmetrical pattern. The deposits are essentially episeptal but not thickened markedly along the middle of the free part of the septum, as in *Ruedemannoceras*. Instead, they tend to thicken against the mural or outer wall of the camera, and may, as in *Ruedemannoceras*, extend some distance inward toward the center of the camera along the anterior wall. Again, though hyposeptal in position, as previously observed by TEICHERT (1933, p. 173-175), these structures are extensions of the original episeptal deposit and not true distinct structures like the hyposeptal deposits of actinoceroids. The details of the pattern can be seen on exfoliated specimens. One such specimen was figured by MILLER, YOUNGQUIST & COLLINSON (1954, pl. 44, figs. 1, 2). The deposits are extremely thin dorsally, thickening gradually laterally and developing a pattern marked first by striations around the circumference which give way to a pitted pattern where the deposit is thicker ventrolaterally. On the ventral side, the deposit is evidently much thickened; here it approaches close to the siphuncle, forming a thickened semicircle around it not very far from it. This region is marked by longitudinal grooves and ridges—so much so, indeed, that this part of the internal mold resembles a weathered actinosiphonate siphuncle.

In spite of the abundant material of *Faberoceras*, only very thin cameral deposits have been observed in sections of shells belonging to this genus and nothing is known of their radial distribution. They are episeptal,

but thin along the septum and thicker along the outer wall of the camerae. No specimens have been found representing parts of *Faberocheras* shells very close to the apex, where more advanced modifications of the deposit would be expected.

No trace whatsoever of cameral deposits has been observed in the Lowoceratidae or Discosoridae. Material of the Lowoceratidae is so meager, that absence of the structures there is negative evidence of little significance. However, there is abundant material of the Discosoridae and no trace of cameral deposits has been found in it.

RANGE OF THE DISCOSORIDA

Review of the stratigraphic and geographic range of the Discosorida shows, first, an amazing discontinuity in the present record, and second, a remarkable confinement of the main groups to well-defined faunal realms, in particular those faunas which have been long recognized as boreal in origin.

Ruedemannoceras is known primarily from the Chazy of the Champlain Valley. Only one other occurrence of the genus is known. This is *Ruedemannoceras stonense* (SAFFORD) from the Murfreesboro limestone of Tennessee. We have had no specimens of this form, but happily the genus is so distinctive in the slight curvature, moderate expansion and broad cross section of the shell, and subcentral broadly expanded siphuncle segments, that there is nothing else which can readily be confused with it. We have accordingly regarded the Murfreesboro limestone as Chazy in age. COOPER & COOPER (1945), on the basis of the brachiopod faunas, supported by the fact that subsurface drilling suggests a very appreciable thickness of sediments between the exposed Murfreesboro and the top of the Canadian, regard these beds as of Black River age. We hold, however, that neither reason is infallible. Even if subsurface recognition of the top of the Canadian is correct, the presence of thick strata below the Murfreesboro would not preclude its age being Chazy. The faunal evidence for Black River assignment of the beds is incomplete and rests primarily on the brachiopods. As bottom-dwellers and sedentary forms, they are more subject to control by environmental factors; they are much more dependent on the environment than the more motile cephalopods. Yet it seems that in much recent work the brachiopod assemblages have overinfluenced assignment of beds to Black River rather than Chazy, and too much emphasis has been placed upon brachiopod types, the appearance of which in typical Black River beds may depend upon a faunal incursion. It seems that such types, mainly generic groups, should be expected in beds of Chazy age, though in a different faunal province. We are therefore still strongly impressed with the fact that the Murfreesboro limestone is the only stratigraphic unit outside of the middle and upper Chazy of the Champlain Valley where *Ruedemannoceras* and *Gonioceras* are found in association. *Gonioceras* is known to range higher but *Ruedemannoceras* is not.

Madiganella, known only from the Ordovician of central Australia, occurs in beds originally regarded by TEICHERT & GLENISTER as approximately Chazy in age.

That their absence probably is real is suggested by preservation phenomena. Though some phragmocones are known, none with traces of such deposits, most specimens are isolated siphuncles. Abrasion has destroyed the shells and the camerae. Had cameral deposits been present, doubtless they would have strengthened the camerae, at least in the adapical part of the shell, and these structures therefore should have been preserved. Although a number of apical ends of discosorid siphuncles are known, they are no more inclined to have camerae attached than are later-formed parts of the phragmocone.

However, little is known of the detailed stratigraphy of this remote region, and the beds yielding *Madiganella* may very well be somewhat younger. As *Madiganella* is more advanced than *Ruedemannoceras* and supplies the only morphological and stratigraphic link between this genus and the Middle Silurian *Pseudogomphoceras*, a position somewhat higher in the Ordovician is possible.

Hecatoceras is known only from the Ordovician of Tasmania. The associated faunas lie within the Trenton-Richmond interval, but as yet cannot be correlated more precisely. F. R. COWPER REED (1936) identified *Cyrtoceras boycii* (now *Ruedemannoceras*) and a *Cyrtogomphoceras* from the Ordovician of the Shan States but his descriptions and figures leave the identification of both forms doubtful.

The next occurrences of discosorids of more definitely known age are in America in beds of essentially Black River age. One is the Simard limestone of Chicoutimi, Quebec. Both SINCLAIR (1953) and FLOWER (1952) regard these beds as of Black River rather than early Trenton age. Here occur *Simardoceras simardense*, *Sinclairoceras haha*, and *Teichertoceras sinclairi*. The other occurrence is in the Platteville limestone of the upper Mississippi Valley, which has yielded *Ulrichoceras beloitense* and *Reedsoceras macrostomum*. It is significant that these faunas mark what has long been considered the first of three incursions of boreal faunas into eastern North America, the second being in the late Trenton Cobourg, and the third being the Richmond of the Cincinnati arch and Anticosti. It is significant that these two faunas show associations of primitive and advanced forms. Morphologically, *Ulrichoceras* is the most primitive member of the Cyrtogomphoceratidae, showing several features reminiscent of the Chazy *Ruedemannoceras*. The other genera belong to the Westonoceratidae, more advanced in reversal of the primitive endogastric curvature to exogastric, and in further specialization of the siphuncle. *Teichertoceras* is logically the most primitive of the Westonoceratidae, retaining endogastric curvature in the early stages and possibly lacking parietal deposits, but from all morphological evidence, *Simardoceras* and *Sinclairoceras* are more advanced types, as is probably the little known *Reedsoceras*. Plainly, these two occurrences of Black River age show that the evolution of the discosorids has progressed very materially. It is of interest to note that the discosorid occurrences are of rather late Black River age. As yet, no members of the

order have been found in strata which can be correlated with the Lowville nor in any strata which may fill the Chazy-Lowville hiatus.

With the exception of *Antiplectoceras* of the Hermitage limestone of Tennessee, which is not well enough known that its discosorid affinities can be any more than a supposition, the next discosorids in America are found in beds of late Trenton age. The Middle Trenton has been considered as marking a withdrawal of boreal and an advance of austral faunal elements. It is not until the return of the boreal elements in late Trenton time, essentially Cobourg time, that the discosorids reappear. Here, at the top of the Trenton in general, where the latest limestone persists, is found a cephalopod fauna containing many genera previously regarded as diagnostic of the much younger Richmond. *Probillingsites*, *Apsidoceras*, *Charactoceras*, *Fremontoceras*, large *Diestoceras*, in contrast to the smaller species which are probably not typical and have a much wider stratigraphic range, *Neumatoceras*, with the discosorids *Winnipegoceras* and *Westonoceras*, are in general quite characteristic of these beds. Where the uppermost beds are shales, as in the Collingwood and Gloucester of the Ottawa Valley, cephalopods are absent, and there persists an impure planktonic black shale association in general. This fact should be noted, for it is possible that in some of the regions discussed, the late Trenton limestone with faunas of Cobourg affinities may well extend higher, being lateral equivalents of these upper shale members of the Ottawa Valley section.

In Quebec, the Terrebonne limestone, and to a lesser extent, the underlying Tetreauville limestone which has yielded fewer cephalopods, contain this fauna. Here are the discosorids *Westonoceras sinclairi*, *W.?* *diestoceroideis*, *Lavaloceras geniculatum*, *L. cartierense*, and *Winnipegoceras sinclairi*. The association contains other cephalopod genera of late Trenton age, notably *Lambeoceras*, *Apsidoceras*, *Fremontoceras*, *Neumatoceras* and large *Diestoceras*. It is here, indeed, that some of these genera, supposedly diagnostic of the Richmond, were first reported in beds of undoubted Trenton age. It is surprising to note that MILLER, YOUNGQUIST & COLLINSON (1954) credit FLOWER (1952) with attributing these beds to the Trenton. The conclusion is one which has been held for at least a generation, and reaffirmed by recent investigations of SINCLAIR (unpublished) and CLARK (1952). Covington and Richmond beds are known in the region and they are very different faunally and lithologically.

Farther west, the Cobourg of northwestern New York and Ontario has yielded fewer cephalopods, but *Probillingsites* is abundant and FLOWER (1952) has reported *Westonoceras* and *Charactoceras* from them. Still farther west an analogous association has been found in the Trenton of Cornell, Michigan. FOERSTE (1932, 1933) described from these beds *Probillingsites*, a fairly large and typical *Diestoceras*, and the discosorids *Teichertoceras husseyi* and *Westonoceras* sp. cf. *W. minnesotense*. FOERSTE referred to these beds as the Cornell member of the Trenton, although they have not yet been formally named and described as far as we are aware. The Cobourg affinities of the fauna are quite evident however.

Still farther west, the Stewartville limestone of the upper Mississippi Valley has yielded rather abundant *Westonoceras*. It may well be that early records of this genus from the underlying Prosser member of the Trenton harken back to a time prior to the recognition of Prosser and Stewartville as distinct entities. FOERSTE (1933, p. 117) expressed similar doubts on the matter. Additional types of significance include *Probillingsites*, *Lambeoceras*, *Charactoceras* and *Ephippiorthoceras*.

Westonoceras makes one other appearance in beds of Trenton age, in the Viola limestone of Oklahoma. Its only other appearance in eastern North America is curiously not in the Trenton, but in the Eden of the Cincinnati region, where *W. ortonii*, *W. ventricosum* and *W.* sp. occur (FLOWER, 1946).

The greatest assemblage of Ordovician discosorids in America is found in those faunas which have come to be considered Red River faunas, using the term in a collective sense. It includes not only the true Red River of the Winnipeg region, but beds extending northward, the Nelson limestone on the west side of Hudson Bay, the Mt. Silliman beds of Baffin Island, the Cape Calhoun beds of northern Greenland, and less well known occurrences between. South from Winnipeg the fauna continues into the lower part of the Bighorn group, the lower part of the Fremont limestone of Colorado, and the lower Montoya of New Mexico and western Texas. Curiously, the discosorids are well represented in the northern extent of these beds but decline and seem to be increasingly replaced by oncoceroid types at the southern end, though actinoceroids and other fossil types are less restricted geographically. It is in these beds that one finds the great concentration of *Cyrtogomphoceras*, *Winnipegoceras*, and *Westonoceras*. Re-analysis of the discosorid types in the present work has led to considerable emendation of generic assignments, as noted in the systematic portion of this paper under the genera in question. The Red River series of Winnipeg contains *Westonoceras manitobense*, *W. albert-saskatwanae*, *W.* sp., *Winnipegoceras laticurvatum*, *W.* sp. cf. *W. royi*, *Cyrtogomphoceras magnum*, *C. whiteavesi*, *C. dowlingi*, *C.?* *intermedium*, and *C.* sp. cf. *C. turgidum*.

On the west side of Hudson Bay, the Nelson limestone has yielded a collection which is smaller, probably because there has been less collecting in this less accessible region, but including *Cyrtogomphoceras nutatum*, *Westonoceras nelsonense*, and *Lavaloceras perplexum*. *W. contractum* is a *Neumatoceras* and *Cyrtogomphoceras shamattawaense* is a species of uncertain position; thus there are no true discosorids in the overlying Shamattawa limestone. Likewise, *W.?* *septentrionale* of the Silurian Attawapiskat limestone is here referred tentatively to *Laureloceras*. *Westonoceras ornatum* is known from the Ordovician of Iglulik Island, north of Hudson Bay (TEICHERT, 1937).

In Baffin Island at Mt. Silliman (or Silliman's Fossil Mount) are beds previously attributed variously to Trenton and Richmond. MILLER, YOUNGQUIST & COLLINSON (1954) refer to them as "Upper Ordovician," in spite of the fact that in the same work WARTHIN finds that the

ostracodes suggest lower Trenton (Hull) affinities, and WHITTINGTON concludes that the trilobites suggest late Trenton affinities. The problem of the faunal analysis will not be discussed in detail here. A more definitive name is needed for these beds and the term Mt. Silliman beds is here proposed. Here again are found abundant *Westonoceras*, *Winnipegoceras*, and *Cyrtogomphoceras*, though the present analysis requires removal of some species previously referred to these genera. The Cape Calhoun beds of northern Greenland contain abundant *Cyrtogomphoceras*, species here referred to *Winnipegoceras*, and *Westonoceras*, of which *Thuleoceras* TROEDSSON is a synonym. It is interesting to note that a group of species of *Winnipegoceras* with short living chambers form a series that is represented by small forms with prominent lateral lobes in northern areas and larger forms with straighter sutures in the south. The series involves *W. tumidum*, *W. reclinatum*, and specimens showing a wider range of proportions included under *W. royi*, the largest of which is from the Selkirk limestone of the Winnipeg region. Ordovician beds of equivalent age in Cockburn Land, northern Baffin Island, have yielded *Teichertoceras* (TEICHERT 1937).

The Lander sandstone of the Bighorn group (MILLER, 1932; FOERSTE, 1935) and the lower part of the overlying dolomites have yielded *Cyrtogomphoceras*, including *C. rotundum*, *C. angustisiphonatum*, *C. vinculum*, *C. popagiense*, *C. contractum*, *C. minor*, *C. landerense*, several *Winnipegoceras*, notable in including forms with long living chambers very close to *W. laticurvatum*, and also some forms with short living chambers, but no known *Westonoceras*. *Landeroceras prolatum* is recorded only from the Bighorn group.

Only one discosorid, *Cyrtogomphoceras contractum*, is known from the lower part of the Fremont limestone of Colorado. As yet no discosorids have been recognized in the Montoya dolomite of New Mexico or western Texas.

It should be noted that FOERSTE (1924, 1932, 1933, 1935) came to the conclusion, though rather reluctantly, that the Red River faunas were Richmond in age. Comparison with Richmond faunas shows that while many Red River genera are found in the Richmond of the Cincinnati arch (FLOWER, 1946) and Anticosti (FOERSTE, 1928), many are completely unknown there, and amazingly, no discosorid types are represented. *Cyrtogomphoceras* is unknown in eastern faunas. *Westonoceras* penetrates late Trenton beds widely, is known in the Eden, but is not reported to extend higher. Penetration of *Winnipegoceras* into eastern faunas is as yet reported only in late Trenton strata of Quebec. These facts suggest a view long held by FLOWER, that the Red River faunas are pre-Richmond and either late Trenton or equivalent to the Covington (Eden and Maysville or some part of them), or both. Precise evaluation within the early Cincinnati and late Trenton involves intricate problems which will be discussed elsewhere.

One interesting point should be brought out in this connection. In flat-lying areas, where strata have gentle dips, the Red River deposits have been differentiated from overlying strata of Richmond age. This applies

to the Red River-Stony Mountain succession of Manitoba, and to the Nelson-Shamattawa succession of Hudson Bay. Farther north, the Richmond is absent or has not been differentiated. Farther south, the strata concerned are in mountain areas, with extent of outcrop limited, and in most places the underlying beds with Red River faunas have not been differentiated from overlying ones with Richmond faunas. Furthermore, in many of these areas original lithological differences have been obscured by dolomitization. Faunal differentiation is also made more difficult and commonly fossils are destroyed. Dolomitization leaves the rock so massive that proper collection *in situ* presents great practical problems. Nevertheless, it is apparent that Richmond assemblages make up a succession of faunas overlying a succession of Red River faunas. Investigations by FLOWER in the Montoya of New Mexico indicate that a Red River succession occupies the lower part, the Upham dolomite. Above it, the Aleman limestone and Cutter dolomite contain a succession of faunas which comprise most and probably all of the Richmond, a conclusion which lends further support to the pre-Richmond age of the Red River faunas. Equivalence of the Red River faunas from New Mexico to Winnipeg, and probably to Greenland seems an escapable conclusion. In view of the extent of the region involved, the faunal changes are amazingly slight, and much less than those encountered in tracing the Middle Ordovician over the appreciably shorter length of the Appalachians.

In northern Europe undoubted discosorids are encountered in the later Ordovician of the Oslo region and the Lyckholm formation of Estonia. The Upper Ordovician of the Oslo region (STRAND, 1933) has yielded a doubtful *Westonoceras*, a *Winnipegoceras*, which, though anomalously small and broad of whorl, seems otherwise to be typical, and contains characteristic genera, not encountered in America, named *Lyckholmoceras*, *Kiaeroceras*, and *Strandoceras*. Of these genera, *Lyckholmoceras* and *Strandoceras* extend into the Lyckholm beds of Estonia (TEICHERT, 1930.) FLOWER found in the collections of the Museum of Comparative Zoology at Harvard a typical *Kiaeroceras* labeled as coming from Estonia, which suggests that this genus may extend into the Lyckholm beds also. TEICHERT (1930) has described some anomalous forms, which unfortunately fail to show even the position of the siphuncle, as *Cyrtogomphoceras? troedssoni* and *Winnipegoceras? sp.* FLOWER (1946) has suggested that the known features of these species are more consistent with placement in the subsequently described genus *Faberoeras*, and they are here tentatively so referred. Some rather inadequately known species from the Bala beds of England, notably *Trochoceras? cinereum* BLAKE and *C. subarcuatum* PORTLOCK, are suggestive of *Faberoeras*, and *C. sonax* is an endogastric form suggestive of the *Cyrtogomphoceratidae* but not typical of either *Strandoceras* or *Lyckholmoceras*, though resembling them more than any other described genera.

The forms thus far discussed belong to associations which have long been considered as boreal faunas in relation to those of North America. In late Trenton time discosorids penetrated the austral faunas of the east-cen-

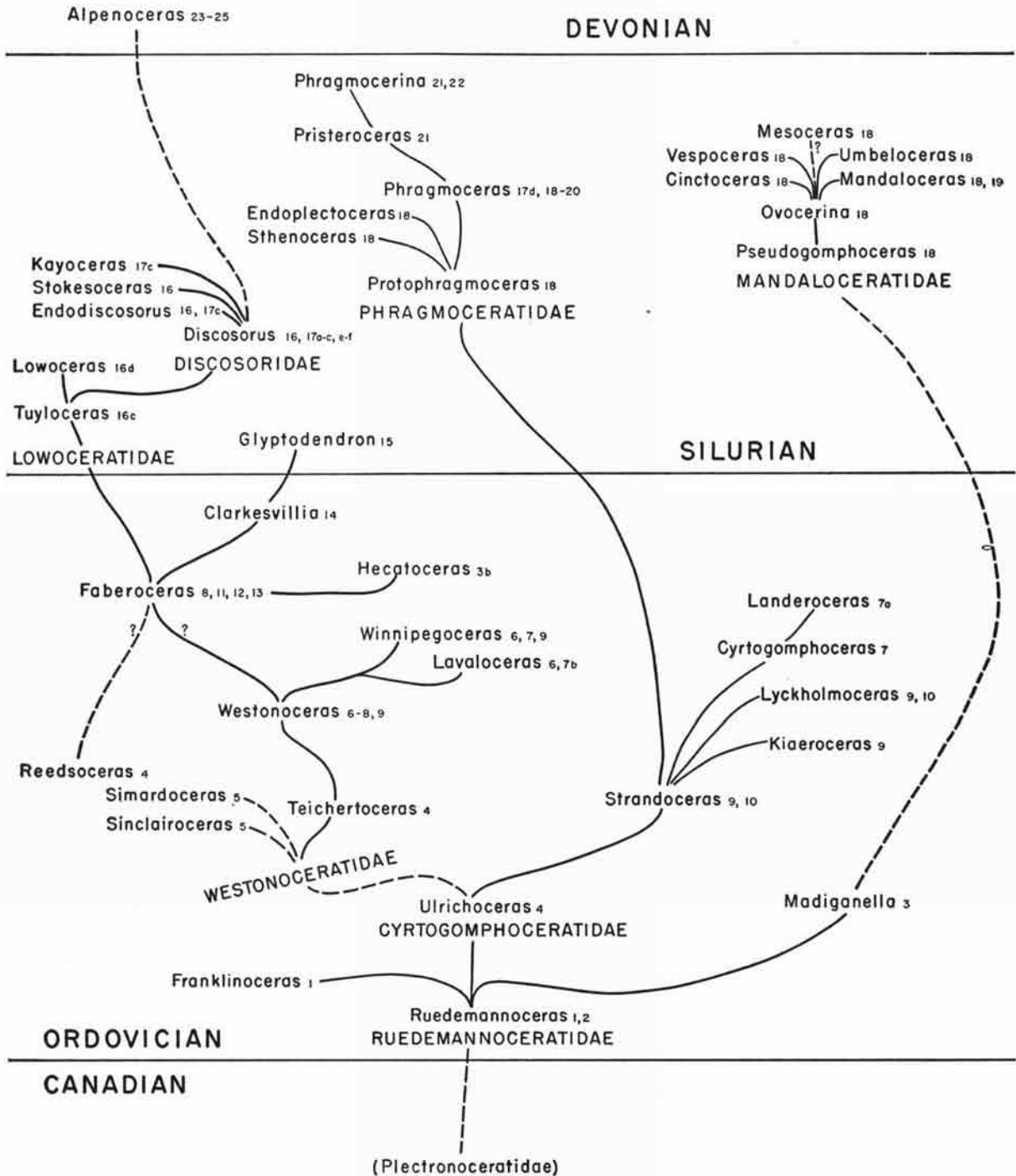


FIGURE 10. Stratigraphic occurrence of genera of the Discosorida, showing general evolutionary relationships.

Position of genera in the system is only approximate, the precise occurrence being indicated by numbers, as follows:

1. Middle and upper Chazyan, Champlain Valley.
2. Murfreesboro limestone, Tennessee.
3. Ordovician, central Australia, 3a, Tasmania.
4. Platteville limestone, northern Mississippi Valley.
5. Simard limestone, Lake St. Jean region, Quebec.

6. Terrebonne limestone, Quebec; Cobourg of Ontario and New York, northern Michigan, and Stewartville of Minnesota.
7. Red River faunas, generalized; 7a, Confined to Lander sandstone of the Big Horn group.
8. Eden, Cincinnati region.
9. Upper Ordovician, Oslo region.

(Continued on facing page)

tral region. The genus *Fabroceras* makes its first appearance concurrently in the contemporaneous Catheys limestone of Tennessee and the Cynthiana limestone of Kentucky. In Kentucky it is joined by *Reedsoceras mcfarlani*. In the same region, *Fabroceras* continues into the Leipers beds, where species attain much greater diversity and show greater specialization of internal structure, the shell becoming costate, the siphuncle larger and in some more central, and in some with parietal deposits extended into endocones. Significantly, one species (*F. magister*) enters the Eden beds of the Cincinnati region, where *Westonoceras* also occurs. Another form, and a more specialized one (*F. elegans*), occurs in the Corryville strata. It has been customary to regard the Catheys and entire Cynthiana as pre-Eden in age, and the Leipers has been considered to be the equivalent of the Fairmount beds of Cincinnati. Fairmount equivalence rests primarily on the fact that it is only in these beds that certain Leipers elements (notably *Orthorhynchula linneyi*) are known to extend as far north as Cincinnati. The simplicity of *Fabroceras magister* and its concordance with Catheys rather than Leipers types, has suggested to FLOWER that perhaps these beds may be in part equivalents of the Eden. Extension of a *Fabroceras* of specialized aspect into the Corryville suggests that the Leipers may include a greater part of the Maysville than has previously been believed, a conclusion which is at least not inconsistent with the appreciable thickness of the formation in southern Kentucky.

Fabroceras is the beginning of a stock which can be traced farther in the east-central region. *Clarkesvillia* differs from it in little other than flattening of the venter in cross section and is convincing as a specialization of the genus in Richmond time. It is known only from the Waynesville part of the Richmond. Interestingly, the entire Richmond contains many stocks which seem to be indigenous and the invasion of boreal elements is actually a gradual or intermittent one. The boreal cephalopod types which have influenced many to consider the Red River and allied faunas as Richmondian, penetrate the region only imperfectly in the early Richmond. *Schuchertoceras* appears in the Waynesville, *Diestoceras* in the Liberty beds above, but the fullest expression of the "boreal" elements is not attained until the late Richmond Whitewater and Saluda beds.

Glyptodendron, of the Lower Silurian Brassfield limestone, is obviously a specialization stemming from *Clarkesvillia* and marks the termination of this part of the discosorids in the austral faunas of east-central North America.

The accompanying diagram (Figure 10) is an attempt to show both the known occurrence of the Discosorida and their evolutionary relationships, which are discussed in detail in the following section. Attempt to portray equivalence in terms of divisions within systems, particularly in the Ordovician, was made difficult by varying and conflicting opinions as to the exact equivalence of many strata. Vertical arrangement of the genera is, of necessity, only approximate and precise occurrence is indicated by numbers explained in the accompanying key. Occurrences may be generalized further as follows: (1) *Ruedemannoceras*, in the Chazy and its probable equivalents. (2) Occurrences in the Platteville and Simard limestones marking early invasion of boreal faunas, which may be labeled broadly as Black River. Strangely, the boreal aspects of the early Black River Lowville are imperfect or else very imperfectly known. The boreal elements show a gradual recession which extends certainly into Rockland and possibly Hull time. FLOWER has suggested that the resulting anomalies in trying to draw a distinction between Black River and "Trenton" faunas would be reduced by placing the boundary higher, possibly at the base of the Sherman Fall division of the Trenton. (3) Faunas of the second, late Trenton boreal invasion, to which the term Cobourg is broadly applied. (4) Faunas of boreal aspect in the north and west, to which, following FOERSTE (1932, 1933, 1935), the term Red River faunas is broadly applied. (5) Late Ordovician faunas of northern Europe. (6) East-central faunas of austral aspect beginning with the late Trenton Catheys and Cynthiana and continuing into Leipers, with rarer representatives in the Eden and Maysville, and continuing on into the Richmond and Brassfield.

The Chazy, Black River and Cobourg supply three discrete glimpses of the evolution of the stock; between them nothing is known and in each reappearance of the stock faunal advances are marked. Much evidence, the appearance of many Red River genera in the late Trenton, appearance of *Westonoceras* in the Eden but not Richmond, and stratigraphic evidence from western sections suggest a pre-Richmond age for the Red River beds. If this is so, we have no record of the evolution of the Discosorida in America in latest Ordovician time. Possibly this is supplied by the northern European faunas but here there are vexatious questions. Equivalence with Richmond beds rests (1) upon genera in the Richmond of Anticosti which now are known to appear as early as late Trenton, and (2) forms suggesting affinities with the Red River faunas, the Richmond age of which is becoming increasingly doubtful.

(Continued from facing page)

10. Lyckholm beds, Estonia.
11. Cynthia-Catheys faunas, Kentucky and Tennessee.
12. Leipers beds of Kentucky and Tennessee.
13. Maysville beds, Cincinnati region.
14. Richmond, Cincinnati region.
15. Brassfield limestone, southern Ohio.
16. North-central Clinton limestones. (a) Timiskaming; (b) Northern Michigan; (c) Hudson Bay; (d) Southampton Island.
17. East-central Clinton. (a) New York; (b) Dayton limestone, Ohio; (c) Hopkinton dolomite, Iowa; (d) Liston Creek limestone, Ind.; (e) Gun River, Anticosti; (f) Jupiter, Anticosti.
18. Étage E₂, Bohemia.
19. Racine-Guelph beds, eastern North America.
20. Middle Silurian, Gotland.
21. Bertie limestone, New York.
22. Manlius limestone, New York.
23. Eifel Devonian, *Stringocephalus* beds and early Upper Devonian.
24. Winnipegosis dolomite, Manitoba.
25. Alpena limestone, northern Michigan.

In Silurian time different stocks show markedly contrasting distributions. The Lowoceratidae and Discosoridae are mainly concentrated in limestones of Clinton age in northern North America, but a handful of species are known to extend outside of that range. In general, the Phragmoceratidae and Mandaloceratidae attain a peak of abundance and variety in later Middle Silurian faunas, without any evident northerly concentration. They are common to the Racine and Guelph associations of North America, and the equivalent Ludlow equivalents, notably Étage E₂ of Bohemia, in Europe.

Most striking is the association of the Discosoridae and Lowoceratidae in northern North America. It is found in the Silurian of northern Michigan, in the Burnt Bluff and Manistique beds, Thornloe limestone (FLOWER, 1946) of Lake Timiskaming, Ekwan limestone on the west side of Hudson Bay, and Silurian of Southampton Island. The general succession of faunas is here quite uniform. First in the Silurian come the faunas dominated by *Virgiana decussata* in beds well recognized at Medinan (Alexandrian) in age. We prefer the older term Medinan with the reservation that the Queenston shale, originally included, is demonstrated to be of Richmondian age and should therefore be removed. They are followed by a fauna widely known as that of the *Leperditia hisingeri fabulina* zone. This horizon must be either late Medinan or very early Clinton, but to which of these it is better assigned seems equivocal from present available evidence. Above it lie beds with corals but particularly characterized by the discosorids *Discosorus* and *Stokesoceras* and the actinoceroids *Huronina* and *Huronella*. Strangely, these beds are absent in the Winnipeg region or else have not been differentiated from overlying strata because the corals (but not the cephalopods) have been found there.

Still higher are found beds with a rich and more mixed cephalopod association, commonly in biohermal beds. The cephalopods are dominantly breviconic types, including many Phragmoceratidae and Mandaloceratidae, specialized oncoceroids, and Ascoceratidae, which show unmistakable affinities with the rich cephalopod associations of BARRANDE'S Étage E₂ of Bohemia, lower Ludlow, widely present in Europe, and the Racine-Guelph faunas of east-central North America.

One is tempted to believe that this is a fauna which entered America by a northerly route, yet it can be traced southward to Indiana and Illinois where it is found overlying a very different association consisting dominantly of orthocones. This fauna, developed in the Joliet and Liston Creek formations, and even more fully displayed farther south in the Laurel limestone and its equivalents in Tennessee, is amazingly similar to that found in Étage E₁ (= Wenlock) of Bohemia. The range of this fauna suggests an entrance from the south, and it must have oc-

cupied the time interval equivalent to that of the more northerly *Discosorus-Huronina* faunas.

A general tendency may be discerned to place all of these limestone faunas rather high in the American Silurian. This practice seems to stem from some of ULRICH'S early correlations. In tracing sections from New York westward, the Clinton beds thin and finally disappear over a region which CUMINGS called the Cataract axis. On the New York side these beds are mainly clastics. Where they reappear on the west of the axis they are dominantly limestone and dolomites, which, because of their coral content and general dissimilarity to the type Clinton, have been long regarded as equivalent to the Lockport in age. Today it is fairly evident that the Lockport corresponds to the Racine. Further, a review of the Shelby faunas indicates (1) that the lower and upper Shelby beds have less in common than CLARK & RUEDEMANN (1903) asserted and (2) that the lower Shelby fauna is a Racine assemblage, whereas the upper Shelby fauna contains many forms of Guelph affinities.

It was suggested to one of us (FLOWER) many years ago by E. R. CUMINGS that many of these limestones, in fact all of the Silurian beds beneath the Racine and its equivalents, are of Clinton age. Further, it is evident that the deposition of Clinton beds must have encompassed a span of time which was very appreciable, necessarily somewhat complex in its history, and quite probably equivalent to the upper half of the Middle Silurian which comprises the Racine and Guelph beds. CUMINGS & SHROCK have shown that in northern Indiana the Silurian succession consists of the Missinewa shale and Liston Creek limestone, which are succeeded by beds ranging in age through Racine and Guelph. There is strong evidence that many Racine types are traceable to ancestral ones in the Liston Creek, Joliet, and the more southerly Laurel limestones, but in Racine time these faunal elements are joined by other stocks new to the region. Possibly the incursion was a gradual one, beginning in Racine and culminating in Guelph-Port Byron time. Certainly there is difficulty in establishing a precise boundary and this suggests a gradual incursion which may not have been strictly contemporaneous everywhere in the east-central region. *Megalomus* has long been regarded as one of the few reliable indicators of Guelph age, but one of us (FLOWER) has found this genus low in the sections at Huntington and Monon, Indiana, in faunas which are otherwise exclusively Racine and not Guelph in aspect.

Taking the Manistique as equivalent to the Liston Creek, it is possible to establish a connection with the most southerly beds containing the *Discosorus-Huronina* association. It should be noted that a few types, notably species of *Discosorus* and *Stokesoceras*, are found in both the Manistique and underlying Burnt Bluff formation.

From the Manistique to the Thornloe limestone of

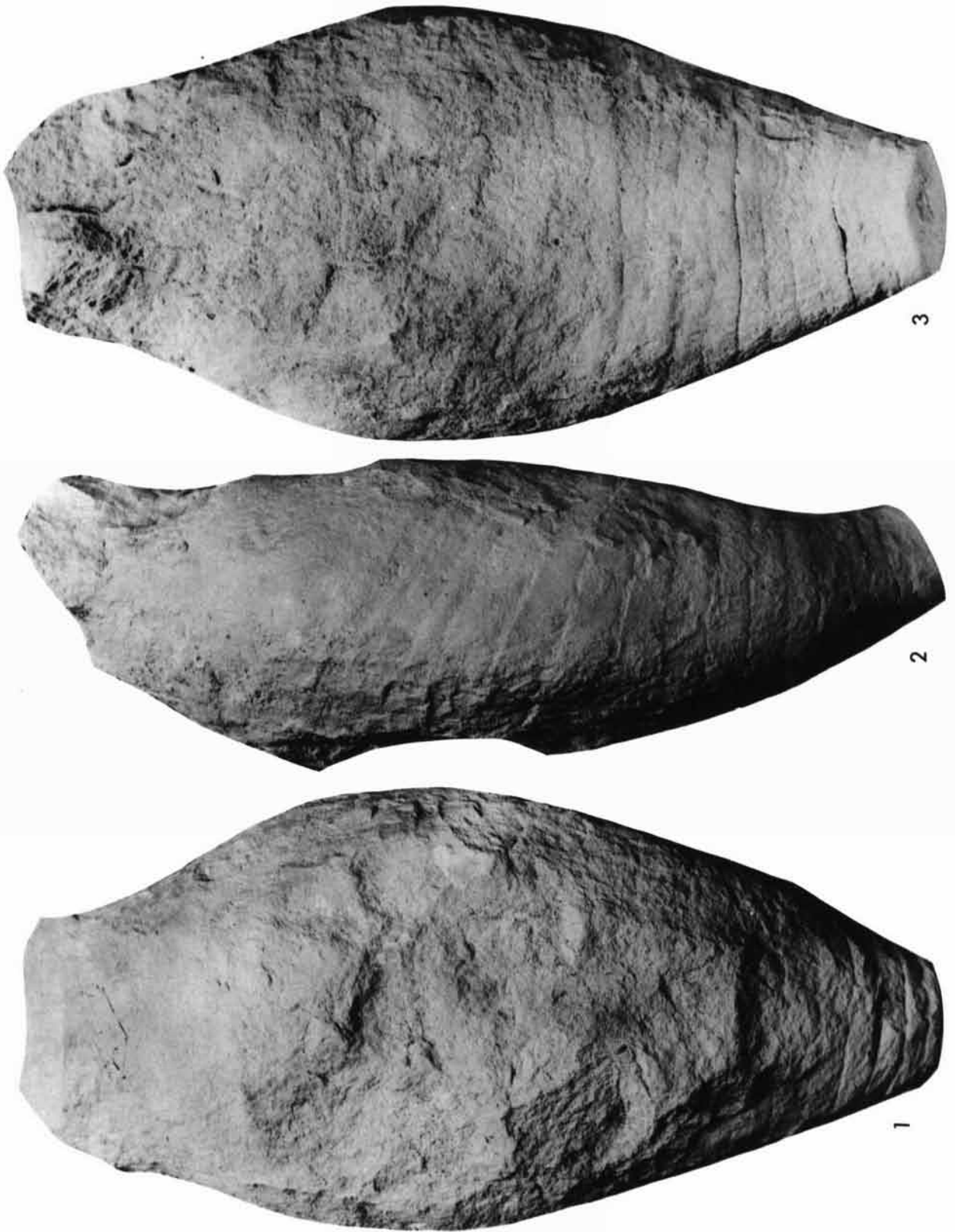
EXPLANATION OF PLATE 7

CYRTOGOMPHOCERATIDAE—*Cyrtogomphoceras*

FIGURE

1-3. *Cyrtogomphoceras nutatum* FOERSTE & SAVAGE, holotype, from Nelson limestone (Ordovician) on the Nelson River, Hudson

Bay; Illinois Geol. Survey collections.—1, Dorsal view, $\times 1$.—2, Lateral view, dorsum at left, $\times 1$.—3, Ventral view, $\times 1$.



FLOWER & TEICHERT—Order Discosorida (Cephalopoda)



FLOWER & TEICHERT—Order Discosorida (Cephalopoda)

Lake Timiskaming, Ekwan of Hudson bay, and unnamed Silurian rocks of Southampton Island, this fauna is fairly constant. Species vary but we find here representatives of *Stokesoceras*, *Discosorus*, and *Endodiscosorus*. Also, *Lowoceras* and *Tuyloceras*, are known only in the range of this fauna.

Certain of the Discosoridae are found outside of this range, always in strata of certain or possible Clinton age. *Kayoceras*, which is little more than a *Discosorus* with a central rather than ventral siphuncle, is known only from the Hopkinton dolomite of Iowa. True *Discosorus* occurs there also. *D. austini* and *D. perexpansum* are found in the Dayton limestone of southern Ohio, a formation which lies low, rather than high, in the Clinton. *D. conoideus* occurs in New York in shales of the Clinton. By-passing the vexations of changing stratigraphic nomenclature, it is evident that it is low in the Clinton, and lies well beneath the marked stratigraphic break which CHADWICK (1918) found dividing the Clinton into two distinct depositional units. In Anticosti *D. gunense* is found in the Gun River beds and *D. infelix* in the overlying Jupiter beds, both recognized as Clinton in age. Correlation with the northern faunas is strengthened by the presence of *Huroniella* in the Gun River and also in the Jupiter beds, where it is joined by species of *Huronia*. Among nautiloids, only *Huronia* extends into the overlying Chicotte beds, which may also be late Clinton rather than Lockport-Racine in age.

The Phragmoceratidae and Mandaloceratidae appear sparingly in beds of Clinton age, that is, belonging in the early half of the Middle Silurian, but representatives of these families are very abundant in the later half, consisting of Racine-Guelph equivalents. In North America, *Tubiferoceras* and *Phragmoceras* appear in the Liston Creek limestone of northern Indiana. *Mandaloceras chaceae* occurs in the late Clinton Irondequoit limestone of New York. *Phragmoceras anticostiense* is found in the Jupiter formation of Anticosti. In Europe, *Phragmoceras imbricatum* occurs in Étage E₁ of Bohemia. Exact equivalence of the Gotland section seems doubtful, but HEDSTRÖM's "horizon I," containing *Phragmoceras* and *Tubiferoceras*, is certainly in the early half of the Middle Silurian, and possibly "horizons II and III" should be grouped there also. A survey of both of these families shows that there is no close accord between the evolutionary sequence of the genera and their order of appearance, as now known in the stratigraphic column. *Tubiferoceras*, morphologically a specialized *Phragmoceras*, is invariably relatively early in appearance. *Phragmoceras* extends much higher than *Tubiferoceras*. Morphologically, Phragmoceratidae with open apertures are simple and logically primitive but none of them occur early. In

fact, *Protophragmoceras*, *Endoplectoceras* and *Sthenoceras* are known only from Étage E₂ of Bohemia. It is there also that most of the Mandaloceratidae are found, all genera being represented. It is primarily *Mandaloceras* which extends its range into the equivalent Racine and Guelph beds of North America. The Trimeroceratidae, potential specialized descendants of the Mandaloceratidae, show the same distribution. The Clinton *Mandaloceras chaceae* is far from showing any aspects which could be called primitive.

Discordance between evolutionary progress and appearance of the genera is not as surprising as first might seem. In so far as our limited knowledge goes, we have had no glimpse of the *Mandaloceras* stock between *Madiganella*, somewhere not very high in the Ordovician of Australia, and the sudden appearance of the Mandaloceratidae in the Middle Silurian. The Cyrtogomphoceratidae occur in North America in beds possibly as old as late Trenton and certainly older than Richmond. It may be that the occurrences of the family in the Oslo region and in the Lyckholm beds of Estonia are not latest Ordovician. At the very least, nothing is known of the stock in Early Silurian time. When both of these families reappear, evolution has plainly progressed considerably and order of appearance of the genera, as well as their distribution, shows selection by paleogeographic and ecological factors in a stock which must have been well differentiated by late Clinton time, when we find the first representatives of both families.

That the Upper Silurian record is meager is not surprising. Cephalopod faunas of this age are scarce and poorly known. *Pristeroceras* and *Phragmoceras* appear in the Bertie waterlime of New York. *Phragmoceras* extends into the Manlius, the latest Silurian.

No Lower Devonian representatives of the order Discosorida are known; this is a time interval for which the cephalopods are rather scarce and our knowledge of them is very incomplete. It is not until the latter half of the Middle Devonian that the last genus, *Alpenoceras* is encountered. It is found in a widely recognized faunal realm, characterized by *Stringocephalus*. It is known from the Stringocephalus limestone in Germany, the equivalent Alpena limestone of northern Michigan, and Winnipegosis dolomite of Manitoba. One fragment of a siphuncle is known from the overlying lower part of the Upper Devonian of Germany. Beyond that point the stock is unknown.

It is surprising that the families Lowoceratidae and Discosoridae are developed most logically from *Fabero-ceras*, of austral Ordovician faunas, and yet their distribution is subarctic in North America, and it is as defi-

EXPLANATION OF PLATE 8 CYRTOGOMPHOCERATIDAE—Landeroceras

FIGURE

1,2. *Landeroceras prolatum* (MILLER). A nearly complete individual (hypotype) from Bighorn dolomite (Ordovician), Lander sandstone member, near Lander, Wyo.; collection of the writer. —1, Ventral view, showing septa and outline of part of siphuncle segments apparently in flattened contact with the

ventral wall of shell in their expanded portions, $\times 1$. —2, Lateral view, venter at left, showing surface markings, $\times 1$; the apparent irregular expansion in early portion possibly represents an original condition. (See also Pl. 5, fig. 9, for section of siphuncle.)

nately a boreal group in Silurian time as are the Cyrtogomphoceratidae and most Westonoceratidae of the Ordovician. It is almost equally remarkable that so far as known, the two families are exclusively confined to strata of Clinton age and that as yet no survivors have

been found in the prolific cephalopod faunas of the later Middle Silurian; also when the stock reappears in the later Middle Devonian, it is again in an association which, as far as North America is concerned, is essentially a boreal one.

EVOLUTION WITHIN THE DISCOSORIDA

GENERAL FEATURES

It is evident from the preceding summary of stratigraphic and geographic distribution of the genera that our knowledge of the discosorid stock is as yet very incomplete. Indeed, it could be said that present knowledge rests upon widely spaced glimpses of the stock, in both space and time. While this discontinuity is significant in itself, for the discosorids show a remarkable distribution that certainly will be of value in tracing faunal migrations and relationships, it necessarily makes the tracing of precise evolutionary developments within the stock more difficult. The difficulties of the markedly incomplete representation of the group in the Ordovician, Silurian and Devonian, have been augmented by rarity of well-preserved material. It is not surprising then that, while identity of the group can be established and its evolution traced in general terms, there remain many more precise matters of relationship upon which no certain answer can be supplied at present.

The general picture of evolution of the stock has already been outlined, and expressed in Figure 3. The primitive family Ruedemannoceratidae is known in the Chazy of North America and Ordovician of central Australia. Genera of this group have expanded siphuncle segments, thick, well-specialized rings, but no other deposits. It is an endogastric stock with the siphuncle relatively close to the center.

The Ruedemannoceratidae gave rise to two distinct stocks. First, with little internal change but development of a contracted living chamber, they gave rise to the essentially Middle Silurian Mandaloceratidae. Second, with inflation of the bullettes, development of a dominantly compressed section, and shifting of the siphuncle from a subcentral to marginal position, they gave rise to the Cyrtogomphoceratidae which are Middle and Upper Ordovician.

Without much internal change other than an apparent slight simplification of the connecting ring, the Cyrtogomphoceratidae gave rise to the Silurian Phragmoceratidae, in which, as in the Mandaloceratidae, specialized contracted apertures developed. However, the Westonoceratidae developed in the early Middle Ordovician, showing more profound advances. The shells reversed their curvature and became exogastric. The siphuncle was distinguished by elaborate rings and swollen bullettes with additional deposits which at first consisted of annulo-siphonate parietal deposits, very much like those of the Pseudorthoceratidae in manner of growth. In later Westonoceratidae the deposits ceased to be confined to the inner surfaces of the individual connecting rings and came to extend throughout an appreciable length of the siphuncles. Thus, structures that started out as a series of discrete segmental deposits developed into a series of continuous endocoines. Such cones have been observed in *Winnipegoceras sinclairi* and several species of *Fabero-ceras*.

In the Silurian Lowoceratidae connecting rings were still swollen into bullettes in early growth stages but they became suppressed in the adult, so that a series of broadly expanded segments with endocoines was produced and the scanty available specimens show a little evidence of the original complexity of the ring. In the Discosoridae the early bullettes are suppressed and the shells are essentially short brevicoines. Anomalously, the last survivor of the stock, *Alpenoceras* of the Devonian, assumes the endogastric form and thus comes to resemble its remote ancestors of the Ruedemannoceratidae and Cyrtogomphoceratidae.

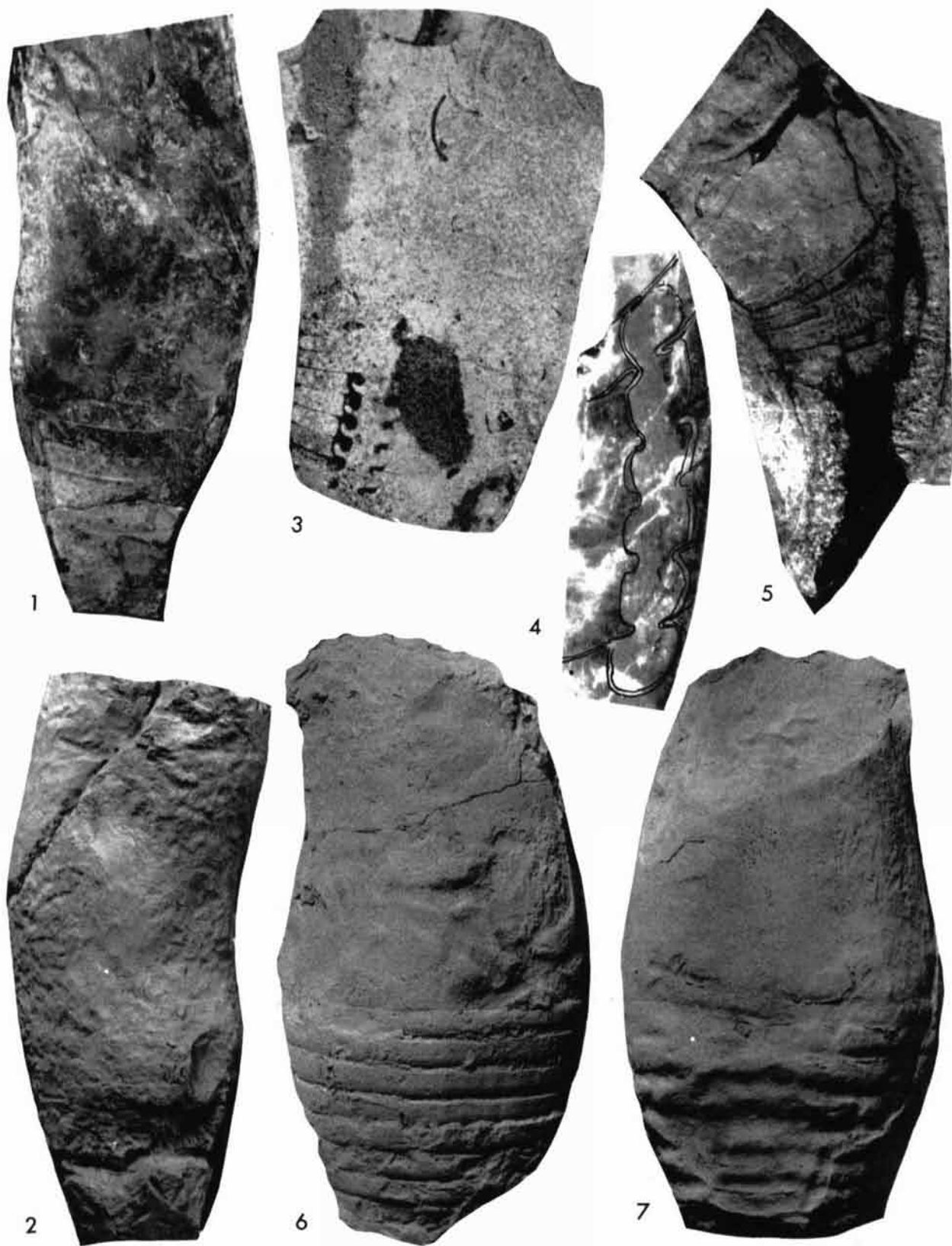
Within this general framework it is possible to trace evolution with greater precision and certainty, though, as previously indicated, some points of vexing uncertainty

EXPLANATION OF PLATE 9

CYRTOGOMPHOCERATIDAE—*Ulrichoceras*; WESTONOCERATIDAE—*Teichertoceras*, *Westonoceras*, *Simardoceras*

FIGURE

- 1-2. *Teichertoceras sinclairi* FLOWER, n. sp., holotype, from Simard limestone (Ordovician) at Ste. Anne de Chicoutimi, Que.; collection of the writer.—1, Left lateral surface, a natural section (later ground and shown in Pl. 5, fig. 10, in enlargement).—2, Right lateral side, showing surface of internal mold, aperture incomplete, $\times 1$.
3. *Ulrichoceras beloitense* FOERSTE, vertical section of holotype, venter on left, showing a dolomite internal mold from which most of the original calcareous shell parts have been removed, including the large bullettes of the siphuncle. From the Platteville limestone, Middle Ordovician, at Beloit, Wisconsin, U. S. Natl. Mus. no. 25302, $\times 2$. See also Pl. 5, fig. 1-4 for exterior of specimen.
- 4,5. *Simardoceras simardense* FLOWER, n. sp., holotype, from Simard limestone (Ordovician), at Ste. Anne de Chicoutimi, Que.; collection of the writer.—4, Section of siphuncle (retouched), $\times 3.4$ —5, Nearly vertical natural section, $\times 1$.
6. *Westonoceras sinclairi* FLOWER, n. sp., holotype, from upper Trenton (Middle Ordovician), at dam on Jacques Cartier River, Que.; collection of the writer. Lateral view, venter at right, rounding of basal part not natural but due to weathering, $\times 1$.
7. *Westonoceras? diestocerooides* FLOWER, n. sp., holotype, from Tetreauville beds, upper Trenton (Middle Ordovician), Trois Rivières, Que.; McGill Univ., Redpath Mus. Lateral view, venter at left, $\times 1$.





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remain in establishing relationships between individual genera (Fig. 11).

RUEDEMANNOCERATIDAE

Ruedemannoceras is the oldest and quite possibly, the most primitive of the known genera of the Discosorida. Therefore, it serves as a natural starting point for discussion of the order, for the genus is one from which all others logically can be derived. It is an endogastric cyrtocone, depressed in cross section, with the venter slightly more flattened than the dorsum and sutures tending to slope forward on the dorsal side in late growth stages. The siphuncle is only slightly ventrad of the center. In earliest stages the necks are short and straight, with the segments slightly expanded between them. The pattern is that of the siphuncular bulbs elsewhere known only in the archaic family Pletronoceratidae (FLOWER, 1954). With growth, the segments become more expanded, the necks lengthen, and as they lengthen the added portion invariably is recurved into brims. The ring becomes complex in structure, developing vincula, granular and chitinoid zones being separated by the first amorphous band and the chitinoid zone set off by a second amorphous band from the two layers of the bullette. Segments become very broadly expanded in the early mature stage but tend to be more spherical and less strongly expanded in late maturity. Cameral deposits are strongly developed. Already one peculiarity of the order—an extremely short mural part of the septum—becomes apparent. *Franklinoceras*, which is associated with *Ruedemannoceras*, is known only from a relatively late growth stage. It differs primarily in its more transverse sutures and strongly compressed section, which is more narrowly rounded dorsally than ventrally. It is closely related to *Ruedemannoceras*, and indeed was at first considered to belong in the genus.

Madiganella, of the Ordovician of Australia, is more advanced than *Ruedemannoceras*. The shells are nearly straight but depressed in section, with the venter slightly flattened as in *Ruedemannoceras*. Sutures are faintly sinuate, developing weak ventral lobes, instead of sloping forward on the dorsum. The outline of segments of the siphuncle is similar to that found in the latest known growth stages of *Ruedemannoceras*. The persistent preservation of a central canal is a new feature. *Madiganella* is a somewhat specialized edition of *Ruedemannoceras*,

the specialization being correlated with the fact that published figures of *Madiganella* represent much later growth stages, with larger shell diameters than in any known *Ruedemannoceras*. The features shown are so much a projection of those noted in passing from early mature to later stages of *Ruedemannoceras* that they could well occur in that genus with further growth. *Madiganella* could well be of Chazyan age, although this is not established by field evidence. The specializations are those which would be expected of a younger form. *Madiganella* is the only known link between the Chazyan *Ruedemannoceras* and the Middle Silurian *Pseudogomphoceras*; the anomalous stratigraphic gap becomes less perplexing if it is remembered that the Larapintine group in which *Madiganella* occurs, embraces a considerable part of the Canadian and higher Ordovician, and may contain several distinct stratigraphic units. It may be that we find here the only known post-Chazyan survivors of the Ruedemannoceratidae. Where in the world survivors of this stock persisted until its next descendant, *Pseudogomphoceras*, appears in Étage E₂ of the Bohemian Silurian, is as yet unknown.

MANDALOCERATIDAE

Pseudogomphoceras, of the Middle Silurian, shows features of the phragmocone which internally duplicate exactly those of *Madiganella*. Gross features are simplified; the sutures are perfectly transverse and the section slightly depressed, but with dorsum and venter equally rounded. The exact form of the aperture is not known but it is clearly contracted strongly. The one known specimen of *P. rigidum* has an incomplete aperture but all evidence suggests that it was very close in form to that of *Ovocerina*.

Ovocerina alphas is a breviconic edition of *Pseudogomphoceras*. The siphuncle is large in diameter, its segments broadly expanded, and filled with a vesicular structure. It differs primarily in lacking any trace of a central tube. The shell expands rapidly and then contracts rapidly, so that in profile the shell wall is convex, instead of straight, in a long early portion. BARRANDE regarded this and allied species as exhibiting natural truncation of the apex, a conclusion which is certainly supported by his figures. Such truncation is not apparent in all species of the genus, however.

Ovocerina is the logical point of origin of several

EXPLANATION OF PLATE 10

WESTONOCERATIDAE—*Teichertoceras*, *Winnipegoceras*, *Fabroceras*

FIGURE

- Winnipegoceras royi* MILLER, YOUNGQUIST & COLLINSON, an exceptionally large form (and yet one seemingly within limits of the species) from the Selkirk limestone (Ordovician) at Tyndall quarries, Manitoba; collection of the writer. Lateral view, venter at right, $\times 1$.
- Teichertoceras husseyi* FOERSTE, holotype, from upper Trenton (Middle Ordovician), near Cornell, Mich.; Univ. Michigan, no. 14461.—2, Lateral view, venter at left, showing weathered surface with siphuncle exposed basally by slight grinding, $\times 1$.—3, Opposite side, showing course of sutures on internal mold, with portions of attached shell, $\times 1$.—4, Siphuncle from lower part of Fig. 2, showing form of segments, thick rings, and swollen bullettes; parietal deposits are absent, $\times 7$.
- Westonoceras* sp., specimen from Ordovician of Baffin Island, precise locality unknown. Thin vertical section of portion of a phragmocone, venter at right, showing cameral deposits on venter, siphuncle segments, and remnants of a central tube in anterior part of siphuncle, $\times 3.2$. (See also Pl. 11, fig. 1; Pl. 12.)
- Fabroceras gracile* FLOWER, n. sp., holotype, from Leipers formation (Upper Ordovician), Cumberland River, near Rowena, Ky.; collection of the writer. Vertical section, venter at right, $\times 1$.

specializations that seem to occur in the Mandaloceratidae, each so independent of others that any attempt to recognize finer groups is extremely difficult. The siphuncle changes in several ways. First, the siphuncle becomes small, slender, and close to the venter, the segments becoming fusiform in outline and empty, and if the rings are still thick and complex, this condition is no longer obvious from casual inspection of specimens. Again, the siphuncle assumes the peculiar form found in typical *Mandaloceras*, in which the early segments are markedly slender, the later ones being very broadly expanded. In conjunction with this type of siphuncle the peculiar structures which BARRANDE called "obstruction rings" appear. They are deposits formed relatively late in history of the siphuncle segment, for they are developed in the early part of the shell and are found to decrease when traced forward, showing the ontogenetic pattern of anulosphonate deposits. They are thickenings of shell material at the septal foramina, from which actinosiphonate rays project for a short distance forward and backward. They are quite similar in form to structures previously regarded as actinosiphonate deposits, though possibly abortive ones. Such deposits are particularly characteristic of the Devonian family Brevioceratidae, a family which seems well established as a member of the Onco-ceratida. The similar appearance of the "obstruction rings" in *Mandaloceras* suggest oncoceroid affinities for this group also. The Mandaloceratidae thus present a very perplexing series of questions. Do they comprise two contemporaneously convergent groups, one of oncoceroid and one of discosorid origin? If so, where is the boundary between them? If not, is the entire group of discosorid origin or of oncoceroid origin? Careful review of the evidence fails to show any possible division between two possibly independent groups. Further, any attempt to subdivide the assemblage fails largely because variations in the pattern of the siphuncle seem to be so completely independent of variation in other shell features, in particular, the aperture and surface markings. Apertures vary from that of *Ovocerina*, with the main part of the aperture rounded but with a prominent and usually very distinctly outlined hyponomic sinus, to those in which the aperture is T-shaped with arms transverse, or, as in the group separated as the genus *Umbeloceras*, with lateral arms curved toward the ventral side. In some species, both with the rounded apertures of *Ovocerina* and the T-shaped ones more typical of *Mandaloceras*, the mid-dorsal part of the aperture is definitely convex, approaching the form of *Eotrimeroceras*. The other major variation in the shell is the development of costae and constrictions. In *Vespoceras* there is a characteristic very marked constriction of the shell that occurs long before the final contraction of the living chamber. In *Cinctoceras* there are strong costae which are reflected variably upon the interior and produce many very shallow constrictions not unlike those found in some specialized species of *Fabro-ceras*. The whole group seems to exhibit such homogeneity and independence of variation of features of shell surface, aperture, and siphuncle, that the conclusion seems inescapable that it represents a natural group rather than contemporaneous convergent homeorphs. The evidence of the internal structure supplies a clear con-

nection with the Discosorida through *Pseudogomphoceras* and *Madiganella*. On the other hand, the affinities of the family with oncoceroids, previously assumed from lack of any better suggestion, are so vague and general that there had been much doubt as to which oncoceroids could be immediate ancestors. As noted in the following section, it is possible that the Mandaloceratidae are the logical origin also of the Trimeroceratidae and this family may also be of discosorid rather than oncoceroid origin.

CYRTOGOMPHOCERATIDAE

Ulrichoceras is the oldest known genus of the Cyrtogomphoceratidae. It shows several features which recall the Ruedemannoceratidae and supplies something of a transition between the families. The siphuncle has swollen bullettes, a new feature and one indicating relationship with higher Cyrtogomphoceratidae, but the cross section is still broad, with flattening on the ventral side. The sutures tend to slope slightly forward on the dorsum and develop slight lobes on the ventral surface. The siphuncle is still much closer to the center of the shell than in more advanced members of the family. That these features recall the Chazyan *Ruedemannoceras* and that *Ulrichoceras*, which possesses them, is the only member of the Cyrtogomphoceratidae so far known from beds of early Mohawkian (essentially Black River age), suggest that *Ulrichoceras* is the most primitive member of the Cyrtogomphoceratidae. The shell is an endogastric one, with a slightly contracted aperture bearing a hyponomic sinus.

Probably *Strandoceras* is the next evolutionary step. It is a compressed cyrtocone with venter narrowly rounded in cross section and with sutures bearing lateral lobes. The siphuncle is close to the venter, its segments broadly expanded, rings thick and bullettes large. It is cyrtoconic and moderately expanding in the young, straighter and more slender in the adult, and the aperture lacks a definite contraction. The genus *Kiaeroceras*, known only from late stages, is an essentially straight edition of *Strandoceras*, similar both in cross section and form and structure of the siphuncle segments. As noted in later discussion, there is more than a suggestion that the early part of the shell was probably slightly endogastric.

Lyckholmoceras is a generalized cyrtocone in form and in this respect quite similar to *Strandoceras*. It is similar in sutures and section, but more gently curved, its most distinctive feature being the relatively slender, slightly expanded segments of the siphuncle.

Cyrtogomphoceras, dominantly a genus of the American Red River faunas, is a compressed brevicone, commonly fusiform in profile, having the aperture definitely though not extremely contracted. The shells are dominantly compressed and the sutures have lateral lobes. Segments of the siphuncle increase very rapidly both in minimum diameter and degree of expansion in the camerae through early growth stages but they may remain the same in proportions or may even contract slightly in latest growth stages. Rings are thick and terminate in swollen bullettes. A few members of the genus are broad in cross section, though most forms are compressed. Most features suggest an origin in the more generalized

Strandoceras, but it is not beyond range of possibility that the broad section is primitive, like the tendency toward contraction of the aperture; if so, the genus may be an off-shoot of the older and more primitive *Ulrichoceras*.

Landeroceras is regarded as little more than a specialization of *Cyrtogomphoceras* in which the shell is straight

and fusiform, so that externally the genus is quite similar to *Diastoceras*, which it fails to resemble in internal structure.

It should be noted that previous interpretations of the *Cyrtogomphoceratidae* (FLOWER, 1946) as an endogastric specialization stemming from the *Westonoceratidae* has

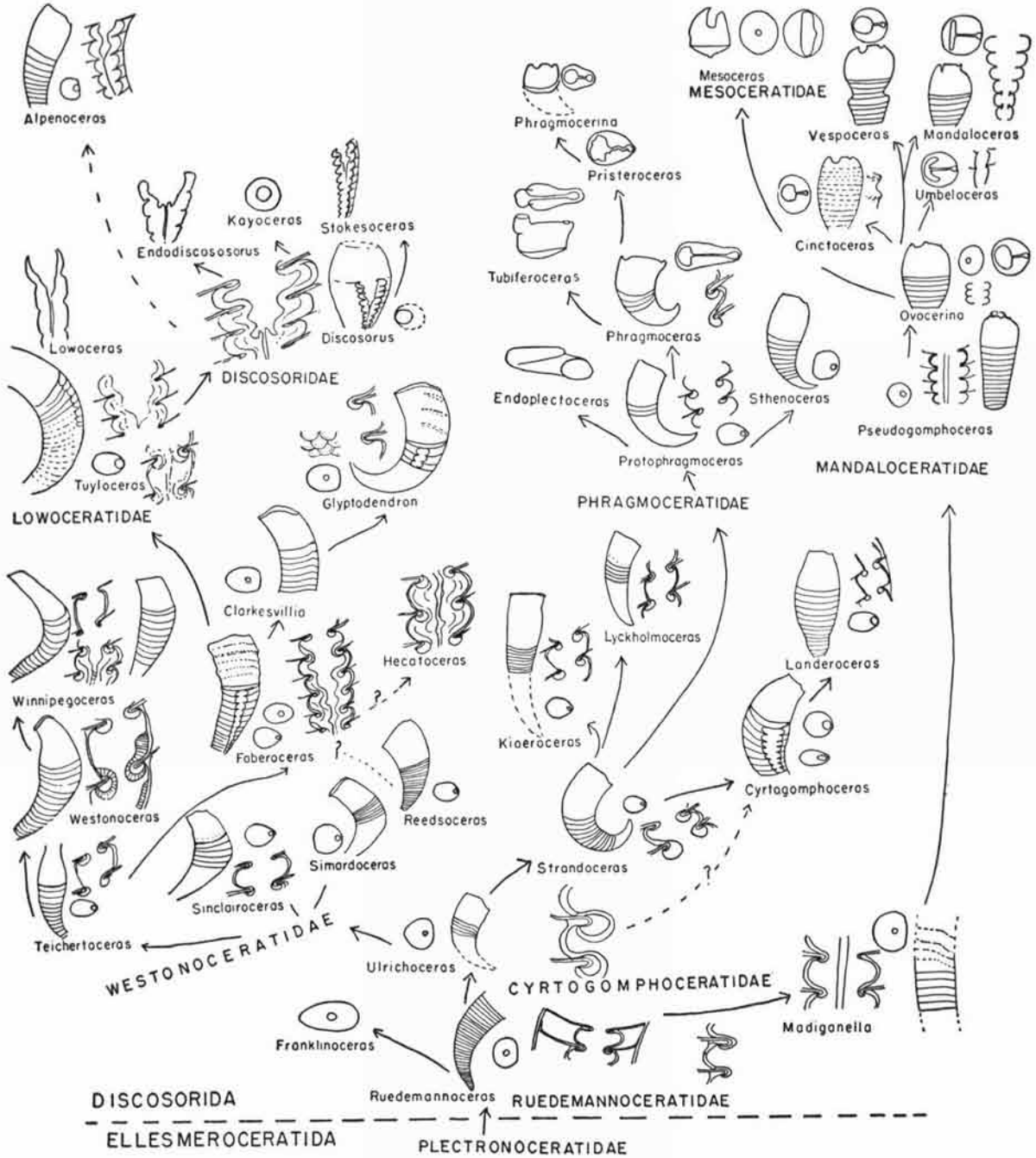


FIGURE 11. General evolutionary pattern of the Discosorida.

Essential features of the genera are shown, and, except for the torticonic *Endoptoceras*, internal molds, cross sections and siphuncles are oriented with the venter to the left. In some places more than one possibility is indicated, favored interpretations be-

ing indicated by solid arrows and less probable alternatives by broken-line arrows. Details of structure and relationship are discussed in the text.

been abandoned in the light of new evidence. Earlier it was not certain that the archaic *Ruedemannoceras* was endogastric. Neither was it clear from the published descriptions and figures that the Cyrtogomphoceratidae apparently possess no parietal deposits; rather, the annular constrictions within the siphuncles are apparently only swollen bullettes, properly interpreted as part of the connecting ring. It is a rather surprising fact that the Cyrtogomphoceratidae now seem to embrace all of the endogastric cyrtocones of the Ordovician. Endogastric shells developed in the Oncoceratidae in the great expansion of that stock in the Silurian, beyond doubt, but the few Ordovician endogastric shells thus far encountered prove without exception to belong to the Discosorida, and most of them to the Cyrtogomphoceratidae.

PHRAGMOCERATIDAE

Though an appreciable gap separates *Strandoceras* from the Ordovician rocks of the Oslo region from *Protophragmoceras* of the Middle Silurian, the two genera are very similar. *Protophragmoceras* is like *Strandoceras* in gross features but has a smaller siphuncle with more heart-shaped and less ellipsoidal segments, thinner rings, and smaller bullettes. As noted in description of the genus, one species at least seems to be specialized by addition of a secondary deposit, the origin and morphological detail of which are unknown. It seems, however, to be an aberrant feature confined to a single species. *Endoplectoceras* is similar in fundamental features of the siphuncle, cross sections, and sutures and is set apart as a torticonic genus, the only one known in the Discosorida.

Sthenoceras is a large shell, less curved generally than others, the mature living chamber becoming straighter and less rapidly expanded, and commonly contracting slightly at the mature aperture. Typical forms have large broadly expanded siphuncles with thick walls and bullettes evident. *Danaoceras* of the Oncoceratida, is a contemporaneous genus of very similar shape but of oncoceroid siphuncular organization. Some Bohemian Silurian species cannot be placed in one or other of these genera on the basis of present incomplete knowledge of their internal structure. In this stock, as in the Mandaloceratidae, there is a possibility of simplification of the internal structure. Some species with siphuncles of small diameter and slender segments without obvious thickening of the rings or swollen bullettes may prove to belong to the discosorid stock.

Phragmoceras agrees in internal features so strongly with *Protophragmoceras* that it is obviously an edition of that genus which achieved a strongly contracted aperture. It is interesting to reflect that this is one of the few instances in which two genera with names derived one from the other and implying relationship prove actually to be related. *Tubiferoceras*, unknown internally, is placed with *Phragmoceras* because in the known features there is evidence of close relationship, almost of intergradation, between the genera. *Pristeroceras* and *Phragmoceras* of the Upper Silurian, unknown internally, are placed here largely because they seem to be logical descendants of *Phragmoceras*. Unless far better-preserved specimens are

found than strata yielding these forms give us reason to expect, the position of these two genera must always remain somewhat uncertain. It should be noted, however, that isolated siphuncles of *Pristeroceras* have been found. While not much is known from their structure, the specimens are of such a nature that if actinosiphonate deposits are present and the genus is allied to the Hemiphragmoceratidae, one may expect the material to show some indication of this type of structure, which it does not.

WESTONOCERATIDAE

The Westonoceratidae are derived from the Cyrtogomphoceratidae and are marked by two main advances—the assumption of an exogastric instead of an endogastric form and appearance of parietal deposits within the siphuncle. Vexingly, it is here that the meager evidence permits more than one possible interpretation of relationships among the genera.

A logical origin of the group is through *Teichertoceras*, which is endogastric in the young but later becomes exogastric, assuming the form characteristic of typical *Westonoceras*. It has also siphuncle segments very similar to those of *Westonoceras*, being subquadrate in vertical section. Bullettes are present. Evidence of parietal deposits is inconclusive. *Westonoceras*, which ranges from late Trenton through Red River and Eden faunas but not higher, is a logical derivative of *Teichertoceras*. It is exogastric throughout. Siphuncle segments are subquadrate in the early portion but may become more rounded later; they have complex rings, small but definite bullettes, parietal deposits, and in some specimens a central tube.

Winnipegoceras appears to be a derivative of *Westonoceras*. Typical forms are long and slender; others have somewhat less slender fusiform shells with shorter living chambers. Curiously, the apertures of both genera have hyponomic sinuses but that of *Westonoceras* slopes adapically gradually from dorsum to venter, while that of *Winnipegoceras* slopes in the reverse direction until a sinus is developed in the mid-ventral region.

Faberooceras is a derivative of *Westonoceras* in which the fusiform contraction of the later part of the shell is lost. Early siphuncle segments, particularly of the older (Catheys and Cynthiana) species, are very similar to those of *Westonoceras* in quadrate outline and internal structure. Later segments become broader, more broadly rounded, particularly in the younger (Leipers and Covington) species. It is in the younger and obviously more specialized species of this genus that the parietal deposits grow over a series of segments and thus develop into endocones. A similar phenomenon occurs in *Winnipegoceras sinclairi*.

Clarkesvillia is an expression of *Faberooceras* in the Richmond which is characterized by flattening of the mid-ventral part of the cross section. Siphuncle segments are still broadly expanded (very broadly expanded in the adult) and have parietal deposits but no endocones. *Clarkesvillia* must have developed from a simple species of *Faberooceras* rather than more advanced ones.

Glyptodendron is a logical extension of *Clarkesvillia* into the Brassfield limestone of the Lower Silurian. It

agrees quite closely with that genus in cross section, shape and sutures but differs in three important features: (1) The siphuncle segments are less broadly expanded and the rings still thick, with bullettes largely suppressed, being small in the latest rings but suppressed in the early ones. (2) The surface has developed a characteristic scaly pattern, on the basis of which the first known fragments of this genus were misidentified as fossil plants. (3) The mature part of the shell bears prominent lateral costae.

While the line of *Faberoceras*-*Clarkesvillia*-*Glyptodendron* is well established, there seems to be more than one possible explanation of its origin. It can, as shown above, be derived from the *Teichertoceras*-*Westonoceras* line. However, there are other possible genera from which it can be derived and these are not yet known from adequate material. *Reedsoceras* is a cyrtocone similar to the simpler *Faberoceras* in aspect, differing mainly in the closely spaced transverse sutures and cross section, which is typically as broadly rounded ventrally as dorsally. Its siphuncle segments are large and broadly expanded but so little is known that the relationship of the genus is uncertain. However, the large size of the shells and large broadly expanded segments are features inherent in the older discosorids and completely foreign to anything known in Ordovician Oncoceratidae. *Reedsoceras* put in its first appearance in the Platteville, associated with *Ulrichoceras*. Vexing are two exogastric genera of the Simard limestone. If *Teichertoceras*, which appears here, gave rise to *Westonoceras*, one would expect that perfect exogastric form would not be achieved until the later half of the Middle Ordovician but both *Simardoceras* and *Sinclairoceras* are perfectly exogastric forms. *Simardoceras*, though unusual in the slender segments of the siphuncle, possesses bullettes. *Sinclairoceras* is more typical in cross section and form but its late siphuncle segments are extremely broadly expanding. For this reason it is a much less likely ancestor of *Westonoceras* than *Teichertoceras*. Clearly, the history of the Westonoceratidae must go back farther than the present known species, which are of late Black River age. The dilemma presented by the essentially contemporaneous appearance of *Teichertoceras*, *Simardoceras*, *Sinclairoceras*, and the much more primitive *Ulrichoceras* of the Cyrtogomphoceratidae can be resolved only when faunas are found containing earlier discosorids, possibly of Lowville age.

Lavaloceras, known only from two species from late Trenton deposits of Quebec, is not indicated on the accompanying diagrams. Its form suggests that it is derived from *Westonoceras* through such species as *W. sinclairi* and *W. diestocerooides* and that it is mainly specialized by broadening of cross section, straightening of the shell, and development of essentially transverse sutures. Its position in the cephalopods must remain tentative, however, for the structure of the siphuncle is not known.

Hecatoceras, known only from isolated siphuncles, is apparently endogastric but is placed in the dominantly exogastric Westonoceratidae because what is known of the structure of the siphuncle indicates probable bullettes, thick rings, and endocones within. The strong development of the endocones indicates that the genus is allied to

Faberoceras. No such structures are known in the dominantly endogastric Cyrtogomphoceratidae.

LOWOCERATIDAE

Tuyloceras, the crucial genus of the Lowoceratidae, is a long slender exogastric cyrtocone with faintly contracted mature aperture, compressed section, and sutures with lateral lobes. In form, it lies between such cyrtocoines as *Faberoceras* and the strongly breviconic Discosoridae. Its early siphuncle segments have the subquadrate form of those of *Westonoceras* and early *Faberoceras* and the bullettes characteristic of both. Within it are endocones like those of *Faberoceras*. The early stages are reasonably explained as recapitulating the essential features of its Ordovician ancestors. Adult segments become more rounded, more broadly expanded, surpassing the condition found in *Faberoceras*, and approaching the proportions of *Discosorus*. Indeed, fragments of late stages of siphuncles alone are not easily distinguished from portions of *Discosorus*. The rings here have lost their bullettes and the one known specimen of the single described species is slightly dolomitized, failing to show clearly the thickness of the ring which has been thus far an inherent discosorid feature. There is some indication also of slight elevation at the tip of the endocone, as found in the Discosoridae.

Lowoceras is known only from a series of segments of a siphuncle. The segments are narrow and filled with endocones. The rings are not evident but plainly no bullettes are present. The series of siphuncle segments indicates that the shell was cyrtoconic and probably slender. In its slender segments it is anomalous but not more so than *Deiroceras*, for example, among the actinoceroids.

DISCOSORIDAE

Discosorus has an essentially straight breviconic shell, which is fusiform, expanding rapidly and then contracting toward the aperture. It remains, however, a faintly exogastric shell. The siphuncle consists of broadly rounded segments which increase very rapidly in size as they are traced forward in the phragmocone. Little is known of the connecting rings. Most sectioned specimens consist of isolated siphuncles from which the rings have been lost. It is evident, however, that the rings show some indication of the type of differentiation noted in older discosorids, though the bullette is no longer thickened and the ring itself is very much thinner than in the ancestral types. The early stages of *Tuyloceras*, which recall the Westonoceratidae so strongly, are lost here and evolution is tachygenetic. A speeding of development and elimination of ancestral stages may be connected with the shorter more rapidly expanded shells or may be a feature explained solely in terms of further specialization and normal tachygenesis. Clearly, the type of structure noted in the adult of *Tuyloceras* persists throughout entire ontogeny. The first segment appears to be rounded and differs from others primarily in its naturally smaller size.

Stokesoceras is little more than a slender version of

Discosorus. Of course, it is impossible to say which of the two genera came from the other. *Kayoceras* is similar to *Discosorus*, being specialized mainly in the migration of the siphuncle toward the center of the shell.

Alpenoceras is an endogastric edition of *Discosorus*. Otherwise, it is not strikingly different, a surprising fact in view of its isolated stratigraphic position. It occurs in Middle and Upper Devonian strata, whereas the other Discosoridae are known only from the early Middle Silurian. It is curious that the last of the Discosorida should

show a reversal to the endogastric curvature which is primitive. It is equally strange that this survivor of the stock should be found in the latter half of the Middle Devonian and as yet unconnected with its ancestors. The structural pattern does not seem to be advanced materially beyond that of its Silurian forerunners. Species from the Eifel Devonian show diaphragms crossing the central canal, but no such structures have been observed in the type species though the section is such that they would show if they existed there.

POSSIBLE DERIVATIVES OF THE DISCOSORIDA

The present investigation has increased the scope of the order Discosorida appreciably, suggesting that further studies may show that other genera should be placed in this order. At the present time some evidence suggests possible discosorid affinities for some forms but adequate material for examination has not been available.

Antiplectoceras FOERSTE (1925, p. 67) is anomalous among Ordovician oncoceroids in its large size and very broadly expanded siphuncle. Both features, though superficial, suggest affinities with the Discosorida. The genus is an exogastric cyrtocone compressed in section with the early part moderately curved and later portion nearly straight and with the aperture contracted into a pattern very much like that of *Phragmoceras*. From what is known of the genus, it seems very likely that it may be included in the Westonoceratidae. The type species, which is the only known representative of the genus is *Antiphragmoceras ulrichi* FOERSTE (1925), from the Hermitage limestone of Tennessee.

The two genera *Danoceras* and *Diestoceras* of the Diestoceratidae both show some features of discosorid affinities. These genera and the little known *Pictetoceras* constitute the Diestoceratidae (FLOWER & KUMMEL, 1950), but there are serious problems in defining the genera and interpreting affinities of the family. These problems have already been outlined (FLOWER, 1946, p. 391ff). *Danoceras* comprises relatively small rather slender brevicones in which the siphuncle is known to be made up of quite slender segments of subtrapezoidal form in longitudinal section. Typical *Diestoceras* includes relatively large gibbous shells in which segments of the siphuncle are much shorter, broader, and subquadrate, but more or less rounded in outline. A small group among these species is known to have a thickening of the ring at the septal foramen from which relatively short and commonly irregular actinosiphonate rays extend forward and backward, but the rays generally do not meet. There remains a group of smaller species for which the siphuncle structure is unknown. These forms currently are assigned to *Diestoceras*, with which they agree in gross features, but their relationship is doubtful. Typical large species of *Diestoceras*, range from late Trenton to Richmond. Many small anomalous species occur also in the later Ordovician, but it should be noted that the earlier Ordovician species, by which *Diestoceras* is traced back through rocks of Black River and Chazy age, belong exclusively to this group.

Because of the actinosiphonate deposits in typical *Diestoceras*, the Diestoceratidae have been referred to the Oncoceratida (FLOWER & KUMMEL, 1950), but it should be noted that no evidence of a close connection of the family with other oncoceroids exists; indeed, the discrepancy between siphuncles of *Danoceras* and typical *Diestoceras* suggests that even as now restricted the family may not be a natural one.

Some evidence suggests possible discosorid affinities for both *Danoceras* and *Diestoceras* but it is not conclusive for either genus. STRAND (1933) pl. 13, fig. 1) figured for *Danoceras* thickenings of the apical end of the connecting rings which he termed bullettes. A similar feature was observed in *Danoceras crater* (FLOWER, 1946) but not figured, and somewhat analogous structures are known in *D. twenhofeli* (FOERSTE, 1928) of Anticosti and *D. ravnii* TROEDSSON (1926, pl. 50). It is not evident, however, that these structures are true bullettes as these structures are now understood. No indication of two-layered structure or differentiation of materials from those comprising the remainder of the ring is observed. It is not beyond the range of possibility that the structures may be only a thickening of the tip of the ring, such as was found to precede development of actinosiphonate deposits in *Valcouroceras* (FLOWER, 1943).

Actinosiphonate rays are produced from swellings of the apical part of the connecting ring in several known species of *Diestoceras*, including the genotype, *D. indianense* (FLOWER, 1946, pl. 41, fig. 10), as well as *D. scalare* (FOERSTE, 1928, TEICHERT, 1933, pl. 14, fig. 48) and *D. pyriforme* (TROEDSSON, 1926; TEICHERT, 1934). However, there are other species which have shown only rings which are markedly swollen at the tips and which are very suggestive of the discosorid bullettes in form. Such structures have been figured for *D. eos* (FLOWER, 1946, pl. 38, fig. 7) and *D. cyrtocerinoides* (FLOWER, 1946, pl. 38, fig. 2). Again these structures fail to show the differentiation of two layers or distinction from the remainder of the ring which is characteristic of true bullettes. Unfortunately, examination of well-preserved material by thin sections is required and all of these forms are so rare that as yet no adequately preserved material is available for such a study.

It is possible that should these forms prove to be of discosorid affinities, the bullettes might be modified to produce short irregular actinosiphonate rays closely approximating those of the Oncoceratida. Such a possibility

is suggested by the development of "obstruction rings" in the Mandaloceratidae. On the other hand, similar discrete actinosiphonate rays stemming from a thickening of the ring at the septal foramen are characteristic of *Valcourceras* of the Ordovician and also of the family Brevioceratidae of the Devonian, being known there in *Stereotoceras*, *Naedyceras*, *Brevioceras*, and *Eleusoceras* (FLOWER, 1939a, 1945). Admittedly, the morphological evidence available at present is ambiguous.

In tracing the Mandaloceratidae to the Discosorida, it was assumed that they were contemporaneous convergent homeomorphs with two other families, the Hemiphragmoceratidae and the Trimeroceratidae. The continuous actinosiphonate deposits extending throughout the length of siphuncles of the Hemiphragmoceratidae indicate that the family is allied to the oncoceroids. No such evidence of oncoceroid affinities is found in the Trimeroceratidae. There the siphuncles are small, slender, empty, and the connecting rings are not markedly thickened. If, as noted in discussion of the Mandaloceratidae, real reduction of the siphuncle occurs from broadly expanded segments and thick rings to slender segments and thin rings, the Trimeroceratidae may stem from the Mandaloceratidae rather than the oncoceroids. *Eotrimero-ceras* FOERSTE (1928) has a relatively open aperture, which approaches that of the Mandaloceratidae in form, notably some species currently assigned to *Ovocerina*. Some species of *Ovocerina* show a faint mid-dorsal sinus of the aperture suggestive of the Trimeroceratidae, in general, and *Eotrimero-ceras*, in particular. Likewise, *Clathroceras*, a brevicone of the aspect of *Ovocerina* except that the exterior of the shell is strongly fluted, may be a member of the Mandaloceratidae. It has, again, a small ventral siphuncle of slender segments without any deposits within or an observable thickening of the connecting ring.

It is remarkable that in two stocks of the Discosorida thinning and simplification of the connecting ring are observed. The first and most evident is the progressive series of the Westonoceratidae, Lowoceratidae, and Discosoridae. The relationship of the families is clearly shown by the retention of endocones in such specialized Westonoceratidae as *Fabero-ceras* and onward through the

series, and the tachygenetic suppression of the thick rings and loss of the swollen bullettes in the progression from *Tuyloceras* to *Discosorus*. Without uniformity of the endocones, it would not have been easy to establish the relationship here. Critical examination of the evidence leads to the conclusion that the Mandaloceratidae comprise a unified stock in which there is a similar simplification of the connecting ring, though in a line in which inflated bullettes were not an inherent feature. A third example of simplification resulting in development of thinner rings and partial suppression of the bullettes as swollen structures, is noted in the progression from *Clarkesvillia* to *Glyptodendron*. That such trends toward simplification of internal structure can be demonstrated three times, suggests that perhaps simplification of the rings may have been carried to greater lengths in other descendants of the Discosorida. One such possible case was suggested by specimens of *Glyptodendron* loaned from the U. S. National Museum. With true *Glyptodendron* were specimens which had been labeled as congeneric but proved to belong to the new genus *Cliftonoceras* and also to *Cumingoceras*. They suggested that further simplification of the siphuncle of the Lower Silurian *Glyptodendron* might have been carried farther in these genera as possible descendants. Review of the evidence led to rejection of the hypothesis in this instance. Obvious differences between these genera and *Glyptodendron* are seen in form and position of the siphuncle segments, as well as in cross section and sutures. The evidence supports the previous interpretation that these genera, united in the Uranoceratidae, developed from the Barrandoceratidae through *Bickmorites*. However, the possibility remains that perfected simplification of internal structures may have produced descendants of the Discosorida in which the features of thick complex ring are lost. There is already evidence of three such trends in the order and others may be recognized. The possibility is a very real one, which deserves consideration in relation to cyrtoconic and breviconic genera of still highly uncertain taxonomic position. It is quite possible that such forms may be recognized among the Middle Silurian cyrtococones of Bohemia, though most such forms appear to belong to the Oncoceratida.

ORIGIN OF THE DISCOSORIDA

The present investigation supplies evidence pointing to the origin of the Discosorida in the archaic Plectronoceratidae, independent of all other cephalopod stocks. The origin of the discosorids seemed at first highly uncertain (FLOWER, 1949, 1946). It could be traced back to the Chazyan, but no farther. It was recognized (FLOWER & KUMMEL, 1950) that there were at least two possibilities, first, an origin in the archaic cephalopods, suggested by the thick rings, and second, origin in the oncoceroids. It was observed that early stages of certain of the Westonoceratidae show strong similarities to the oncoceroids. Particularly striking is a similarity between *Fabero-ceras sonnenbergi* of the Cynthiana limestone and species of *Oonoceras* in the same formation. Certain difficulties, however, were recognized in this hypothesis. Simi-

larities between *Fabero-ceras* and *Oonoceras* are superficial, depending on exogastric curvature, compressed section, lateral lobes, and the rather small ventral siphuncle; generally, derivation of the discosorids through the Westonoceratidae from the Oncoceratida, would have required elimination of the family Ruedemannoceratidae, which contains the oldest and apparently simplest discosorids. Further, significant differences exist in the connecting rings, those of the discosorids being primarily thick, whereas those of the oncoceroids are primarily thin and secondarily thickened but with the thickening internal and developing in its fullest extent into actinosiphonate deposits.

The present investigation has led to the complete rejection of the hypothesis of an oncoceroid derivation of

the Discosorida. It is now evident that the Westonoceratidae can be traced back through the Cyrtogomphoceratidae to the Ruedemannoceratidae. Relationships are reaffirmed by the evident homologies in structures within the connecting ring which had not been known previously. Recognition of the derived condition of the exogastric Westonoceratidae, in contrast to the primitive endogastric nature of the Ruedemannoceratidae and Cyrtogomphoceratidae, left a possible oncoceroid origin as a possibility which required no further consideration.

The fact that the discosorids have thick connecting rings as a primitive feature, allies them with the oldest cephalopods, for thick rings are a feature of the Ellesmeroceratida, which are retained in the Endoceratida and Tarphyceratida but lost in other orders. Discovery of early stages of *Ruedemannoceras* with siphuncular bulbs, a feature known elsewhere only in the archaic Plectronoceratidae (FLOWER, 1954), suggested a possible origin in that family independent of all other cephalopod stocks. Recapitulation is not perfect. In *Ruedemannoceras* the siphuncle is subcentral from the earliest stage, instead of ventral. Though the mature shells are endogastric, the apex could possibly be interpreted as exogastric. Thickening and flattening of the septa at the transition from siphuncular bulbs to cyrtocoanitic segments with recurved septal necks is still an unexplained anomaly. However, there is a gradual widening of the siphuncle at the septal foramen, a gradual increase in expansion of the segments, and gradual growth of the septal neck with the new part developed into a brim which increases until it becomes at least three times the length of the neck.

Taking account of this remarkable ontogenetic succession, recapitulation of the siphuncular bulbs in the Plectronoceratidae suggests an origin of the Discosorida in this family, independent of all other cephalopod stocks. The Ellesmeroceratidae are younger than the Plectronoceratidae and probably descended from them (FLOWER, 1954, fig. 7). Though early stages of the Ellesmeroceratidae are poorly known, *Eremoceras* at least shows conclusively that no such recapitulation occurs (FLOWER, MS). Also, no recapitulation of siphuncular bulbs is discernible in the early stage of any cephalopods which, from other evidence, are regarded as evolving from the Ellesmeroceratidae, either directly or through more specialized families. Recapitulation of this sort is lacking in the Michelinoceratida, Endoceratida, Actinoceratida, and Tarphyceratida.

TEICHERT & GLENISTER (1954) have described *Apocrinoceras* from the Canadian of Australia. This genus is a small annulated orthocone with a small marginal siphuncle which resembles that of the discosorids in its combination of expanded segments with recurved septal necks and very thick connecting rings. This genus seemed to be a welcome addition to the Discosorida, supplying the first representative of the order to be recognized in beds as old as Canadian. It was hoped that this form would reduce the morphological, as well as the stratigraphic gap between the discosorids and the ellesmeroceroids. Further examination, however, showed that *Apocrinoceras* presents so many anomalies as a discosorid that it seems necessary to regard it as belonging to a completely different line, one resembling the discosorids in general pattern of the siphuncle but quite unrelated to them. It became apparent that the resemblance between the siphuncles of *Westonoceras* and *Apocrinoceras* did not extend to *Apocrinoceras* and *Ruedemannoceras*. Yet all evidence indicates that *Ruedemannoceras* is primitive in relation to *Westonoceras*. If one postulates derivation of *Westonoceras* from *Apocrinoceras*, he must also postulate that *Ruedemannoceras* does not belong to this general stock. Homologies of the connecting ring of *Ruedemannoceras* with *Westonoceras* and other discosorids require rejection of this interpretation. Though the connecting rings of *Apocrinoceras* show differentiation of structure only faintly, bullettes are wanting and the only indicated structure is a longitudinal banding of the ring in several layers. This type of structure is completely foreign to the discosorids but is typical of the Ellesmeroceratida. The most anomalous feature of *Apocrinoceras* as a potentially primitive discosorid is its form, for the primitive discosorids are cyrtocoones, in fact, primitively endogastric cyrtocoones. Nothing suggests the ancestry of discosorids in orthoconic shells or annulated ones. Therefore it seems possible that this genus may belong to some ellesmeroceroid stock quite independent of derivation of the discosorids from the Plectronoceratidae.

Happily, new evidence establishes the position of *Apocrinoceras* quite clearly. Two other genera, *Desioceras* and *Glenisteroceras* resemble this genus in being tiny annulated shells with small siphuncles which are somewhat expanded within the camerae. The expansion of the segments is less here, however, and these genera supply a transition into the Protocycloceratidae, which are straight annulated orthocones with essentially tubular siphuncles, thick rings, longitudinally banded when seen

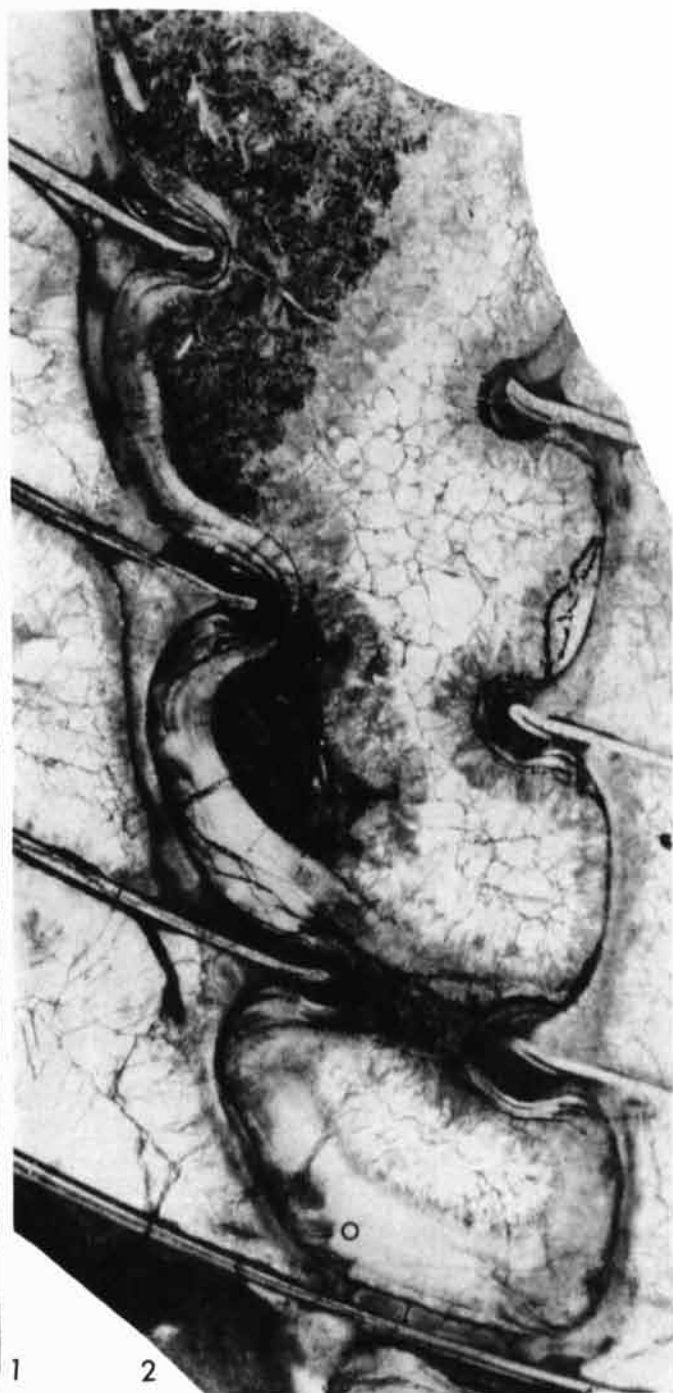
EXPLANATION OF PLATE 11

WESTONOCERATIDAE—*Westonoceras*, *Faberoceras*

FIGURE

1. *Westonoceras* sp., specimen from Ordovician of Baffin Island, precise locality unknown. Portion of thin vertical longitudinal section, venter at right, showing differentiation in connecting ring (most evident on dorsal side of lower two segments) and poor demarcation of ring from material in camerae on the venter, $\times 9$; parietal deposits are complete ventrally, forming a continuous lining of siphuncle, but dorsally they are largely confined to rings surrounding the bullettes.
2. *Faberoceras* sp., specimen from Leipers beds (Upper Ordovician), near Rowena, Ky.; collection of the writer. Portion of

thin section, slightly off center apically, and tangential to the bullette at the base, $\times 9$. Above the basal septum, which is complete, a tangential section through the bullette shows a suggestion of radial differentiation of structure. On the venter, at the left side of the figure, is seen a very abrupt anterior termination of the bullettes, some differentiation in the free part of the ring, and the vinculum short and nearly divided by the granular zone. Dorsally the bullettes are much more abbreviated anteriorly, the free part of the ring largely granular, and the vinculum shows variations from one segment to the other, doubtless due largely to replacement.





FLOWER & TEICHERT—Order Discosorida (Cephalopoda)

in section; the Protocycloceratidae are traceable back to the Ellesmeroceratidae (FLOWER, 1954, fig. 7) and, indeed, *Walcostoceras* is so transitional between the families that it has been difficult to decide in which group it should be placed. Clearly, acceptance of this stock as origin of the discosorids would require complete rejection of the recapitulation shown by the early stages of *Ruedemannoceras*. While, of course, it is not necessary to interpret the early stages of *Ruedemannoceras* as palingenetic, this explanation is logical and likely. On the other hand, rejection of a direct origin of the discosorids in the Plectronoceratidae and acceptance instead of an origin in the Apocrinoceratidae and Protocycloceratidae involve anomalies of form and structure which it would be difficult, and probably impossible, to justify.

As yet, no forms are known connecting *Ruedemannoceras* of the Chazyan with the Plectronoceratidae. Ca-

nadian Plectronoceratidae show in adult stages the development of a tubular siphuncle like that of the Ellesmeroceratidae and more specialized Canadian families. Probably the Discosorida have to be traced back to a distinct origin in *Plectronoceras* of the Cambrian. That such a gap exists is not as surprising as it might appear. In spite of advances in knowledge of Canadian cephalopods, TEICHERT & GLENISTER (1954) found in their investigation of Australian Canadian cephalopods that only one form could be assigned to a previously described genus. It is obvious that many species await description and that much remains to be learned of the morphology of these shells. This is particularly true among the smaller orthoconic and cyrtoconic shells and it is among the latter that the Canadian ancestors of discosorids are probably to be found.

ECOLOGY

The discosorids are primarily cyrtocoines, at first endogastric as observed in the Ruedemannoceratidae, Cyrtogomphoceratidae, and Phragmoceratidae, becoming exogastric in the Mandaloceratidae, Westonoceratidae, Loweroceratidae, and Discosoridae. Yet in *Mandaloceras* itself there is a slight reversal of curvature, *M. verneuli* being endogastric; *Hecatoceras* of the Westonoceratidae and *Alpenoceras* of the Discosoridae also revert to an endogastric form. Much uncertainty exists as to the mode of life of endogastric cyrtocoines, almost no opinions on the position of the shell in life having been published. That a transition can occur from endogastric to exogastric shells in the Discosorida, and occasionally, to endogastric from exogastric ones, suggests that probably no great difference in the mode of life is involved. A similar and more gradual transition exists between the primitive cyrtocoines of the Oncoceratida and some Silurian endogastric derivatives of the stock. It then seems logical to assume that the endogastric cephalopods lived much as did the exogastric ones, with the apex of the shell directed obliquely upward.

Many discosorids have the aperture little contracted, if at all. Such forms appear to have been bottom-dwellers, either benthonic crawlers or epibenthonic swimmers which frequently came to rest.

Shells with visored apertures present a special problem, especially when it is recalled that such forms developed several times independently in entirely different lines of descent, as cited in following numbered statements. (1) In the Gasconade (= Tremadoc) some species

currently assigned to *Burenoceras* of the Ellesmeroceratidae develop shells with constricted apertures which are almost exact duplicates, though in miniature, of *Phragmoceras*. (2) *Antiphragmoceras* in the Ordovician of Tennessee develops an aperture and shell that are quite like those seen in true *Phragmoceras* except that the shell is exogastric, not endogastric. (3) In the Middle Silurian true *Phragmoceras* and its relatives develop. (4) In the Devonian, *Bolloceras* is an almost exact duplicate of *Phragmoceras*; yet its concavosiphonate actinosiphonate siphuncle suggests derivation from the Oncoceratida through the exogastric Nothoceratidae. (5) In the Middle Silurian, the Hemiphragmoceratidae have similar shells and similar apertures, though curvature is exogastric. One genus, *Hemiphragmoceras*, very closely approaches *Phragmoceras* itself in aspect. (6) In the Middle Silurian, the Mandaloceratidae develop from another part of the Discosorida and possibly they gave rise to the Trimeroceratidae.

Considering such examples of convergence in shell form, it is evident that these breviconic shells were specialized for a mode of life which was clearly advantageous, but vexingly, we cannot yet say with certainty what that mode of life was.

It is uncertain whether the animals living in such shells primarily were swimmers or perhaps even floaters, as suggested by MILLER & FURNISH (1937), or whether they were essentially bottom-dwelling forms capable of squeezing a considerable part of their body through the constricted aperture, like the gastropod *Cypraea*. On this

EXPLANATION OF PLATE 12

WESTONOCERATIDAE—*Westonoceras*

Westonoceras sp. Further enlargement of thin section shown on Pl. 10, fig. 5 and Pl. 11, fig. 1, $\times 15$, venter on left. On the upper left most of the short wedge-shaped mural part of the septum is seen. White calcite adjacent to it represents extensively replaced cameral deposits. The ventral wall of the siphuncle shows small bullettes, but the remainder of the ring is only faintly differentiated from the material in the camerae. Parietal

deposits have grown to completion ventrally, and show clear lamellar structure. Dorsally the ring is thicker, clearly set off from material in the camerae. The 3 complete segments show on the dorsum variations in the structure of the free part of the ring. The incomplete anterior segment exhibits a sharp anterior termination of the bullette, orad of which there is only granular material.

question various suggestions but no single convincing answer has been offered. DEECKE (1912) suggested a bottom-dwelling mode of life and PRELL (1921) assembled evidence in support of this hypothesis, although his erroneous assertion that a secondary shell layer covered the original shell exterior, and his suggestion that *Phragmoceras* might be the ancestor of the Octopoda, make one inclined to discount his discussion entirely. In favor of his view, for which neither of these questionable points is essential, it may be observed (1) that these shells are commonly developed in shallow-water associations with a dominantly benthonic association and (2) that protrusion of the head for crawling is theoretically possible. Against the bottom-dweller hypothesis is the conclusion that prominence of the hyponomic sinus suggests a prominent hyponome and therefore an animal which moves primarily by jet propulsion and swimming. The symmetry of the aperture suggests that it is adapted for the protrusion of special organs, probably the eyes and perhaps both eyes and tentacles. On the other hand, we have the suggestion made by ABEL (1924, p. 196) that such animals might have been plankton-feeders whose head could have remained permanently in the living chamber.

Compressed slightly curved fusiform shells are another adaptive form, less evident, because the species are less well known, being dominantly developed in the boreal Ordovician faunas. Such shells were developed in specialized members of both the endogastric *Cyrtogomphoceratidae*, notably in *Cyrtogomphoceras* itself, and in *Westonoceras* and *Winnipegoceras* of the *Westonoceratidae*. Indeed, so striking is the convergence of form, that, for example, only by studies of internal morphology did it become evident that the species described as *Winnipegoceras dowlingi* by FOERSTE belong in fact to *Cyrtogomphoceras*. As first suggested for *Westonoceras* by TEICHERT (1933, 1935) such forms may well have been moderately successful swimmers.

It has been emphasized in the chapter on distribution and range that from Black River time to close of the Ordovician, at least, the discosorids were dominantly confined to boreal associations. Further inquiry is needed to indicate whether control was purely paleogeographical, in terms of confinement to strictly isolated epeiric seas, or whether the control was ecological. If ecological, temperature is the logical explanation, and by all analogy, the boreal faunas, with shells of bizarre shapes, great size, and strong calcification, should be tropical in contrast to the temperate austral ones. It is significant that the discosorids do not show distribution in close accord with lithofacies, as do the actinoceroids. The Selkirk lime-

stone is a close duplicate (except in color and rarity of chert) of the Chaumont limestone of New York. It differs primarily in color from the doubtless equivalent lower Montoya of the Franklin Mountains of western Texas. All of these associations contain abundant endoceroids and actinoceroids. Endoceroids are too little known to evaluate their differences, although we know that true *Vaginoceras* occurs in Black River beds but has not as yet been recognized in the Red River faunas. The picture of actinoceroids is different. *Actinoceras* and *Goniceras* dominate the Black River beds; *Armenoceras* and *Lambeoceras* are the commonest elements of the Selkirk limestone. Similar environments seem to be represented by these massive limestones with dolomitic mottlings and similar associations of cephalopods, gastropods and corals. However, the discosorids are common to the Selkirk and Dog Head members of the Red River, which are rather different lithologically. The Dog Head is a thin-bedded, well-bedded, rather argillaceous limestone and in it the cephalopods commonly show the upper and not the undersides preserved. Similar preservation is rare in the Cincinnati and typical only in one other association in our experience, namely the Chazy as exposed on the shore of Lake Champlain at Valcour, New York. Significantly, as the Red River faunas are traced southward, the discosorids decline. They are still present in the Big Horn group of Wyoming and scarce in the lower Fremont of Colorado, but as yet none have been found in the Burnum limestone of central Texas, where *Armenoceras* dominate the fauna.

One genus, *Faberoceras*, is confined to Ordovician faunas of austral aspect. As pointed out in the discussion of evolution, there is some question as to the origin of this genus, but whether its ancestor was *Westonoceras* or *Reedsoceras*, it sprang from a stock known only meagerly from boreal associations in Black River time. *Faberoceras* is known from the late Trenton Catheys and Cynthiana and penetrates the overlying Leipers, where, indeed, it attains its fullest development. We know one species from the Eden of Cincinnati and another from Corryville beds. More doubtful are species in the Bala of England and Lyckholm of Estonia. *Clarkevillea* is a continuation of this stock into the Richmondian and is to be regarded as a modification of the austral *Faberoceras*, not as one of the boreal elements popularly said to characterize Richmond deposits of the Cincinnati arch. The early Richmond boreal cephalopods include only a few forms, notably the *Ascoceratida*. It is not until the later Richmond (Whitewater, Saluda) that the real boreal invasion of the cephalopods is consummated. Even

EXPLANATION OF PLATE 13 WESTONOCERATIDAE—*Westonoceras*

FIGURE

1-3. *Westonoceras alberta-saskatunae* FLOWER, n. sp., holotype, from quarries in Selkirk member of Red River beds (Ordovician), near Tyndall, Man.—1, Lateral view, venter at left, $\times 1$.—2, Vertical section of basal part, $\times 1$.—3, Part of siphuncle from same section showing outline of vestigial bullettes and trace of a central tube in one segment, $\times 2.3$. (See also Pl. 14, fig. 4,5.)

4-6. *Westonoceras* sp., phragmocone from same beds and locality as cited for Figs. 1-3.—4, Lateral view of portion sectioned vertically, venter at right, $\times 1$.—5, Basal part of opposing adoral fragment showing unusual cross section in which venter is as broadly rounded as dorsum, $\times 1$.—6, Siphuncle from same section showing detail of outline of segments and very small bullettes, $\times 2.8$.

Both specimens in collection of the writer.





then it is questionably perfect; many types of mollusks, brachiopods, and bryozoans trace their lineage back to indigenous Covington forms. The discosorid stock still continues in the form of *Glyptodendron* of the Lower Silurian Brassfield of the same region.

The mode of life and environment of the Lowoceratidae and Discosoridae is again a matter on which no opinions have been ventured in print. This is small wonder, for the mode of life of cephalopods inhabiting these shells, which consisted more of heavy siphuncle than anything else, is perplexing. The Discosoridae, together with the Huroniidae, have their peak development in calcareous beds of northern North America in early Middle Silurian time. Corals are the only other dominant faunal elements in the typical association. Of the environment we can say little with certainty. It is evident that most of the discosorids and Huroniidae were washed around considerably prior to burial; that is why isolated siphuncles are commonly found and phragmocones are exceptional in these beds. However, beyond this point we cannot go with any assurance in the present state of our knowledge. Whatever the environment, it is perhaps significant that the stock disappears from view until we encounter the Devonian *Alpenoceras*, again in boreal faunas of North America, though here clearly allied to the *Stringocephalus* limestone faunas of Germany.

In contrast, the Phragmoceratidae and Mandaloceratidae are dominantly developed in the late Middle Silurian and have a wide distribution in that epoch. They succeed the *Discosorus-Huronia* faunas in northern North America but are actually more widespread. In Indiana and more southerly successions in eastern North

America, the Phragmoceratidae and Mandaloceratidae occur in associations overlying the Liston Creek dolomite and Laurel limestone and the Joliet of Wisconsin, which are dominated by a very different assemblage, consisting essentially of orthocones and *Cummingsoceras*. A closely allied fauna is found in an equivalent position (E_1 of BARRANDE) in Bohemia, and the succeeding E_2 fauna has much in common with the Racine-Gueph succession (including the Mandaloceratidae and Phragmoceratidae) of eastern North America. Commonly, but not exclusively, the Racine-Guelph faunas are found in association with bioherms, but this does not hold for the Liston Creek dolomite.

In summary, knowledge of the mode of life of all these forms leaves much to be desired. All occur in benthonic associations and reversal of curvature in individual stocks suggests that there may have been no profound difference in the mode of life of exogastric and endogastric shells. Forms with small siphuncles, which prevail in most groups, and compressed cross sections, notably developed in the Westonoceratidae, are more convincingly interpreted as dominantly swimmers rather than as benthos. On the other hand, shells with large siphuncles, like those of the Discosoridae, could hardly have belonged to other than benthonic or epibenthonic animals. It is still uncertain whether the visored shells of the Phragmoceratidae and Mandaloceratidae, represent dominantly benthonic animals or swimmers or floaters. Regrettably, until we can deduce with more certainty than we can now, the physical environments in which these cephalopods lived, we cannot come closer to an ecologic interpretation of the conditions governing the remarkable distribution of the discosorids in the Paleozoic.

PART 2. TAXONOMY

By ROUSSEAU H. FLOWER

Order DISCOSORIDA Flower in Flower & Kummel, 1950

The order Discosorida is characterized primitively by the combination of broadly expanded siphuncle segments and thick connecting rings. The rings are complex, showing a differentiation of structure peculiar to the order, notably the development of an anterior vinculum and an apical bullette consisting of two layers. Early stages of the oldest genus, *Ruedemannoceras*, show the siphuncular bulbs known elsewhere only in the archaic family Plectronoceratidae (FLOWER, 1954) and the dis-

cosorids are regarded as stemming from this ancient family, independent of all other cephalopods.

Internal structure is highly plastic. Primitively the bullettes are uninflated and the siphuncle empty in the Ruedemannoceratidae. Similar internal simplicity is inherited in the primitive members of the Mandaloceratidae at least. Bullettes are swollen in the Cyrtogomphoceratidae and their descendants, the Phragmoceratidae. Parietal deposits are added to the pattern in the Westonocera-

EXPLANATION OF PLATE 14

WESTONOCERATIDAE—*Winnipegoceras*, *Westonoceras*

FIGURE

1-3. *Winnipegoceras obesum* FLOWER, n. sp., holotype, from Tetreauville limestone, late Trenton (Middle Ordovician), Ruisseau Rouge, northwest of Crabtree Mills, Que.; collection of Dr. G. W. SINCLAIR.—1, Ventral view, $\times 1$.—2, Septal view, venter below, $\times 1$.—3, Lateral view, venter at right, $\times 1$.

4-5. *Westonoceras albertaina-saskatwanae* FLOWER, n. sp., holotype, from Selkirk member of Red River series (Ordovician), at quarries near Tyndall, Man.; collection of the writer.—4, Ventral view, $\times 1$.—5, Dorsal view, $\times 1$. The sectioned anterior portion failed to preserve any of the internal structure. (See also Pl. 13, fig. 1-3.)

tidae and in specialized genera of this family are increased into endocones. Endocones persist into the Silurian *Westonoceratidae*, where mature parts of the shells show a loss of the swollen bullette and a general thinning and simplification of the ring, a feature which occurs throughout ontogeny in the *Discosoridae*.

Shells are dominantly cyrtocoines, primitively endogastric, becoming exogastric in the *Westonoceratidae* and their descendants as well as in the *Mandaloceratidae*. Exceptional types belonging to these exogastric stocks revert to endogastric curvature. Simplification of the connecting rings has been observed in the *Mandaloceratidae* and in *Glyptodendron* of the *Westonoceratidae*. Such simplification, when unaccompanied by such specialized structures as the endocones of the *Discosoridae*, may produce shells very difficult to distinguish from the *Oncoceratida*.

Representatives of the *Discosorida* occur in boreal and central parts of North America, central and northern Europe and Australia. They have a known stratigraphic range from Chazyan to the Upper Devonian but are chiefly developed in Middle and Upper Ordovician and Silurian deposits.

Family RUEDEMANNOCERATIDAE Flower, 1940

Shells in this family are simple endogastric cyrtocoines with uncontracted apertures bearing a shallow hyponomic sinus. The siphuncle, which is located ventrad of the center, shows clear siphuncular bulbs in the earliest stage of the type genus, later giving place to broadly expanded segments with strongly recurved septal necks. Connecting rings are thick, the vinculum, granular and chitinous zones, the two amorphous bands and the two layers of the bullette being well differentiated, but the bullette is uniform in thickness with remainder of the ring. No organic deposits are developed against the interior of the siphuncle wall but traces of a central tube are present in some shells, particularly in *Madiganella*. The siphuncle segments are more strongly expanded and the rings thicker on the dorsum than venter. Sutures are either straight, tending to slope forward from venter to dorsum, or they may develop faint sinuate lobes on the venter. The cross section, dominantly broad, has the venter either broadly flattened or more broadly rounded than the dorsum.

Discussion. This family contains *Ruedemannoceras*, the oldest genus of the *discosorids* thus far known. By its lack of annular deposits in the siphuncle and inflated bullettes it is primitive in relation to the *Cyrtogomphoceratidae*, *Westonoceratidae*, and their descendants. As originally conceived, the family contained only *Ruedemannoceras*, a cyrtocoine shell of broad cross section and nearly central siphuncle. At first it was assumed that the genus was probably exogastric, this condition being more common than endogastric curvature among nautiloids generally. However, in *Ruedemannoceras* no good direct evidence of orientation was apparent. The siphuncle is so nearly central that it could be regarded as either slightly dorsad or ventrad of the center. No conchial or septal furrows could be seen, and neither the aperture nor growth

lines which might supply evidence of a hyponomic sinus, have been observed. However, *Madiganella* shows growth lines that indicate the presence of a hyponomic sinus on the concave side of the shell. Thin sections of *Ruedemannoceras* show that the connecting ring is thicker, its structures more clearly differentiated, and its segments somewhat more expanded on the convex than on the concave side. Analogy with other genera where orientation is better established, notably *Westonoceras*, indicate that these features characterize the dorsal side of the siphuncles of the older *Discosorida*. Also, the cameral deposits are most strongly developed against the concave side of the shell, and they are almost universally concentrated on the venter in the nautiloids.

The writer previously had tentatively referred *Yabeites* ENDO to the *Ruedemannoceratidae*. As a slightly curved shell with a subcentral siphuncle composed of broadly expanded segments, it seemed the only possible related genus known at that time. TEICHERT has restudied the genus (*vide litt.*) and confirmed KOBAYASHI's conclusion that it is an actinoceroid. However TEICHERT & GLENISTER (1954) described *Madiganella*, which they referred originally to the *Cyrtogomphoceratidae*. It agrees with *Ruedemannoceras* in its broad cross section, slightly flattened venter and nearly central position of the siphuncle. Though replacement makes impossible the study of the details of the thick connecting ring, it is evident that there is no inflation of the bullette such as characterizes the *Cyrtogomphoceratidae*. Further, late stages of *Ruedemannoceras* show a decrease in curvature in rate of expansion, and in expansion of the segments siphuncle from broadly elliptical to spheroidal. In all of these features *Ruedemannoceras* very closely approaches features found in *Madiganella*, which is known only from large and obviously relatively late portions of the phragmocone.

One form, otherwise similar to *Ruedemannoceras*, differs from it in having a strongly compressed cross section. It is here described as a new genus named *Franklinoceras*. As yet, no species are known bridging the gap in the matter of cross section, and recognition of a distinct genus here simplifies definitions. The difference is probably not a great one, however, and it may be noted that it has not proved feasible to attempt a separation of *Cyrtogomphoceras* on a similar basis.

Ruedemannoceras and *Franklinoceras* occur in the Chazyan of the Champlain Valley, New York and Vermont. *Madiganella* is known only from Lower Ordovician rocks of central Australia.

Genus RUEDEMANNOCERAS Flower, 1940

Type species—*Cyrtoceras boycii* WHITFIELD

Ruedemannoceras FLOWER, 1940, Geol. Soc. America., Bull. 51, p. 1969.

—FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 427.

—FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 612.

Shell endogastric, cross section wider than high, venter slightly flattened, dorsum more rounded in early stages but both dorsum and venter more evenly rounded in later growth stages. Sutures closely spaced, sloping forward from venter to dorsum, obliquity increasing as growth progresses, but without definite lobes. Early portion of conch essentially straight, after which curvature and expansion are pronounced, but the latest observed

stages show reduction in curvature and rate of expansion. Neither aperture nor growth lines known. Shell surface, as far as known from small fragments, essentially smooth.

Siphuncle only slightly ventrad of the center throughout growth, early segments showing siphuncular bulbs with short septal necks parallel to axis of siphuncle. By about 5th septum, septal necks have increased in length, the increased portion being recurved to form brims. Already the degree of expansion within the siphuncle has increased. With further growth expansion increases and brims become longer. In early ephebic stage siphuncle is composed of segments much higher than long, strongly expanded, and more markedly expanded and with thicker rings on the dorsal side. Rings, thick from the initial portion, develop differentiation of structures already described in discussion of morphology—bullette, granular zone, 1st amorphous band, chitinous zone, 2nd amorphous band, and inner and outer layers of bullette. In latest observed growth stages segments of the siphuncle become less strongly expanded in the camerae, and are spheroidal instead of broadly elliptical. Structure of the connecting ring apparently remains unchanged.

Discussion. RUEDEMANN (1906), in a paper noteworthy as the only one in North America in a 20-year period which made intelligent use of HYATT'S (1900) classification, referred the genotype of *Ruedemannoceras* to *Cyrtactinoceras* HYATT. That genus is a slender cyrtococone of the Silurian, exogastric, with a ventral hyponomic sinus. Sutures in late growth stages slope forward on the concave dorsum. The siphuncle is slightly removed from the venter, and segments are expanded in the early ephebic stage but are longer than high, gradually becoming more slender adorally. Annular deposits in the siphuncle grow orad and apical from their point of inception at the tip of the septal neck and the junction of two adjacent connecting rings. Deposits are annular. The form of the deposits and the gradual adoral simplification of the outline of the siphuncle show that *Cyrtactinoceras* is a curved Silurian derivative of the dominantly orthoconic and dominantly Ordovician Stereoplasmoceratidae. This genus is not known to contain any other species than the type species, *C. rebelle* (BARRANDE).

Ruedemannoceras is very distinctive as a closely septate cyrtococone with a siphuncle of broadly expanded segments, located between the center and concave side. As noted in discussion of the family Ruedemannoceratidae, in the absence of conchial or septal furrows or a hyponomic sinus, orientation of the shell as endogastric or exogastric was for a long time very uncertain and now is established by analogy with other genera. The type species is happily represented by material showing the structure of the siphuncle and in particular, of the connecting ring, and further is the only member of the discosorids represented by material showing extremely early segments of the siphuncle.

As yet only two occurrences of the genus are known, in the middle and upper Chazyan of the Champlain Valley and in the Murfreesboro limestone of central Tennessee.

Ruedemannoceras boycii (Whitfield)

Pl. 1; Pl. 2, fig. 1-10; Pl. 3, fig. 1, 2, 4-6; Pl. 5, fig. 7

Cyrtoceras Boycii WHITFIELD, 1886, *Am. Mus. Nat. Hist., Bull.*, v. 1, p. 326, pl. 29, fig. 4.

Cyrtactinoceras boycii RUEDEMANN, 1906, *New York State Mus. Bull.* 90, p. 489, pl. 35, fig. 1-4; text-fig. 46-47.

Cyrtactinoceras champlainense RUEDEMANN, 1906, *ibid.*, p. 491, pl. 34, fig. 3, pl. 36, fig. 1-2; text-fig. 48-50.

Cyrtactinoceras boycii GRABAU & SHIMER, 1910, *North American Index Fossils*, v. 2, p. 117, fig. 1352.

Cyrtactinoceras champlainense GRABAU & SHIMER, 1910, *ibid.*, v. 2, p. 117.

Ruedemannoceras boycii FLOWER, 1940, *Geol. Soc. America, Bull.* 51, p. 1970.

Shell cyrtococonic, moderately curved beyond a small nearly straight initial portion, moderately expanding, rate of expansion and curvature both reduced in latest observed stages. Mature living chamber and aperture unknown. Cross section wider than high, ventral side slightly flattened in early ephebic stage, but dorsum and venter almost equally rounded in later stages. Sutures very closely spaced, straight and transverse in young but sloping increasingly forward on convex dorsal side of shell in later growth stages. Portions of phragmocones are known extending up to a shell height of nearly 40 mm., but most specimens are fragments of considerably earlier portions of the shell. Absence of conchial and septal furrows is explicable in terms of roughness of known surfaces of internal molds of all specimens. Thin sections show that mural part of septum is extremely thick and short extending less than half the length of the very shallow camerae. Probably the septal furrow is not developed.

Siphuncle shows peculiar early ontogenetic progression noted separately in the following section. Early ephebic segments are very broad and broadly expanded (Pl. 1; Pl. 2, fig. 8). Height across septal foramen slightly greater than length of the segment and where expansion in the camerae is at its maximum, height of segment is at least three times its length.

Septa thicken slightly at point where they are recurved into septal necks. Length of neck extremely short, about one-sixth of length of segment, and brim narrowly free from transverse part of septum, twice length of neck on dorsum and slightly longer on venter. Owing to its thickness, ring is broadly adnate to septum at its anterior and posterior ends. Expansion of segment is much more marked dorsally than ventrally. Differences in areas of adnation slight at adoral ends of ring but that on dorsum nearly twice as great as on venter adapically. Differentiation of structures within the ring has been discussed in preceding section. In later growth stages (Pl. 2, fig. 3, shown in greater enlargement in Pl. 3, fig. 2) segments of siphuncle show decrease in both maximum and minimum height of segments in proportion to their length. Septal necks are shorter, extent of brims and extent of expansion becomes more nearly equal on the dorsum and venter and maximum height of segment is only about 1.5 times its length. This occurs where the shell height is 18 to 22 mm. and length of segment about 3 mm. A still later stage is shown in Pl. 3, fig. 1 (horizontal section) in which segments appear more nearly subquadrangular. This section was made from a weathered surface in which prominence of bullettes suggested that they might be slightly distended as in the *Cyrtogomphoceratidae* and *Westonoceratidae*. Examination of polished section shows that bullettes are not swollen and their original prominence in natural weathered section was clearly the effect of differential weathering and indication of differences in texture of material or both between the bullette and remainder of the ring.

Early stages. A vertical section through the apex removed from the specimen shown on Pl. 2, fig. 2-4, shows a series of 12 camerae (first and last incomplete). This section, 7 mm. in length, shows a remarkable ontogenetic succession in the form of the siphuncular segments. The apex of the shell is bluntly rounded, for a length equal to the first 6 camerae, after which it is extremely slender, and then assumes the fairly rapid expansion which persists over much of the shell, at its adoral end. Curiously, the apex alone shows

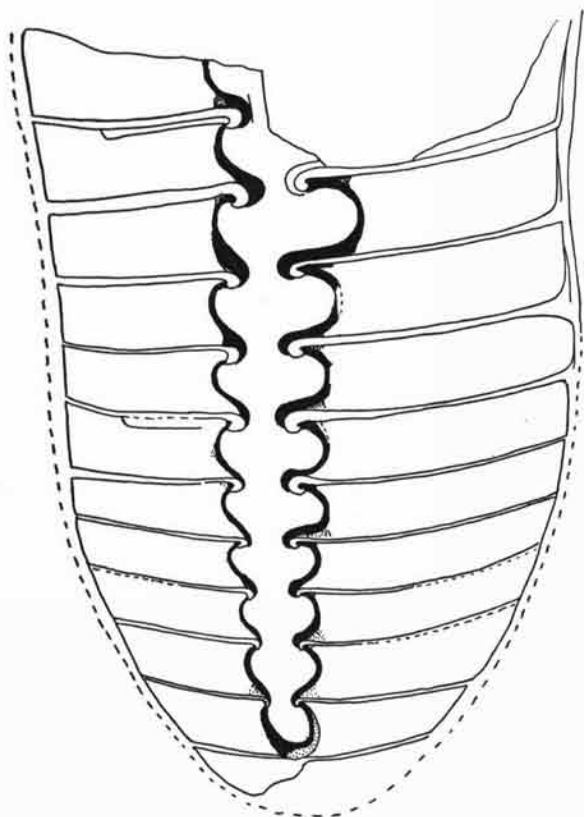


FIGURE 12. Initial part of the shell of *Ruedemannoceras boycii*.

Outline drawing of section (Pl. 2, figs. 9, 10) showing ontogenetic progression from siphuncular bulbs to broadly expanded segments typical of *Ruedemannoceras*. The section is essentially vertical, venter on left, about $\times 10$. Missing portions of the apex are restored.

a slight curvature in the initial part in which greater convexity of the ventral profile, at left, leads one to interpret this part of the shell alone as exogastric (Pl. 2, fig. 9-10).

The first camera is incomplete, but from the part preserved, outline of the shell apex can be restored without any serious doubt. The apex of the siphuncle is lost, being outside of the plane of the section in the 2nd camera, but the anterior end of the segment is well displayed. Here septal necks are thicker than the free part of the septum, short, and essentially orthochoanitic. Expansion of the segment is confined to that region outlined by the connecting ring alone.

In the next two segments inflation of the segment in the camerae is increased, the outline becomes more broadly rounded, but necks are still short and essentially orthochoanitic. From the 5th to 7th segments the necks become thicker, longer, and more definitely recurved. The 7th to 9th septa show an unusual change, thickening and becoming nearly flat as seen in section, through septa nearer the apex, as well as those located adorally, show normal curvature with anterior side concave. Here the mural part of the septum can be seen as unusually thick and so short as to extend forward for less than half the length of the extremely shallow camera. Meanwhile the siphuncle has continued its change of form, with anterior segments still more broadly expanded, expansion on the dorsal side more marked than on venter, at the extreme anterior

end of the section a faint differentiation of the bullette. Camerae in this section are filled with calcite. If any cameral deposits were present here, as seems probable, they have been lost by alteration. Calcite also occupies the cavity of the siphuncle and is clearly inorganic. The structures of the section are shown in text-figure 12.

Figure 13 shows a slightly later stage that overlaps the anterior end of the preceding section. This specimen, though preserving the structures well, shows them in only faint color variation, as is commonly true of the specimens from the massive dove-gray limestones associated with *Stromatocentrum* reefs in the upper Chazyan Valcour limestone. This section was ground as nearly vertically as possible on a naturally broken surface, and does not quite attain the plane of symmetry. The portion shown in Pl. 3, fig. 6, has a maximum length of 38 mm. The section exposes the siphuncle only in the lower two-thirds of the specimen. Both camerae and siphuncle are filled with white calcite and structures are differentiated only by faint color contrast. A further enlargement of the apical portion (Pl. 3, fig. 6) shows the initial part more clearly. The apex is incomplete; probably the basal part represents the third or fourth actual chamber. Segments are slender initially, septal necks short and straight, with only faintest suggestion of recurved brims. The free connecting rings outline segments expanded, though only moderately, in the camerae. The succeeding 9 camerae show the unusual thick extremely flat septa noted in the anterior end of the preceding specimen. In these camerae expansion of the siphuncle increases, the brims become more strongly developed, and segments assume the proportions which are retained throughout a good portion of the shell, resembling those very closely shown in Pl. 1, which persists to a point where the shell is 25 mm. high, at which point segments become narrower and spherical rather than depressed-elliptical in aspect. The section shows also traces of possible cameral deposits, but replacement is such that it is here very difficult to distinguish organic from inorganic calcite in the camerae.

Cameral deposits. Except in the camerae close to the anterior end of the phragmocone and those of the extreme apex, *Ruedemannoceras* exhibits rather extensive cameral deposits. Evidence of the structure is plain in all sections but recrystallization and replacement has obscured the structures to such an extent that it is usually difficult to distinguish inorganic from organic calcite. One section (Pl. 2, fig. 1) shows camerae in which the deposits are preserved as white calcite against a black limestone matrix at the adoral end. Here it can be seen that the deposits have nearly filled the camerae on the concave ventral side of the siphuncle, but on its dorsal side there are only episepal deposits which partially fill the camerae. They are unusual in pattern, for they are thick close to the siphuncle, thin as they approach the dorsal wall of the shell, and in this growth stage are not developed at all against the mural wall of the camera. When traced through successively adapical camerae, the deposits on the dorsum increase, not by increased thickness on the episepal deposit, but instead, by its continuation over the dorsal wall of the camera and well onto its anterior surface. The usual discrete relationship of episepal and hyposeptal deposits is absent, however. (See Pl. 5, fig. 7.)

Discussion. This species is a highly distinctive one in the Chazyan of the Champlain Valley. The cyrtoconic form, broad section and subcentral siphuncle composed of broadly expanded segments distinguish it readily from all other forms. RUEDEMANN (1906) recognized two species in the association. After examination of a considerable suite of specimens, including RUEDEMANN's types, it was necessary to conclude that while there is some variation in proportion among individuals, it is impossible to recognize a clear boundary between two species. The feature upon which *C. champlainense* was differentiated from *C. boycii* consists of differences found to exist between earlier and later growth stages. RUEDEMANN's specimens show close thick rather flat septa, and a cross

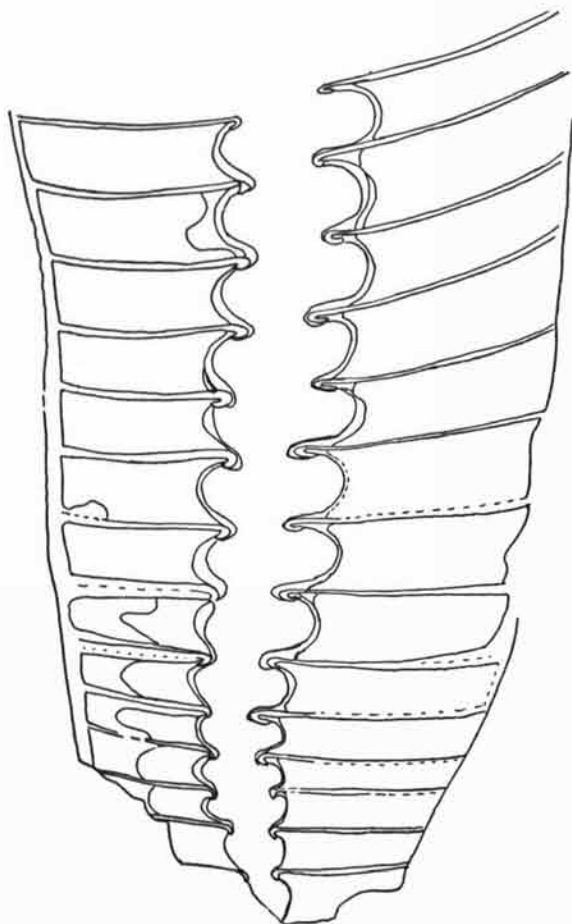


FIGURE 13. Early stage of *Ruedemannoceras boycii*.

Outline drawing based on the section shown in Pl. 3, figs. 5, 6. The interval represented is slightly later than that shown in text-fig. 12. Note extremely thick and flat septa at transition from siphuncular bulbs to normal cyrtocoanitic segments. About $\times 9$.

section in which the dorsum is rather conspicuously flattened. They are well shown in the early portion of the specimen figured on Pl. 2, fig. 2-4, where they are succeeded by the more rounded section, more distant and more normally curved septa of typical *R. boycii*. For this reason, it has seemed best to regard the two species as actually one. It is possible that several species are represented in the Chazyan associations, but from the present material, which is believed to represent the largest accumulation of specimens ever assembled, a division into two species is not possible. All available material is fragmentary and it may be that additional specimens will call for a revision of this interpretation. Possibly more than two species actually occur. The most complete specimen figured here (Pl. 2, fig. 2-4) appears to become slightly straighter at an earlier growth stage than does the holotype; also, it shows the development of subspherical segments, a feature apparently connected with late maturity, of which WHITFIELD'S type gives no indication. It could, therefore, possibly be a distinct species. Again, the specimen shown in Pl. 2, fig. 5-7, appears to be a shell somewhat more rapidly expanding than our other material. The camerae are slightly deeper and segments of the siphuncle slightly less strongly expanded than in corresponding parts of other specimens. While certainly variations in proportions comparable with those on which it is customary to erect species occur, I have refrained from

recognizing two or more species, feeling that variation in proportions within a single species is reasonable.

Types. The holotype of the species is in the collection of the American Museum of Natural History. Additional material figured by RUEDEMANN is in the New York State Museum, and in collections of the University of Vermont. Specimens figured in this work are in the collection of the writer, to be deposited in the collection of the New Mexico Bureau of Mines, nos. 62-67.

Occurrence. In the Chazy limestone of the Champlain Valley, New York and Vermont. The species is unknown in the lower Chazyan Day Point limestone, but is common to the Crown Point and Valcour limestones. Specimens are from a number of localities, those figured being confined to the middle Chazy (Crown Point limestone) from the type Chazyan section, just southwest of Chazy, New York, and from exposures of the Valcour limestone along the road leading east from the main highway just south of Chazy and east to Little Monty Bay.

Ruedemannoceras stonense Safford

Cyrtoceras? stonense SAFFORD, 1869, Geol. Tennessee p. 290, pl. 4 (G3), fig. 2a-c.

This species is known only from a portion of a phragmocone with cross section slightly wider than high, septa straight and very closely spaced, siphuncle clearly central and composed of short segments broad at the septal foramen and broadly expanded within the camerae. So distinctive is the genus *Ruedemannoceras*, that there can be no doubt that this species shows the essential features of the genus.

Discussion. I have not seen specimens of *Ruedemannoceras stonense*, having been unable to locate Safford's type and neither my own desultory collecting nor the more extensive collections of the U. S. National Museum have yielded any additional specimens. It is interesting to note that the Murfreesboro limestone agrees with the middle and upper Chazyan and differs from all other known formations in containing the genera *Gonioceras* and *Ruedemannoceras* in association. Though current trend is to interpret the Murfreesboro limestone as post-Chazyan, I cannot but wonder whether the supposedly more advanced types of brachiopods necessarily indicate a younger-than-Chazyan age or whether their later appearance in more easterly sections may be the result of faunal migrations.

Occurrence. Murfreesboro limestone of the central basin of Tennessee.

Doubtful Records of *Ruedemannoceras*

Cyrtoceras cf. boycii COWPER REED, 1936, Palaeontologica Indica, new ser. v. 21, p. 99, pl. 5, fig. 19.

It is desirable here to record this tentative specific reference to the type species of *Ruedemannoceras*. The specimen, from the Ordovician of the southern Shan States, is very incomplete and the description brief. The illustration shows a weathered natural section, apparently from the dorsal or ventral side of a cyrtococone with relatively central siphuncle like that of *Ruedemannoceras*, but the illustration of the siphuncle indicates that it is tubular. From the published evidence it is uncertain to what genus this specimen should be assigned, but it is not convincing as a *Ruedemannoceras*, and not adequate as a basis for extending the recorded geographic range of the genus to southern Asia.

Genus FRANKLINOCERAS Flower, n. gen.

Type species—*Franklinoceras elongatum* FLOWER, n. sp.

This genus is erected for a single remarkable species known only from a late growth stage. It resembles *Ruedemannoceras* in being a cyrtococonic shell with subcentral

broadly expanded siphuncle. Segments of the siphuncle are short, broad at the septal foramen, broadly expanded and broadly rounded in outline within the camerae. The ring shows evidence of appreciable thickness as in *Ruedemannoceras*. Gross features of the shell show differences by which this genus is set apart from *Ruedemannoceras* and also *Madiganella*. The cross section is extremely narrow, the convex dorsal side broadly rounded, the ventral side narrowly rounded and possibly originally subangular. The sutures are straight and transverse, showing neither the tendency to slope forward on the convex side apparent in late stages of *Ruedemannoceras*, nor the slight ventral lobes developed commonly in *Madiganella*.

Only the genotype from Chazyan strata of the Champlain Valley is known.

Franklinoceras elongatum Flower, n. sp.

Pl. 3, fig. 3, 7.

The holotype consists of an appreciable portion of a living chamber and 12 camerae of a large slender cyrtococone. Cross section strongly compressed, greatest width of the shell being attained about half way between convex dorsal side and center. Venter relatively narrowly rounded. The holotype, 100 mm. long, increases beyond the basal 20 mm., which is incomplete, from a height of 42 mm. to 53 mm. in a length measuring 10 mm. on the convex dorsum and 45 mm. on the concave venter. Radii of curvature for dorsum and venter uniform throughout length of specimen, 250 mm. for dorsum and 200 mm. for venter. The apical 38 mm., as measured on the dorsum, represents 11 camerae and a greatly abbreviated 12th camera, the last 2 mm. deep, others averaging 3 mm. and showing no appreciable variation. A vertical section shows the siphuncle, largely destroyed in the adoral part of the phragmocone, consisting of short broad, broadly expanded and broadly rounded segments similar to those of *Ruedemannoceras*. An indication of rings of appreciable thickness can also be seen but there are no deposits in the siphuncle or camerae. In the lower part of the specimen a segment 3 mm. long increases from 3 mm. at the septal foramen to 7 mm. within the camera. Here the siphuncle is exactly central, the expanded portion being 15 mm. from both dorsum and venter. Sutures, as exposed on the internal mold, are straight and transverse. No trace of the shell surface remains. Maximum length of the living chamber (42 mm.) is attained on the convex side of the shell. This is a convincing length for a mature living chamber but since it is incomplete, the course of the aperture cannot be determined and it is possible that the living chamber was somewhat longer originally.

Discussion. The compressed section and simple sutures which distinguish the genus from allied forms, serve also to distinguish this, the only species known as yet. If the rate of expansion indicated on the extant part was uniform, the complete shell had a length of 25 to 30 cm., but it is quite probable that, as in the related *Ruedemannoceras*, the early portion of the shell was more rapidly expanding, and the shell may not have extended for more than 20 cm.

Holotype. Collection of the writer, no. 68.

Occurrence. From the *Maclurites* ledges of the middle Chazyan, from the type section of the Chazyan just southwest of Chazy, New York.

Genus MADIGANELLA Teichert & Glenister, 1952

Type species—*Madiganella magna* TEICHERT & GLENISTER

Madiganella TEICHERT & GLENISTER, 1952, *Jour. Paleont.*, v. 26, p. 743.

This genus is as yet known only from relatively small portions, all of appreciably large cross section, and obvi-

ously representing relatively late portions of the phragmocones. Shells are slender and nearly straight; indeed, the genus was first described as orthoconic. However, both the genotype and the unnamed species here illustrated, show a slight concavity in the profile of the siphonal side, and one at least shows the opposite side to be very slightly convex. Suture pattern relatively simple, sutures being largely transverse but showing a faint tendency, apparently variable among the species, toward development of a slight lobe on the siphonal side. On this side also the shell tends to be slightly flattened in cross section. The siphuncle, located between center and concave side, with segments broad in proportion to the shell cross section at the septal foramen, its segments broadly and evenly rounded within the camerae. Septal necks extremely short, strongly recurved, narrowly free. Rather extensive replacement in all material thus far examined has altered the original structure of the connecting ring. The appreciable thickness of the ring in *M. magna* (Pl. 4, fig. 7) is probably increased in the apical portion by addition of inorganic material. Adoral segments show an original thickness that is very suggestive of *Ruedemannoceras*. The 2nd segment from the anterior end shows further a buttress-like structure, possibly comparable to that noted on the ventral side of *Ruedemannoceras*, and certainly the apical part of the ring is differentiated in texture from the remainder, being comparable to the bullette of *Ruedemannoceras*. One can see in the same segment a suggestion of a vinculum. In thickness of rings and outline of segments, both *M. magna* and *M. sp.* are comparable to *Ruedemannoceras*. A singular feature of *Madiganella* is the persistent preservation within the siphuncle of a central tube (Pl. 4, fig. 47; Pl. 5, fig. 8). The tube appears to have a hard, probably a calcified wall. Its irregularity in preservation as well as in form and position, is probably a preservation phenomenon rather than an original feature, as noted in discussion of the structure in the earlier section on discosorid morphology.

Madiganella sp. shows markings on the surface which are apparently rather widely spaced growth lines of unusual prominence. They match the course of the septa and equal them in spacing except on the concave side of the shell where they slope adapically. These structures have nothing to do with the septa and have such a scant relief that they are not visible on a whitened specimen (as seen by comparing Pl. 4, fig. 5 and 6 which show the same view of the same specimen whitened and in natural color). They are evidently growth lines and the downward curve is an indication of a hyponomic sinus on the concave side of the shell.

Discussion. *Madiganella* appears to be very closely related to *Ruedemannoceras*. Its known siphuncle segments are very similar to those in late (but not early) stages of *Ruedemannoceras*. In both genera the siphuncle lies slightly off center toward the side of the shell which is slightly concave in longitudinal section and slightly flattened in cross section. With little doubt the two genera are to be oriented similarly and are closely related. *Madiganella* then may be interpreted as a modification of *Ruedemannoceras* in which the shell becomes much larger and nearly straight. The sutures are essentially transverse but are reported as being faintly sinuate, de-

veloping slight ventral lobes. This sinuate pattern is a natural modification of the oblique sutures of *Ruedemannoceras*. The persistent central canal is, of course, a unique feature not known in *Ruedemannoceras*.

TEICHERT & GLENISTER, at the time of their original description of the genus, reported having several undescribed species in addition to *Madiganella magna* and "*Orthoceras tatei*" ETHERIDGE, which they indicate as a member of the genus. It will suffice to note that *Madiganella* is known as yet only from the Ordovician of Australia and according to TEICHERT its precise stratigraphic position in the Ordovician is uncertain. He suggests that the beds, originally regarded as Chazyan, may well be actually somewhat younger. Certainly the Larapintine group, from which these fossils come, appears to contain several units of different ages. *Catoraphiceras* indicates a late Canadian age and *Bathmoceras* probably very latest Canadian. *Bactroceras* and *Cyclendoceras* suggest a post-Canadian age. That *Madiganella* appears to be considerably more advanced than *Ruedemannoceras* and that its logical descendant, *Pseudogomphoceras*, does not put in an appearance until Silurian time, both suggest that a post-Chazyan position of *Madiganella* in the Ordovician is probable.

TEICHERT & GLENISTER (1952) have compared *Madiganella* to both *Fabroceras* and several genera of the Cyrtogomphoceratidae. Affinities with *Ruedemannoceras*, instead, are indicated by the absence of parietal deposits within the siphuncle, invariably well developed in *Fabroceras* and indeed characteristic of the entire family Westonoceratidae; also, the uninflated bullettes are a feature which serves to set the Ruedemannoceratidae apart from both the Cyrtogomphoceratidae and Westonoceratidae.

Additional species of *Madiganella* are soon to be described by GLENISTER. Notes on the species are therefore confined to bibliographic citations and notes on the specimens illustrated to show the features on the genus. Dr. TEICHERT has kindly supplied a photograph of *M. magna* and Dr. GLENISTER has loaned the specimen here noted as *M. sp.*

Madiganella magna Teichert & Glenister

Pl. 4, fig. 7

Madiganella magna TEICHERT & GLENISTER, 1952, Jour. Paleont., v. 26, p. 744, pl. 105, fig. 1-2.

This species, known from relatively small portions which by their size are late portions or phragmocones, is nearly orthoconic. Exteriors are quite generalized and have not yet been figured. The original illustrations of TEICHERT & GLENISTER show good vertical sections but only the smallest indication in one segment of the central tube. A more extensive portion shows the tube (Pl. 4, fig. 7) and better suggests a thickening of the connecting rings. The enlargement shown by TEICHERT & GLENISTER (Pl. 105, fig. 2) indicates thickening of the rings on the dorsal side of the siphuncle but not on the ventral side, a feature consistent with its relationship to *Ruedemannoceras* and orientation in relation to this genus.

The holotype, in the University of Adelaide (no. NTO-10), is from Ellery Creek, in the Heavitree Range of central Australia.

Madiganella tatei (Etheridge)

Orthoceras tatei ETHERIDGE, 1893, Southern Australia Parliamentary Papers, no. 52, p. 6-8, pl. 1.

Madiganella tatei (ETHERIDGE) TEICHERT & GLENISTER, 1952, Jour. Paleont., v. 26, p. 733.

Larapintine group, Ordovician, central Australia.

Madiganella sp.

Pl. 4, fig. 1-6; Pl. 5, fig. 8

Under this designation is illustrated and discussed a specimen of *Madiganella* which is one of several to be described specifically by Dr. GLENISTER. It is here figured in order to show essential features of the genus more thoroughly than in the only previously published description. The shell is nearly straight but the ventral side is markedly concave when seen in profile, though convexity on the weathered dorsal side is not evident. The siphuncle is somewhat more centrally located than in *M. magna* and the septa are less deeply curved. These two features combine to produce segments of the siphuncle which are less markedly oblique in vertical section than those of *M. magna* and thus more closely comparable to segments of a late growth stage of *Ruedemannoceras* here illustrated (Pl. 3, fig. 2). The cross section is well arched on the dorsum, strongly rounded ventrolaterally, and only slightly convex, thus showing a definite flattening, on the venter.

The specimen (maximum length 52 mm.) contains 10 camerae of essentially equal length. The height and width of the cross section are equal. The septa are essentially transverse, with only faintest traces of lobes dorsolaterally and ventrally separated by faint saddles on the strongly rounded ventrolateral regions. The siphuncle is twice as far from the dorsum as from the venter, whereas in *M. magna* it is between three and four times. The curvature of the septa is slightly less in vertical section than in that species. Siphuncle segments are less oblique in vertical section but the form of the segment and their size in relation to the shell as a whole are quite similar in the two species. The connecting rings were apparently originally thick but extensive replacement has evidently altered their structure considerably. Alteration has affected material in the camerae also, but probably such a large shell represents a portion of the phragmocone too near the living chamber for cameral deposits to be developed there. The central tube can be seen passing irregularly through most of the anterior four segments of the specimen. It is somewhat bent and is surrounded by matrix.

The figured specimen, from collections of the University of Adelaide, is from the Ordovician of Maree Bluff, central Australia.

Family CYRTOGOMPHOCERATIDAE

Flower, 1940

The family Cyrtogomphoceratidae contains shells which are dominantly compressed endogastric cyrtocoones with the siphuncle close to the ventral side. The apical end of the connecting ring is expanded into markedly swollen bullettes, segments of the siphuncle being dominantly short and broadly expanded; ring markedly thickened. Parietal or other deposits in the siphuncle are wanting.

As noted in discussion of the evolution of the Discosorida, the Cyrtogomphoceratidae are regarded as stemming from the Ruedemannoceratidae. They represent the next grade in specialization of the siphuncle, for the connecting ring develops swollen bullettes at its tip but parietal or other deposits which characterize the Westonoceratidae are wanting. Further, the Cyrtogomphoceratidae are evidently allied to the Ruedemannoceratidae in the endogastric form of the shell, although previously this was not apparent when the direction of curvature of the Ruedemannoceratidae was uncertain. The Westonoceratidae must have developed relatively early from the Cyrtogomphoceratidae, for both families are found to be differentiated in late Black River time. The Westonoceratidae are specialized in the development of parietal de-

posits and in reversal of curvature of the shells from endogastric to exogastric. Though dominantly endogastric, some members of the family are straight or nearly so. It has long been apparent that *Landeroceras*, a straight brevicone that is strikingly homeomorphic with the contemporaneous *Diestoceras*, is a straight breviconic edition of *Cyrtogomphoceras*. It was not previously clear whether *Kiaeroceras* belonged here or in the Westonoceratidae (FLOWER, 1946). Restudy of the types indicates that the shell of *Kiaeroceras* is faintly endogastric and that structure of its siphuncle is comparable to that of the Cyrtogomphoceratidae, whereas it lacks accessory internal deposits of the Westonoceratidae.

The Phragmoceratidae are descendants of the Cyrtogomphoceratidae in the Silurian. They differ in the thinner and simpler nature of the connecting ring, as well as by the specialized apertures, and there is some indication of a development of parietal deposits here attained independent of the Westonoceratidae. The morphological boundary between the Phragmoceratidae and Cyrtogomphoceratidae is so placed as to include in the Phragmoceratidae a small group of Silurian genera with open apertures. In the siphuncle structure they seem to be allied with the associated *Phragmoceras* rather than with their Ordovician forerunners as indicated both by simplicity of the connecting ring and the appearance of accessory deposits within the siphuncle, as noted in discussion of *Protophragmoceras*.

Genus ULRICHOCERAS Foerste, 1928

Type species—*Ulrichoceras beloitense* FOERSTE

Ulrichoceras FOERSTE, 1928, Denison Univ. Bull., Sci. Lab., Jour., v. 23, p. 211.

Shell cyrtoconic, endogastric, fairly rapidly expanding to middle of living chamber, adoral portion slightly contracted to aperture. Cross section slightly wider than high, subtriangular, dorsum and ventrolateral regions strongly rounded, with intervening regions less convex. Sutures describe broad lobes on the ventral face, rising laterally, becoming faintly sinuate and transverse or rising, though less markedly on dorsum. Siphuncle located between center and venter, relatively large in diameter at septal foramen; segments short in proportion to the diameter at septal foramen, broadly rounded but not markedly expanded, broadest at their anterior ends. Septal necks unknown, but they must have been either narrowly separated from the septum or actually recumbent. Rings are thickened with their apical ends developing strongly inflated bullettes.

A broad conspicuous hyponomic sinus is indicated on

the venter but the remainder of the aperture is unknown. It was evidently either transverse or may have sloped forward slightly on the dorsum. No traces of surface markings other than faint growth lines impressed on the internal mold are known.

Discussion. The original description of the genus and species was accompanied only by line drawings and no information on the shell interior was available. The writer concluded from examination of the type that probably it is a discosorid, as indicated by endogastric form, broad cross section, and large siphuncle somewhat removed from the venter. Dr. TEICHERT borrowed the type and received permission to section it, and though the original hard parts of septa and siphuncle were found to have been largely dissolved, the section tended to confirm previous opinions as to affinities of the genus. Though the preserved internal structure is rather inadequate, its pattern is consistent with that of the Cyrtogomphoceratidae. With crucial parts dissolved away, it was not at first evident whether large cavities at the septal foramina represented parietal deposits or bullettes or both. Subsequent study of other forms showed that the ontogenetic pattern, in which the cavities tend to increase rather than to decrease in size as ontogeny progresses, is consistent with the nature of bullettes and completely inconsistent with parietal deposits, which one would not expect to find preserved in a region so close to the living chamber.

Similar broadly expanded segments, broadest and most rounded at the anterior end, are found in some Silurian Oncoceratidae. There, also, the ring is thickened, and may be annular at the septal foramen. That this is a case of morphological convergence is indicated by the discordance in age of the two types and the fact that all Silurian forms are exogastric cyrtocoones with narrow cross section, having siphuncles extremely close to the ventral wall. BARRANDE (1877) has figured some such structures, notably in *Oonoceras diprion* (pl. 499, fig. 18), *Cyrtoceras opportunatum* (pl. 541, fig. 5), and *Orthoceras viduum* (pl. 526, fig. 5).

Any attempt to place *Ulrichoceras* with oncoceroids encounters some serious discrepancies. There is a stratigraphic gap from early Middle Ordovician to late Middle Silurian, where the only similar endogastric oncoceroids occur. Also, it is now evident that endogastric cyrtocoones belonging to the Oncoceratida are absent in the Ordovician; all such forms have been found to belong to the Discosorida. As previously noted, gross features of the shell, such as broad cross section, position of the

EXPLANATION OF PLATE 15

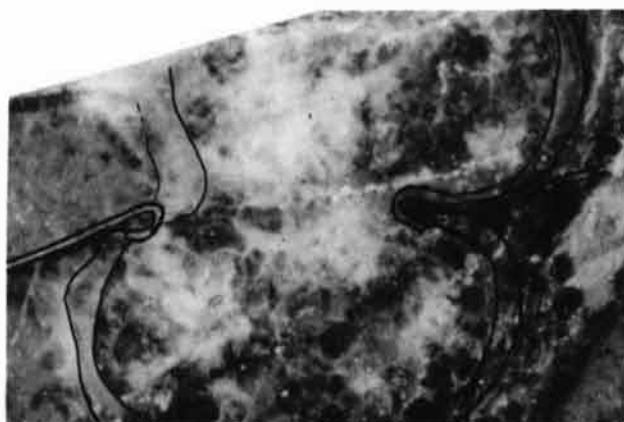
CYRTOGOMPHOCERATIDAE—*Kiaeroceras*; WESTONOCERATIDAE—*Sinclairoceras*, *Winnipegoceras*

FIGURE

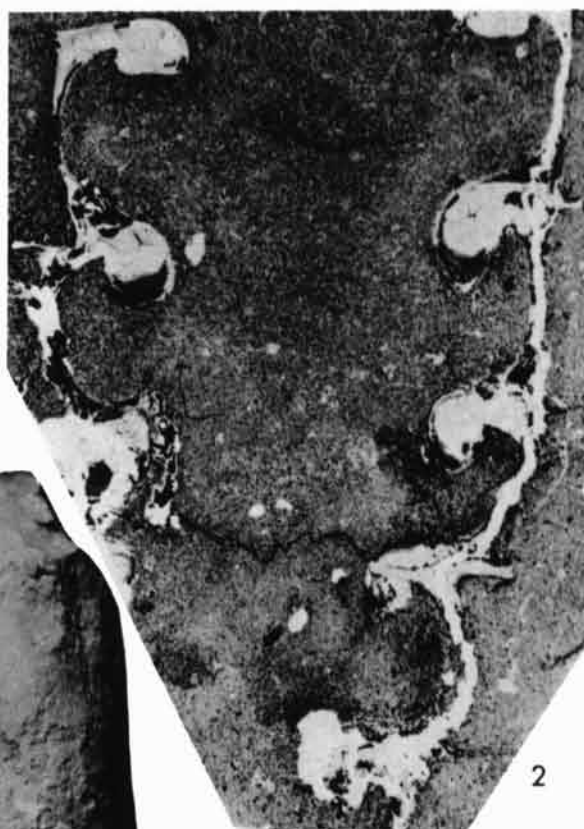
1. *Sinclairoceras haha* FLOWER, holotype, from Simard limestone (Ordovician), Ste. Anne de Chicoutimi, Que.; collection of the writer. Vertical section through siphuncle at anterior end of phragmocone (retouched), venter on right, $\times 8$.
2. *Kiaeroceras frognoeyense* STRAND, from Trinucleus limestone (Ordovician), Frognoya, Ringerike, Norway; Univ. Oslo, Paleont. Mus., no. I 2013; courtesy of Dr. TRYGVE STRAND. Thin

section of siphuncle showing bullettes but with fine structure replaced.

- 3-5. *Winnipegoceras sinclairi* FLOWER, holotype, from Terrebonne limestone (Middle Ordovician), St. Bartholomew, Que.; collection of the writer.—3, Lateral view, venter at left, $\times 1$.—4, Ventral view, $\times 1$.—5, Vertical section of only siphuncle segments preserved (from base of specimen) showing extremely rapid thickening of deposits with diaphragms crossing central tube, venter on left, $\times 6$.



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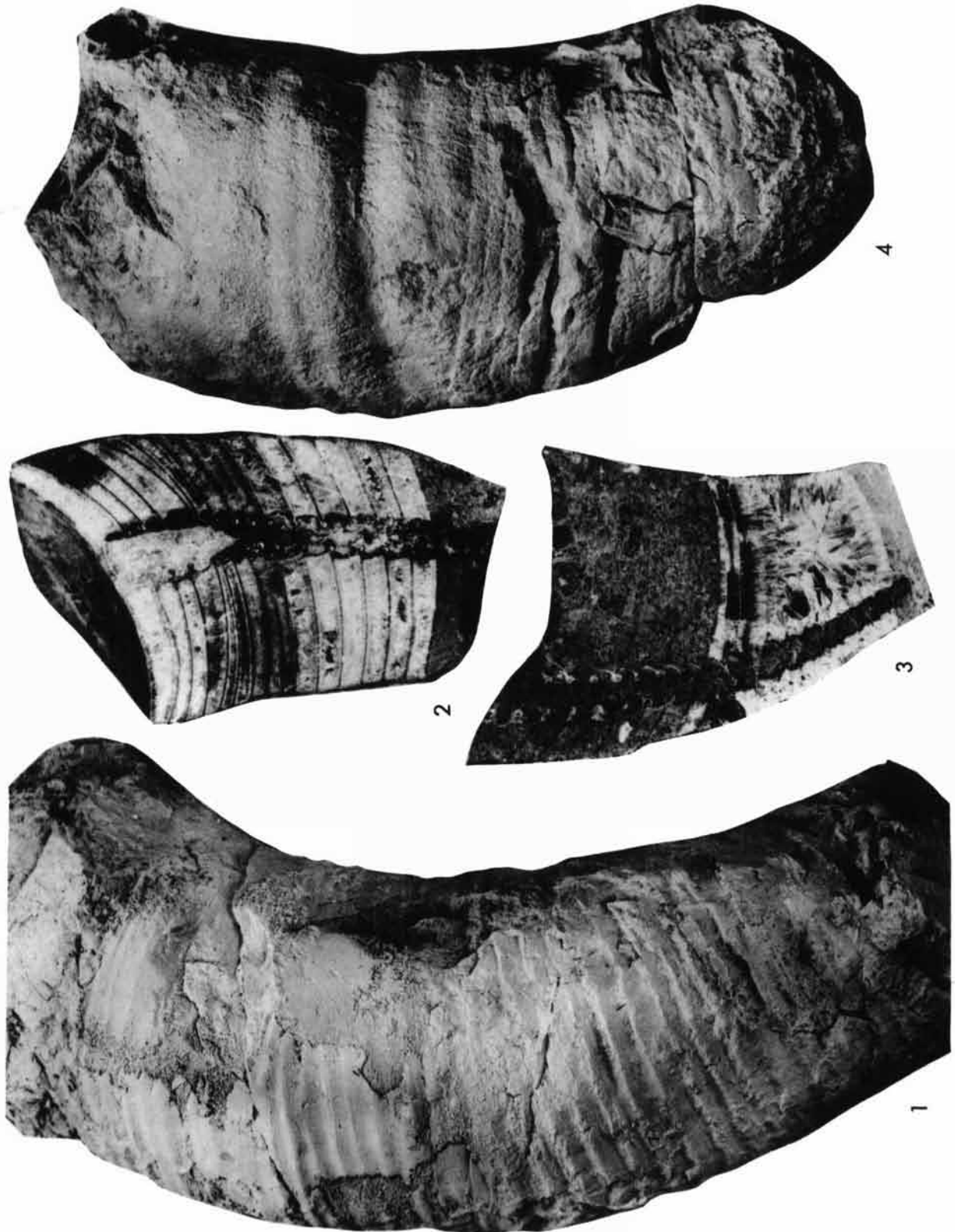
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FLOWER & TEICHERT—Order Discosorida (Cephalopoda)

siphuncle some distance from the ventral wall, and tendency of the sutures to slope forward from venter to dorsum, all recall the Ruedemannoceratidae. Obviously the siphuncle is similar to that of higher *Cyrtogomphoceratidae* and probably the swollen cavities represent dissolved bullettes. *Ulrichoceras* is thus logically interpreted as a primitive member of the *Cyrtogomphoceratidae*, being the oldest known genus and retaining some features indicative of its origin in the still older and simpler *Ruedemannoceratidae*.

Ulrichoceras beloitense Foerste

Pl. 5, fig. 1-4; Pl. 9, fig. 3; text-fig. 14

Ulrichoceras beloitense FOERSTE, 1928, Denison Univ. Bull., Sci. Lab., Jour., v. 33, p. 211, pl. 47, fig. 1 A-C.

The only known specimen of this species is the holotype, which is 50 mm. long, including eight camerae and a nearly complete living chamber. It is an internal mold in dolomite, gently curved, moderately expanding to a point beyond middle of living chamber, where shell contracts slightly laterally and more markedly dorsally. Cross section shows flattened, only slightly convex venter and strongly rounded ventrolateral and dorsal sides, giving a faintly subtriangular form that is slightly wider than high throughout. Shell increases in a length of 45 mm. from 24 mm. and 21 mm. at base to 32 and 30 mm. near the middle of living chamber. Sutures visible ventrally and laterally but indicated dorsally only at base of specimen. The eight camerae occupy a length laterally of 17 mm., last three being very slightly shallower than earlier ones, a sign of maturity. Sutures describe broad shallow rounded lobes on venter, rising toward the sides and becoming sinuate, so that they are more nearly transverse on the dorsal half of the specimen. They may be transverse mid-dorsally or may still slope forward enough to develop very faint dorsal saddles.

At the base of the specimen the siphuncle is round in cross section, unusually large and well removed from the venter. It is 4 mm. across and 4 mm. from the venter, 12 mm. from the dorsum. A segment 5.5 mm. in maximum height is only 2 mm. in length. Segments expand only moderately within the siphuncle, widening most and being most strongly rounded at their anterior ends; the two sides of the rings approach each other gradually in approaching adapical ends of segments, meeting the adapical septa either with no area of adnation or only a very small one. Connecting ring markedly thicker on ventral than dorsal side but its material has been removed by solution. The cavity widens at the septal foramen in each segment, and is slightly greater in adoral than adapical segments. Ontogenetic increase in size of the cavity suggests that it represents a dissolved bullette and not a parietal deposit. The septal necks have been dissolved also and their precise form is unknown, except that they were evidently short and strongly recurved. The thickened ring on the ventral side is very similar in form to that figured here for *Cyrtogomphoceras* (Pl. 6, fig. 1-2) and little doubt attaches to interpretation of the structure as a thick ring with swollen bullette.

The aperture is very incompletely preserved and so rough that little can be determined as to its form other than presence of a

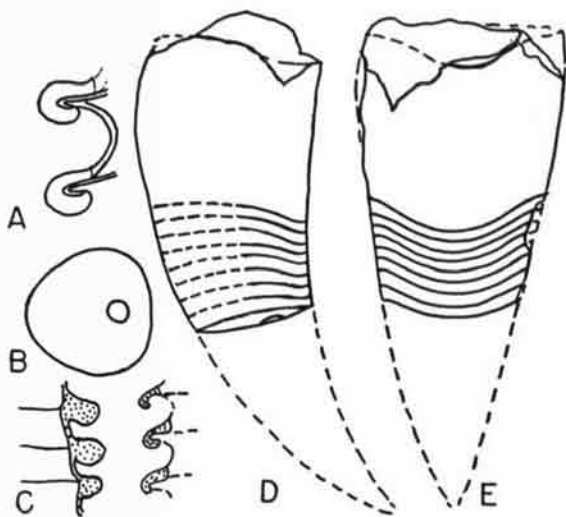


FIGURE 14. *Ulrichoceras beloitense* FOERSTE

A, Restoration of part of dorsal wall of siphuncle, showing inflated bullette; $\times 4$.—B, Cross section at base of holotype; $\times 0.75$.—C, Portion of siphuncle, venter at left, showing structures lost by solution; enlarged. D, Lateral view with apex and aperture restored; $\times 0.75$.—E, Ventral view; $\times 0.75$.

broad hyponomic sinus which occupied most of the ventral face and was broader and shallower than ventral lobes of the sutures.

Discussion. Characters of the genus also serve to distinguish this species. In view of removal of siphuncle structures by solution, interpretation of them rests largely on analogy with related genera, including the more primitive and older *Ruedemannoceras* and younger, more specialized members of the *Cyrtogomphoceratidae*.

Holotype. U. S. Natl. Mus., no. 25302.

Occurrence. Platteville limestone (upper buff member,) at Beloit, Wis. The species is notable as the only representative of the *Cyrtogomphoceratidae* so far known from beds of early Mohawkian age.

Genus STRANDOCERAS Flower, 1946

Type species—*Protosphragmoceras tyriense* STRAND

Strandoceras FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 434.

Shell a compressed endogastric cyrtocone with living chamber straighter and more slender than earlier portion. Cross section compressed, venter more narrowly rounded than dorsum, commonly subangular. Sutures with shallow lateral lobes, sloping forward slightly on dorsum in late stages. Aperture open, with shallow hyponomic sinus on venter. Siphuncle close to venter, with large broadly rounded segments, necks with short brims

EXPLANATION OF PLATE 16

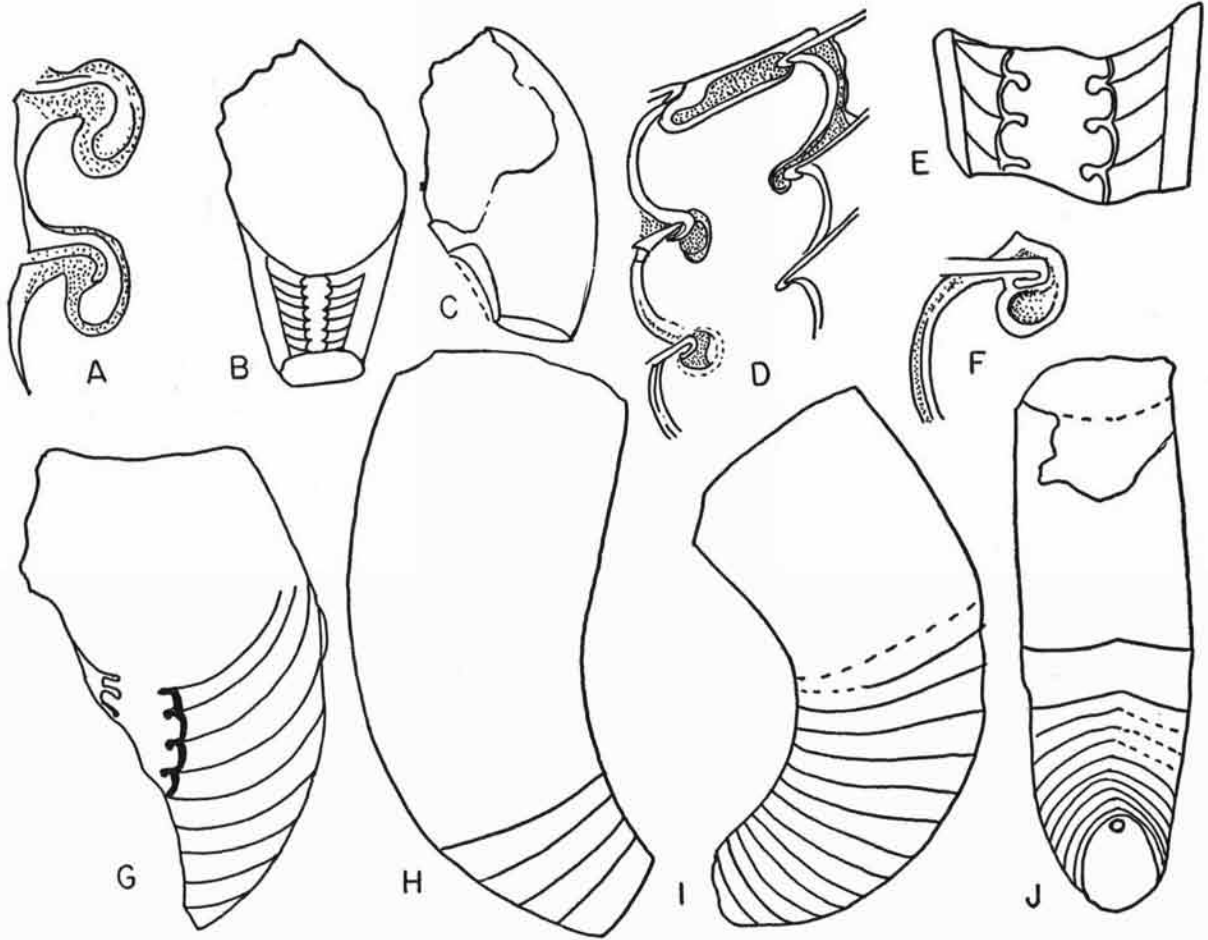
WESTONOCERATIDAE—*Fabroceras*

FIGURE

1-2. *Fabroceras multinctum* FLOWER, paratypes from Leipers beds (Upper Ordovician), along Cumberland River near Rowena, Ky.—1, Paratype showing lateral surface of late growth stage with fine numerous transverse ridges, and faint longitudinal markings apparent only near anterior end, $\times 1$ (Univ. Cincinnati, no. 24211).—2, Vertical section showing abnormal crowding of camerae at middle and typical rapid enlargement of siphuncle, $\times 1$ (Shideler collection); structure

shown in more detail on Pl. 17, fig. 3.

3-4. *Fabroceras percostatum* FLOWER, specimens from Leipers beds (Upper Ordovician), along Cumberland River, near Rowena, Ky.—3, Vertical section of paratype, $\times 1$ (Univ. Cincinnati, no. 24215); shown in more detail on Pl. 18, fig. 1.—4, Lateral view of holotype (Univ. Cincinnati, no. 24214) showing extreme development of costae and annular constrictions noted in the genus, $\times 1$.

FIGURE 15. General features of *Strandoceras*.

A. Siphuncle wall of *S. tyriense* (STRAND) showing large bullettes; $\times 4$, after STRAND.

B, C. *S. schmidti* (TEICHERT); B, ventral view; C, lateral view, venter at left; both $\times 0.75$, after TEICHERT.

D. *S. tyriense* (STRAND), portion of longitudinal and essentially vertical section of siphuncle, slightly tangential at anterior end, venter at right; $\times 4$, after STRAND.

E. *S. sphynx* (SCHMIDT), horizontal longitudinal section of siphuncle; $\times 1$, after TEICHERT.

F. *S. tyriense* (STRAND), septal neck showing large bullette and portion of free part of connecting ring; $\times 4$, after STRAND.

G, H. *S. sphynx* (SCHMIDT); G, vertical section, venter at left, $\times 0.75$; H, lateral view, $\times 1$, after TEICHERT.

I, J. *S. tyriense* (STRAND), exterior of holotype, $\times 0.5$; I, lateral view, venter at left; J, ventral view, after STRAND.

EXPLANATION OF PLATE 17

WESTONOCERATIDAE—*Faberoceras*

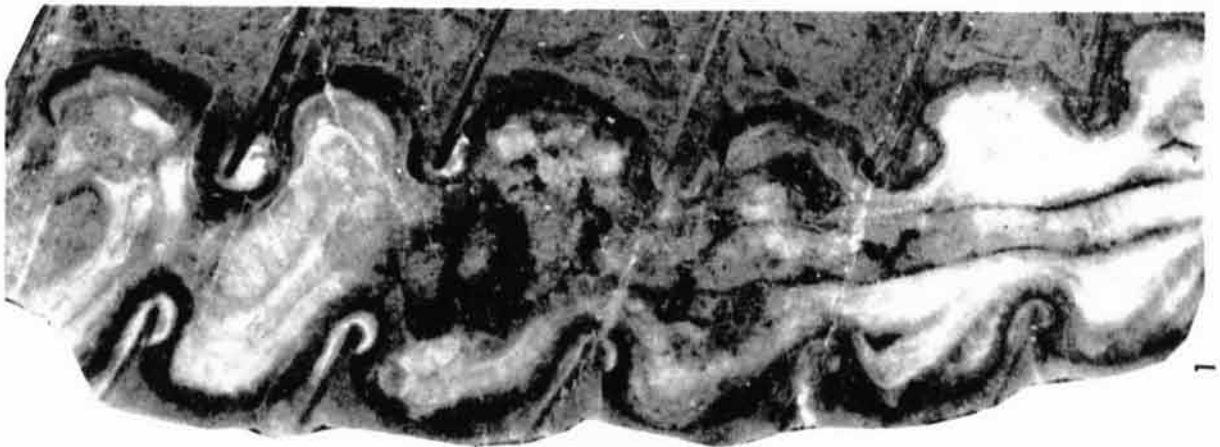
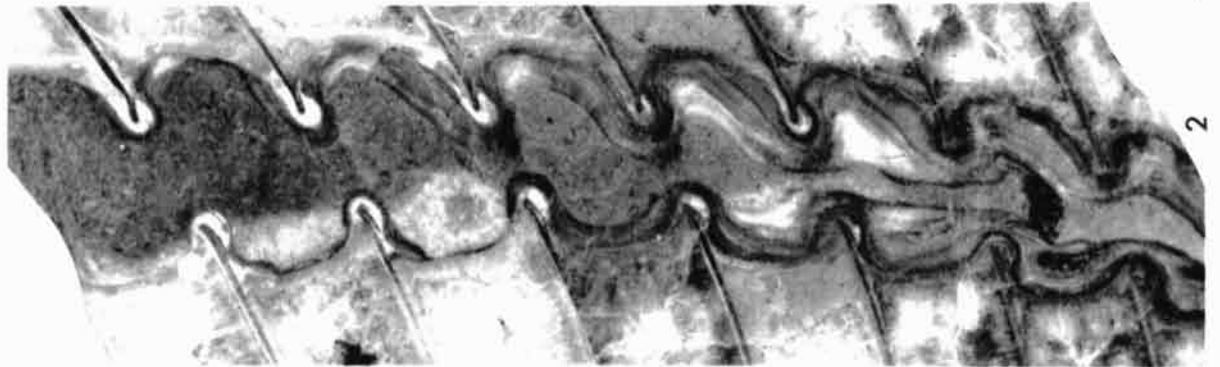
FIGURE

1. *Faberoceras* sp. Vertical section of siphuncle, $\times 6$, venter on left. Adorally the inner layer of the bullettes is replaced by white calcite; it is extended anteriorly on the venter, but abbreviated on the dorsum. The interior of the siphuncle is filled with endocones, and the wall of the very broad central canal is shown in the apical half, the adoral half being slightly off center.
2. *Faberoceras* sp. cf. *F. shideleri* FLOWER. Section of siphuncle, $\times 4$, showing bullettes replaced by white calcite (most prominent adorally), thick rings, and endocones; near the base cen-

tral tube shows interruption, apparently representing a diaphragm, which rarely is observed in this genus.

3. *Faberoceras percostatum* FLOWER. Section of siphuncle showing details in form of segments, $\times 3.2$ (shown $\times 1$ in Pl. 16, fig. 2). The crowding of septa is apparently abnormal here but the marked expansion of the siphuncle and rounding of its segments is not. Within are endocones, which give way in interior part to forward-growing parietal deposits.

All from Leipers beds (Upper Ordovician), along Cumberland River, near Rowena, Ky.; specimens shown in Figs. 1 and 2 from collections of the writer, in Fig. 3 from Shideler collection.



3

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1

FLOWER & TEICHERT—Order Discosorida (Cephalopoda)



narrowly separated from free part of septum; rings markedly thickened, with large two-layered bullettes.

Discussion. The genus was erected for Ordovician species previously referred to *Protophragmoceras*, which were of obvious discosorid organization, the siphuncle being very much like that of *Cyrtogomphoceras* in its broadly rounded segments, thick rings, and large bullettes. The strong cyrtococon curvature, slender form, and reduction of expansion in the living chamber distinguish the genus from other members of the Cyrtogomphoceratidae. *Lyckholmoceras*, which most nearly resembles *Strandoceras* in form, has a much more slender siphuncle. *Kiaeroceras* differs in the essentially straight anterior part of the shell.

Protophragmoceras is probably a Silurian descendant of *Strandoceras*, distinguishable by its smaller siphuncle with segments showing greatest expansion and most markedly rounded outline in the anterior end and with septal necks apparently very short and recumbent. A considerable stratigraphic gap separates these two genera, *Strandoceras* being confined to the early Upper or late Middle Ordovician of the Scandinavian and Baltic regions, whereas *Protophragmoceras* is thus far known only from the later half of the Middle Silurian (Étage E₂) of the Bohemian basin.

The known species have been adequately illustrated and described. The accompanying figure (Fig. 15A-J) shows their essential features largely as illustrative of the genus.

Strandoceras tyriense (Strand)

Text-fig. 15A, D, I, J

Protophragmoceras tyriense STRAND, 1933, Norsk Geol. Tidsskr., Bind 14, p. 93, pl. 12, fig. 1a, b; pl. 13, fig. 2-4.
Strandoceras tyriense FLOWER, 1946, Bull. Am. Paleont., v. 29, p. 434.

Lower Trinucleus limestone, Frogøy Island, Ringerike, and Gastropod limestone, Stavnestangen, Ringerike, Norway; upper Middle Ordovician or lower Upper Ordovician.

Strandoceras sphynx (Schmidt)

Text-fig. 15E, G, H

Phragmoceras sphynx SCHMIDT, 1858, Archiv. für Naturk. Liv-, Esth- und Kurlands, v. 1, ser. 2, p. 200.
Protophragmoceras sphynx TEICHERT, 1930, Paläont. Zeitschr., Band 12, p. 298, pl. 7, fig. 20; pl. 8, fig. 24, text-fig. 3, 4.
STRAND, 1933, Norsk Geol. Tidsskr., Bind 14, p. 93.

This species is recorded from the Lyckholm formation of Estonia and Gastropod limestone of Norway; upper Middle Ordovician or lower Upper Ordovician.

Strandoceras? sp.

Protophragmoceras sp. STRAND, 1933, Norsk Geol. Tidsskr., Bind 14, p. 96, pl. 11, fig. 11.

The early portion of a phragmocone resembling that of *Strandoceras tyriense* in form has been described and illustrated by STRAND who reports that it has the same sort of siphuncular structure as "*Protophragmoceras tyriense*." Little doubt of its assignment to *Strandoceras* exists therefore, even though internal structures have not been figured.

This fossil occurs in the Sphaeroid limestone, Gjøvik, Hadeland, Norway; upper Middle Ordovician or lower Upper Ordovician.

Strandoceras schmidtii (Teichert)

Text-fig. 15B, C

Codoceras schmidtii TEICHERT, 1930, Paläont. Zeitschr., Band 12, p. 297, pl. 8, fig. 25-26.

Strandoceras schmidtii is based on a shorter and more rapidly expanding shell (as compared with other species) from the Lyckholm beds of Estonia. Except for the more rapid expansion it is typical of the genus. True *Codoceras* has a subcentral actinosiphonate siphuncle and is known only from the Middle Silurian.

This species may be recorded from the Lyckholm beds (upper Middle or lower Upper Ordovician) of the Baltic region.

Genus LYCKHOLMOCERAS Teichert, 1930

Type species—*Lyckholmoceras estoniae* TEICHERT

Lyckholmoceras TEICHERT, 1930, Paläont. Zeitschr., Band 12, p. 301.
STRAND, 1933, Norsk Geol. Tidsskr., Bind 14, p. 89.

Shells assigned to *Lyckholmoceras* are large endogastric cyrtococones with moderate curvature and expansion of early stages reduced in the adoral portion. Cross section compressed, venter much more narrowly rounded than dorsum, sutures essentially transverse, with slight lateral lobes. Siphuncle composed of relatively slender segments but with thick rings and vestigial bullettes. Aperture with a ventral hyponomic sinus.

In curvature and reduction of expansion at the adoral end of the shell, this genus is intermediate between *Strandoceras* and *Kiaeroceras*, but it differs markedly from both in its much more slender siphuncle. The large size of the shell, the endogastric form and the thickening of the ring indicate classification of the genus in the Cyrtogomphoceratidae.

The genus is confined to the later Ordovician (Lyckholm beds) of Estonia and the Oslo region of Norway.

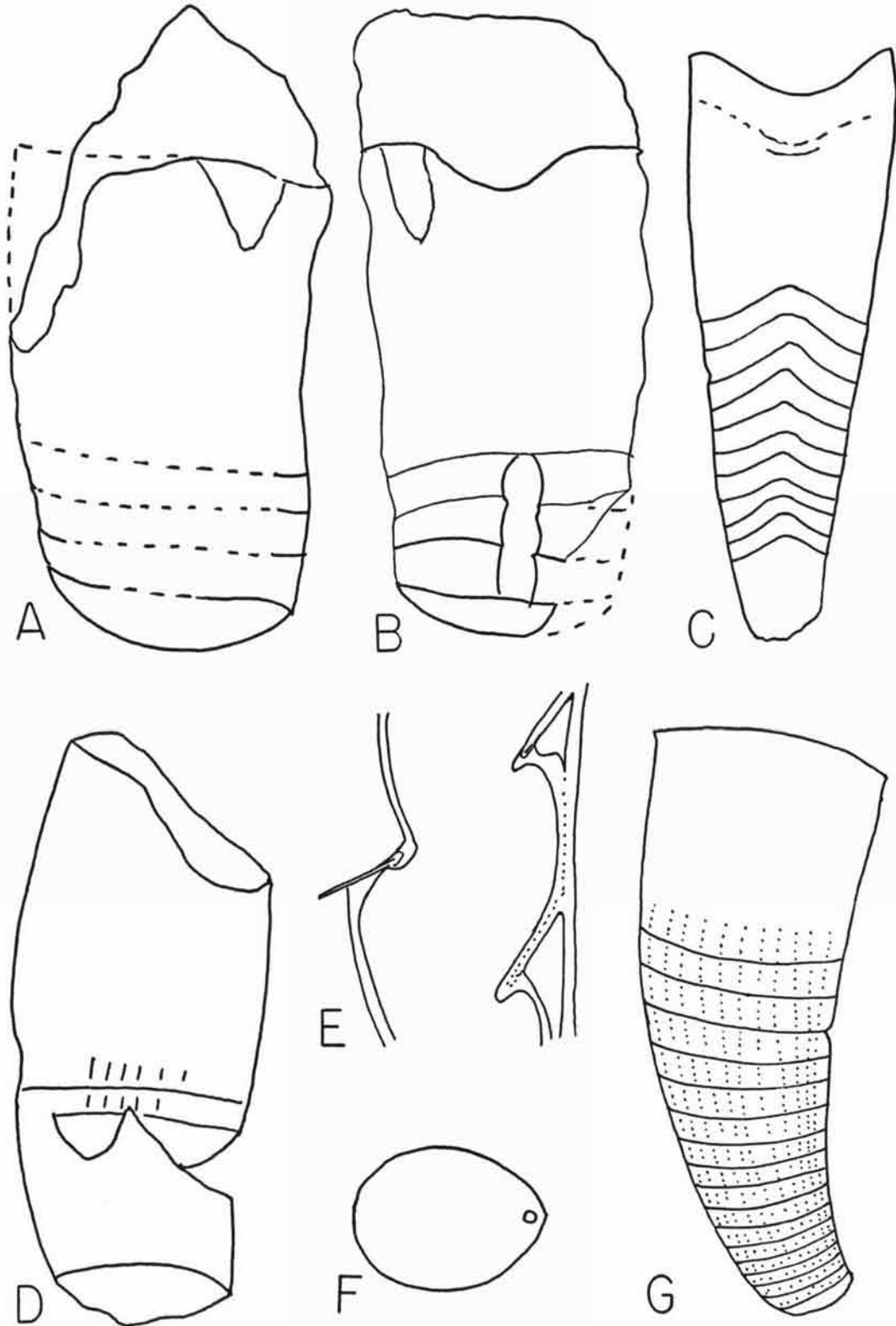
EXPLANATION OF PLATE 18 WESTONOCERATIDAE—*Faberocheras*

FIGURE

1. *Faberocheras percostatum* FLOWER. Section of apical portion of siphuncle of paratype (Univ. Cincinnati, no. 24215), about $\times 4$. The anterior end (upper part of figure) shows the 8th segment from the anterior end of the specimen. From the 8th to 17th camerae (representing an unusual distance) only thick connecting rings and bullettes are evident. Parietal deposits cover the bullettes in the remaining adapical camerae, shown in section slightly off center here.

2. *Faberocheras multinctum* FLOWER. Section of siphuncle showing details of texture of connecting rings. Note clear anterior termination of bullettes, particularly on ventral side (at left), and lamellar structure of endococones; portion of thin section, $\times 9$ (shown on Pl. 19, fig. 1). Collection of the writer.

Both from Leipers beds (Upper Ordovician), near Rowena, Ky.

FIGURE 16. Characters of *Lyckholmoceras*.

A, B. *L. estoniae* TEICHERT; *A*, lateral view, with restorations indicated, $\times 1$; *B*, ventral view, $\times 1$.—*C, G.* *L. norvegiae* STRAND; ventral and lateral views, $\times 0.75$.—*D, E.* *L. constrictum* STRAND; *D*, lateral view, $\times 0.75$; *E*, siphuncle, venter at right, $\times 6$.—*F.* *L. norvegiae* STRAND; diagrammatic cross section.

Lyckholmoceras constrictum Strand

Text-fig. 16D, E

Lyckholmoceras constrictum STRAND, 1934, Norsk. Geol. Tidsskr., Bind 14, p. 91, pl. 8, fig. 5; pl. 13, fig. 5.

Trinucleus limestone, Ringerike, Norway; Ordovician.

Lyckholmoceras estoniae Teichert

Text-fig. 16A, B

Lyckholmoceras estoniae TEICHERT, 1930, Paläont. Zeitschr., Band 12, p. 301, pl. 9, fig. 30-31.

Lyckholm beds, Estonia; Ordovician.

Lyckholmoceras norvegiae Strand

Text-fig. 16C, G

Lyckholmoceras norvegiae STRAND, 1934, Norsk. Geol. Tidsskr., Bind 14, p. 89, pl. 11, fig. 1 a-b, 2.

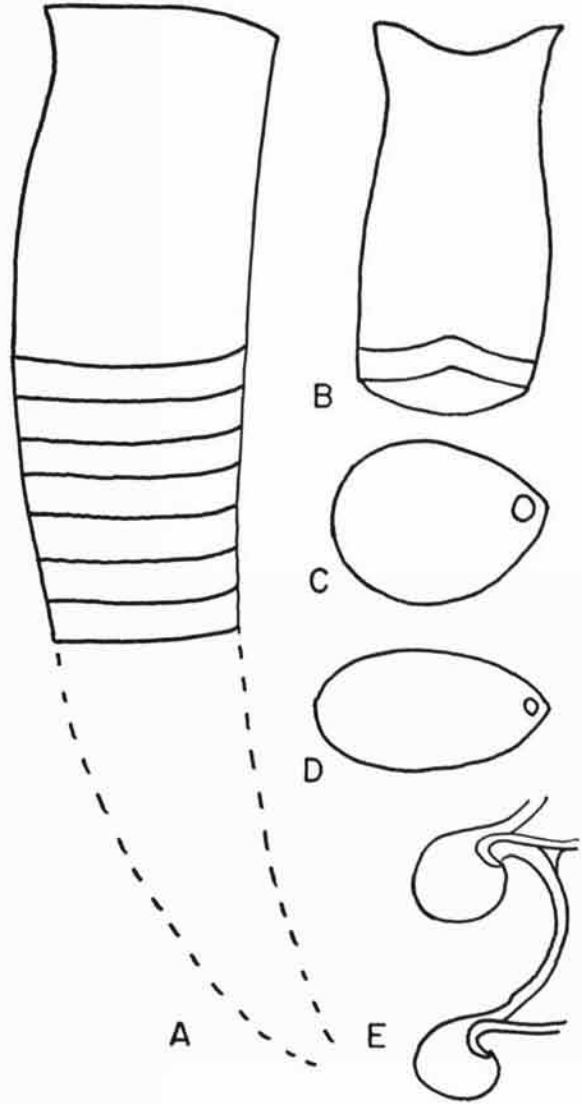
Trinucleus limestone, Ringerike, Norway; Ordovician.

Genus KIAEROCERAS Strand, 1933Type species—*Kiaeroceras frognoeyense* STRAND*Kiaeroceras* STRAND, 1933, Norsk. Geol. Tidsskr., Bind 14, p. 97.
FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 612.

Shells slender, essentially straight, known species quite large, contracting slightly over mature living chamber, some with slightly flaring aperture. Cross section compressed, venter in all species more narrowly rounded than dorsum. Sutures show faint lateral lobes separated by prominent ventral fainter dorsal saddles. Aperture with hyponomic sinus. Siphuncle close to venter, septal necks short, hardly recurved, connecting rings markedly thickened, with very prominent bullettes which extend well into the siphuncle cavity. No parietal or accessory deposits within siphuncle have been found. Shell surface with only growth lines, usually indicating the hyponomic sinus.

Discussion. The large essentially straight shells comprising this genus are seemingly intermediate between the exogastric Westonoceratidae and endogastric Cyrtogomphoceratidae. However, their stratigraphic position relatively high in the Ordovician makes one suspect this simple interpretation. The absence of any parietal deposits and similarity of the large bullettes with those of *Cyrtogomphoceras* and *Strandoceras* suggest that this genus is allied to the Cyrtogomphoceratidae rather than to the dominantly exogastric Westonoceratidae.

Through the kindness of Dr. STRAND, I have been able to examine the type material of *Kiaeroceras frognoeyense* and photographs of thin sections of the siphuncle of this species which were supplied are reproduced here. An opaque tangential section through the siphuncle exposed on specimen I-1346, illustrated by STRAND (pl. 9, fig. 4), shows broadly expanded segments with definitely thick rings, as well as some differentiation of inner and outer layers of the bullettes. This section seems to have septal necks which extend well within the bullettes and are recumbent. The two thin sections, though showing so recrystallized a condition as to leave doubt concerning the septal necks, suggest a very different interpretation. (1) The first (illustrated on Pl. 29, fig. 7), from specimen 12149 of the Paleontologisk Museum of Oslo,

FIGURE 17. General features of *Kiaeroceras*.

Outline drawings based on types.—A-C, *K. frognoeyense* STRAND; A, lateral view showing portion of shell (composite of holotype and paratype) with apex restored; B, ventral view (holotype) showing ventral saddles and hyponomic sinus; C, cross section, venter at right; all $\times 0.5$.—D-E, *K. herocyense* STRAND; D, diagrammatic cross section, $\times 0.5$; E, restoration of part of siphuncle wall showing necks, rings and inflated bullettes, $\times 4$.

is a vertical section, where, as usual with siphuncles close to one wall of the shell and not at the point of greatest depth of the septum, segments are markedly oblique. The septal neck on the dorsum, seen in the penultimate septum of the illustrated section, is short and recurved but free. That on the venter is essentially parallel with the axis of the siphuncle. The remainder of the siphuncle is represented by light calcite within which there is very poor differentiation. It is evident that the rings are thickened. The calcite extends outward from the normally expected outer boundary of the connecting ring. It is

possible that some inorganic calcite deposited against the outer surface of the ring is incorporated in this material but probable that a good part of the light area, at least, represents a connecting ring which has been thickened by addition of material to its outer surface. The ends of the connecting rings are clearly thickened into prominent bullettes, but within them there is no longer any clear differentiation of structures. (2) A second section (Pl. 15, fig. 2), taken from specimen No. I-2013, Paleontologisk Museum of Oslo, is apparently a horizontal longitudinal section, for the two sides of the siphuncle are essentially similar in outline. Again, replacement has obscured so much of the original differentiation that the septal necks and connecting rings are largely indistinguishable. The penultimate septum on the lower right shows, however, what appears to be a good septal neck, short, scarcely recurved, and not unlike what might be expected at this point from the vertical section noted above. Rings are thickened and produced into prominent bullettes at the septal foramina. Some segments show the apical surface bearing a dark area, which is part of an original outer layer. The anterior segment shows in the upper left a thickening of the anterior end of the ring, so that it is adnate to the adoral septum, a feature found in other discosorids. A prominent outward thickening of the ring like that seen in the preceding section is lacking.

Essential features of *Kiaeroceras* are illustrated in Figure 17.

This genus is confined to later Ordovician beds of the Baltic region.

***Kiaeroceras frognoeyense* Strand**

Pl. 15, fig. 2; Pl. 29, fig. 7; text-fig. 17A-C, E

Kiaeroceras frognoeyense STRAND, 1933, Norsk. Geol. Tidsskr., Bind 14, p. 97, pl. 9, fig. 4; pl. 12, fig. 2a-b.

Trinucleus limestone, Frognoya, Ringerlike, Norway; Ordovician.

***Kiaeroceras* sp. cf. *K. frognoeyense* Strand**

Kiaeroceras cf. *frognoeyense* STRAND, 1933, Norsk. Geol. Tidsskr., Bind 14, p. 98, pl. 1, fig. 7.

Lyckholm formation, Piersal, Estonia; Ordovician.

***Kiaeroceras heroeyense* Strand**

Text-fig. 17C

Kiaeroceras heroeyense STRAND, 1933, Norsk. Geol. Tidsskr., Bind 14, p. 99, pl. 9, fig. 5.

Gastropod limestone, Herøya, near Porsgrund, Norway; Ordovician.

Genus CYRTOGOMPHOCERAS Foerste, 1924

Type species—*Oncoceras magnum* WHITEAVES

Cyrtogomphoceras FOERSTE, 1924, Denison Univ. Bull., Sci. Lab., Jour., v. 20, p. 267.

FOERSTE & SAVAGE, 1927, Same, v. 22, p. 87.

FOERSTE, 1929, Same, v. 24, p. 232.

TROEDSSON, 1929, Meddelelser om Grønland, Bind 71, p. 96.

TEICHERT, 1930, Paläont. Zeitschr., Band 12, p. 296.

FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30,

p. 71.

FLOWER, 1940, Geol. Soc. America, Bull., v. 51, p. 1961.

ROY, 1941, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 146.

FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 433.

MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America,

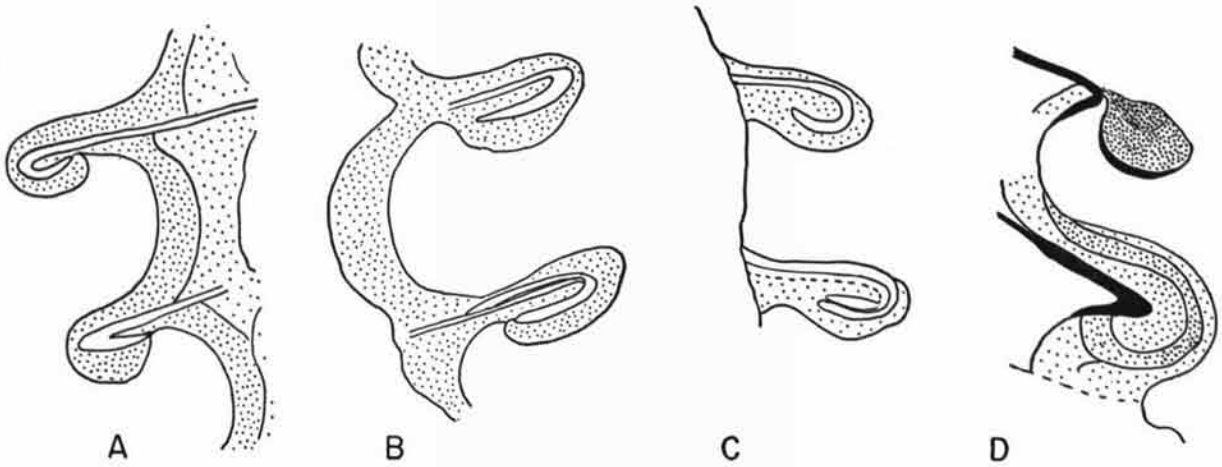
Mem. 62, p. 104.

Large fusiform endogastric brevicones, expanding rapidly apically, gibbous over anterior end of phragmone or base of living chamber, the living chamber contracting conically. Aperture with ventral hyponomic sinus. Ventral profile convex, curvature reduced near aperture; dorsum straight or concave apically, convex over gibbous region, straight or concave to aperture. Cross section compressed in typical species, but circular or even slightly broader than high in others. Sutures typically with faint lateral lobes, and sloping increasingly forward on dorsum in late growth stages. Siphuncle large, relatively close to the concave venter. Shell apparently thin, as specimens are commonly distorted. Surface with growth lines, ranging from relatively smooth to coarsely fasciculate.

Siphuncle slightly removed from venter, with short and broad segments broadly expanded within camerae, free part of each segment strongly rounded, brims narrowly free or recumbent and connecting rings generally broadly adnate to septa at both ends. Rather commonly, particularly in early growth stages, siphuncle segments increase very markedly in diameter throughout a relatively short series of camerae, as shown by the illustrated sections of *Cyrtogomphoceras dowlingi* (Pl. 6, fig. 5), *C. nutatum* (Pl. 6, fig. 3-4), and *C. rotundum* (Pl. 5, fig. 5). Later growth stages commonly show a series of segments essentially uniform in size.

Some sections suggest that in late maturity size of siphuncle segments may actually decrease slightly, though a possibility remains that this effect may be more apparent than real. Also this may appear in sections which are central apically but slightly excentric adorally, thus failing to attain maximum diameter of the segments. However, such contraction is suggested by one section (FOERSTE, 1928, pl. 8, fig. 2) of *C. intermedium* and in this species seems to be real rather than adventitious.

Details of siphuncle structure unfortunately can be ascertained only from a few specimens. TROEDSSON (1926) has published figures of thin sections of *C. turgidum* and *C. curvatum* but his illustrations represent only small parts of segments and it is impossible from these figures alone to distinguish between structures of the connecting ring and any possible parietal deposits. TROEDSSON's figure (1926, pl. 2, fig. 2) of *C. turgidum* was previously interpreted (FLOWER, 1946, p. 433, text-fig. 18G) as showing an apical swelling of the true connecting ring and a parietal deposit. His section (Fig. 19D) shows a recurved but free brim with the apical part of a connecting ring which thickens as it passes around the inside of the septal neck. A faint differentiation may represent inner and outer layers of the bullette or may be a bullette thickened by parietal deposits, the two being replaced so that they seem very similar in structure and composition, the boundary between them being faint. Within is a calcareous deposit that is thin adorally and thick adapically, as far as its identity can be traced, which if the previous layer is a parietal deposit, can only be an endocone. Its tendency to thicken adapically in the inflated part of the segments suggests an endocone and is atypical of parietal deposits, which elsewhere are thinner in the expanded part of the segment if any difference in thickness occurs. Apically, recrystallization obscures the structures. Ador-

FIGURE 18. Structure of the siphuncle wall in *Cyrtogomphoceras*.

Cyrtogomphoceras sp. (Pl. 6, fig. 1, 2). *A*, Dorsal wall showing necks, rings thickened into bullettes, and an apparent secondary thickening on the outside of the original ring. *B*, Ventral wall of same specimen, showing what can be observed of septal necks and rings, anterior neck being differentiated only in part, the adapical one with apparent double layers (almost certainly part of this structure is the inner layer of a bullette).—*C*, *Cyrtogomphoceras curvatum* TROEDSSON, portion of the siphuncle

wall (based on TROEDSSON, 1926, pl. 59, fig. 3), showing structures essentially similar to those in *A* and *B*.—*D*, *Cyrtogomphoceras turgidum* TROEDSSON (based on TROEDSSON, 1926, pl. 2, fig. 2) showing a portion of siphuncle wall with a large bullette only at the anterior septal foramen, adapical one showing apparently a bullette of two layers, and an accessory deposit over it, the interpretation of which is doubtful but suggests a parietal deposit. (*A-C*, $\times 5$; *D*, about $\times 8$).

ally, a small rather discrete "lunule" seems to hang tenuously from the innermost part of the septal neck.

TROEDSSON'S (1926, pl. 59, fig. 3) figure of *C. curvatum* shows recurved septal necks and structures which clearly are only thick rings enlarged into bullettes (Fig. 18C).

A portion of a phragmocone of *Cyrtogomphoceras* sp. cf. *C. rotundum* which was sectioned (Pl. 5, fig. 5) shows adoral increase in diameter of the siphuncle segments and their strongly rounded outline, but all original calcareous structures have been lost by solution. Six segments of the siphuncle are clearly outlined (with the dorsal wall of a 7th) in a length of 40 mm. The basal segment expands from 3 to 11 mm. and the adoral one from 16 to 25 mm. Evidently the rings were fairly thick, swollen into bullettes around the strongly recurved septal necks. The greater amount of material removed in adapical segments suggests that either the wall was much thicker in this region or else that slight parietal deposits existed which have been removed by solution along with primary structures of the siphuncle wall. Probably only primary structures are involved, as incipient parietal deposits would be expected to appear here, if at all, confined to the region of the septal foramen, an interpretation with which this section seems widely inconsistent.

The figured specimen, from the Lander sandstone of the Bighorn group, from the south side of the middle fork of the Popo Agie River, 10 miles west of Lander, Wyoming, is no. 2050 in the U. S. Natl. Museum.

A specimen from the Mt. Silliman beds of Baffin Island figured by MILLER, YOUNGQUIST & COLLINSON (1954, pl. 43, fig. 5) as *Cyrtogomphoceras* sp., was ground

vertically to expose the siphuncle. Though differentiation of structure proved to be slightly less than was originally hoped, this specimen (Pl. 6, fig. 1, 2) retains parts of 7 siphuncle segments. Clearly the septal necks are strongly recurved, brims long, parallel to the transverse part of immediately adjacent septa but narrowly free. They are surrounded by bullettes (clearly seen in the lower right of Pl. 6, fig. 1). The rings are thick, with some differentiation by color variation in the opaque section, but not adequate for clear delineation of the regions (Fig. 18A,B). Where the free part of the neck approaches the septa at either end it tends to be thickened. Though only slightly developed on the dorsum, the thickening is greatly accentuated on the ventral side and there is there a secondary later thickening, since parts of the original outer boundary of the connecting ring can be discerned.

Cyrtogomphoceras nutatum (Pl. 6, fig. 3, 4) shows only a faint trace of bullettes in the adapical septal foramen. *C. dowlingi* shows the outline of the siphuncle segments, though solution has made the outline irregular, particularly in anterior segments, but the original fine structures cannot be determined. Obviously small bullettes may occur adapically but no thick accessory deposit is present.

From these sections it seems evident that *Cyrtogomphoceras* has a siphuncle in which the rings are thickened and bullettes are typically swollen. TROEDSSON'S figure of *C. turgidum* (here reproduced in text-fig. 18D) suggests a bullette only in the anterior segment shown. Possibly some of the calcareous structure surrounding the adapical one of the two septal necks could be a parietal deposit but the section shows too small a

portion to permit definite interpretation. It may be that some inorganic calcite is involved here; possibly it is a thickened bullette. If it is a parietal deposit, perhaps thickened into an endocone, it is exceptional and is a feature for which no other evidence has been found in *Cyrtogomphoceras*.

Evidence of cameral deposits in *Cyrtogomphoceras* is very poor. Possibly they were wanting and at the most their development must have been very slight. Rather many specimens are known showing the siphuncle slightly askew in cross section and a few of these available for examination at first hand show that distortion of the shells through pressure from compaction of the sediments contributes to this condition, indicating that the phragmocone was weak. Specimens from the Selkirk member of the Red River formation belonging to the larger species commonly show such flattening, which is remarkable in view of the fact that the external shell is unusually thick.

Discussion. The form of this genus is particularly characteristic. Strangely, without knowledge of the position of the siphuncle, and consequently, of orientation, some species look very much like *Westonoceras* or *Winnipegoceras*. Indeed, a fortuitous find of a specimen showing adequate internal structure, shows that *Winnipegoceras dowlingi* FOERSTE is a true *Cyrtogomphoceras*.

The genus is confined to boreal Ordovician faunas of Red River aspect. It is as yet unknown in the lower part of the Montoya, the Upham dolomite. In the Fremont limestone of Colorado it is represented only by *C. contractum*. In the Bighorn group, described species include *C. landerense*, *C. minor*, *C. perexpansum*, *C. popoagiense*, *C. rotundum* and *C. vincinum*, all from the Lander sandstone member. The equivalent Whitewood dolomite of South Dakota has yielded *C. foerstei* and *C. thompsoni*. The Red River series of Manitoba contains *C. dowlingi*, *C. intermedium*, *C. whiteavesi* and *C. sp. cf. C. turgidum*, all from the Dog Head member, and *C. magnum* and *C. sp. cf. C. rotundum* from the Selkirk member. The next occurrence of equivalent beds, Nelson limestone, has yielded *C. nutatum* but *C. shamattawaense* from the overlying Shamattawa limestone is so atypical that it cannot be considered in discussing the range of the genus. The Mt. Silliman beds of Baffin Island have yielded *C. baffinense*, *C. furnishii*, *C. milleri*, and *C. schucherti* and from the Cape Calhoun beds of northern Greenland *C. curvatum*, *C. sacculus*, and *C. turgidum* have been collected.

Reports of *Cyrtogomphoceras* in northern Europe (TROEDSSON, 1926; TEICHERT, 1931) and southeastern Asia (COWPER REED, 1936) are based on specimens which now are either definitely assigned to other genera or are so inadequately known that while their reference to *Cyrtogomphoceras* seems dubious, they cannot be placed in any other genus with certainty.

Cyrtogomphoceras is confined to Red River faunas, late Middle or early Upper Ordovician, northern North America.

Cyrtogomphoceras dowlingi (Foerste)

Pl. 6, fig. 5, 6

Winnipegoceras dowlingi FOERSTE, 1928, Michigan Univ., Geol. Mus. Contrib., v. 3, p. 58, pl. 8, fig. 1.
FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 217.

Shell strongly compressed, much higher and rather more gibbous than typical *Winnipegoceras*, to which it was originally referred, although its position in this genus seemed anomalous. I have been fortunate enough to secure a topotype specimen which, when sectioned, shows that the species has the typical structure of *Cyrtogomphoceras* and therefore the species is now referred to this genus.

The topotype specimen agrees closely with the holotype, which preserves only one side of the adoral camerae and living chamber. The topotype has a length of slightly more than 150 mm., extremity of the aperture being obscure. Only one side of the shell is preserved but its original cross section obviously was extremely flattened laterally. The shell has a height of 21 mm. at the base, where the width was probably about 15 mm., increasing to 62 mm. in a length of 50 mm. on the straight venter and 75 mm. on the strongly convex dorsum. In this interval eight camerae occur, increasing in depth on the dorsum from 9 to 14 mm. Sutures slope slightly adapically on the dorsum in the early part but become transverse and then slope adorally on the venter. In the next three camerae the sutures develop prominent lateral lobes and are extended markedly forward on the convex dorsum. Three well-preserved camerae average 12 mm. in depth dorsally, and on the extreme dorsum are obscure traces of two additional sutures. The four adoral camerae occupy a length of 55 mm. on the dorsum, beyond which the shell continues for 40 mm. apparently representing only the basal half of the living chamber.

A vertical section of the basal part of the specimen shows a siphuncle close to the straight side of the shell. Preservation of the early segments is poor, but it is evident that the segments are broadly expanded in the camerae and that they enlarge with extreme rapidity from adapical to adoral camerae. Where the shell height is 60 mm., a segment 6 mm. long enlarges from 15 to 23 mm. In cross section the siphuncle is strongly compressed, 17 mm. wide and 30 mm. high at the break in the mid-length of the specimen.

The only feature in which the present specimen is atypical of *Cyrtogomphoceras dowlingi* is a slight convexity of the ventral profile at mid-length of the specimen, and it is not evident that this is really as atypical as it appears, for in this region the venter of the holotype is incomplete.

The holotype (Geol. Survey of Canada, no. 7152) and hypotype, deposited in the New Mexico Bureau of Mines, are both from the Dog Head member of the Red River series, from Little Tamarack Island, Lake Winnipeg; Ordovician.

Cyrtogomphoceras nutatum Foerste & Savage

Pl. 6, fig. 3, 4; Pl. 7, fig. 1-3

Cyrtogomphoceras nutatum FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 87; pl. 17, fig. 2A, B.

A large *Cyrtogomphoceras*, holotype and only known specimen being broad in cross section. FOERSTE & SAVAGE regarded the present condition of the fossil as due to flattening after death and burial, a conclusion which is amply supported not only by some irregularity in its form but also by obvious distortion of a septal surface exposed near the mid-length of the specimen.

The adapical seven camerae were sectioned. They show a siphuncle in which segments expanded very rapidly from camera to camera, 1st to 6th segments increasing in maximum diameter from 4 to 10 mm. The 7th segment is too obscure for measurement. The siphuncle segments are imperfectly preserved; their outlines, though indicated by faint color variation throughout, fail to show

original structure. The connecting ring, septal necks, and any accessory structures have been dissolved. The basal segment shows an outline which is stylolitic. At its adoral end, penetrating within the stylolitic boundary, can be seen the tips of septal necks surrounded by small but prominent bullettes. Fainter indications of similar structures are found in the next two adoral segments, but farther adorally the whole outline of the siphuncle becomes fainter, and evidently original structures have been more completely dissolved, leaving the siphuncle outline as indicated only by slight differences in color and texture between matrix which entered through the siphuncle and matrix which penetrated the camerae, evidently through the break which removed much of the dorsal wall of the shell.

Holotype (Savage collectoin, Illinois Geol. Survey, no. 42 HB) from the Nelson limestone horizon 4, Nelson River, Hudson Bay; Ordovician.

Cyrtogomphoceras angustisiphonatum Miller

Cyrtogomphoceras? angustisiphonatum MILLER, 1932, Connecticut Acad. Arts, Sci., Trans., v. 31, p. 296, pl. 31, fig. 2, 3.

A relatively small species known from a single fragmentary specimen which does not show the form of the shell clearly, yet undoubtedly a true *Cyrtogomphoceras*. Shell a compressed endogastric brevicone with relatively large siphuncle.

The position of the species seemed doubtful when it was believed that *Cyrtogomphoceras* was related to *Diestoceras*, with which it practically intergrades in shell form, but the siphuncle of *Cyrtogomphoceras* indicates that it belongs to the Discosorida. The very large siphuncle is a secondary feature, but one safely employed inasmuch as all *Diestoceras* possess siphuncles of relatively small diameter.

The species occurs in the Lander sandstone member of Bighorn dolomite; Ordovician.

Cyrtogomphoceras baffinense Foerste

Cyrtogomphoceras baffinense FOERSTE, 1928, Michigan Univ., Geol. Mus. Contrib., v. 3, p. 63, pl. 4, fig. 1; pl. 11, fig. 4.

MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 105, pl. 53, fig. 1-3 (non ROY, 1941; nec MILLER, YOUNGQUIST & COLLINSON, 1954, pl. 43, fig. 6).

A medium-sized species with moderately spaced septa. The specimen figured by ROY (1941) under this name and refigured by MILLER, YOUNGQUIST & COLLINSON is a smaller species with much more closely spaced septa, here named *Cyrtogomphoceras schucherti*.

The species occurs in the Mt. Silliman beds, Ordovician, of Baffin Island.

Cyrtogomphoceras contractum Foerste

Cyrtogomphoceras contractum FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 77, pl. 15, fig. 1-3.

A moderate-sized species rather suggestive of *Cyrtogomphoceras baffinense*. It occurs in the Fremont limestone near Canyon City, Colo.; Ordovician.

Cyrtogomphoceras curvatum Troedsson

Cyrtogomphoceras curvatum TROEDSSON, 1929, Medd. om Grønland, Bind 71, p. 96, pl. 56; pl. 58, fig. 1; pl. 59, fig. 3.

A larger and more gibbous form than *Cyrtogomphoceras baffinense*, notable mainly as one of the few species in which the siphuncle structure is known in some detail, as noted under the generic discussion. It occurs in the Cape Calhoun beds of northern Greenland; Upper Ordovician.

Cyrtogomphoceras furnishi Roy

Cyrtogomphoceras furnishi ROY, 1941, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 148-9, fig. 108a-c.

MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 106, pl. 43, fig. 1-3.

A small rather closely septate species known from a single specimen. ROY (1941) has figured a section showing one segment of a siphuncle which is typical in breadth at the septal foramen and marked expansion within the camerae.

The species is known from the Mt. Silliman formation of Baffin Island; Ordovician.

Cyrtogomphoceras intermedium (Whiteaves)

Oncoceras (magnum? var.) intermedium WHITEAVES, 1897, Canada Geol. Survey, Paleozoic Fossils, v. 3, pt. 3, pp. 221-2, text-fig. 13.

Cyrtogomphoceras intermedium FOERSTE, 1928, Univ. Michigan, Geol. Mus. Contrib., v. 3, p. 65, pl. 8, fig. 2.

FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 223.

A relatively slender fusiform shell, moderately large. The type is ground to a vertical longitudinal section, displaying the form of the siphuncle segments clearly, but the fine structure cannot be made out well. Adoral siphuncle segments are slightly contracted; it is not evident that this may not be due to a section which is very slightly oblique and thus not intersecting the anterior segments at their point of greatest diameter.

The species occurs in the Dog Head member of Red River formation, Lake Winnipeg region of Manitoba; Ordovician.

Cyrtogomphoceras landerense Foerste

Cyrtogomphoceras landerense FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 74, pl. 15, fig. 5.

A moderately large species comparable with *Cyrtogomphoceras curvatum* in size, but more similar to *C. baffinense* in vertical profile.

The species is found in the Lander sandstone member of Bighorn dolomite, northwestern Wyoming; Ordovician.

Cyrtogomphoceras magnum (Whiteaves)

Oncoceras magnum WHITEAVES, 1890, Royal Soc. Canada, Trans., v. 7, sec. 4, p. 79, pl. 15, fig. 1.

WHITEAVES, 1897, Canada Geol. Survey, Paleozoic Fossils, v. 3, pt. 3, p. 220.

Cyrtogomphoceras magnum FOERSTE, 1924, Denison Univ. Bull., Sci. Lab., Jour., v. 20, p. 267.

FOERSTE, 1928, Univ. Michigan, Geol. Mus. Contrib., v. 3, p. 59, pl. 6, fig. 1.

FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 232.

One of the largest known species of *Cyrtogomphoceras*, apparently represented by a single specimen 187 mm. long, attaining a maximum height of 105 mm. FOERSTE'S (1928) photograph of the type is very slightly reduced. Regrettably, details of siphuncle structure are unknown in this species, which is the type of the genus. The large diameter of the siphuncle is such, however, as to leave no doubt as to the close affinities between this and species better known internally.

Cyrtogomphoceras magnum occurs in the Selkirk member, Red River formation, Manitoba; Ordovician.

Cyrtogomphoceras? milleri (Roy)

Diestoceras milleri ROY, 1941, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 152, 180, fig. 111.

Cyrtogomphoceras milleri MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 63, p. 107, pl. 31, fig. 2.

This species, known from a single specimen that is evidently crushed vertically and shows only the siphonal ventral side clearly, was placed by ROY in *Diestoceras*, a conclusion eminently justified by the form and general appearance of the specimen. MILLER, YOUNGQUIST & COLLINSON based their change of generic assignment primarily on the forward slope of the adoral sutures as seen toward the sides of the siphonal view of the specimen. While this feature could easily be attributed to distortion which has affected

the whole specimen, I am inclined to accept their reference of the species to *Cyrtogomphoceras* on the basis of the very short and very broad segments of the siphuncle, as seen partially exposed on the surface. Such segments are characteristic of *Cyrtogomphoceras*, whereas siphuncle segments of *Diestoceras* are uniformly smaller, narrower, generally longer than wide, subquadrate scalariform in vertical section, and typically actinosiphonate.

The species is known from the Mt. Silliman formation, Baffin Island; Ordovician.

Cyrtogomphoceras minor Foerste

Cyrtogomphoceras minor FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 78, pl. 15, fig. 4.

A relatively small species known only from a living chamber. It is typical of the genus in its forward slope of the sutures on the dorsum, ventrally placed rather large siphuncle, and endogastric curvature.

The species occurs in the Lander sandstone member, Bighorn dolomite, Wyoming; Ordovician.

Cyrtogomphoceras popoagiense Foerste

Cyrtogomphoceras popoagiense FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 75, pl. 14, fig. 3-4.

A moderate-sized rather slender fusiform species reminiscent of *Cyrtogomphoceras laticurvatum* of the Red River series.

The species is recorded from the Lander sandstone member, Bighorn dolomite, Wyoming; Ordovician.

Cyrtogomphoceras rotundum Miller

Cyrtogomphoceras rotundum MILLER, 1932, Connecticut Acad. Arts, Sci., v. 31, p. 294, pl. 30, fig. 1; pl. 31, fig. 1.
FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 76, pl. 14, fig. 1.

A moderately large species notable in breadth of cross section, which is nearly circular instead of compressed. Portion of a phragmocone of this species is illustrated (Pl. 5, fig. 5). This specimen is a fragment with a maximum length of 70 mm. It expands from a height of 35 mm. and width of 32 mm. at the base where the siphuncle segment (removed by solution) leaves a cavity 7 mm. wide and 9 mm. high. The specimen includes 8 and possibly 9 camerae, the septa and sutures being lost in the basal part, with a dorsal length of 75 mm. and a ventral length of 35 mm.

This species occurs in the Lander sandstone of the Bighorn group, Ordovician, of Wyoming.

Cyrtogomphoceras perexpansum Foerste

Cyrtogomphoceras perexpansum FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 73, pl. 13, fig. 1.

Known from a single specimen, the dorsal side of which is poorly preserved. It is notable as the largest known species of the genus, exceeding *Cyrtogomphoceras magnum* in size, for the complete shell is estimated at 350 mm. in length and 140 mm. in width. The cross section is apparently very slightly compressed. The siphuncle has not been observed.

This species occurs in the Lander sandstone member, Bighorn dolomite, Wyoming; Ordovician.

Cyrtogomphoceras sacculus Troedsson

Cyrtogomphoceras sacculus TROEDSSON, 1929, Meddel. om Grønland, Bind 71, p. 98, pl. 57, fig. 3; pl. 58, fig. 5-6.

A rather small species with ventral profile relatively gently curved. Possibly when complete it had the slender fusiform outline of *Cyrtogomphoceras intermedium* and *C. popoagiense*, both of which are somewhat larger species. TROEDSSON has figured (in line drawings) two vertical sections of this species showing the siphuncle segments to be typical in form.

This species is described from the Cape Calhoun beds of northern Greenland; Ordovician.

Cyrtogomphoceras turgidum Troedsson

Cyrtogomphoceras turgidum TROEDSSON, 1929, Meddel. om Grønland, Bind 71, p. 98, pl. 57, fig. 3; pl. 58, fig. 5-6.

A rather small, strongly gibbous, closely septate species. TROEDSSON has shown in outline drawings two vertical sections through this species and photographs of a thin section on which the interpretation of the siphuncle structure of the genus is based. Probably the fragment shown by TROEDSSON on pl. 58, fig. 4, is not conspecific with the others, for it appears to be portion of a phragmocone of a larger species with more distant septa.

The species occurs in the Cape Calhoun beds of northern Greenland; Ordovician.

Cyrtogomphoceras sp. cf. *turgidum* Troedsson

Cyrtogomphoceras cf. *turgidum* FOERSTE, 1928, Michigan Univ., Geol. Mus. Contrib., v. 3, p. 65, pl. 7, fig. 4.
FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 233.

The specimen which FOERSTE figured under this name is a somewhat smaller and more gibbous form than typical *Cyrtogomphoceras turgidum*. If the gibbosity is due to slight lateral flattening, the species is actually a much smaller one. Until more material is studied, its specific relationships will necessarily remain somewhat doubtful.

The species is known from the Dog Head member of Red River formation, Manitoba; Ordovician.

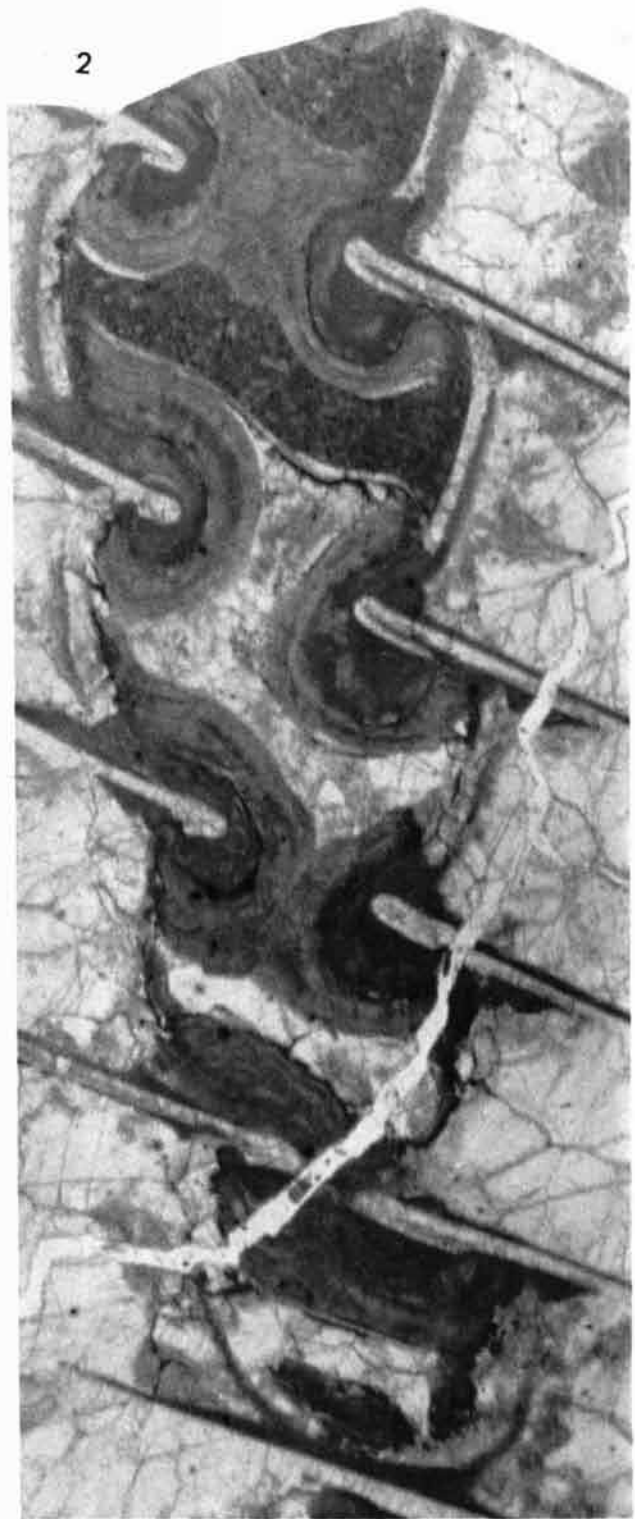
EXPLANATION OF PLATE 19

WESTONOCERATIDAE—*Fabroceras*

1. *Fabroceras multicinctum* FLOWER, from Leipers beds (Upper Ordovician), Cumberland River, near Rowena, Ky. Vertical thin section through portion of siphuncle, $\times 4.8$, showing adoral enlargement of segments, thick rings, small bullettes, and parietal deposits which form endocones exclusively; portion of central tube shown adapically (bottom part of figure). The apical part of this section is shown in greater detail on Pl. 18, fig. 2.
- 2-3 *Fabroceras* sp., from Leipers beds (Upper Ordovician), Cumberland River, near Rowena, Ky.—2, Thin section of part of siphuncle showing septal necks and tangential section through bullette, $\times 22$; light prismatic material above and below bullette comprises parietal deposit, isolating bullette from matrix in siphuncle. Between center and innermost part of the recurved neck at left a trilobite tail is embedded in the bullette. —3, Portion of same section showing recurved neck (white) at left and trilobite tail just to right, $\times 33$.
- 4.5 *Fabroceras* sp. cf. *F. saffordi* FLOWER, specimen from Catheys beds (upper Middle Ordovician), Ft. Nagly, Nashville, Tenn. —4, Vertical section, venter at right, $\times 1$. —5, Basal segments of siphuncle showing bullettes unusually thick on anterior surface of septa, parietal deposits lacking, about $\times 4$.
6. *Fabroceras* sp., from Leipers beds (Upper Ordovician), Cumberland River, near Rowena, Ky.; Shideler collection. Section through siphuncle, venter at right, showing subquadrate form of segments like those of *Westonoceras*; bullettes and parietal deposits present, $\times 1$.

All specimens, except as noted for Fig. 6, in collections of the writer.





Cyrtogomphoceras schucherti Flower, n. sp.

Cyrtogomphoceras baffinense ROY, 1941, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 147, fig. 107.
Cyrtogomphoceras baffinense? MILLER, YOUNGQUIST & COLLINSON, Geol. Soc. America, Mem. 62, p. 105 (partim), pl. 43, fig. 6, (non pl. 53, fig. 1-3, which is typical *C. baffinense*).

This form is obviously different from *Cyrtogomphoceras baffinense* in its smaller size, very closely spaced septa, and position of its point of greatest gibbosity much closer to the base of the mature living chamber. It seems to be allied more closely to *C. turgidum*, discussed above, but is a less gibbous form, greatest shell height being attained close to the living chamber instead of some distance below the base of the living chamber. The type shows segments of the siphuncle partially exposed by weathering on the concave ventral side; in form they are typical of *Cyrtogomphoceras*.

Holotype, Chicago Nat. Hist. Mus., no. P-28871. From the Mt. Silliman formation, Baffin Island; Ordovician.

Cyrtogomphoceras vicinum Foerste

Cyrtogomphoceras vicinum FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 76, pl. 14, fig. 2.

A typical moderate-sized species with rather distant septa on venter, which is strongly curved in profile in the anterior part of the phragmocone. The type shows obscure growth lines which slope adapically as they approach the convex side of the shell.

The species occurs in the Lander sandstone member, Bighorn dolomite, Wyoming; Ordovician.

Cyrtogomphoceras whiteavesi (S. A. Miller)

Oncoceras gibbosum WHITEAVES, 1889, (non HALL), Royal Soc. Canada, Trans., v. 7, sec. 4, p. 80, pl. 15, fig. 2-3.

Oncoceras whiteavesi S. A. MILLER, 1897, North American Geol. Paleont., Appendix 1, p. 697.

— WHITEAVES, 1897, Canada Geol. Survey, Paleozoic Fossils, v. 3, pt. 3, p. 222.

Cyrtogomphoceras whiteavesi FOERSTE, 1928, Univ. Michigan, Geol. Mus. Contrib., v. 3, p. 61, pl. 7, fig. 1-3.

— FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 232.

Cyrtogomphoceras whiteavesi is a moderate-sized short and gibbous form in which the typical broad short segments of the siphuncle are known. There is no adoral contraction of the siphuncle, as suggested by the section of *C. intermedium*.

This species is found in the Dog Head member, Red River series, Manitoba; Ordovician.

Cyrtogomphoceras foerstei Miller & Furnish

Cyrtogomphoceras foerstei MILLER & FURNISH, 1937, Jour. Paleont., v. 11, p. 548, pl. 68, fig. 1, 2.

A rather slender form reminiscent of the associated *Cyrtogomphoceras nutatum*. It occurs in the "dolomite member" of the Whitewood formation, South Dakota; Ordovician.

Cyrtogomphoceras thompsoni Miller & Furnish

Cyrtogomphoceras thompsoni MILLER & FURNISH, 1937, Jour. Paleont., v. 11, p. 549, pl. 68, fig. 3.

A slender form, evidently belonging to the same general species group as *Cyrtogomphoceras foerstei*. It occurs in the "dolomite member" of the Whitewood formation, South Dakota; Upper Ordovician.

Unnamed Species of Cyrtogomphoceras

Cyrtogomphoceras sp. I ROY, 1941, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 149, fig. 109

This fragment from the Mt. Silliman beds of Baffin Island comprises part of a phragmocone representing a relatively large species, one obviously attaining a greater size than *Cyrtogomphoceras baffinense*, the largest named species known from the Mt. Silliman exposures.

Cyrtogomphoceras sp. II ROY, 1941, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 149, fig. 110.

The fragment figured under this designation is a small shell comparable in size to *Cyrtogomphoceras furnishi* but slightly smaller and with septa much more widely spaced.

Cyrtogomphoceras sp. MILLER, YOUNGQUIST & COLLINSON, 1954 Geol. Soc. America, Mem. 62, p. 108, pl. 43, fig. 4-5.

This specimen, from the same locality and horizon as those above, shows an anterior portion of a typical rather small *Cyrtogomphoceras* which is weathered on one side so as to expose the siphuncle. The form is here refigured (Pl. 6, fig. 1-2,) and referred to in the generic discussion.

Cyrtogomphoceras sp. SWEET, 1955, Jour. Paleont., v. 29, p. 81, pl. 18, fig. 1.

This specimen, from the Lander sandstone of the Bighorn dolomite in Wyoming, is a moderate-sized shell with essentially circular cross section when mature, notable mainly for showing a clear straight transverse aperture on the convex side of the shell, indicating that this side is dorsal.

Species Incorrectly Assigned to Cyrtogomphoceras

Cyrtogomphoceras? shamattawaense FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 88, pl. 19, fig. 1A, B.

A slender shell with living chamber contracting gently from a point shortly beyond its base, scarcely endogastric, broadly depressed in cross section, and with rather distinct subparallel sutures not sloping markedly forward on the convex side in later growth stages. It clearly has no relation to typical *Cyrtogomphoceras*, but from the extant descriptions and figures it is impossible to say what its relationships are. *Lavaloceras* FLOWER (1952) is somewhat similar in form, certainly more so than *Cyrtogomphoceras*.

The species is from the Shamattawa limestone on the west side of Hudson Bay.

Cyrtogomphoceras stensioei TROEDSSON, 1926, Meddel. om Grønland, Bind 71, p. 108, pl. 63, fig. 5; pl. 64, fig. 1, 2.

Diestoceras stensioei TEICHERT, 1930, Paläont. Zeitschr., Band 12, p. 294.

This species from the Lyckholm beds of Estonia has been assigned to *Diestoceras* by TEICHERT, a conclusion supported by form of the shell and its narrow siphuncle. In general aspect and proportions it appears to be quite close to species from the Richmond of the Cincinnati region.

EXPLANATION OF PLATE 20**WESTONOCERATIDAE—Fabroceras****FIGURE**

1. *Fabroceras* sp. cf. *F. multinctum* FLOWER. Series of siphuncle segments showing adoral enlargement and rounding of form, with thick rings, small bullettes, and clear development of endocones; opaque section, $\times 8$.
2. *Fabroceras* sp. Thin section of siphuncle slightly off center and therefore with parietal deposits seeming to join across mid-

dle of section, $\times 11$; main part of connecting ring replaced (represented by coarse light granular material) and sharply differentiated from large bullettes, vinculum clearly shown on dorsal side, at right.

Both from Leipers beds (Upper Ordovician), Cumberland River, near Rowena, Ky.; collections of the writer.

Cyrtogomphoceras? troedssoni TEICHERT, 1930, Paläont. Zeitschr., Band 12, p. 296, pl. 9, fig. 32, 33.
Faberoceras troedssoni FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 452.

This is a cyrtoconic slender species with one side convex and the other concave, instead of essentially straight as in typical *Cyrtogomphoceras*. The sutures are simple, with slight lateral lobes; siphuncle is unknown; the surface bears prominent transverse markings and a prominent cincture or constriction some distance before the aperture. At the time when the species was described, assignment to *Cyrtogomphoceras* seemed most suitable, though TEICHERT recognized that it was far from being a typical species. The subsequent discovery of shells of very similar form and ornament in the Leipers formation of Kentucky led the writer to assign this species to *Faberoceras*, erected for reception of these forms.

Lyckholm beds, Ordovician, Estonia.

?*Cyrtogomphoceras turgidum* TROEDSSON, COWPER REED, 1936, Palaeont. Indica, new ser., v. 21, Mem. 3, p. 101, pl. 5, fig. 21.

COWPER REED (1936) has figured and described from Nyaungkiang, Shan States, a small strongly curved portion of a phragmocone which he assigned tentatively to *Cyrtogomphoceras turgidum* TROEDSSON. Judging from the illustration it is not evident that this is a true *Cyrtogomphoceras*, but it is also impossible to say to what genus it should be assigned. The specimen fails to expose its siphuncle.

Genus LANDEROCERAS Foerste, 1935

Type species—*Diestoceras prolatum* A. K. MILLER

Landeroceras FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 69.
 FLOWER, 1940, Geol. Soc. America, Bull., v. 51, p. 1970.
 FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 516.
 FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 613.
 MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 103.

Shell straight, fusiform, compressed in cross section, venter and dorsum about equally rounded. Shell gibbous over anterior part of phragmocone, then contracting subconically over the remainder and the living chamber to a small aperture with shallow hyponomic sinus. Sutures straight and transverse or with a broad lobe in ventral region. Siphuncle large, broadly expanded, with adapical end of segments broadly in contact with shell wall. Segments oblique in vertical section, scalariform; connecting rings broadly adnate to mural and free parts of septa at adapical end on venter; adnate to septa beyond neck at adoral end on dorsum. Necks short, recurved but free on venter, recumbent on dorsum. Bullettes surround necks

and brims, connecting ring being thickened particularly where it joins septum on dorsal side. The surface bears rather coarse transverse markings.

Discussion. This genus was based upon a species originally assigned by MILLER to *Diestoceras*. The more slender fusiform shape of the shell is the primary basis for distinguishing *Landeroceras*, which FOERSTE compared only with *Diestoceras*. The broadly ovate areas of contact of the siphuncle with the ventral wall of the shell are so much like those of *Cyrtogomphoceras* and so unlike anything known in *Diestoceras*, that FLOWER (1940) referred the genus to the Cyrtogomphoceratidae of the Discosoroidea, now Discosorida. Subsequently, sectionable material has served to demonstrate the discosorid affinities of the genus. MILLER, YOUNGQUIST & COLLINSON state that the genus is close to *Diestoceras* but that its conch is more elongate and more gradually contracted adorally. Unfortunately, the structures indicate that *Diestoceras* is typically actinosiphonate, whereas *Landeroceras* is a typical discosorid. The resemblance between these genera is purely homeomorphic.

Some problems relate to the taxonomic value assignable to variations among individual specimens. From present evidence it is concluded that only a single rather variable species is known. The genus is known thus far only from the Lander sandstone member of the Big Horn dolomite, Upper Ordovician.

Landeroceras prolatum (Miller)

Pl. 5, fig. 9; Pl. 8; text-fig. 19

Diestoceras prolatum MILLER, 1932, Connecticut Acad. Arts, Sci., v. 31, p. 291, pl. 28, fig. 8.
Diestoceras flexuosatile MILLER, 1932, Same, v. 31, p. 288 (partim), pl. 29, fig. 3 (non fig. 1, 2).
Landeroceras prolatum FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 69, pl. 5, fig. 6, 7.

A large straight fusiform shell with sutures somewhat variable in their expression of a shallow ventral lobe. The figured hypotype, somewhat more complete than previously known specimens, is 270 mm. long. The basal 40 mm. is poorly preserved, tapering to a point which is quite clearly not the true apex but adventitious. The shell expands (in a length of 75 mm.) from this part (56 mm. wide and 58 mm. high) to 75 and 78 mm. at the maximum cross section, located 50 mm. below the base of the living chamber where the shell has contracted to 58 and 64 mm. The sutures here

EXPLANATION OF PLATE 21

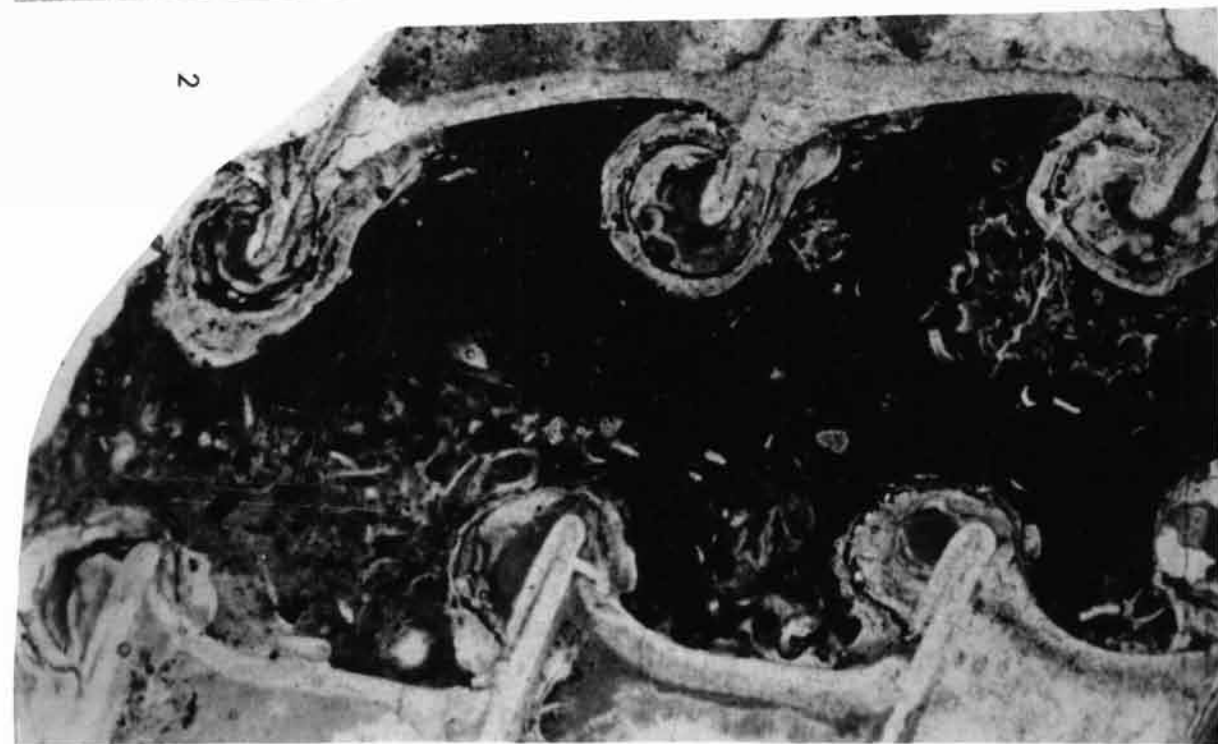
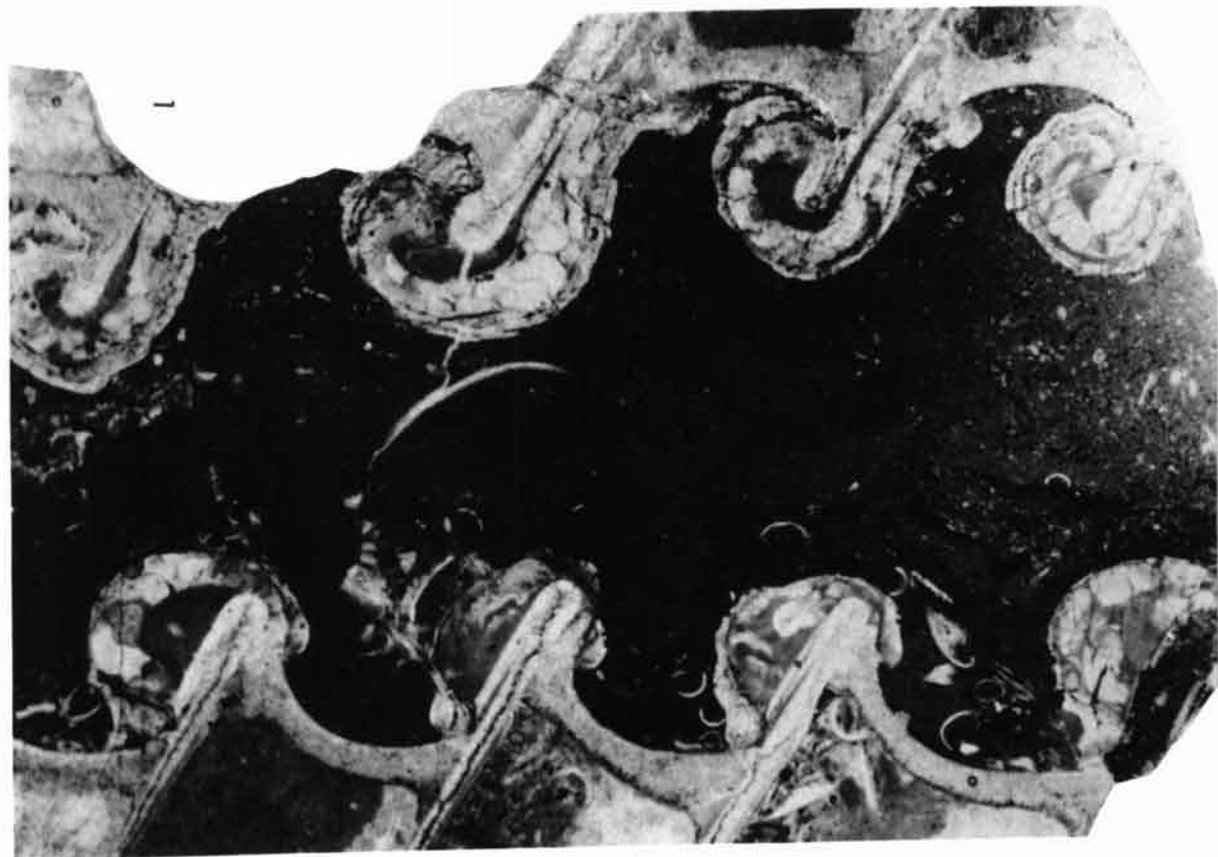
WESTONOCERATIDAE—*Faberoceras*

FIGURE

1-2. *Faberoceras* sp., from Leipers beds (Upper Ordovician), Cumberland River, near Rowena, Ky.; collection of the writer. Adapical (1) and adoral (2) parts of a single thin section, about $\times 15$, showing 9 segments of the siphuncle which exhibit variations in preservation and ontogenetic progression. (Slightly retouched to strengthen outline of septal necks and structures of connecting ring.) Brims long on dorsum toward left and short on venter. Bullettes increase in degree of inflation as traced adorally. Adorally the two zones of the bullette are clearly differentiated, but they cannot be differentiated from one another apically because of replacement. The anterior end of the bullettes is short on the dorsum, longer on the venter. On the ventral side of segments 7-9 at the anterior end (figure 2), there is a marked increase of the inner zone of the bullette

along the anterior part of the septum, and in segment 9 the apical and adoral parts, separated in earlier segments, form a continuous band. The vinculum is clear on the dorsum of segments 2-4, but it becomes smaller and divided by the granular zone in anterior segments. Differentiation of the free part of the ring is obscure in apical segments, discernible but variable as a result of replacement in segments 5 and 6, and developed into obscure longitudinal banding in anterior segments. Deposits form endocones in the three apical segments, are discrete parietal deposits in segment 4, showing deposit complete on venter but immature on dorsum; incomplete ventrally and completely absent dorsally in segment 5, present only on the venter in segments 6 and 7, and completely absent in segments 8 and 9. Segments numbered from apical end. (Same section as FLOWER, 1946, pl. 30, fig. 1.)





FLOWER & TEICHERT—Order Discosorida (Cephalopoda)

are oblique, sloping adapically on the ventral side. The living chamber has a maximum ventrolateral length of 60 mm. and dorsolateral length of 45 mm. The aperture is 40 mm. wide and 45 mm. high. On the ventral side is a sinus 15 mm. wide and 8 mm. deep.

Sutures slope downward broadly in crossing the venter; the hypotype specimen differs from those previously found in that adoral camerae become strongly oblique instead of transverse and losing ventral lobes. The 10 clearly marked adapical camerae are subequal in length, averaging 10 mm., succeeding ones being 9, 7, 6 and 4 mm. in length, respectively, after which an apparent camera of 3 mm. is followed by closely spaced septal markings, four in 7 mm. on the venter, some being strongly crenulate (regarded as gerontic incomplete septa constituting the basal zone).

The siphuncle, exposed on the internal mold, is seen as broadly rounded markings at the adapical end of each camera. Plainly, it is so expanded as to lie in contact with the shell wall, or rather, the mural part of the septum, which never is evident.

A vertical section (Pl. 5, fig. 9), through the siphuncle shows the structures rather obscurely but clearly enough to indicate form and structure of the segments. The segments are oblique and scalariform in vertical section. On the venter the neck is recurved but not recumbent, the segment expands and the connecting ring soon comes in contact with the ventral wall of the camera which it follows to the next adapical septum. It is broadly adnate to the septum along which it continues to the tip of the neck as usual. On the dorsum the brim is recumbent, the connecting ring which springs from its tip being broadly adnate to the adoral septum, then becoming free and curving strongly inward, before reaching the next septum which it joins with scarcely any area of adnation. The ring is thickened, with thickening particularly evident where the free part of the ring joins the adoral septum on the dorsal side. Here triangular thickened areas are seen in vertical section, giving the outside of the segment an angular and scalariform appearance. At the septal foramina are clear indications of small annuli like those of *Westonoceras* in structure but smaller in size. A segment of the siphuncle 10 mm. long located 60 mm. from the apex measures 7 mm. across the septal foramen and expands to 13 mm.

Discussion. This species is interpreted as somewhat variable in lobation and obliquity of the sutures. The alternative interpretation would require (1) that MILLER's holotype, which has only transverse sutures should be considered as one species, (2) that FOERSTE's form with ventral lobes but with later sutures becoming essentially transverse should be considered as a second species, and (3) that the specimen here figured, in which lobes persist to latest stages with adoral sutures sloping adapically on the venter and in which the aperture is slightly inclined in the opposite direction, should be considered a third species. So close are all these specimens in general proportions that it seems evident that the differences apparent in late stages are most reasonably attributed to variation within the species.

FOERSTE described but did not figure the siphuncle in section for this species. Probably his section was obscure; that of the present specimen is so obscure that details are poorly displayed in a

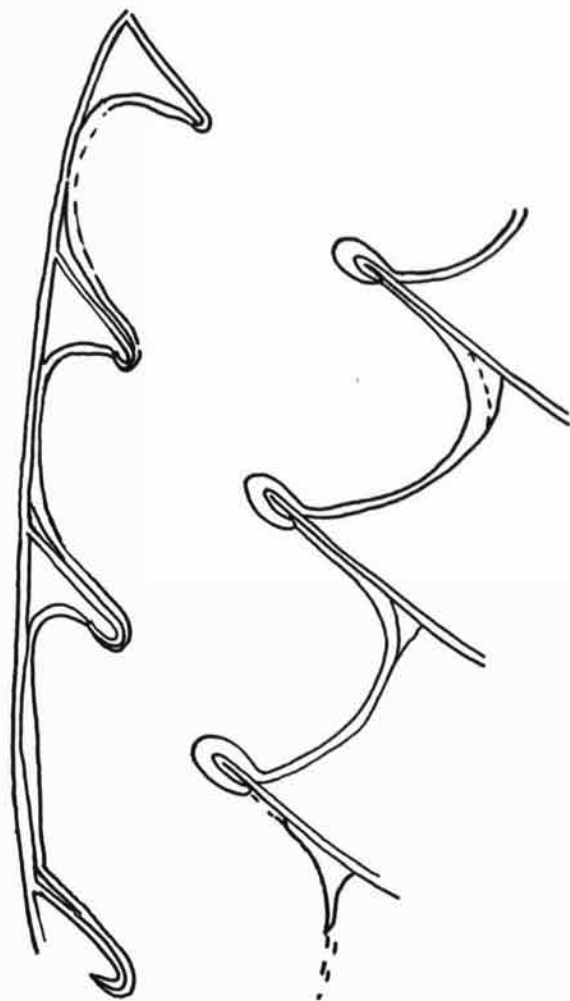


FIGURE 19. Siphuncle of *Landeroceras prolatum*.

Vertical section of siphuncle, $\times 3$, venter on left, based upon section shown in pl. 5, fig. 9.

photograph, and therefore a drawing (Fig. 19) has been prepared synthesizing structural features observed in four fairly well preserved segments. The specimen represented is preserved in hard dolomitic sandstone which penetrated the conch, and except for regions close to the shell wall and siphuncle, the septa were destroyed.

I agree with FOERSTE that a paratype of *Diestoceras flexuosatile* is to be assigned to *Landeroceras prolatum*, but that the holotype,

EXPLANATION OF PLATE 22

WESTONOCERATIDAE—*Fabroceras*

FIGURE

1, 2. *Fabroceras* sp., from Leipers beds (Upper Ordovician), Cumberland River, near Rowena, Ky.; collection of the writer. Slightly overlapping photographs of a single thin section from portion of the phragmocone of an immature individual, about $\times 12$, showing texture of connecting rings and ontogenetic modifications. Noteworthy is the gradual increase of the inner layer of bullettes over the anterior side of septa on the ventral

side (toward left) as growth progresses and variable replacement of outer layer of bullettes on the dorsum. The dorsal side shows variation in form of the vinculum and more definite layering in the free part of connecting rings than does the ventral side. Thin parietal deposits are developed ventrally, that in the apical segment extending a third of the way forward along the free part of the connecting ring. Parietal deposits are wanting dorsally.

showing a siphuncle which is relatively small and somewhat removed from the venter is, as far as available evidence indicates, a true *Diestoceras*.

Types. Holotype, Univ. Missouri; hypotypes, U. S. Natl. Mus., 2 specimens, Univ. Missouri, one specimen, and the present hypotype in the collection of the writer.

Occurrence. Lander sandstone member of the Bighorn dolomite, Ordovician, from various localities in Wyoming.

Family WESTONOCERATIDAE Teichert 1933

When first proposed, the family Westonoceratidae contained only the genus *Westonoceras*. Subsequently, it has grown in scope (TEICHERT, 1934; FLOWER, 1940, 1946; FLOWER & KUMMEL, 1950) and a few genera are added in the present work. As now conceived, the family includes discosorids consisting dominantly of compressed exogastric cyrtocoines. The bullette is inflated throughout the family, and within the siphuncle parietal annulo-siphonate deposits are developed in all known genera. Primitively, these deposits are segmental, very much as in the Pseudorthoceratidae, but in advanced Westonoceratidae they surpass their original limits, grow throughout a series of segments, and, one growing over another, to form a pattern of endocoines terminating in a central canal.

As noted in discussion of evolution, some doubt attaches to precise phyletic relationships of the various genera of the family. One endogastric form (*Hecatoceras*) is included here because its specialized siphuncle, well supplied with endocoines, suggests that it is a derivative of rather specialized Westonoceratidae. These structures are not known in any of the Cyrtogomphoceratidae.

Genus TEICHERTOCERAS Foerste, 1933

Type species—*Teichertoceras husseyi* FOERSTE

Teichertoceras FOERSTE, 1933, Denison Univ. Bull., Sci. Lab., Jour., v. 28, p. 140.

Teichertoceras includes slender cyrtocoine shells of compressed section with dorsum broadly and venter narrowly rounded, sutures typically with lateral lobes, and siphuncle of rather slender subquadrate segments slightly removed from venter. The shell becomes gibbous over the anterior part of the phragmocone and exogastric, tapering gently to a somewhat extended aperture. The shell differs from *Westonoceras* primarily in that early portion of the phragmocone is slightly curved endogastrically. Siphuncle segments are very similar to those of *Westonoceras* in form; rings are thick, terminating in swollen though not greatly enlarged bullettes; parietal deposits not observed in the siphuncle but they may be present.

Discussion. *Teichertoceras* differs from *Westonoceras* primarily in early endogastric curvature of the shell. Other differences, notably absence of parietal or other deposits in the siphuncle, may be more apparent than real, owing to limitation of present available material. On the other hand, as a genus which must be regarded as a relatively primitive one in the Westonoceratidae, possibly it has not yet developed parietal deposits such as characterize the family generally. Of the oldest species, *T. sinclairi*, only the anterior part of the siphuncle has been observed, and parietal deposits, if present, would not

be expected close to the living chamber. In *T. husseyi*, also, the observed part of the siphuncle is rather too near to the living chamber to show such deposits. Accordingly, failure to observe these structures is not necessarily an indication of their absence.

Theoretically, some difficulty is encountered in recognizing *Teichertoceras* as distinct from *Westonoceras*. The anterior portion of the shell is exogastric and general resemblance between the genera is strong. Further, it is possible that some gradation exists between typical *Westonoceras* with exogastric apical part, *Thuleoceras* with apical portion essentially straight, and *Teichertoceras* with endogastric curvature, particularly since no clear line can be drawn between *Westonoceras* and *Thuleoceras*, this latter therefore being correctly classed as a synonym of *Westonoceras*. However, practical difficulties, except when dealing with extremely short early fragments of shells, is not as great as one would expect. It is possible that some species for which early parts of the shells are unknown cannot be distinguished properly. If so, some species currently assigned to *Westonoceras* may belong in *Teichertoceras*, but this is a matter which can only be determined as more complete material of the species becomes available.

Curiously, *Teichertoceras* is represented by one species of essentially Black River age, which is thus older than any known *Westonoceras*, though younger species of Trenton (Cobourg) age are contemporaneous with *Westonoceras* species which are quite typical. The apparent greater age of *Teichertoceras* suggests that it is relatively primitive. Since the endogastric curvature is a primitive feature of the Discosorida and dominates the Ruedemannoceratidae and Cyrtogomphoceratidae, its presence in the early stage of *Teichertoceras*, one of the oldest of the Westonoceratidae, may have a recapitulatory significance.

Teichertoceras sinclairi Flower, n. sp.

Pl. 5, fig. 10; Pl. 9, fig. 1, 2

Westonoceras sp. FLOWER, 1952, Jour. Paleont., v. 26, p. 26.
SINCLAIR, 1953, Am. Jour. Sci., v. 251, p. 845.

A rather large *Teichertoceras* of generalized outline, with moderately compressed cross section, dorsum relatively broadly rounded, and venter narrower than dorsum. In profile, venter is slightly concave and dorsum slightly convex in earliest stage where shell height is 22 mm. and width estimated at 20 mm.; at 30 to 50 mm. from base, dorsal profile becomes strongly convex, gibbous, and a maximum shell height of 40 mm. is attained. The dorsal profile then becomes concave and the ventral profile convex. At the extreme adoral end, dorsum and venter are nearly parallel and the usual conical contraction of the shell to the mature aperture is lacking. The holotype, 80 mm. in length, retains the phragmocone over the basal 46 mm., with 10 camerae that range in depth from 3.5 to 4.5 mm. Shell expands rapidly to region of dorsal gibbosity attained on the anterior part of phragmocone. The width here is uncertain but it is equal to or slightly greater than the height. Beyond this region width decreases and height remains little altered over the region of the concave dorsum. The apertural end, probably slightly distorted, is 42 mm. high and 34 mm. wide (estimated). Fragments suggest that the aperture is incomplete, originally having extended at least 10 mm. farther.

Sutures obscure, but evidently with very poorly developed lateral

lobes, a natural condition in view of the relatively broad cross section of the shell. Anterior camerae show no trace of shortening commonly associated with maturity. Siphuncle slightly removed from venter. The observed segments (near anterior end of phragmocone) are elongate subquadrate in vertical section but with free part of ring slightly curved, convex outwardly, rounding being most pronounced in anterior segments. Necks short, recumbent, anterior end of ring more broadly in contact with septum dorsally than ventrally, adapical end of ring joining adapical septum with a slight area of adnation ventrally but apparently none dorsally. Bullettes are developed, being larger in anterior than adapical segments. No additional deposits are observed but would not be expected in segments of the siphuncle so close to the living chamber. Likewise, no cameral deposits are evident.

Discussion. This species is of particular interest because of its status as one of the oldest of the *Westonoceratidae* and oldest known species of *Teichertoceras*. Unfortunately, the Simard limestone, which yielded the type, is one from which it is almost impossible to extract cephalopods with good surfaces and the surface of this fossil (an internal mold) is extremely rough. Also, the specimen appears to have been distorted considerably. When first found, the specimen was observed only as a natural weathered section, which showed siphuncle segments essentially like those found in *Westonoceras*. Extraction of the specimen showed however, that the apex is endogastric and that this form belongs to *Teichertoceras* rather than to *Westonoceras*. The natural section was smoothed by grinding for closer study of the siphuncle. The section is not strictly vertical, and the mid-ventral region being lost, the extant part extends on the dorsum beyond the mid-dorsal line.

In relation to the only other described species of *Teichertoceras* (*T. husseyi*), this is a much larger form, broader in cross section, with dorsum prominently gibbous before shell attains a convex profile on the venter, and though the living chamber tends to taper, it lacks conical contraction toward the aperture such as characterizes *T. husseyi* and as is characteristic of *Westonoceras* and *Winnipegoceras*. In general aspect, the form of this species is anomalous. Since only two species of the genus are known, one can hardly state that this form is atypical but clearly the general pattern of *T. husseyi*, which continues into most representatives of *Westonoceras* and *Winnipegoceras*, is not attained in this early and probably primitive species.

Holotype. Collection of the writer.

Occurrence. Simard limestone, bed 4 of SINCLAIR'S (1953) section, Ste. Anne de Chicoutimi, Quebec; Middle Ordovician.

Teichertoceras husseyi Foerste

Pl. 10, fig. 2-4

Teichertoceras husseyi FOERSTE, 1932-33, Denison Univ. Bull., Sci. Lab., Jour., v. 27, pl. 33, fig. 2A-E (1932); v. 28, p. 140 (1933).

FOERSTE has described and illustrated the holotype of this species which is still its only known representative; his description need not be repeated. The species is a relatively small and slender one, having essential features of a *Westonoceras* except that the early portion of the shell is gently (but definitely) endogastric. The type preserves one side of an internal mold, the opposite side being a natural weathered section. The apical portion was slightly ground to permit study of the siphuncle in more detail. The segments are subquadrate in form, rings evidently thick and expanded into bullettes over the area of septal foramina. The segments studied (extending from the 14th to 21st camerae apical of the base of living chamber) exhibit no parietal or other deposits. At the apical end the shell has a height of 8 mm., indicating that the original initial part of the shell could hardly have been far distant.

Holotype. Univ. Michigan. Mus. Paleont. no. 14461.

Occurrence. Beds of Trenton age at Cornell, 13 miles north of Escanaba, Mich. FOERSTE lists this form as from the "Cornell

member of the Trenton." So far as I have been able to ascertain, such a stratigraphic unit has never been formally proposed. The association of *Diastoceras*, *Westonoceras*, and *Probillingsites* from this locality suggests equivalence of the fossil-bearing beds with the Cobourg division of the Trenton.

Teichertoceras sp. cf *T. husseyi* Foerste

Oncoceras minnesotense CLARK, 1897, Minnesota Geol. Survey, v. 3, pt. 2, p. 798, pl. 58, fig. 16-18b (partim).
Westonoceras minnesotense FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 312, pl. 48, fig. 3.
Teichertoceras? clarkei FOERSTE, 1932, Same, v. 32, explanation pl. 33, fig. 4.
Teichertoceras cf. *husseyi* FOERSTE, 1933, Same, v. 33, p. 142.

This designation is given to a small portion of a phragmocone, which has been sectioned vertically to show the siphuncle. Reference of the specimen to *Teichertoceras* depends on its slight though definite endogastric curvature. The figured specimen (Univ. Minnesota, no. 258B) was originally included among the types of *Westonoceras minnesotense*, but that species is restricted and does not have an endogastric early stage. The fossil comes from Lime City, Minn., occurring in beds originally regarded as Prosser but possibly Stewartville, which was not differentiated from the Prosser at the time this material was collected.

Teichertoceras sp.

Teichertoceras sp. TEICHERT, 1937, Rept. 5th Thule Exped., v. 1, no. 5, p. 88, pl. 17, fig. 13-15.

Under this designation TEICHERT figured and described a small portion of a phragmocone, obviously slightly endogastric, which is typical of *Teichertoceras*. It has shorter camerae than *T. husseyi* and appears more rapidly expanding, but the latter difference could be the result of slight flattening which the specimen has suffered. Although this fossil is from drift at Cape Griffith, on the south coast of Cockburn Island, it is obviously from the Ordovician and noteworthy as the only evidence to date of the occurrence of *Teichertoceras* in the Arctic.

Genus WESTONOCERAS Foerste, 1924

Type species—*Cyrtoceras manitobense* WHITEAVES

- Westonoceras* FOERSTE, 1924, Denison Univ. Bull., Sci. Lab., Jour., v. 20, p. 253 (*Westonoceras* on p. 196).
 — FOERSTE, 1926, Same, v. 21, p. 331.
 — TROEDSSON, 1926, Meddel. om Grønland, Bind 71, p. 90.
Thuloceras TROEDSSON, 1926, Same, Bind 71, p. 93.
Westonoceras FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 54.
Westonoceras FOERSTE, 1928, Michigan Univ., Mus. Paleont., Contrib., v. 3, no. 3, p. 48.
 — FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 219.
 — FOERSTE, 1930, Same, v. 24, p. 311.
 — FOERSTE & TEICHERT, 1930, Same, v. 25, p. 280.
 — FOERSTE, 1933, Same, v. 28, p. 115.
 — TEICHERT, 1933, Palaeontographica, Band 78, Abt. A, p. 207, 216.
 — STRAND, 1933, Norsk Geol. Tidsskr., Bind 14, Heft 1, p. 73, 112 (footnote).
 — TEICHERT, 1934, Meddel. om Grønland, Bind 92, no. 10, p. 36-38.
 — TEICHERT, 1935, Am. Jour. Sci., ser. 5, v. 29, p. 5.
 — FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 59 (*Thuloceras* definitely included as synonym of *Westonoceras*).
 — FLOWER, 1940, Geol. Soc. America, Bull., v. 51, p. 1969.
Westonoceras ROY, 1941, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 140.
Westonoceras FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 428, 438.
 — FLOWER & KUMMEL, 1951, Jour. Paleont., v. 24, p. 612.
 — FLOWER, Jour. Paleont., v. 26, p. 26.
Westonoceras TEICHERT & GLENISTER, 1952, Jour. Paleont., vol. 26, p. 744 (footnote).
Westonoceras TEICHERT & GLENISTER, 1954, Bull. Am. Paleont., vol. 38, no. 150, p. 65 (footnote).
 — MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 84 (*Sinclairoceras* and *Neumatoceras* are regarded as probable synonyms).

Name of genus. As shown in the synonymy given above for this genus, variant spellings of the name (*Westonoceras* and *Westonoceras*) have been used by authors, not only by different authors but by the same author at different times. Since these

names are objective synonyms, only one of them can be valid and this automatically makes the other invalid. Which of the two names is valid and which is invalid? It is perfectly clear under application of International Rules (see Copenhagen Decisions, 1953, p. 43-45) that during the past 30 years (1926-56) the spelling of this name which was to be recognized as valid is *Westenoceras* and not *Westonoceras*, in spite of statement by FOERSTE & TEICHERT (1930) that FOERSTE (1924) intended to name the genus after a person named T. C. WESTON and in spite of the fact pointed out by MILLER (cited by TEICHERT & GLENISTER, 1954) that both *Westenoceras* and *Westonoceras* are spellings used in FOERSTE'S (1924) original publication. According to the Rules, these are "original spellings" which have equal standing until a "first subsequent user" employs one of them, thus casting the die for all time unless and until provisions of the Rules affecting this choice of name are complied with in manner that establishes legally valid change. It happens that FOERSTE (1926) himself was "first subsequent user" of the name *Westenoceras* and, all other considerations being irrelevant, this serves to invalidate *Westonoceras*. So the nomenclatural situation stands.

The technical points just reviewed have either not been known to most authors writing about these cephalopods or if known have been ignored, because widely prevailing usage has accepted the name *Westonoceras*. In 1933 TEICHERT recognized this spelling when he introduced the family name *Westonoceratidae*, which has validity under current Rules even if its type genus should be spelled *Westenoceras*, the family name then being construed to have derivation from a junior objective synonym (*Westonoceras*) of the type genus *Westenoceras*. This is unhappy, not to say foolish, because the single-letter difference of "e" in the generic name and "o" in the family name would commonly be misinterpreted by readers as a printer's error. Surely it is desirable that spelling of the family and its type genus should agree. To accomplish this one may not advisedly ignore the Rules, because instability of nomenclature would persist. The alternatives then are given of applying to the International Commission on Zoological Nomenclature for exercise of its plenary powers to (1) set aside *Westonoceratidae* in favor of *Westenoceratidae* (a name yet unknown in paleontological literature) or (2) replace *Westenoceras* (presently valid) by *Westonoceras* (presently invalid). Obviously the second choice is preferable. A mechanism is given (Copenhagen Decisions, art. 75, p. 45) for validating the change from *Westenoceras* to *Westonoceras* if this procedure is used prior to adoption of the new code of Rules which in recent years has been in preparation; this consists simply of publishing the proposed change in the *Bulletin of Zoological Nomenclature* subject to so-called "challenge procedure" (not likely to be exercised and at very most requiring reference to the Commission for a decision).

For the purposes of this monograph on the Discosorida and the nautiloid volume of the *Treatise on Invertebrate Paleontology*, which is in preparation, proposal to recognize *Westonoceras* instead of *Westenoceras* is submitted to ICZN for publication in the *Bulletin of Zoological Nomenclature* and *Westonoceras* is herein adopted with the notation "ICZN pending."

Description. Shell compressed, a humped exogastric cyrtococone. Early part slender, gently exogastric to straight but rapidly increasing in rate of expansion and convexity of ventral profile as adoral end of phragmocone is approached. Venter there humped and strongly convex but this convexity later reduced, and living chamber tapers, contracting gently toward aperture. Cross section compressed, dorsum broadly rounded, venter narrow, commonly subangulate. Sutures with lateral lobes, tending to slope increasingly forward on the venter in late growth stages. Internal molds typically show shallow longitudinal grooves on phragmocone, these comprising molds of incipient cameral deposits.

Siphuncle close to ventral wall of shell but narrowly separated from it. Siphuncle segments are slightly oblique in vertical outline, owing to strong obliquity of septa as they approach margin of shell but they are essentially subquadrate. Septal necks typically recumbent, with recurved inner tip commonly bent forward slightly in siphuncle. Rings thick, with dense amorphous anterior region clear, anterior crystalline and apical chitinous regions usually not distinct, variable in expression but tip invariably differentiated into a bullette of two layers with amorphous dense material separating it from main part of ring evident in some specimens. The ring is thicker on dorsal than ventral side. Parietal deposits are typically developed, commonly grown forward from their point of origin around the bullette so as to form a continuous lining within the siphuncle. Deposits are initiated at the septal foramen and grow gradually forward over the interior of the ring until they meet the next adoral deposit. Deposits in any section are more advanced on ventral side of the siphuncle than on its dorsal side. As in the Pseudorthoceratinae (FLOWER, 1939), parietal deposits form first on venter and grow laterally toward dorsum. Some sections therefore show isolated masses of deposit on the dorsum at middle of a siphuncle segment, quite distinct from annular deposits formed at septal foramina (Pl. 12, lower right side of siphuncle). The section illustrated (Pl. 10, fig. 5; Pl. 11, fig. 1; Pl. 12) shows clearly thick rings on the dorsal side (already described in the general discussion of morphology), parietal deposits and trace of a central tube at anterior end of section, which is completely enclosed by matrix. Cameral deposits are also shown here. MILLER, YOUNGQUIST & COLLINSON (1954), p. 94, fig. 12) have shown another section exhibiting a central tube and have figured fragments (Pl. 44, fig. 1, 2) showing cameral deposits in an advanced stage of growth. Curiously, the rather coarse-pitted and transversely banded pattern gives way to one of longitudinal markings around the region of the siphuncle, so much so that an actinosiphonate siphuncle is suggested.

Westonoceras is separated only with great difficulty from *Teichertoceras* when specimens consist only of early stages of the phragmocone. In some species of *Westonoceras*, early portions of the shell are definitely exogastric, (Pl. 13, fig. 1-6) but in others the early portion becomes nearly or perfectly straight. It is only a step from "typical" exogastric early stages to those which are faintly endogastric. Doubt must be expressed concerning the correctness of generic allocations of many species. The matter is not an important one, for the two genera are closely similar in form and structure, and obviously they are very closely related. The earlier appearance of *Teichertoceras* stratigraphically, together with the fact that known species of this genus appear to be somewhat simpler in organization of the siphuncle, suggests that *Teichertoceras* is the primitive radicle from which *Westonoceras* developed. Likewise, differences which separate *Westonoceras* from *Winnipegoceras* are matters primarily of degree insofar as shell form is concerned, and the outlines of siphuncle segments of the two genera are quite similar. One cannot be as definite about details of structure, for specimens of *Winnipegoceras* showing well-preserved si-

phuncles in which details of structure can be studied are still far from adequate. However, the present evidence indicates no important differences.

MILLER, YOUNGQUIST & COLLINSON (1954) have assigned species to *Westonoceras* primarily upon the basis of form, internal structures of many specimens not having been studied. Their suggestion that *Sinclairioceras* may prove to be a synonym of *Westonoceras* is opposed not only by differences in form but by very dissimilar conformation of the siphuncle segments, which are far too rounded for *Westonoceras* and lack strongly inflated bullettes. They suggest also that *Neumatoceras* may be a synonym of *Westonoceras*. While it is true that the siphuncle of the type species of *Neumatoceras* is rather poorly preserved, I have had opportunity to study its structure in other species, mainly undescribed forms, and find that in outline and structure the siphuncles in this genus are oncoceroid, being narrower and more evenly rounded in outline than in the *Westonoceratidae*, also lacking bullettes or complex thickened rings such as occur in this family. Further, as has been pointed out (FLOWER, 1946), *Neumatoceras* grades in the Ordovician into typical oncoceroids, notably *Oncoceras* and *Beloitoceras*, to such an extent that little doubt of its relationship is allowed. Anomalously, in asserting the unity of *Neumatoceras* with *Westonoceras* MILLER, YOUNGQUIST & COLLINSON have assigned to *Westonoceras* not only some typical representatives of *Neumatoceras* but a number of true species of *Oncoceras* and *Beloitoceras*, notably forms of the *Oncoceras duncanianae* and *Beloitoceras amoenum* groups (FLOWER, 1946). Proper generic reassignment of these species is made in following pages.

Form variation in *Westonoceras* is such that certain species approach very closely to the shape of some other genera (notably of the *Oncoceratidae*), and study of internal structure is usually necessary in order to ascertain whether a particular species belongs to the *Westonoceratidae* or *Oncoceratidae*. Where such investigation has not been undertaken, lamentable confusion has resulted.

Range of species. *Westonoceras* is quite characteristic of faunas of Red River affinities, which extend from Cape Calhoun (northern Greenland) through various localities in the Arctic Archipelago (notably of the Mt. Silliman beds of Baffin Island) and west side of Hudson Bay to the typical Red River deposits of the Winnipeg region in Manitoba. The genus has not been found in more southerly extensions of the Red River faunas, as in the lower Bighorn, Fremont, or Montoya groups, all of Ordovician age. However, it ranges into more easterly beds long accepted as late Trenton and Eden in age. It appears in the Viola limestone of Oklahoma, Stewartville limestone of Minnesota, and Cobourg equivalent (late Trenton) of northern Michigan, Cobourg of New York (and probably adjacent Ontario), and Tetreauville limestone of Quebec. Southward, curiously, its only extension is marked by very rare examples, not in the Cynthiana or Catheys beds, where other late Trenton migrants sometimes are found, but in Eden beds of the Cincinnati region. The genus is completely unknown in beds of Richmond age in the Cincinnati region, Ontario, and Quebec, or in the prolific Rich-

mond faunas of Anticosti. One species is assigned to the genus from the Gastropod limestone (considered to be Upper Ordovician) of the Oslo region, Norway, but its form is not typical and generic assignment seems somewhat doubtful.

Westonoceras manitobense (Whiteaves)

- Cyrtoceras manitobense* WHITEAVES, 1890, Roy. Soc. Canada, Trans., v. 7, sec. 4, p. 80, pl. 13, fig. 3-5; pl. 15, fig. 4.
 WHITEAVES, 1897, Canada Geol. Survey, Paleozoic Fossils, v. 3, pt. 3, p. 223.
Oncoceras manitobense CLARKE, 1879, Minnesota Geol. Survey, Paleont., v. 3, pt. 2, p. 799.
Cyrtoceras manitobense SCHUCHERT, 1900, U. S. Natl. Mus., Proc., v. 22, p. 799 (partim).
Westonoceras manitobense FOERSTE, 1924, Denison Univ. Bull., Sci. Lab., Jour., v. 20, p. 253.
Westonoceras manitobense FOERSTE, 1928, Michigan Univ., Geol. Mus. Contrib., vol. 3, p. 49, pl. 5, fig. 1; pl. 11, fig. 5.
 FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 220, pl. 38, fig. 2-3.

Probably more than one species is included under this specific name. WHITEAVES figured three specimens. One of these which FOERSTE (1928) took as type (whether by WHITEAVES label or by his own selection is not clear) is a relatively small form in which lobes of the sutures are concentrated on the ventral third of the lateral face. A second specimen refigured by FOERSTE (1929) is simpler in profile, but a much larger form, with lobes of its sutures plainly deepest in the dorsal half of the section. At the same time, portion of a phragmocone apparently conspecific with the second specimen (judging by its proportions) was also figured. This shows, better than any other fossil figured from the Red River fauna, the form of siphuncle segments and bullettes which characterizes *Westonoceras*.

The holotype, from Big Island (now Hecla Island) in Lake Winnipeg, is from the Dog Head member of the Red River series, Ordovician. It is no. 1879 in the collection of the Geological Survey of Canada.

Westonoceras sp. cf. *W. manitobense* (Whiteaves)

- Westonoceras* cf. *manitobense* FOERSTE & TEICHERT, 1930, Denison Univ. Bull., Sci. Lab., Jour., v. 25, p. 284, pl. 55, fig. 1A, B.

FOERSTE & TEICHERT have assigned tentatively to WHITEAVES' species from the Red River beds a portion of phragmocone with gently exogastric form and moderately spaced septa bearing even faint lateral lobes; this fossil comes from the Stewartville horizon beneath the Fernvale limestone at Louisiana, Mo. The specimen seems comparable both in spacing of septa and nature of sutures to *W. manitobense*. The figured specimen is in the U. S. Natl. Museum.

Westonoceras alberta-saskatunanae Flower, n. sp.

Pl. 13, fig. 1-3; pl. 14, fig. 4, 5

This is a giant *Westonoceras*, the type incomplete basally where it has a shell height of 35 mm. and estimated width of 25 mm.; length of specimen 240 mm. It expands to a gibbous region with a height of 78 mm. and width of 48 mm. and contracts to an aperture of 50 and 25 mm., the contraction occupying the last 125 mm. of the shell as measured on the venter. The cross section is unusually narrow. At the base the venter is a little more narrowly rounded than the dorsum, but not subangular, as at a position 128 mm. farther toward the living chamber, where it is 70 mm. high and 44 mm. wide, with dorsum broadly rounded and venter subangular. The siphuncle has been observed in the basal 9 camerae which were sectioned vertically. Here, in a length of 52 mm., are 9 segments of the siphuncle, the basal one incomplete. At the base the segments are broad and short, a segment 6 mm. long expanding from 3 mm. at the septal foramen to 7 mm. At the anterior end of this section the segments

increase to 7 mm. in length but the expansion is little changed, being here 4 to 7 mm. The adapical segments are filled with calcite, apparently inorganic. Thick rings are evident and small bullettes are developed but these are not apparent at the anterior end of this section. Farther adorally the siphuncle is not preserved. The apical part shows that the siphuncle is typical of *Westonoceras* in position, form of segments, thick rings, and bullettes.

Camerae are moderate in depth throughout, increasing only gradually adorally from 5 mm. at the base to 12 mm. in the 17th (penultimate) camera, the last being shortened to 10 mm. Sutures have moderate lateral lobes, the lobation being median and not concentrated markedly on either dorsum or venter as in some species. Sutures slope increasingly forward on the venter, particularly in the last few camerae where the shell is markedly gibbous. The living chamber appears to be short, conical, and essentially complete. It is 74 mm. long ventrally and 65 mm. dorsally. It contracts in height from 76 to 50 mm. and in width from 56 to 25 mm. In profile the dorsal side of the shell is faintly concave adapically, becoming faintly convex over the middle of the phragmocone, and concave over the base of the living chamber, then straight and very faintly convex at the aperture. The ventral profile is convex throughout, but shows slight convexity adapically, greatly increased over the gibbous portion, and then greatly reduced from there to the aperture. The last camera is slightly contracted. Next to it, a good basal zone is present at the extreme base of the living chamber.

Discussion. This is one of the largest species of *Westonoceras*. In size *W. greggi* is most nearly comparable but it has much more transverse sutures and a more angular profile on both dorsum and venter, where in *W. alberta-saskatunae* the curvature is uniformly more sinuate. Our species is slightly larger and adoral camerae markedly deeper. It is of interest that the living chamber has such a shape that if found alone it probably would be attributed to *Winnipegoceras* rather than *Westonoceras*. While this raises a perplexing question as to whether some species with relatively short living chambers which currently are referred to *Winnipegoceras* would be better placed in *Westonoceras*, it is reassuring support for the affinities of these two genera.

The holotype is in the collection of the writer, at the New Mexico Bureau of Mines. It is from the Selkirk limestone (Ordovician), from quarries near Tyndall, Man.

Westonoceras nelsonense Foerste

Westonoceras nelsonense FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 223, pl. 38, fig. 1.

This species is similar to *Westonoceras manitobense* in profile but is a larger more robust form. Structure of the siphuncle is typical of the genus but segments are rather more rounded in outline within the camerae than usually observed. Bullettes are developed. The sutures have only slight lateral lobes which are concentrated on the dorsal two-thirds of the shell, giving way ventrally to a broad saddle.

The type specimen (Canada Geol. Survey, no. 7147) is from the Nelson limestone of the Nelson River area, Hudson Bay.

Westonoceras gouldi Foerste

Westonoceras gouldi FOERSTE, 1928, Michigan Univ., Geol. Mus. Contrib., v. 3, p. 52, pl. 5, fig. 2; pl. 11, fig. 1A-C.
Westonoceras cf. gouldi FOERSTE, 1928, Same, v. 3, p. 54, pl. 1, fig. 3A, B; pl. 11, fig. 2A, B.

MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 89, pl. 41, fig. 1-3; pl. 42, fig. 1; pl. 43, fig. 7.

This species is characterized by a shell that is strikingly trapezoidal in vertical profile, with straight dorsum and venter nearly straight on either side of the region of greatest gibbosity where the outline becomes almost angular. Sutures are straight in the young, sloping forward on the dorsum and later becoming more transverse. A prominent ventral saddle develops only at and

beyond the gibbous region. FOERSTE's description and illustration of the species show the typical cross section and siphuncle outline and indicate the presence of bullettes. MILLER, YOUNGQUIST & COLLINSON attribute to the species a small fragment which, in section, shows cameral deposits and form of the siphuncle segments with thick rings and large bullettes but it is not evident from description or photograph whether the bullettes are supplemented by parietal deposits.

The species, known only from the Mt. Silliman beds (Ordovician) of Baffin Island, is a highly characteristic member of the genus.

Westonoceras greggi Roy

Westonoceras greggi ROY, 1931, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 141, fig. 104.

MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 91, pl. 42, fig. 2.

This species has an exceptionally large shell with sutures swinging forward on the dorsum in early stages and without conspicuous lateral lobes. The profile is subtrapezoidal as in *Westonoceras gouldi* but the shell is more slender in proportion to length.

The species is known from a single specimen (Chicago Nat. Hist. Mus., no. P28868) from the Mt. Silliman beds (Ordovician) of Frobisher Bay, Baffin Island.

Westonoceras putnami Foerste

Westonoceras putnami FOERSTE, 1928, Michigan Univ., Geol. Mus., Contrib., v. 3, p. 51, pl. 5, fig. 3; pl. 11, fig. 3A, B.

FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 220.

MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 92, pl. 43, fig. 8.

A small slender *Westonoceras*, with gibbous part of shell convex in profile over a rather long interval, so that the whole shell has the aspect of an *Oncoceras* rather than a *Westonoceras*. FOERSTE has published an outline drawing of the siphuncle in section which shows subquadrate segments well removed from the venter, as typical of *Westonoceras* and of a sort never found in true oncoceroids.

This species is known only from the type, collected from the Mt. Silliman beds (Ordovician) of Putnam Highland, Baffin Island.

Westonoceras deckeri Foerste

Westonoceras deckeri FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 60, pl. 4, fig. 1.

A moderate-sized species with nearly straight dorsum slightly convex over anterior part of the phragmocone and venter strongly curved over the gibbous region but nearly straight adapically and adorally from there. Sutures with shallow broad even lateral lobes. Internal structure not observed but there can be no doubt as to generic affinities, because form is that of a typical *Westonoceras* and not resembling other genera in shape.

The type, in the collection of Dr. Charles Decker, is from the Viola limestone (Ordovician) west of Bromide, Okla.

Westonoceras sinclairi Flower, n. sp.

Pl. 9, fig. 6

The holotype is a large *Westonoceras* exposing one good lateral surface, the opposite side being weathered and terminating roughly in a plane surface that passes obliquely from a point near the shell aperture to the posterior extremity on the side illustrated. The specimen has a maximum length of 100 mm., of which the basal 43 mm. represents a phragmocone, incomplete on both dorsum and venter adapically; it contains 8 subequal camerae. Sutures are essentially straight and transverse, with only faintest

suggestion of lateral lobes, possibly attributed to slight lateral flattening of the specimen. Dorsal profile convex and gibbous over the anterior part of phragmocone and remaining convex over the basal half of the living chamber, then becoming slightly concave and nearly straight to the aperture. Ventral profile convex over upper part of phragmocone and base of living chamber, curvature decreasing and becoming essentially straight as the aperture is approached. The shell evidently was originally compressed in cross section and more narrowly rounded ventrally than dorsally. The greatest shell height, of 56 mm., is attained essentially at the base of the living chamber; the shell contracts in the remaining 58 mm., as measured laterally, to an aperture 42 mm. high and 32 mm. wide. The aperture, part of which is attained on the dorsum of the specimen, is rough and obscure. The ventral side of the shell probably is close to the original aperture, but does not quite attain it.

Septa are rather strongly curved as exposed in vertical section. Where the shell height is 53 mm., a septum is 18 mm. in depth, approximately equal to the length of 3 camerae. The penultimate camera shows part of the siphuncle in natural section with a segment 5 mm. long and 11 mm. high, which is broader and shorter than in other species of *Westonoceras* but otherwise typical in outline. It shows indication of thickening of the ring, possibly supplemented by parietal deposits, at the septal foramen. The exterior of the phragmocone displays longitudinal markings such as commonly are found on phragmocones of this genus.

Discussion. *Westonoceras sinclairi* is characterized by its relatively large size, essentially straight and transverse sutures, and general roundness of the profile, as a result of which the geniculate nature of the ventral profile, characteristic of many species, is not particularly evident here. The adapical part of the shell, where weathering has removed both dorsum and venter, exaggerates the apparent roundness. Probably both dorsal and ventral profiles of the adapical region were essentially straight and diverging only moderately. Absence of any obliquity of earliest septa in relation to others suggests that the early part of the shell is essentially straight.

Type. Collection of the writer.

Occurrence. Ordovician, Upper Trenton near dam on the Jacques Cartier River, Portneuf sheet, Quebec.

Westonoceras? diestoceratoides Flower, n. sp.

Pl. 9, fig. 7

This species is based on a faintly exogastric brevicone, evidently flattened slightly by pressure, with the better of its two lateral surfaces somewhat weathered. The shell is essentially straight adapically, with sides rapidly diverging, the venter being slightly convex and the dorsum essentially straight. The venter then becomes more curved over the gibbous part of the shell, curvature being reduced gradually until it practically disappears near the aperture. The dorsum becomes strongly convex for a short space over the gibbous region, and then straight, approaching the venter rapidly toward the aperture. Sutures are straight and transverse basally but tend to slope forward on the venter in the extreme adoral portion. No good lateral lobes are developed. The original cross section is obviously distorted. In its present condition the specimen suggests a section more narrowly rounded dorsally than ventrally, which judging from the condition of the specimen and comparison with other species, may not at all denote the original form. Internal structures largely are lost but evidence of a septal foramen near the ventral side of the shell is preserved, though the outline of siphuncle segments is not shown.

The type has a length of 100 mm., increasing from a height of 35 mm. to 55 mm. in the basal 35 mm. and decreasing to 40 mm. in the adoral 55 mm. The point of greatest gibbosity lies well below the base of the living chamber. The 10 extant camerae of the phragmocone occupy a ventral length of 55 mm. and dorsal length of 45 mm. Apical sutures are straight, the last few

septa showing faint dorsolateral lobes and extending forward farther ventrally than dorsally. The living chamber contracts subconically, is compressed and exogastric, with converging venter and dorsum, the venter convex and dorsum straight.

Discussion. This species is even more rounded in outline than *Westonoceras sinclairi*, a fact which gives it very much the aspect of a *Diestoceras*. However, the evidence of exogastric curvature and ventral siphuncle indicate that its resemblance to *Diestoceras* is adventitious, being partly the result of slight distortion which the type specimen has undergone. *W. sinclairi* is closer in proportions to *W. diestoceratoides* than any other so far described. This new species differs in its more rounded form, less evident exogastric curvature, adoral slope of the anterior septa on the venter, and development of the region of greatest gibbosity at a slightly earlier stage.

Holotype. McGill University; collected by Dr. T. H. Clark.

Occurrence. Ordovician, Tetreauville limestone equivalent (uppermost Trenton), Three Rivers, Quebec.

Westonoceras ventricosum (Miller)

Cyrtoceras ventricosum S. A. MILLER, 1875, Cincinnati Quart. Jour. Sci., v. 8, p. 131-132, text-fig. 16.

Cyrtoceras ventricosum JAMES, 1886, Cincinnati Soc. Nat. Hist., Jour., v. 8, p. 246.

— S. A. MILLER, North American Geol. Paleont., p. 435, fig. 731.

— NICKLES, 1902, Cincinnati Soc. Nat. Hist., Jour., v. 20, p. 73.

— BASSLER, 1915, U. S. Natl. Mus., Bull., 92 v. 1, p. 358.

— CHAPPARS, 1936, Ohio Jour. Sci., v. 36, p. 18.

Westonoceras ventricosum FLOWER, 1946, Bull. Am. Paleont., no. 116, p. 441, pl. 9, fig. 1; pl. 14, fig. 3, 4.

This species, from the Southgate beds of the Eden at Cincinnati, is known only from portions of phragmocones. They are clearly attributable to *Westonoceras*, belonging with species in which early portions of the shell are slightly but quite definitely exogastric.

Westonoceras ortoni (Meek)

Orthoceras Ortoni MEEK, 1872, Acad. Nat. Sci. Philadelphia, Proc. (for 1872), p. 330.

— MEEK, 1873, Ohio Geol. Survey, Paleont. v. 1, p. 155, pl. 13, fig. 8.

— S. A. MILLER, 1875, Cincinnati Quart. Jour. Sci., v. 2, p. 130.

— JAMES, 1886, Cincinnati Soc. Nat. Hist., Jour., v. 8, p. 239.

— LESLIE, Pennsylvania Geol. Survey, Rep. Progr., v. 4, p. 555.

Cyrtoceras ortoni NICKLES, 1902, Cincinnati Soc. Nat. Hist., Jour., v. 20, p. 73.

Westonoceras? ortoni FOERSTE, 1932, Denison Univ. Bull., Sci. Lab., Jour., v. 27, pl. 33, fig. 3A, B; Same, v. 28 (1933), p. 117.

— FLOWER, 1946, Bull. Am. Paleont., no. 116, p. 444.

This species is still known only from the type specimen, and from its cross section and form there can be no doubt as to its status as a typical *Westonoceras*. The location of the type, for some time unrecorded, is now known to be the Museum of Comparative Zoology of Harvard. It is from the Southgate member of the Eden beds of Cincinnati.

Westonoceras ornatum (Troedsson)

Cyrtoceras manitobense SCHUCHERT, 1900, U. S. Natl. Mus., Proc., v. 22, p. 170 (partim).

Thuleoceras ornatum TROEDSSON, 1926, Meddel. om Grönland, Bind 72, p. 94, pl. 1, fig. 3, 4; pl. 55, fig. 4-9.

Thuleoceras ornatum FOERSTE, 1928, Denison Univ. Bull., Sci. Lab., Jour., v. 23, p. 98, pl. 8, fig. 2-5; pl. 23, fig. 8.

Westonoceras ornatum TRICHERT, 1937, Rept. 5th Thule Exped. v. 1, no. 5, p. 87, pl. 17, fig. 11, 12.

The specimens assigned to this species consist of portions of phragmocones, representing relatively apical parts of large shells. They are straight, moderately expanding, and compressed in cross section, with venter narrowed and subangulate, and sutures bearing lateral lobes, all characteristic of *Westonoceras*. FOERSTE (1935) finally definitely assigned *Thuleoceras* as a synonym of *Westonoceras*, a course which is fully substantiated, for early stages of *Westonoceras* grade from straight to faintly exogastric to such an extent that it is quite impossible to draw a definite line between these forms when early stages alone are available.

TROEDSSON (1926) has figured this species showing a section of several camerae, and also thin sections of smaller portions, showing the thick rings and bullettes of *Westonoceras*. In one section (TROEDSSON, 1926, pl. 1, fig. 3) the bullettes are apparently supplemented by annular parietal deposits insofar as can be judged from the photograph.

This species is widespread in the Arctic. TROEDSSON's original material is from Cape Calhoun. SCHUCHERT's material, refigured by FOERSTE and assigned to this species, is from the Mt. Silliman beds of Baffin Island. TEICHERT assigned to the species specimens from Iglulik Island. MILLER, YOUNGQUIST & COLLINSON included SCHUCHERT's specimens with some additional material under the name *Westonoceras?* spp. Admittedly, species differentiation is difficult and hazardous on the basis of short bits of phragmocone such as generally have been assigned to this species, and caution is properly applied to identification of the species in areas remote from the type locality. It is, however, significant that *W. ornatum* is mainly Arctic where small straight bits of phragmocone seemingly referable to it are extremely common. Probably the specimens from Baffin Island here figured (Pl. 10, fig. 5; Pl. 11, fig. 1; Pl. 12,) is close to or identical with this species but there seems to be little point in attempting a specific designation for such a short fragment. Its importance lies in the morphological details it reveals, as discussed in the first part of the present work.

Westonoceras sp. (Mt. Silliman)

Westonoceras thompsoni MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 93 (partim), pl. 51, fig. 6-7, text-fig. 12.

Of the four specimens figured as *Westonoceras thompsoni*, the holotype is a member of the *Beloitoceras amoenum* group, another specimen is a fragment of uncertain generic position with much deeper camerae (Pl. 48, fig. 6-8), and the remaining two are short portions of phragmocones of *Westonoceras*. One is shown in lateral and septal aspect (Pl. 51, fig. 6, 7) and while not absolutely conclusive, the position of the siphuncle well away from the venter and the nature of the cross section suggest true *Westonoceras*. The other is represented by a line drawing (text-fig. 12, p. 94) which indicates traces of cameral deposits, a siphuncle composed of typical subquadrate segments (less trapezoidal here than in many forms, because the siphuncle is well removed from the venter) and sutures more nearly transverse than prevails close to the ventral side. The rings are indicated as thick and bullettes not clearly shown, but attention is called to "a median longitudinal structure which may possibly be organic." This structure appears to be a central tube similar to that here figured for another *Westonoceras* (Pl. 10, fig. 5; Pl. 11, fig. 1). In our specimen the tube is fragmentary; in the one figured by MILLER, YOUNGQUIST & COLLINSON it is more complete and relatively undistorted. Regrettably, it is not evident from their description whether the calcite which surrounds this tube is inorganic or organic.

The figured specimen, from the Mt. Silliman beds (Ordovician) of Baffin Island, is in the U. S. National Museum.

Westonoceras sp. (Selkirk)

Pl. 13, fig. 4-6

The specimen here described is portion of a phragmocone 65 mm. long, expanding from 9 and 15 mm. to 25 and 35 mm. It is slightly exogastric in curvature with elliptical cross section and venter scarcely more narrowly rounded than dorsum adapically and only slightly more narrowed adorally. Sutures nearly transverse basally, sloping forward slightly more at the anterior end but lacking lateral lobes such as one expects in *Westonoceras*. Siphuncle segments are exposed in the 12 basal camerae which increase in length from 3 to 5 mm. in the length of 6 mm. They are subtrapezoidal, typical of *Westonoceras* in structure and outline but with the free part of the connecting ring slightly more curved than is typical. An adoral segment 5 mm. long increases from 2 mm. at the septal foramen to a height of 6 mm. in the camerae. Bullettes are small and inconspicuous, the remainder of the siphuncle being filled with homogeneous calcite in which no organic structures are evident. The rings are thick and the entire structure is typical of *Westonoceras* except for absence of any sign of parietal deposits, which, as noted above, are not seen in all species.

Discussion. This specimen is worthy of note because it is typical of *Westonoceras* internally and yet externally extremely generalized in cross section and sutures. It is probably an early portion of a relatively large species, but of which one is dubious. It suggests that some of the more generalized early portion of phragmocones which have been assigned to *Westonoceras* may really belong there, but such assignments cannot be accepted as definite when investigation of the structure of the siphuncle has not been made. *Westonoceras? septentrionale* is close to this species in aspect, differing largely in its appreciably more slender form, but as FOERSTE & SAVAGE point out, its internal structure is not typical of *Westonoceras*, and assignment of the species to this genus is dubious. The difficulty lies in the fact that early stages of oncoceroids may present the same general aspect in cross section, expansion, and suture pattern. Sections have shown that many such specimens are oncoceroids.

It is also not impossible that this specimen could be an early stage of *Winnipegoceras*. If so, it will strengthen the affinities between the two genera. The present specimen shows obvious *Westonoceras*-like features but none indicating definite affinities with *Winnipegoceras*, other than fairly strong exogastric curvature and rounding of the venter in cross section. Neither feature is conclusive in the present state of our knowledge.

The figured specimen, which is from the Selkirk limestone (Ordovician) at quarries near Tyndall, Man., is in collections of the writer.

Westonoceras iowense Foerste & Teichert

Westonoceras iowense FOERSTE & TEICHERT, 1930, Denison Univ. Bull., Sci. Lab., Jour., v. 25, p. 281, pl. 55, fig. 2A, B.

This species is known from an appreciable portion of a phragmocone, slightly curved exogastrically and typical in cross section,

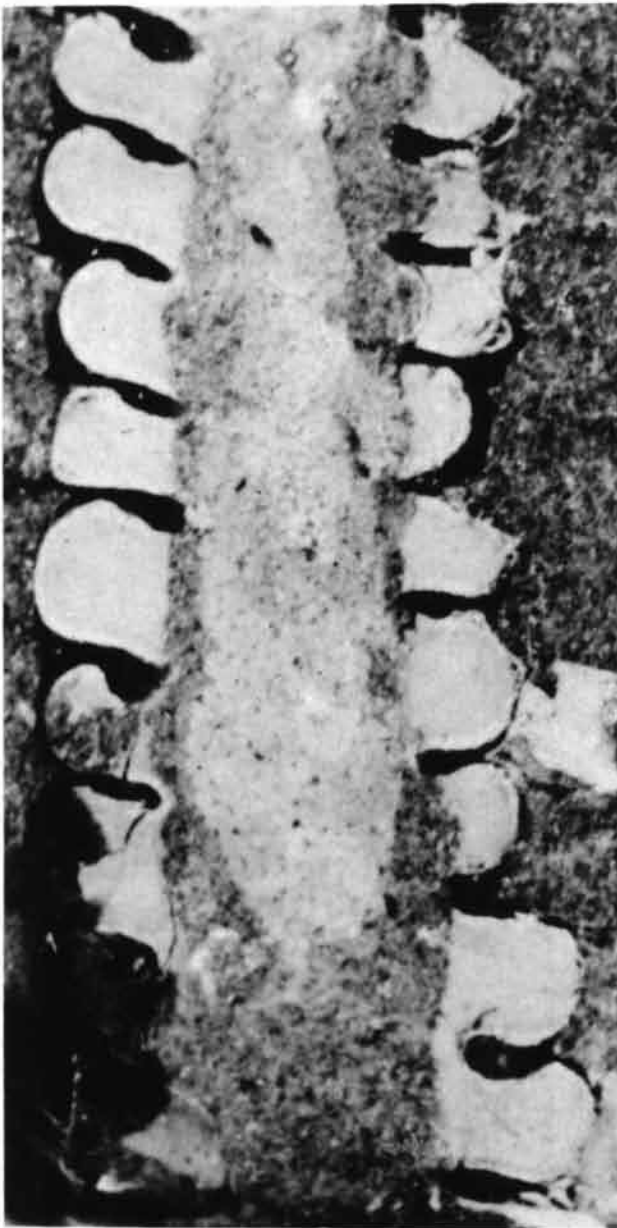
EXPLANATION OF PLATE 23

WESTONOCERATIDAE—*Faberoceras*

FIGURE

1-4. *Faberoceras elegans* FLOWER, holotype, from Upper Ordovician Corryville beds, Cincinnati region; Univ. Cincinnati Mus., no. 22860.—1, Vertical section from basal portion of siphuncle showing obscure septal necks which are recrystallized and not distinct from the strongly developed bullettes, about

×7.—2, Adoral portion of siphuncle showing somewhat different form of anterior segments, thick rings, and (in part) septal necks, bullettes not developed, about ×7.—3, Septal view from base of specimen, venter at right, ×7.—4, Entire vertical section, ×1.6, portions of which are more enlarged in figs. 1 and 2.



1



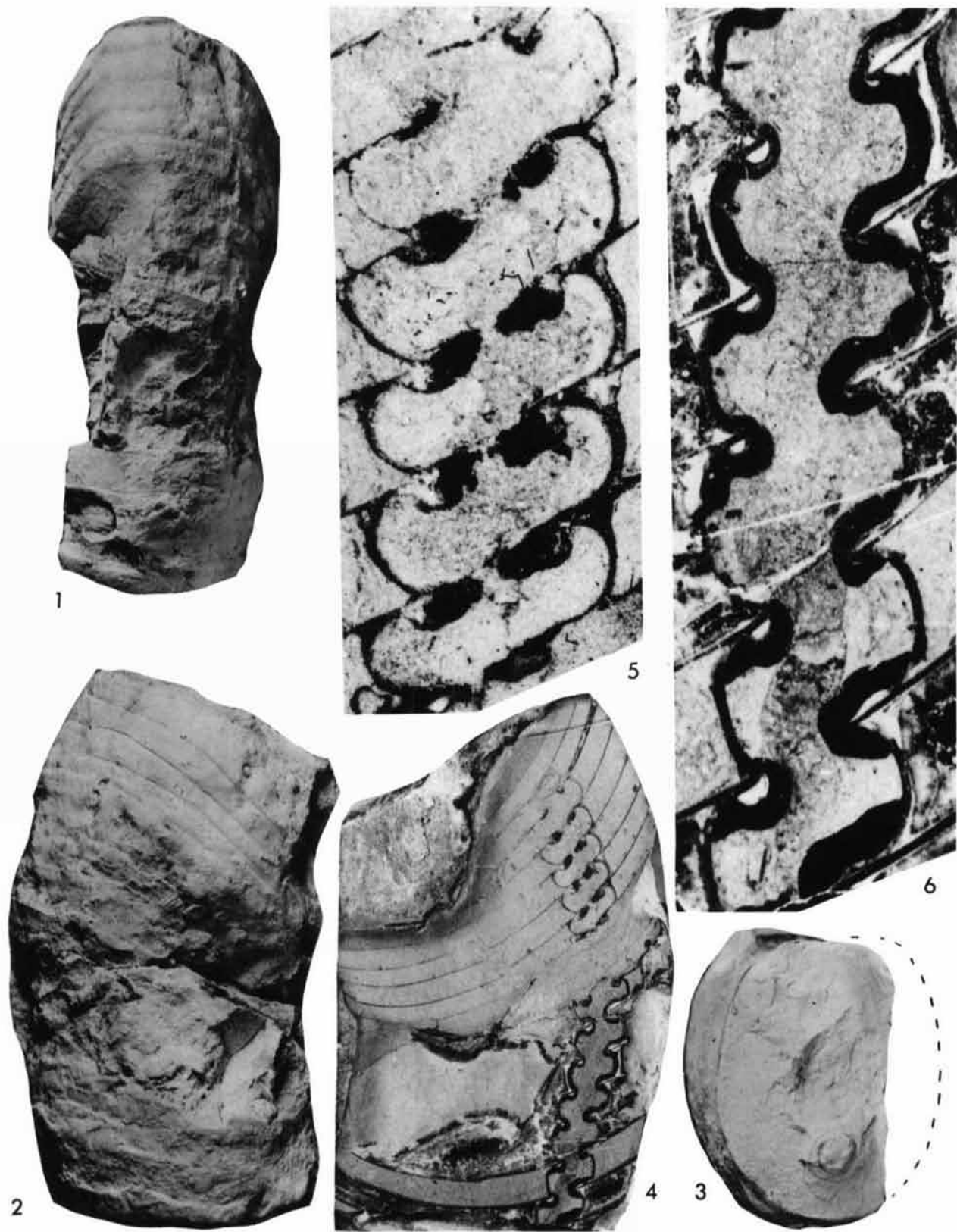
2



3



4



being broadly rounded dorsally and narrow ventrally and with siphuncle segments typical in form and position.

The holotype (U. S. Natl. Mus. no. 83005) is from the Stewartville limestone (Ordovician), 2 miles west of Clermont, Iowa.

Westonoceras sp. cf. *W. iowense* Foerste & Teichert

Cyrtoceras manitobense SCHUCHERT, 1900, U. S. Natl. Mus., Proc., v. 22, p. 170 (Atpatok Island specimen only).
Westonoceras cf. iowense FOERSTE & TEICHERT, 1930, Denison Univ. Bull., Sci. Lab., Jour., v. 25, p. 283, pl. 55, fig. 3A-C.

FOERSTE & TEICHERT have refigured specimens, showing that in form of the shell and structure of the siphuncle they belong to *Westonoceras*. The known specimens consist of rather short septal sections of phragmocones, probably from the early part of a large shell. The five specimens (U. S. Natl. Mus., no. 33061) are from Red River equivalents (Ordovician) of Akpatok Island, Ungava Bay.

Westonoceras minnesotense (Clarke)

Oncoceras minnesotense CLARKE, 1897, Minnesota Geol. Survey, v. 3 pt. 2, p. 798, pl. 58, fig. 16-18, text-fig. 10.
Westonoceras? minnesotense FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 312, pl. 48, fig. 3 (non fig. 4).
Thuloceras minnesotense TROEDSSON, 1926, Meddel. om Grønland, Band 71, p. 94.
Westonoceras minnesotense FOERSTE, 1932, Denison Univ. Bull., Sci. Lab., Jour., v. 27, pl. 33, fig. 1; 1933, v. 28, p. 116.

This species is known apparently only from early portions of the phragmocone, which is essentially straight, with sutures sloping markedly forward and forming dorsal saddles, and with the siphuncle (figured by CLARKE) clearly typical of *Westonoceras* in structure.

Some perplexity attends the exact stratigraphic position of this species. The revision from the Galena to Prosser is a matter of stratigraphic refinement but as FOERSTE notes, the occurrence may actually be in the Stewartville and not in the underlying Prosser limestone. Ordovician.

Westonoceras sp. cf. *W. minnesotense* (Clarke)

Westonoceras cf. minnesotense FOERSTE, 1933-34, Denison Univ. Bull., Sci. Lab., Jour., v. 27, pl. 33, fig. 5A, B; v. 28, p. 117.

This is known only from a fragment of phragmocone, too short to permit accurate generic diagnosis. It is from the upper Trenton (Ordovician), evidently a Cobourg horizon, near Cornell, Mich.

Westonoceras sp. (Cobourg)

Westonoceras FLOWER, 1952, Jour. Paleont., v. 26, p. 26.

In a small collection from the Cobourg limestone at Adams, south of Watertown, New York, made by Dr. R. RUEDEMANN, is a small fragment of phragmocone which is unmistakably that of a *Westonoceras*. FLOWER (1952) has made brief mention of this specimen and it is important to emphasize this record once more as the only one linking *Westonoceras* of Michigan with occurrence of the same genus in Quebec, all in late Trenton associations of Cobourg aspect. The specimen, which is too small and incomplete to merit description or illustration is in the collection of the New York State Museum.

Westonoceras? osloense Strand

Westonoceras osloense STRAND, 1933, Norsk Geol. Tidsskr., Bind 14, p. 73, pl. 10, fig. 5 a, b.

Nothing is known of the siphuncle of this species, based on a single specimen 90 mm. long. The shell is faintly exogastric, only moderately gibbous and compressed, with sutures sloping forward increasingly on the venter. The rather deep camerae throughout the length of the type suggest that this is a member of the Westonoceratidae, such camerae being highly atypical of oncoceroids of similar proportions, if not completely foreign to them. The species is rather generalized in shape, merging perhaps better with *Winnipegoceras* than *Westonoceras*. I refer this species questionably to *Westonoceras* in view of the lack of information concerning internal structure and the rather generalized form of this fossil. As the only recorded species of *Westonoceras* in northern Europe, the situation is vexing, leaving the occurrence of *Westonoceras* there as questionable. The species, known from a single specimen, is from the *Trinucleus* limestone (Ordovician) of Oslo, Norway.

Species Formerly Assigned to Westonoceras

The following species at one time or another have been placed in *Westonoceras* but now are assigned to other genera. For convenience, they are listed here under *Westonoceras*. Fuller discussion of reasons for changing generic designations will be found under the revised generic assignment, either in the main part of the text (those which are judged to be true discosorids) or in the appendix (for those which are assigned to other orders).

FORMER DESIGNATION	PRESENT DESIGNATION
<i>W. baffinense</i> (SCHUCHERT)	<i>Beloitoceras? baffinense</i>
<i>W. cornulum</i> (SCHUCHERT)	<i>Beloitoceras cornulum</i>
	<i>Cyrtorizoceras</i> sp. 1, sp. 2
	<i>Neumatoceras</i> sp. 1, sp. 2
	<i>Neumatoceras</i> (or <i>Beloitoceras</i>) sp.
	<i>Neumatoceras contractum</i>
<i>W. contractum</i> (FOERSTE & SAVAGE)	
<i>W. sp. cf. W. breviposticum</i>	<i>Neumatoceras medium</i>
<i>W.? rallense</i> FOERSTE & TEICHERT	<i>Elrodoceras? rallense</i>
<i>W. latum</i> TROEDSSON	<i>Winnipegoceras latum</i>
<i>W. askerense</i> STRAND	<i>Danoceras? askerense</i>
<i>W. septentrionale</i> FOERSTE & SAVAGE	<i>Laureloceras? septentrionale</i>
<i>W. thompsoni</i> MILLER et al.	<i>Beloitoceras thompsoni</i>
<i>W. tumidum</i> (SCHUCHERT)	<i>Neumatoceras tumidum</i>
	<i>Westonoceras sp.</i>
<i>W. washburni</i> MILLER et al.	<i>Oncoceras washburni</i>
<i>W. wilsonae</i> MILLER et al.	<i>Beloitoceras wilsonae</i>
<i>W. sp.</i> FOERSTE & SAVAGE	<i>Lavaloceras? perplexum</i>

Genus WINNIPEGOCERAS Foerste, 1928

Type species—*Cyrtoceras laticurvatum* WHITEAVES

Winnipegoceras FOERSTE, 1928, Michigan Univ. Geol. Mus. Contrib., v. 3, no. 3, p. 56.
FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 215.
TEICHERT, 1930, Paläont. Zeitschr., Band 12, p. 292.

EXPLANATION OF PLATE 24

WESTONOCERATIDAE—*Clarkesvillia*

FIGURE

1-6. *Clarkesvillia halei* FLOWER, holotype, from Waynesville beds (Upper Ordovician), Clarkesville, Ohio; Univ. Cincinnati collections.—1, Ventral view, $\times 1$.—2, Lateral view, venter at left, $\times 1$.—3, Apical view, venter beneath, $\times 1$.

4, Vertical section, $\times 1$.—5, Adoral segments of siphuncle showing very broad outline and bullettes, $\times 3$.—6, Ad-apical segments showing more slender form, smaller bullettes, and parietal deposits within the siphuncle, $\times 4$.

- FOERSTE, 1935, Denison Univ. Bull., Sci. Lab., Jour., v. 30, p. 38.
- ROY, 1941, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 143.
- FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 428, 432.
- FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24 p. 612.
- MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 99.

Typical *Winnipegoceras* comprises shells consisting of compressed exogastric cyrtocoines which are gently expanded and curved in the young, becoming gibbous and more strongly curved in the mature shell near the anterior end of the phragmocone, then with curvature markedly reduced, shell contracting gently to aperture. The living chamber is slender, very long in typical species, but short in others. The anterior part may be essentially straight and either gently contracting or tubular. The aperture generally slopes gradually adapically from dorsum to venter, with obliquity accentuated mid-ventrally by the hyponomic sinus. Sutures typically show lateral lobes. The siphuncle is only slightly removed from the venter, its segments being contracted rather abruptly at the septal foramen and subquadrate in some as in *Westonoceras* but in others with outline less angular and more rounded. In general, segments are longer in proportion to their maximum diameter than in *Westonoceras* and therefore more slender. Bullettes are swollen, though generally relatively small. One specimen is known showing parietal deposits extended into endocoines.

Winnipegoceras includes two species groups which seem to be rather well differentiated. Typical forms have an extremely long living chamber that contracts gently toward the aperture and in some shells is essentially tubular in the anterior part. Other species have very short living chambers that contract conically, usually rather gently, to the aperture. It is possible that some species have been included in the forms with short living chambers where this feature is more apparent than real and the living chamber is short because it is incomplete. The apparent difference in length of the living chamber is a useful criterion for recognition of the two species groups. Recognition of these groups as distinct genera (or subgenera) seems unwise in the present state of our knowledge, for differences in living chambers are not matched by differences in other features of the shells and no reason is found for suspecting that the two stocks are not closely related.

Forms with long living chambers (Fig. 20) include *Winnipegoceras laticurvatum*, from the Red River beds of Lake Winnipeg together with two specimens referred to this species from the Bighorn dolomite, *W. youngquisti* from the Ordovician beds near Churchill, Man., and *W. fragmentaricum* from the Ordovician of the Oslo re-

gion, Norway. Forms with definitely short living chambers include *W. sinclairi* and *W. obesum* of the late Trenton of Quebec, *W. royi* of the Mt. Silliman beds of Baffin Island and Red River series of Winnipeg, *W. latum* and *W. reclinatum* of the Cape Calhoun beds, and seemingly *W. bighornense* of the Bighorn group and *W. sp.* of the Matepedita series of Quebec, and a number of other forms which are figured but not named.

Careful review of the species has been required because some forms are unknown internally and of dubious generic position. A few such species are retained in the genus with notation of their doubtful features. Others definitely referred are excluded from *Winnipegoceras* and assigned to genera as recorded in the appendix to the present work, but these are listed here for convenience with indication of their new generic position: *W. dowlingsi* FOERSTE (to *Cyrtogomphoceras dowlingsi*); *W. humei*, MILLER, YOUNGQUIST & COLLINSON (to *Oncoceras humei*); *W. sp.* FOERSTE, from the Cat Head limestone (to *Neumatoceras sp.*); *W. sp.* TEICHERT (to *Fabero-ceras? sp.*).

Many species are yet known only from single specimens and many fail to show the internal structure. On such evidence as exists, some of these forms cannot be retained in *Winnipegoceras* but are referable instead to genera of the Oncoceratidae. Conversely, a few forms previously attributed to the Oncoceratidae are found on review to be widely disparate with known oncoceroids and more consistent with a position in *Winnipegoceras*. Various species of *Winnipegoceras*, known by their internal structure to be typical, approach general proportions of the oncoceroid genus *Neumatoceras*. The obvious if superficial feature that such species of *Winnipegoceras* are large, whereas those of *Neumatoceras* are very small, has proved of great practical value and reliability.

Knowledge of internal structure depends on a relatively small number of specimens which have been sectioned to show the siphuncle. FOERSTE (1928, Pl. 9, fig. 10,) has figured a section of *Winnipegoceras laticurvatum* (here illustrated in Fig. 20B) showing a suite of siphuncle segments which are elongate and somewhat variable in form, probably from slight crushing of the specimen. As is so commonly true of specimens like this one from the Dog Head member of the Red River group, preservation of the siphuncle is rather poor and this section even fails to show bullettes clearly. No evidence of parietal or other deposits within the connecting rings is found. ROY (1941) figured part of a siphuncle showing a similar subquadrate slender segment, this

EXPLANATION OF PLATE 25

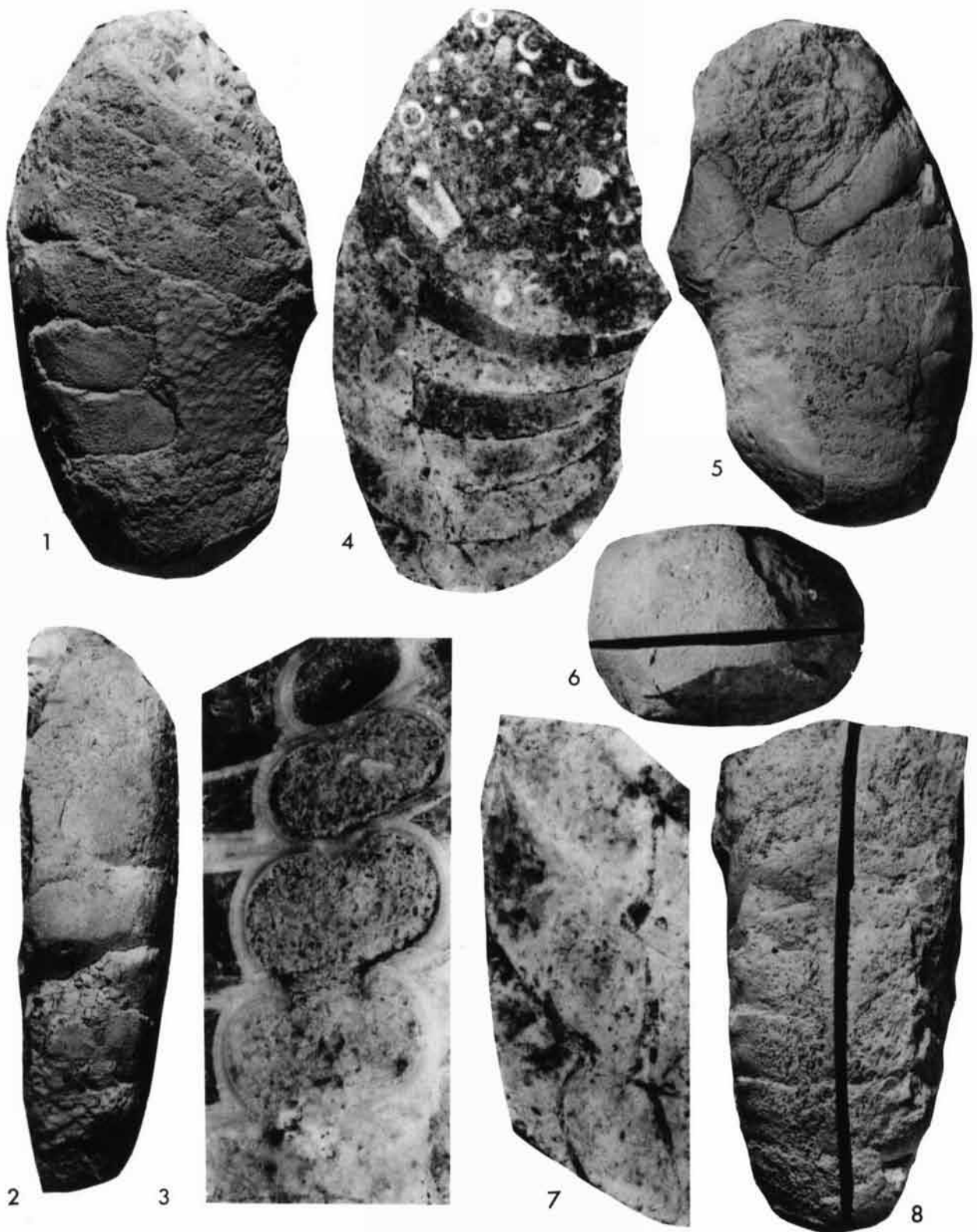
WESTONOCERATIDAE—*Glyptodendron*

FIGURE

1-3. *Glyptodendron subcompressum* (BEECHER), hypotype, from Brassfield limestone (Lower Silurian), at Brown's quarry, 2 miles west of New Carlisle, Ohio; U. S. Natl. Mus., no. 125275. —1, Lateral view of a nearly complete living chamber, venter at left, $\times 1$. —2, Septal view, $\times 1$. —3, Ventral view of basal part. The side shown at left being weathered progressively deeper from the basal septum to the adoral end; the characteristic pitted surface of the genus is shown, $\times 1$.

4-5. *Glyptodendron subcompressum* (BEECHER), portion of phragmocone representing an early growth stage, from same locality and horizon as specimen illustrated in Figs. 1-3; U. S. Natl. Mus. no. 125276. —4, Nearly vertical section cutting dorso-lateral wall with slightly more than half of ventral surface but less than half of the dorsal surface preserved, $\times 1$. —5, Portion of basal part of siphuncle showing thick rings and absence of bullettes, $\times 2.8$.





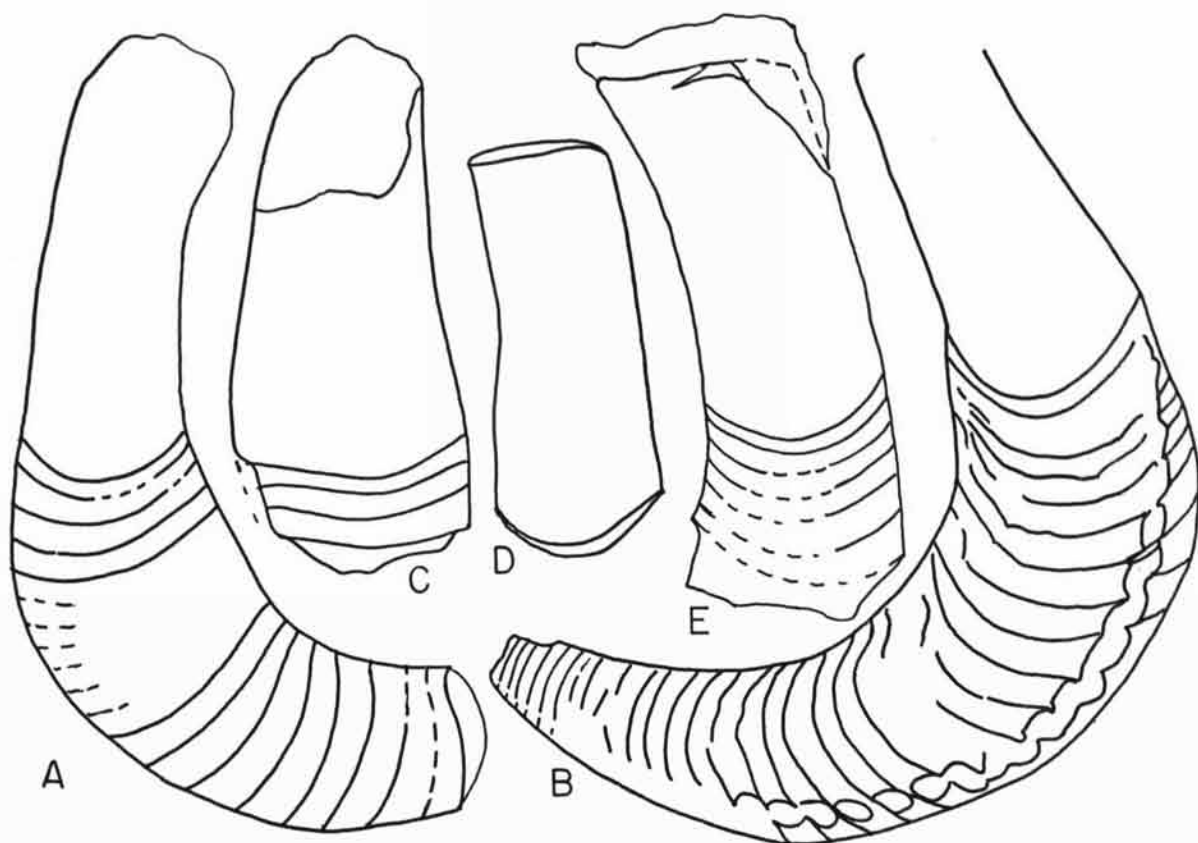


FIGURE 20. Typical species of *Winnipegoceras* with attenuated living chambers.

A,B. *W. laticurvatum* (WHITEAVES), two specimens from the Red River beds of Manitoba figured by FOERSTE showing variations in proportions; $\times 0.75$.

C. *W. youngquisti* FLOWER, n. sp., lateral view, showing great height of shell at base of living chamber, which is shorter and more strongly contracted than in *W. laticurvatum*; $\times 0.75$.

D,E. *W. sp. cf. W. laticurvatum* (WHITEAVES); D, specimen from the Bighorn group, similar to A, but slightly smaller, figured by MILLER & CARRIER; E, specimen from the Lander sandstone, Bighorn group, closely comparable to the paratype shown in B, figured by FOERSTE; $\times 0.75$.

being in the anterior part of the phragmocone of a species later set apart as *W. royi*. TROEDSSON (1926) has figured sections of *W. reclinatum* (which he referred to *Maelonoceras*) and *W. latum* (which he placed in *Westonoceras*) showing in line drawing structures which are certainly bullettes. Material of *Winnipegoceras* is rare, difficult to obtain, and more difficult to find well preserved enough to show internal structure adequately. Happily, I had one specimen of my own, the holotype of

W. sinclairi, from the Terrebonne limestone of Quebec. Though the Terrebonne beds usually show internal structure of the cephalopods poorly preserved or completely wanting, this specimen proved exceptional. Anterior septa were broken and the siphuncle was wanting there, but at the base of the specimen two segments and part of a third segment of the siphuncle were preserved. Here, within segments quite typical of the genus in outline, were found deposits thickened into endocones, surrounding a central

EXPLANATION OF PLATE 26

WESTONOCERATIDAE—Glyptodendron, Cliftonoceras

FIGURE

1-3. *Glyptodendron subcompressum* (BEECHER), specimen from Brassfield limestone (Lower Silurian), at Brown's quarry, 2 miles west of New Carlisle, Ohio; U. S. Natl. Mus., no. 125276. —1, Lateral view showing sutures and portion of shell with surface markings, $\times 1$. —2, View of incomplete ventral side, $\times 1$. —3, Section of anterior part of siphuncle showing short broad segments and faintly developed bullettes, $\times 2.5$.

4-8. *Cliftonoceras quadratum* FLOWER, n. sp., from "Clifton lime-

stone" (old label), identified by FOERSTE as Brassfield limestone (Lower Silurian), at Clifton, Tenn.; U. S. Natl. Mus., no. 67236. —4, Vertical section, venter at left, slightly enlarged. —5, Lateral view showing internal mold and retaining a small piece of the smooth shell surface, $\times 1$. —6, Septal view, venter at left, $\times 1$. —7, Basal part of siphuncle of section illustrated in Fig. 4, showing recurved neck on dorsum and broad area of adnation on venter, $\times 2.5$. —8, Ventral view, $\times 1$.

tube traversed by irregularly spaced diaphragms (Fig. 22).

The genus *Winnipegoceras* occurs in Ordovician strata of North America and northwestern Europe.

Winnipegoceras laticurvatum (Whiteaves)

Cyrtoceras laticurvatum WHITEAVES, 1895, Canadian Records Sci., v. 6, p. 395.
WHITEAVES, 1897, Canada Geol. Survey, Paleozoic Fossils, v. 3, p. 224, fig. 14.

Winnipegoceras laticurvatum FOERSTE, 1928, Michigan Univ., Geol. Mus. Contrib., v. 3, pt. 3, p. 56, pl. 9, fig. 1-2.

FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 216.
(non) ROY, 1941, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 143, fig. 105.

The type of this species is a slender cyrtocone, compressed, gently exogastric in the young, with curvature increasing gradually over a gibbous region at the anterior end of the phragmocone, and living chamber very long, tapering, and conically contracted to the aperture. Sutures with well-developed lateral lobes. Siphuncle slightly removed from venter, its segments subquadrate and trapezoidal in vertical section. Early segments have essentially the outline of those in *Westonoceras*; adoral segments are still subquadrate but longer and more slender. Preservation of the siphuncle wall in the type is poor; the thick ring, bullettes or other expected structures have not been observed.

It is worthy of note that the two specimens figured by WHITEAVES and later by FOERSTE show some variation in size and proportions. The holotype is a relatively small shell with the apical part very slightly curved, suggesting that this specimen (Fig. 20A) is considerably less curved apically than the second, slightly larger specimen (Fig. 20B).

The species is typically developed in the Dog Head member of the Red River series (Ordovician) of Manitoba. I have observed an apparently conspecific form in the Selkirk member at quarries near Tyndall, Man.

Winnipegoceras sp. cf. *W. laticurvatum* (Whiteaves)

Text-fig. 20D,E

Winnipegoceras laticurvatum FOERSTE, 1935, Denison Univ. Bull. Sci. Lab., Jour., v. 30, p. 38, pl. 4, fig. 2.

MILLER & CARRIER, 1942, Jour. Paleont., v. 16, p. 540, pl. 78, fig. 6.

Under this designation are considered two fragmentary specimens from the Lander sandstone of the Bighorn group with long living chamber comparable in length to that of the paratype (compare Figs. 20B,E) from the Red River beds of Manitoba but with the aperture seemingly somewhat less markedly contracted vertically. That the apical part of the shell, representing parts of 6 camerae, seems slightly less curved and the whole shell somewhat less rapidly contracting vertically, may be adventitious.

MILLER & CARRIER have figured an isolated living chamber (Fig. 20D) from the Lander sandstone which is almost identical in proportions to that of the holotype of the species (compare Figs. 20A, D) but differing in that the lateral lobe of the suture is strongest close to the dorsum.

The proper specific assignment of these specimens is something of a problem. Both are admittedly very close to *Winnipegoceras laticurvatum*, insofar as they are known, but our knowledge of them is very incomplete. Assignment of them to *W. laticurvatum* seems convincing from evidence at hand but judgment must be reserved. For several years *W. laticurvatum* was the only recognized species of *Winnipegoceras*, and not only these specimens but others which are quite clearly different were assigned to this species. At the present time the two specimens are assigned tentatively to *W. laticurvatum*. Only one known species of the genus (the diminutive *W. fragmentarium* STRAND from the Oslo Ordovician) is typical in having long gently contracted living chamber and certainly it is questionable whether all specimens of

Winnipegoceras which are typical in having long slender living chambers should be considered as conspecific.

The two described specimens are from the Lander sandstone of the Bighorn group (Ordovician) of Wyoming.

Winnipegoceras youngquisti Flower, n. sp.

Text-fig. 20C

Winnipegoceras laticurvatum MILLER & YOUNGQUIST, 1947, Jour. Paleont., v. 21, p. 415, pl. 56, fig. 2.

This is a *Winnipegoceras* with very shallow camerae and faint lateral lobes. Shell height at base of the living chamber is appreciably greater than in true *W. laticurvatum*, and the living chamber, which is slender and long as in that species, is atypical in contracting gently and uniformly to the aperture, whereas in *W. laticurvatum* the rate of contraction, gentle at first, is reduced adorally until the anterior part of the living chamber is nearly cylindrical rather than conical. In all probability this is a true *Winnipegoceras* but differences in form, spacing of septa, and the presence of faint lateral lobes indicate that it should not be placed in *W. laticurvatum*, being recognized rather as a distinct species. So great are the differences that the only alternative course would be to recognize only a single species in the genus *Winnipegoceras*.

The species, known from a single specimen, is from Ordovician rocks at Battery Point, just northwest of Churchill, Man.

Winnipegoceras fragmentarium Strand

Text-fig. 23C, D

Winnipegoceras fragmentarium STRAND, 1933, Norsk Geol. Tidsskr., bind 14, p. 75, pl. 11, fig. 8a-b.

This is a diminutive species, which in vertical profile shows gentle tapering contraction from the anterior part of the phragmocone to the living chamber. The living chamber is relatively slender in proportion to its height. The shape of the extant part of the shell suggests that the earlier portion may well have contained a gibbous strongly curved region, which is to be expected in *Winnipegoceras*. Nothing is known of the siphuncle. In two respects this species is not closely comparable with any known true *Winnipegoceras*, for the sutures slope strongly forward on the dorsal side, showing only faintest lateral lobes, and the cross section of the shell is broad, being essentially circular instead of strongly compressed. In spite of these differences, and lack of information concerning the siphuncle, the species has the aspect of a *Winnipegoceras*, and fails to suggest any other known genus. It is from the Gastropod limestone (Ordovician) of Ringerike, Norway.

Winnipegoceras latum (Troedsson)

Text-fig. 21D,E

Westonoceras latum TROEDSSON, 1926, Meddel. om Grønland, bind 71, p. 90, pl. 54, fig. 2, 3.

This is a small species as compared with other representatives of any of the *Westonoceratidae*. Externally it has the aspect of a *Beloitoceras* in which the shell is gibbous well below the base of the mature living chamber. Two features are atypical of *oncoceroids* and typical of the *Westonoceratidae*: first, the camerae are unusually deep and exceptionally uniform in length throughout the length of the specimen, second, the siphuncle is well removed from the ventral margin of the shell and composed of rather elongate but definitely subquadrate segments such as are characteristic of *Westonoceras* and *Winnipegoceras*. The slight degree of gibbosity, implication of a missing long slender stage seen in the remarkably uniform length of the camerae in the gibbous portion, and the slender tapering living chamber, all suggest that this species is better placed in *Winnipegoceras* than in *Westonoceras*. It is known from the Cape Calhoun beds of northern Greenland.

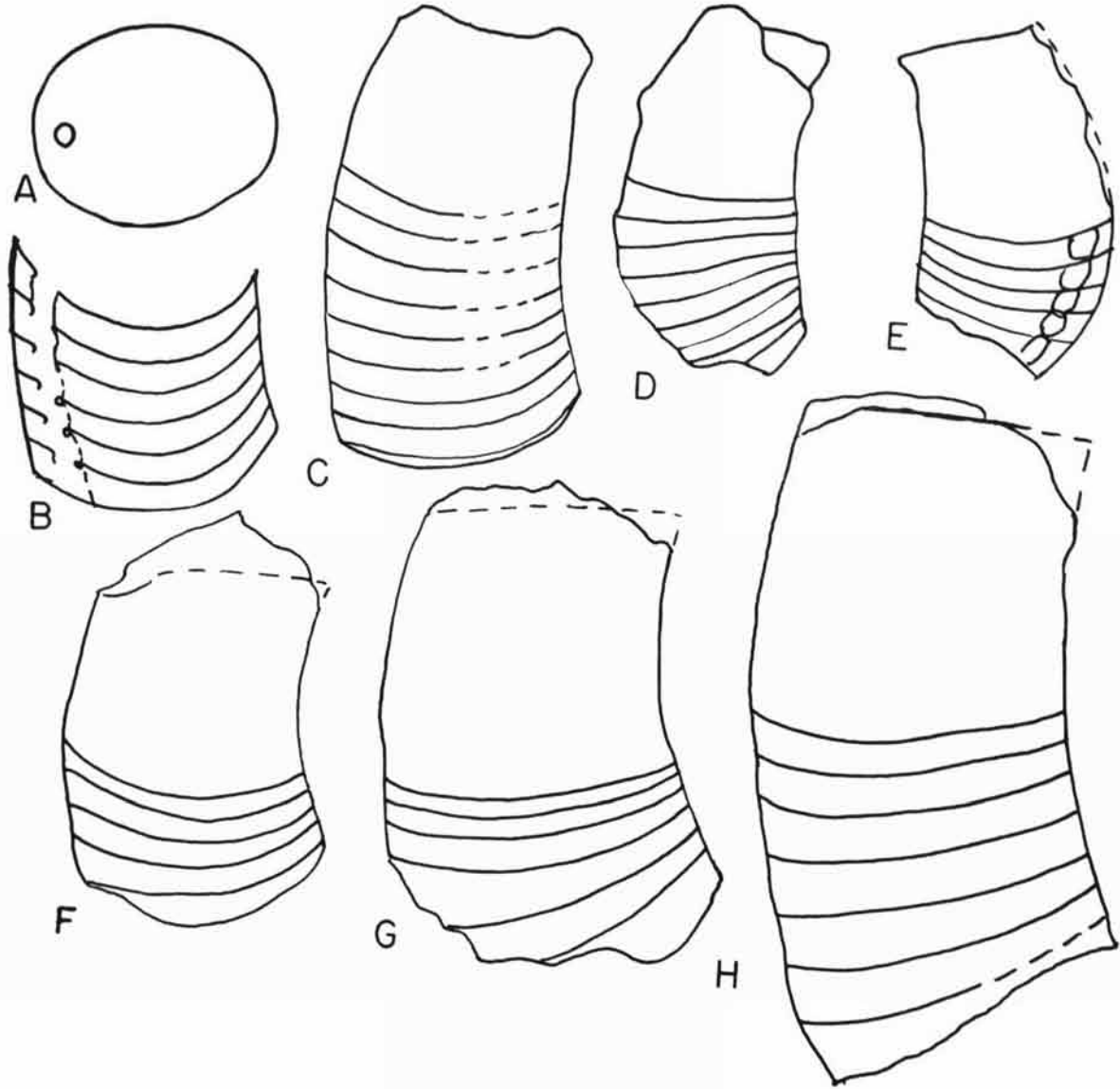


FIGURE 21. Specimens of *Winnipegoceras* with short living chambers.

A progressive series of shells with short living chambers assigned to *Winnipegoceras* is illustrated. Ranging from right to left in the upper row and from left to right in the bottom row, they display a progressive increase in size, reduction in the degree of contraction, reduction of curvature, and reduction in depth of lateral lobes of the sutures, these changes corresponding roughly to the occurrence of the fossils from the northern extremity of their range to southern localities (all $\times 0.5$).

A-C. *W. reclinatum* (TROEDSSON), Cape Calhoun beds, Green-

land; A, cross section; B, longitudinal section, showing traces of bullettes; C, lateral view, venter at left.

D-E. *W. latum* (TROEDSSON), Cape Calhoun beds, Greenland; D, lateral exterior; E, section from opposite side.

F-H. *W. royi* MILLER, YOUNGQUIST & COLLINSON; F, G from Mt. Silliman beds, Baffin Island; H from Selkirk limestone, Red River series, Manitoba; F, lateral view of holotype; G, lateral view of a larger form; H, lateral view of a specimen here attributed to the species. All $\times 0.75$.

Winnipegoceras reclinatum (Troedsson)

Maelonoceras? reclinatum TROEDSSON, 1926, Meddel. om Grønland, bind 71, p. 91, pl. 55, fig. 1-3.

This is a large exogastric shell, faintly gibbous, but slender in relation to *Westonoceras*. In size and proportion it is intermediate between *Westonoceras* and *Winnipegoceras*, being placed in the latter genus mainly on the basis of its slender form, broad

extent and slight swelling of the gibbous region, deep camerae with gentle lateral lobes, and nature of the cross section, which is not narrowed ventrally as in typical *Westonoceras*. The ventral siphuncle is made up of rather slender subtrapezoidal segments in which traces of bullettes are preserved, thus indicating affinity of this species with the *Westonoceratidae*. It is known only from the Cape Calhoun beds of northern Greenland.



FIGURE 22. Vertical section of the siphuncle of *Winnipegoceras sinclairi*.

The section shows the basal part of the holotype, with venter at left, $\times 8$. The break in the septa on the dorsal side simulates septal necks. The thick rings are difficult to differentiate from parietal deposits, but are clearly thickened apically into bullettes. Growth lines are evident in parietal deposits, here thickened into cones, but complicated by recrystallization. The central tube is transversely by diaphragms.

Winnipegoceras royi Miller, Youngquist & Collinson

Pl. 10, fig. 2; text-fig. 21F-H

Neumatoceras? tumidum Roy, 1941, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 146, fig. 106 a-d.

Winnipegoceras royi MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 101, pl. 32, fig. 1-2; pl. 52, fig. 4-5.

The holotype is a living chamber with four camerae of a compressed exogastric brevicone, rather slender, large. The ventral siphuncle as illustrated by Roy is imperfect, but seems to consist of elongated subquadrate segments such as characterize *Winnipegoceras laticurvatum*, a fact which corroborates generic assignment of the species. MILLER, YOUNGQUIST & COLLINSON have placed in the same species an individual in which height of the shell at base of the living chamber is considerably greater, adoral camerae deeper, and vertical contraction of the living chamber

toward the aperture somewhat more gentle. This specimen is intermediate in proportions between the holotype and a larger, more slender shell in which contraction of the living chamber is still more reduced. This specimen, however, is from the Selkirk limestone at quarries near Tyndall, Manitoba. It is necessary to point out that information on variation is inadequate to indicate whether the three described specimens, differing as they do in size and proportions, represent variation within a species or three distinct species. One could hardly include the two Mt. Silliman specimens in *W. royi* and exclude the Selkirk specimen. Admittedly not enough specimens are known to permit reliable solution of the problems of specific assignment presented by these specimens.

The Selkirk limestone specimen here illustrated is 130 mm. long. Only one side is preserved; this shows 7 camerae and an essentially complete living chamber. The shell height decreases gradually from 75 to 55 mm., the 7 camerae occupy the basal 75 mm. on the venter. The sutures show only faint lobes and slope forward increasingly on the venter as growth progresses. The living chamber has a ventral length of 65 mm. and decreases in height from 65 to 55 mm. The cross section is compressed, the venter and dorsum being about equally rounded. Probably the original width of the shell was about two-thirds of the height.

Winnipegoceras sp.

Winnipegoceras laticurvatum (WHITEAVES) ROY, 1941, Field Mus. Nat. Hist., Geol. Mem., 2, p. 143, fig. 105.

Winnipegoceras aff. *W. laticurvatum* MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 100, pl. 52, fig. 1-3.

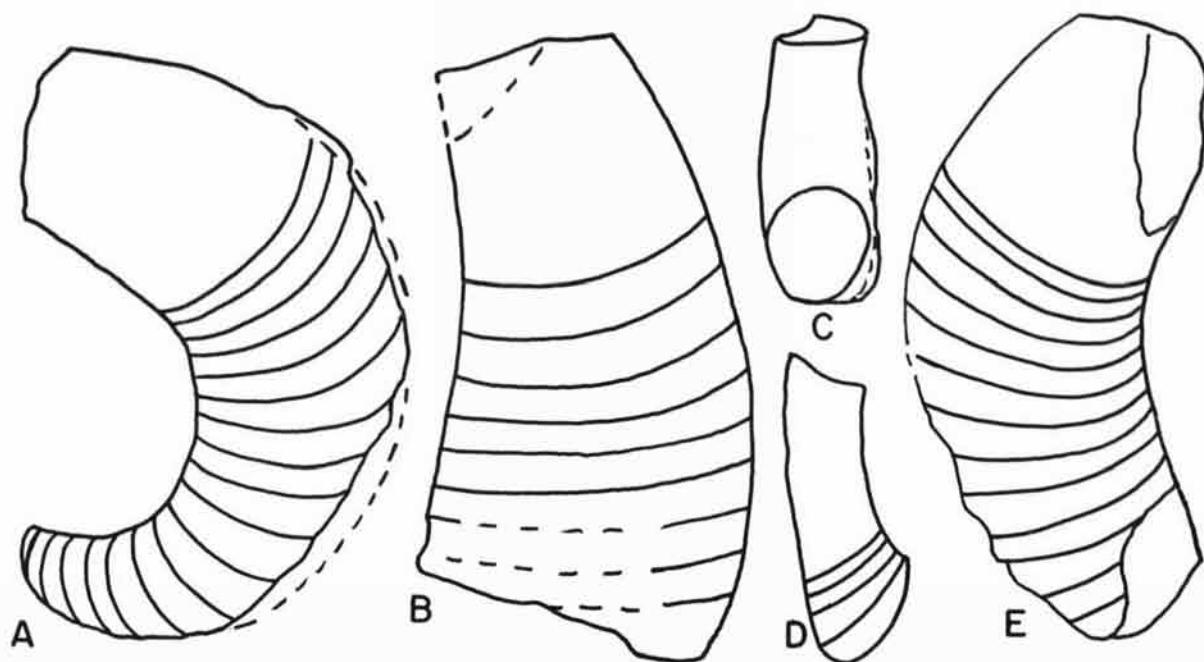
ROY assigned to *Winnipegoceras laticurvatum* an extremely slender shell, very gently contracting toward the aperture, which, without information concerning the siphuncle, could be considered as a member of the genus *Oonoceras*, which has a similar though commonly less marked contraction of the mature living chamber. MILLER, YOUNGQUIST & COLLINSON have figured a specimen which they assign tentatively to *W. laticurvatum*. This one appears to be justifiably placed in *Winnipegoceras*, for the anterior part of the phragmocone is faintly gibbous and the shell agrees more closely with *Winnipegoceras* in general aspect, particularly in the character of the lateral lobes and the rather deep camerae. This form seems to have a complete or nearly complete living chamber; it is clearly much less gibbous over the phragmocone and seems to be more comparable with other species which agree with the present form in having a short living chamber. *W. reclinatum* (TROEDSSON) is a similar but larger species. *W. latum* TROEDSSON is slightly smaller, more gibbous, and has less well-developed lateral lobes of the sutures.

Winnipegoceras sinclairi Flower

Pl. 15, fig. 3-5; text-fig. 22

Winnipegoceras sinclairi FLOWER, 1952, Jour. Paleont., v. 26, p. 48, pl. 10, fig. 6, 8.

This species is based on an internal mold retaining a living chamber and a very considerable part of the phragmocone. The proportions are fully described in the original publication but the present paper gives more adequate illustrations of the species, this time at natural size. The base of the specimen was sectioned in hope of learning more about internal structure of the genus. Although the siphuncle is largely destroyed, parts of the three basal segments are preserved, showing rather unusual thick deposits within the siphuncle, here illustrated and described. Thick parietal deposits are extended until they appear to be developed into endocones. This feature has elsewhere not been noted in the genus, and indeed, is paralleled in the Ordovician only by the genera *Fabroceras* and *Hecatoceras*. Comparable cones are developed in the Lowoceratidae and Discosoridae of the Silurian. A central tube crossed by diaphragms is duplicated only in the Devonian *Alpenoceras* described by SCHINDEWOLF (1942).

FIGURE 23. Aberrant species of *Winnipegoceras*.

A, *Winnipegoceras* sp., specimen identified by MILLER & FURNISH (1937) as *W. laticurvatum*, from the Matepédia series of Quebec; $\times 0.75$.

B, *Winnipegoceras* sp., an unusually high compressed shell from the Whitewood dolomite, South Dakota; $\times 0.75$.

C, D, *W. fragmentarium* STRAND, from the Gastropod limestone of the Oslo region, Norway; C, dorsal view; D, lateral view, venter at left; both $\times 0.75$. This is a form with long living cham-

ber belonging to the *W. laticurvatum* group, anomalous in its tiny size and broad cross section.

E, *Winnipegoceras?* *bighornense* (MILLER & CARRIER), from the Bighorn group, comparable in proportions to *W. reclinatum* and *W. royi* (text-fig. 20) and also comparable to *W. sp.* (text-fig. 23A) from which it differs mainly in the reduced curvature; $\times 0.5$.

(All are drawn from original figures.)

The structure shown in this specimen is illustrated in Pl. 15, fig. 5, and in text-fig. 22. The siphuncle structures are preserved in varying colors of rather dark calcite, gray to nearly black, against a dark gray faintly brownish matrix. The segments are slender, scalariform, the ring adnate at the adoral end on the dorsum, at the apical end on the venter, a condition fairly typical of ventral siphuncles in exogastric cyrocones. The free part of the segment is nearly straight, curving inward at the adapical end on the dorsum and at the adoral end on the venter. The ventral septal neck is seen best in the adoral end of the apical camera, where the neck is scarcely recurved. Necks are harder to discern on the dorsum but are evidently short, recurved, narrowly escaping being recumbent. A singular feature of the specimen is the appearance presented of short recurved necks where the septum meets the extreme exterior of the siphuncle. This condition can hardly be real and is apparently the result of fracture and distortion.

Of the most adoral of the three segments, only the connecting ring is preserved on the dorsal side. It shows an inner brownish fine-textured layer, faintly lamellar, with a suggestion of differentiation within it, the adoral end being denser and darker than the remainder, while the tip is again darker but terminates in a small bullette of light calcite about a darker center. Outside the primary layer of the ring is some light coarse-grained calcite, orad of which is darker denser material separating the ring here from a portion of the anterior septum. The recurved neck and attendant structures are destroyed. In the next segment the septal neck can be seen, though only with difficulty. The ring is thick, with accompanying structures destroyed. In the next segment the septal

neck can be made out, though only with difficulty, and is portrayed more clearly in the text figure than in the photograph. The ring on the dorsal side is thick but its structure is largely not evident except at its apical end where a small bullette composed of an outer light and an inner dark layer can be seen. On the ventral side, the anterior end of the ring is poorly preserved but over most of the length, the original thickness of the ring is clearly evident and its tip can be seen passing within the adapical septal neck, swollen to form a bullette. In the adapical segment the structure of the ring is not evident ventrally. Dorsally its original thickness is supplemented by some material on the outside but it is not evident from the opaque section whether this material is organic or adventitious.

The adapical segment and a half shows clearly a tube in the center of the siphuncle crossed by curved diaphragms, concave anteriorly. The calcite between the tube and connecting ring is somewhat puzzling, owing probably in large part to partial recrystallization. The adapical segment shows (most clearly on the dorsum) lines indicating the surface of growing parietal deposits which have later thickened to form endocones around the central tube. Traces of some more oblique lines within this area on both dorsum and venter indicate the position of anterior extremities of successive endocones which tend to be irregularly inflated, more or less in accordance with the expansion of the siphuncle segments in the camerae. In the adapical two segments several such sinuate lines, light-colored in relation to surrounding material, can be seen. The second segment on the dorsum shows lines of growth of the deposit, marking gradual thickening of the parietal deposits, particularly in the adapical half of the segment, leaving an endocone cavity widest in the anterior half of the segment.

Allowing for vicissitudes of replacement and recrystallization, the structures shown here are similar to those marking the endocones developed from parietal deposits in *Fabroceras* and *Hecatoceras* and not unlike structures observed in the Discosoridae.

Winnipegoceras? obesum Flower, n. sp.

Pl. 14, fig. 1-3

This species is known only from a rather smooth and apparently somewhat waterworn internal mold of a living chamber. The cross section is compressed throughout, with venter narrowly and dorsum broadly rounded, greatest width being about two-thirds the distance from venter to dorsum. The dorsal profile is very faintly convex in the adapical half, becoming very faintly concave in the adoral half. Taking the dorsal profile as a vertical line, the suture of the last septum is inclined forward from dorsum to venter, but develops only a shallow lateral lobe. The ventral profile converges toward the dorsum as traced from base to aperture of the living chamber, the outline being slightly convex throughout its length and modified only by a slight preoral constriction near the aperture. The living chamber has a dorsal length of 50 mm. and a ventral length of 48 mm. The aperture clearly slopes adapically on the venter to form a hyponomic sinus.

The shell contracts to a height of 45 mm. and width of 33 mm. at aperture. At base the siphuncle is 7 mm. high and 6 mm. wide, located about 4 mm. from the venter. The form and structure of its segments is not apparent.

Discussion. Lacking knowledge of the structure of the siphuncle, reference of this species to *Winnipegoceras* is tentative. However, all known features, such as proportions of the living chamber and the size and position of the siphuncle, are consistent with placing this species in the genus *W.?* *obesum* is a much larger species than the associated *W. sinclairi*, its cross section is broader in proportion to height, the sutures slope more gently forward from dorsum to venter, and the lateral lobes are much less marked. Proportions of the living chamber are rather close to those of the holotype of *W. royi* but the shell contracts more rapidly as the aperture is approached and the sutures are more transverse and display fainter lateral lobes.

Holotype. Collection of G. W. Sinclair.

Occurrence. Ordovician, Terrebonne limestone, upper Trenton, from Ruisseau Rouge, northwest of Crabtree Mills, Quebec.

Winnipegoceras? bighornense (Miller & Carrier)

Text-fig. 23E

Richardsonoceras bighornense MILLER & CARRIER, 1942, Jour. Paleont., v. 16, p. 539, pl. 77, fig. 5.

This is a relatively large slender exogastric cyrtocone, with camerae unusually deep for an oncoceroid but comparable to those in *Winnipegoceras*. It is atypical of *Oonoceras* (of which the genus *Richardsonoceras* appears to be a synonym) in gentle vertical contraction of the shell in the anterior part of the phragmocone and entire length of the living chamber. The living chamber appears to be short but incomplete adorally. *W.?* *bighornense* (Fig. 23E) appears to be closely comparable in proportions to species of *Winnipegoceras* with short living chambers, similar to but not conspecific with *W. sp.* MILLER & FURNISH (1937) in nature of the sutures and intermediate between that form and the group of *W. reclinatum* and *W. royi*.

Nothing is known of the siphuncle. Where form alone must be the basis of taxonomy in these shells, it is nevertheless clear that this species is closely comparable to species of *Winnipegoceras* and not to any true oncoceroids.

The species is known from the Bighorn dolomite (Ordovician) of Medicine Mountain, in the Big Horn Mountains of Wyoming.

Winnipegoceras? sp. A

Text-fig. 23A

Winnipegoceras sp., CRICKMAY, 1932, Am. Jour., Sci., ser. 5, v. 24, p. 379.
Winnipegoceras sp. aff. W. laticurvatum MILLER & FURNISH, 1937, Jour. Paleont., v. 11, p. 551, pl. 69, fig. 1.

The form here indicated is a considerably flattened shell from phyllites of the Matepedia series, near Matepedia, Quebec. Although the specimen is very poorly preserved, it does not seem at all probable that the features which it shows can be the result of distortion of any typical *Winnipegoceras*. The shell is more uniformly and strongly curved than in any known species, the shell height increases gradually, and decreases very gently as the aperture is approached. The living chamber is short, the sutures develop very deep and prominent lateral lobes. Without the internal structure some problem always exists in assigning a species such as this on the basis of form alone. I agree that *Winnipegoceras* is a more logical identification than any other for this species, but clearly, placement of it in the genus opens the way for inclusion of still others which are strongly curved, with deep lateral lobes and distant septa, expanding gently in the early part, and contracting in equally gentle manner toward the aperture. One such form is *Richardsonoceras bighornense* MILLER & CARRIER (1942, Jour. Paleont., v. 16, p. 539, pl. 77, fig. 5) and indeed it would not be a great step further to include *Exomegoceras wyomingense* MILLER & CARRIER (1942, *op. cit.*) also. Insofar as gross shell proportions are concerned, the apparent bridging of species from oncoceroids to discosorids is obviously a matter of homeomorphy. It seems necessary to reject the reference of this specimen to *W. laticurvatum*; its assignment to *Winnipegoceras* is logical yet dubious in the absence of knowledge of the internal structure. The specimen is from the Matepedia series (Ordovician) of Quebec.

Winnipegoceras sp. B

Text-fig. 23B

Winnipegoceras sp., MILLER & FURNISH, 1937, Jour. Paleont., v. 37, p. 550, pl. 69, fig. 2.

This is a strongly compressed shell which attained a relatively great height and rather deep camerae before contracting gently adorally. It has a rather short living chamber. A trace of an apparent siphuncle lies close to the venter. While a little anomalous in form, *Winnipegoceras* seems a more likely generic resting place for this species than any other.

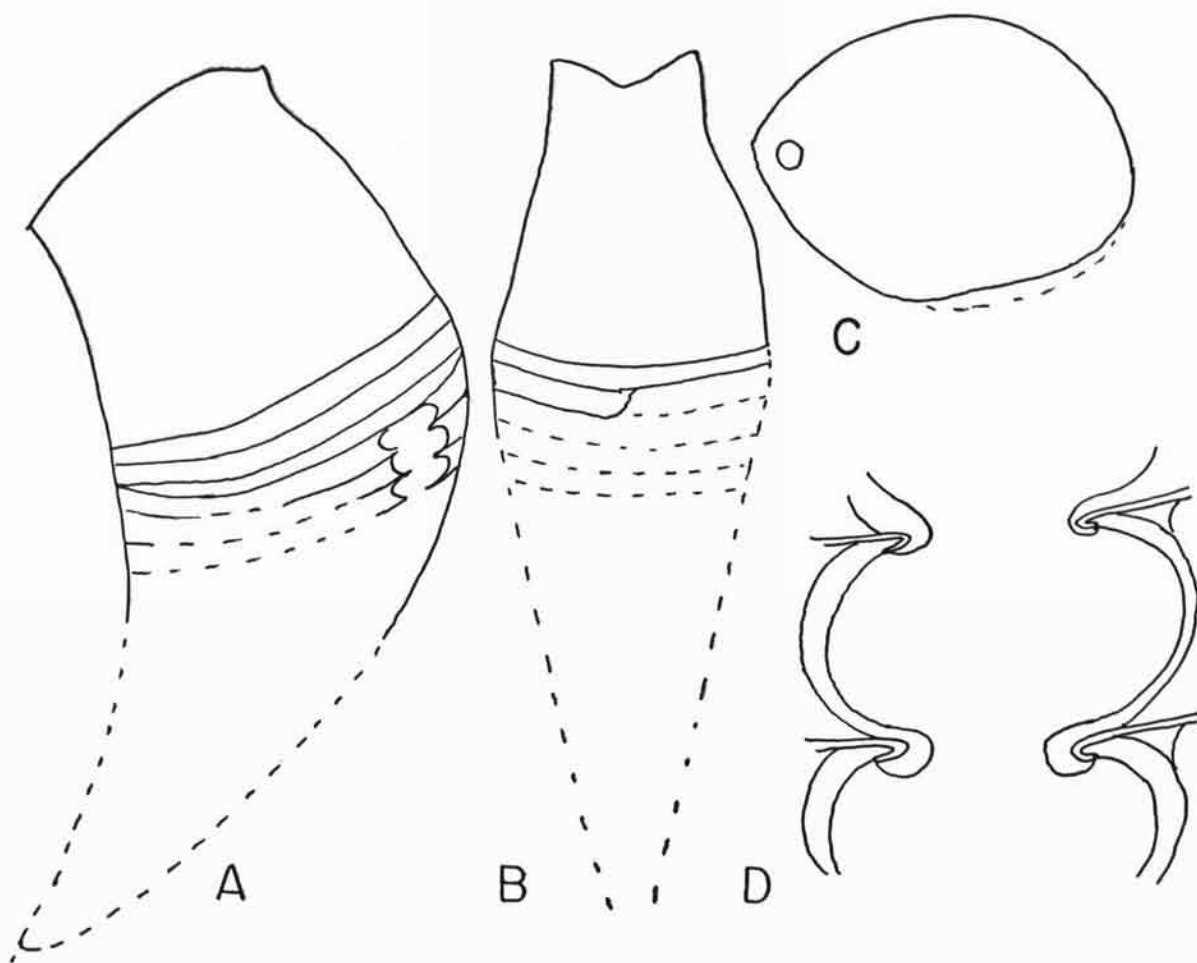
The species is from the middle of the Whitewood dolomite (Ordovician) of South Dakota.

Genus SINCLAIROCERAS Flower, 1952

Type species—*Sinclairoceras haha* FLOWER

Sinclairoceras FLOWER, 1952, Jour. Paleont., v. 26, p. 47.

Shell a compressed exogastric brevicone with venter narrowly and dorsum broadly rounded in cross section. Dorsum slightly concave, flaring slightly at aperture. Venter convex, only slightly so in early part, diverging rapidly from dorsum, becoming very strongly humped just before base of mature living chamber, then nearly straight and approaching dorsum. Sides converge to aperture from a point apical of base of living chamber. Main part of aperture slopes slightly forward from dorsum to venter but is modified by a hyponomic sinus. Sutures are transverse in adoral part of shell and show shallow lateral lobes. Siphuncle close to venter, with segments (known only in adoral parts of phragmocone) broad, broadly expanded, and broadly rounded in out-

FIGURE 24. *Sinclairoceras haha* Flower

A, Lateral view, adoral part complete, middle shown in section, apex restored; $\times 1$.—B, Ventral view, apex restored; the oblique view is responsible for the apparent anterior lobes of the sutures; $\times 1$.—C, Septal view, outline partially restored; $\times 1$.—D, Siphuncle, vertical section; \times .

line. Apical end of ring broadly adnate ventrally but not dorsally. Recrystallization has obscured details of the rings, but it is noteworthy that bullettes are very poorly developed in this form.

Sinclairoceras is presently known only from the Simard limestone, early Middle Ordovician of Quebec.

Discussion. *Sinclairoceras* is still known only from the holotype of *S. haha*. The shape of the shell indicates that the genus is a member of the Westoniceratidae. It differs from *Westoniceras* in being shorter, the apical end less slender and humping of the anterior part less marked. Lateral lobes of the sutures are shallow and no prominent ventral saddle is developed in the anterior end as in *Westoniceras*. The siphuncle, known only from a few anterior segments, is filled with coarse inorganic calcite, so that original structures are rather poorly shown. The thick rings, as well as the short very broadly expanded segments, are discosorid features but anomalously there is no evidence of swollen bullettes. Absence of parietal deposits is not significant, for they are never present in anterior segments of the siphuncle, but other genera of

the Westoniceratidae show well-developed bullettes there. Replacement is a possible explanation but bullettes are generally quite persistent structures, even where alteration of other parts is advanced. That the genus may be an oncoceroid is possible but unlikely. No Ordovician Oncoceratidae are known to approach this genus in proportions or to possess such short broad and broadly rounded siphuncle segments.

MILLER, YOUNGQUIST & COLLINSON (1954) suggest that *Sinclairoceras* may be related to, and may even be a synonym of *Westonocoeras*. A relationship is probably but in view of internal as well as external differences, synonymy is not. In the same work, *Westoniceras* is so broadly interpreted as to include a number of oncoceroids quite unlike *Westoniceras* in internal structure.

Sinclairoceras haha Flower

Pl. 15, fig. 1; text-fig. 24

Sinclairoceras haha FLOWER, 1952, Jour. Paleont., v. 26, p. 48, pl. 9, fig. 14-16, text-fig. 1.

No new information is available concerning this species and it is unnecessary to repeat the description. One correction should be

made, namely that the text figure accompanying the original description is natural size, and not reduced to 0.7. The siphuncle is refigured here, its features having been discussed in connection with the genus.

The holotype and only known specimen, in the collection of the writer, is from bed 4 (SINCLAIR, 1953) of the Simard limestone (Ordovician) from a quarry at the edge of Ste. Anne de Chicoutimi, Quebec.

Genus SIMARDOCERAS Flower, n. gen.

Type species—*Simardoceras simardense* FLOWER, n. sp.

Shell an exogastric cyrtococone, moderately expanding, venter almost uniformly convex in profile, curvature slightly increasing over anterior part of phragmocone and decreasing over the anterior part of the living chamber. Dorsal profile concave apically, becoming straight and then very slightly convex over anterior part of phragmocone and base of living chamber and faintly concave near aperture. Cross section notable in being wider than high in late growth stages, dorsum more flattened and venter more rounded. Sutures not observed except in natural section, obviously sloping forward on venter in late growth stages and probably with lateral lobes very poorly developed, if at all.

Siphuncle ventral, with subquadrate segments, longer than broad, with thick connecting rings and faint annular expansion in apical segments over septal foramen, which may possibly be a thickening of the ring alone without parietal deposits.

Discussion. This genus is erected for a remarkable species which in aspect resembles a rather large *Oncoceras* but which is peculiarly different from that genus in its broad cross section and evident discosorid organization of the siphuncle. The genus may well be related to *Winnipegoceras*, which it resembles rather closely in form of siphuncle segments. The living chamber is somewhat produced at the aperture, though the extent of this production, not clearly shown, is evidently slight. While it thus approaches some species of *Winnipegoceras* with short living chambers in vertical profile, it differs from all of them in its very broad cross section, which, with slender siphuncle segments, distinguish it from the associated *Sinclairoceras*, where also the aperture is more contracted.

As noted in discussion of phylogeny, *Sinclairoceras*, *Simardoceras* and *Reedsoceras* are anomalous in that their presence in beds of Black River age suggests more than

one evolutionary explanation of the *Westonoceratidae*. The associated *Teichertoceras* is a logical beginning of the family, giving rise to *Westonoceras* and then other genera. *Sinclairoceras*, *Simardoceras*, and *Reedsoceras* precede *Westonoceras* in appearance, however, and incomplete evidence suggests a possible origin of *Fabero-ceras* in these genera, rather than in *Westonoceras*. Yet the internal structures show affinities of *Fabero-ceras* with *Westonoceras*, rather than with any of these three Black River genera. Information concerning internal structure of all three genera is so scant, however, as to be inconclusive and clarification of the problem must await study of better material than is now available.

Simardoceras simardense Flower, n. sp.

Pl. 9, fig. 4, 5; text-fig. 25A,B

Moderate-sized exogastric brevicone of oncoceroid aspect, distinctive in its broad cross section and showing discosorid affinities by structure of its rather broad siphuncle segments. Cross section apparently depressed throughout, with dorsum more flattened than venter. Shell expands from a height of 12 mm. at the base to 35 mm. at adapical end of living chamber. Dorsum with basal radius of curvature of 40 mm., then becoming straight over the anterior half of phragmocone, faintly convex over base of living chamber, and faintly concave, nearly straight near the aperture. Ventral profile only very slightly convex basally, with radius of curvature about 100 mm., a condition which persists over the basal 40 mm. of the type, in which height increases from 12 to 25 mm. Curvature of the venter increases, radius decreasing to 60 mm. over the anterior gibbous part of the phragmocone, then becoming rapidly straighter and scarcely convex over the living chamber to the aperture.

The living chamber has a basal height of 40 mm. and decreases to 32 mm. at the aperture. The dorsal length is 32 mm. and ventral length 41 mm. owing to greater convexity of the ventral profile. Features of the aperture have not been observed. Sutures straight as far as observed and in adoral part of the phragmocone tending to slope forward on the venter. In vertical profile the septa are exceedingly shallow in curvature. The adoral camerae, of which six can be clearly observed, average 4 mm. in length on the ventral side. The siphuncle is close to the venter. A segment 4 mm. long expands from 2 mm. at the septal foramen to a width of 4 mm. Septal necks, made out only with difficulty, are only slightly recurved on the ventral side and recumbent on the dorsal side. They are surrounded by small annular deposits. Connecting ring broadly adnate to septum on the dorsum adorally and on the venter adapically, free part of the connecting ring remarkably thickened. Aside from small annuli, no organic deposits have been observed within the siphuncle. Surface features of the shell are not displayed.

EXPLANATION OF PLATE 27

LOWOCERATIDAE—*Tuyloceras*, *Lowoceras*; DISCOSORIDAE—*Discosorus*

FIGURE

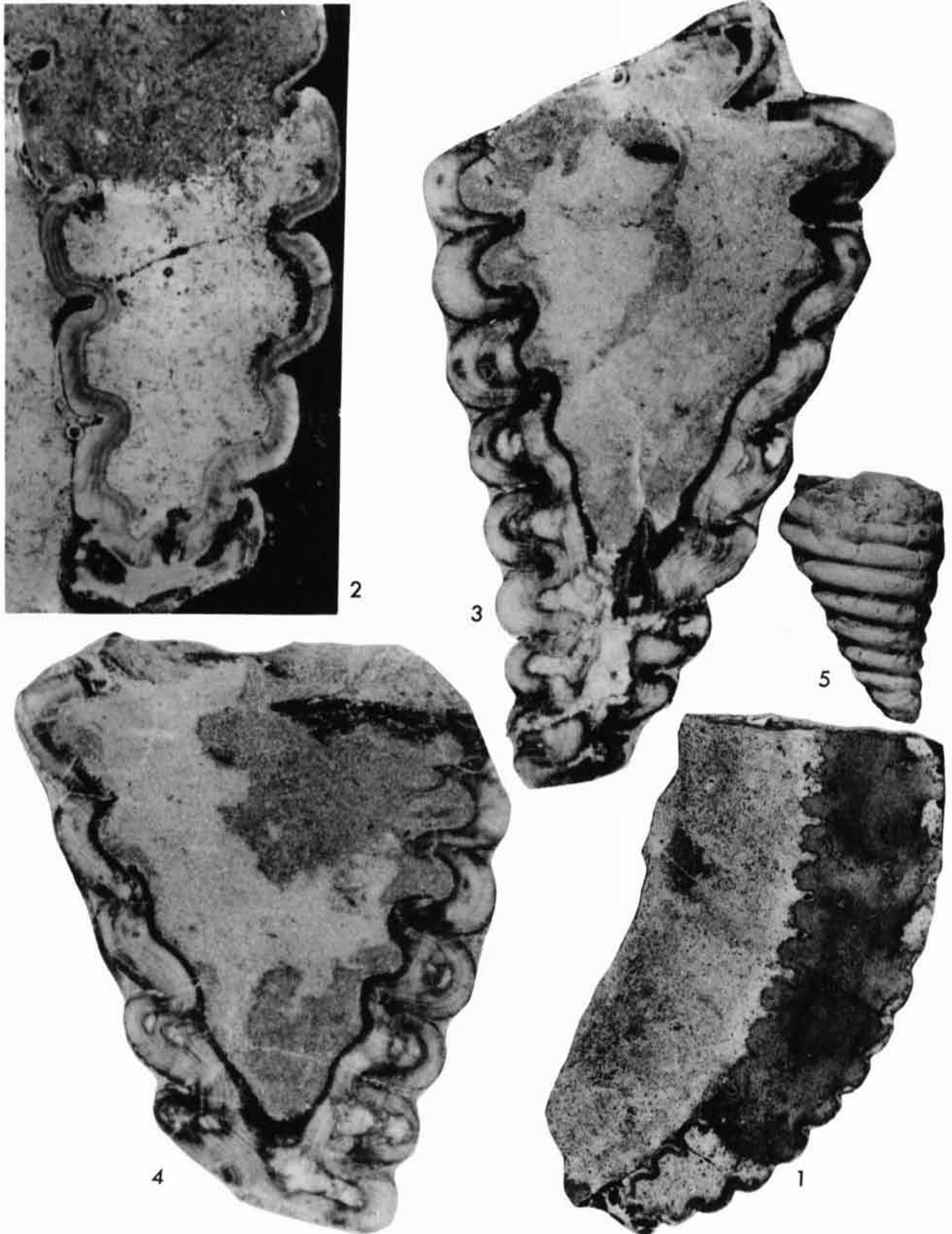
1,2,6,8. *Tuyloceras percurvatum* FOERSTE & SAVAGE, holotype, from Ekwon limestone (Silurian), Ekwon River, Hudson Bay; Univ. Illinois, Savage collection, no 4OHB.—1, Lateral view of adapical portion with part of venter ground away to give vertical section through siphuncle, $\times 1.5$.—2, Siphuncle from apical portion, $\times 4.6$.—6, Lateral view of shell, venter at left, $\times 1$.—8, Ventral view, $\times 1$. (See Pl. 28, fig. 1,2.)

3,7. *Discosorus* sp. cf. *D. ehlersi* FOERSTE, specimens from Thornloe

limestone (Middle Silurian), Lake Timiskaming; Canada Geol. Survey collection.—3, Ventral view, $\times 1$.—7, Lateral view of silicified siphuncle etched from matrix, venter at right, showing typical form and tiny (apparently initial) expanded segment, $\times 1$.

4-5. *Tuyloceras southamptonense* FOERSTE & SAVAGE, holotype, $\times 1$, Silurian, Southampton Island, Canada Geol. Survey no. 7846.—4, Vertical section, venter on left, showing endocones, without bullettes.—5, Opposite side, showing exterior of siphuncle.





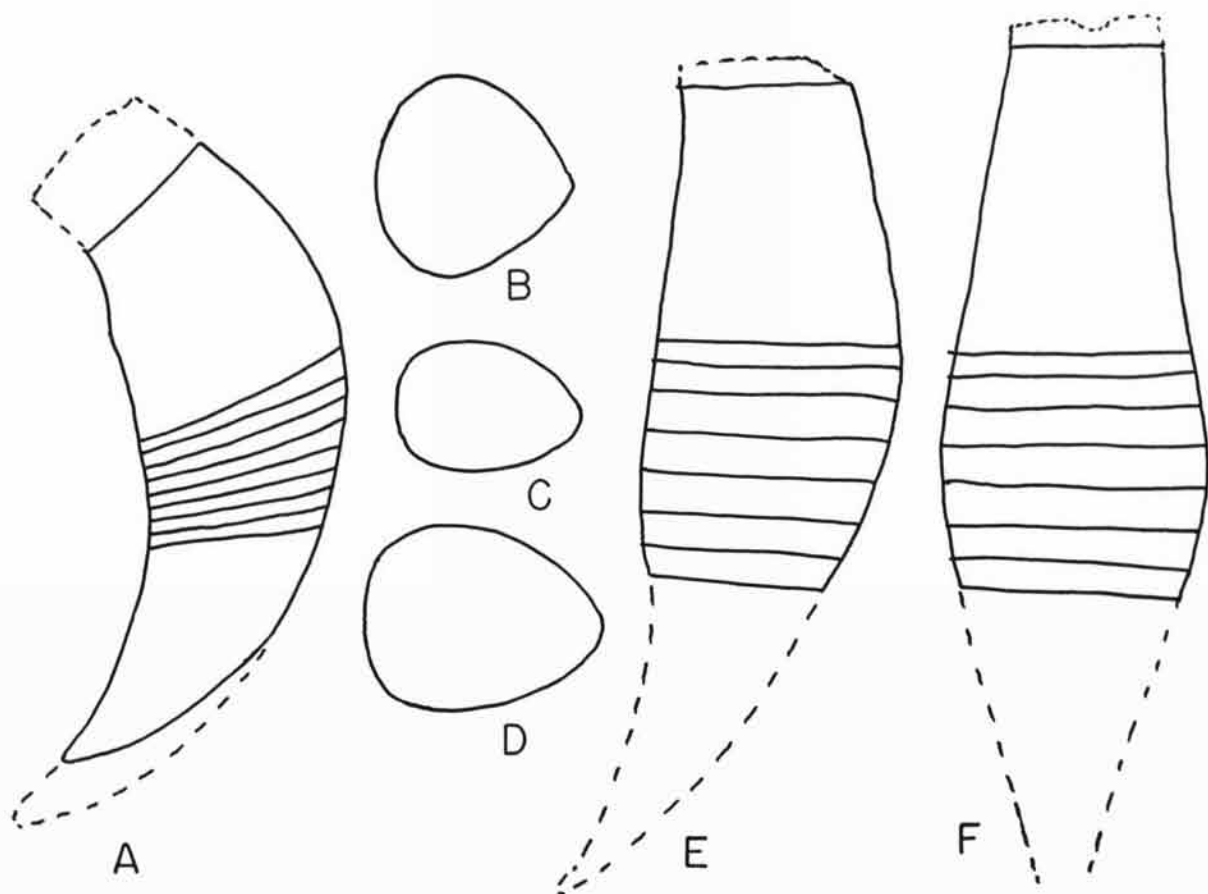


FIGURE 25. General features of *Simardoceras* and *Lavaloceras*.

A, B, Simardoceras simardense; *A*, lateral view, apex and aperture restored; *B*, cross section of shell near aperture, venter at left.—*C-F, Lavaloceras cartierense*; *C*, cross section near aperture; *D*, cross section at gibbous portion; *E*, lateral view, venter at right; *F*, ventral view; in *E* and *F* aperture and apex are restored. All approximately $\times 0.75$.

Discussion. This species is based on a single remarkable specimen from the Simard limestone of Chicoutimi, Quebec. As with other cephalopods of that association, internal structures are well displayed but it has proved almost impossible to observe the surface. Extraction of the surface of the living chamber proved unsuccessful, but a cross section near the adoral end supplied needed information as to cross section. The greater part of the phragmocone is filled with friable calcite, making its extraction impossible. A series of sections was taken, one of which displayed beautifully preserved segments of the siphuncle. The specimen as illustrated is a natural weathered section, essentially vertical. The true vertical plane, however, extends down beneath the

exposed surface on the ventral side; actually, therefore, slightly more than half of the specimen is preserved.

The type proved almost impossible to remove from the matrix. A portion of the living chamber is preserved but it shows no unusual features. It should be noted that the type, as figured, is cut across the adoral end. These sections show that the shell continued somewhat farther adorally, but its exact extent, though evidently not more than 10 mm., cannot be determined with any accuracy.

As noted under the generic discussion, this is a shell of oncoceroid aspect, peculiar in the breadth of cross section and the siphuncle shows the thick ring of Ordovician discosorids. Affinities

EXPLANATION OF PLATE 28

LOWOCERATIDAE—*Tuyloceras*; DISCOSORIDAE—*Discosorus*

FIGURE

1,2. *Tuyloceras percurvatum* FOERSTE & SAVAGE, from Ekwon limestone (Silurian), Ekwon River, Hudson Bay; Univ. Illinois, Savage collection, no. 40HB.—1, Vertical section through anterior part of phragmocone showing initial rapid expansion, and later nearly uniform portion of siphuncle segments; endocones present in basal portion, $\times 1$.—2, Basal portion of same section showing outline of siphuncle segments, endocones, and hump at aperture of central canal, septal necks

mainly removed by solution, $\times 3$. (Same specimen as illustrated on Pl. 27, fig. 1,2,6,8.)

3-5. *Discosorus conoideus* HALL, from lower Clinton shales (Middle Silurian) near Walcott, N.Y.; collection of the writer.—3,4, Opposite sides of section showing form of segments, traces of septal necks, endocones (lamellar structure visible), hump, and endotube, $\times 3$.—5, Exterior of same specimen prior to sectioning, $\times 1$. (See Pl. 29, fig. 2.)

with *Winnipegoceras* are suggested, but it differs from all members of that genus, which it approaches only remotely in form, by the extreme breadth of cross section.

Holotype. Collection of the writer.

Occurrence. From the Simard limestone (Ordovician), of Ste. Anne de Chicoutimi, Quebec. The exact horizon is not certain but it is somewhere in beds 4 to 6 of SINCLAIR (1953), probably in bed 4.

Genus LAVALOCERAS Flower, 1952

Type species—*Lavaloceras geniculatum* FLOWER

Lavaloceras FLOWER, 1952, Jour. Paleont., v. 26, p. 52.

The genus *Lavaloceras* was erected for brevicones, exogastric but nearly straight, dorsal profile slightly convex basally, nearly straight adorally, venter with early part not definitely known, but probably more convex apically than the dorsum, becoming strongly curved, geniculate in profile over anterior part of the phragmocone, essentially straight from there to the aperture, and approaching the dorsum quite rapidly. Sutures are straight and transverse. Siphuncle ventral, its structure still not known save that segments apparently expand rather strongly within the camerae. Cross section broadly rounded dorsally, more narrowly rounded ventrally. Proportions vary, but the section tends to be broader than in most Ordovician brevicones and may be slightly wider than high.

Discussion. The simple sutures and broad cross section set this genus apart from both *Winnipegoceras* and *Westonoceras*. Species of both genera, however, approach *Lavaloceras* in one feature or another to such an extent as to suggest intergradation and a real relationship rather than homeomorphy. Regrettably, the upper Trentonian of Quebec, which has yielded all of the species definitely assigned to the genus, is notorious for poor preservation of cephalopod interiors and no specimen of *Lavaloceras* from there has as yet yielded a good siphuncle. The position of the genus as a member of the Discosorida or of the Oncoceratida is therefore open to question and cannot be settled until better material can be studied. However, the fact that associated species of *Westonoceras* (notably *W. sinclairi* and *W. diestoceroides*) approach *Lavaloceras* in aspect and a similar

though less marked resemblance is found to species assigned to *Winnipegoceras*, suggest a close relationship among all three of these genera. That this may be false, however, is shown by apparent similarities between *Landeroceras* and *Diestoceras* and the ease with which oncoceroids can be confused with *Westonoceras* and *Winnipegoceras*. The species in question are as similar in form to known oncoceroids as to the discosorids with which they have been classed, but no oncoceroid species or genera are known to approach species of *Lavaloceras* at all closely in either form or size.

Lavaloceras geniculatum Flower

Lavaloceras geniculatum FLOWER, 1952, Jour. Paleont., v. 26, p. 52, pl. 10, fig. 3, 4.

Terrebonne limestone, upper Trenton, Ordovician, Quebec.

Lavaloceras cartierense Flower, n. sp.

Pl. 4, fig. 8, 9; text-fig. 25C-F

The type and only known specimen consists of a living chamber and six adoral camerae. The shell is worn on one lateral surface and may have been flattened laterally by pressure. The cross section is slightly higher than wide, a condition which may not have been natural. The dorsal half of the specimen is essentially semicircular in cross section, unusually broad, with venter more narrowly rounded and slight ventrolateral flattening. Dorsal profile very slightly concave adorally, nearly straight, and slightly convex at extreme apical end of the type. Venter slightly convex basally, suggesting slight geniculation over the anterior part of the phragmocone, slightly convex but nearly straight over the anterior few camerae and entire length of the living chamber.

The basal two camerae are incomplete ventrally. What remains suggests that they lie at the anterior end of a fairly rapidly expanding part of a nearly straight but faintly exogastric shell. Together they have a length of 10 mm. dorsally. Beyond them the shell is 44 mm. high and 42 mm. wide, increasing to 44 and 46 mm. in 10 mm., and then gently contracting to a width of 30 mm. and height of 35 mm. at the aperture, 50 mm. dorsally and 60 mm. ventrally. The living chamber has a basal width of 40 mm. and height of 44 mm., a dorsal length of 40 mm. and ventral length of 50 mm.

The six camerae, of which the last is only slightly shorter than the penultimate one, have sutures which are perfectly straight and transverse. The internal mold of the phragmocone shows faint longitudinal markings, as in *Westonoceras*.

The siphuncle is all but unknown. A faint indication of the septal foramen is found close to the venter. A section through

EXPLANATION OF PLATE 29

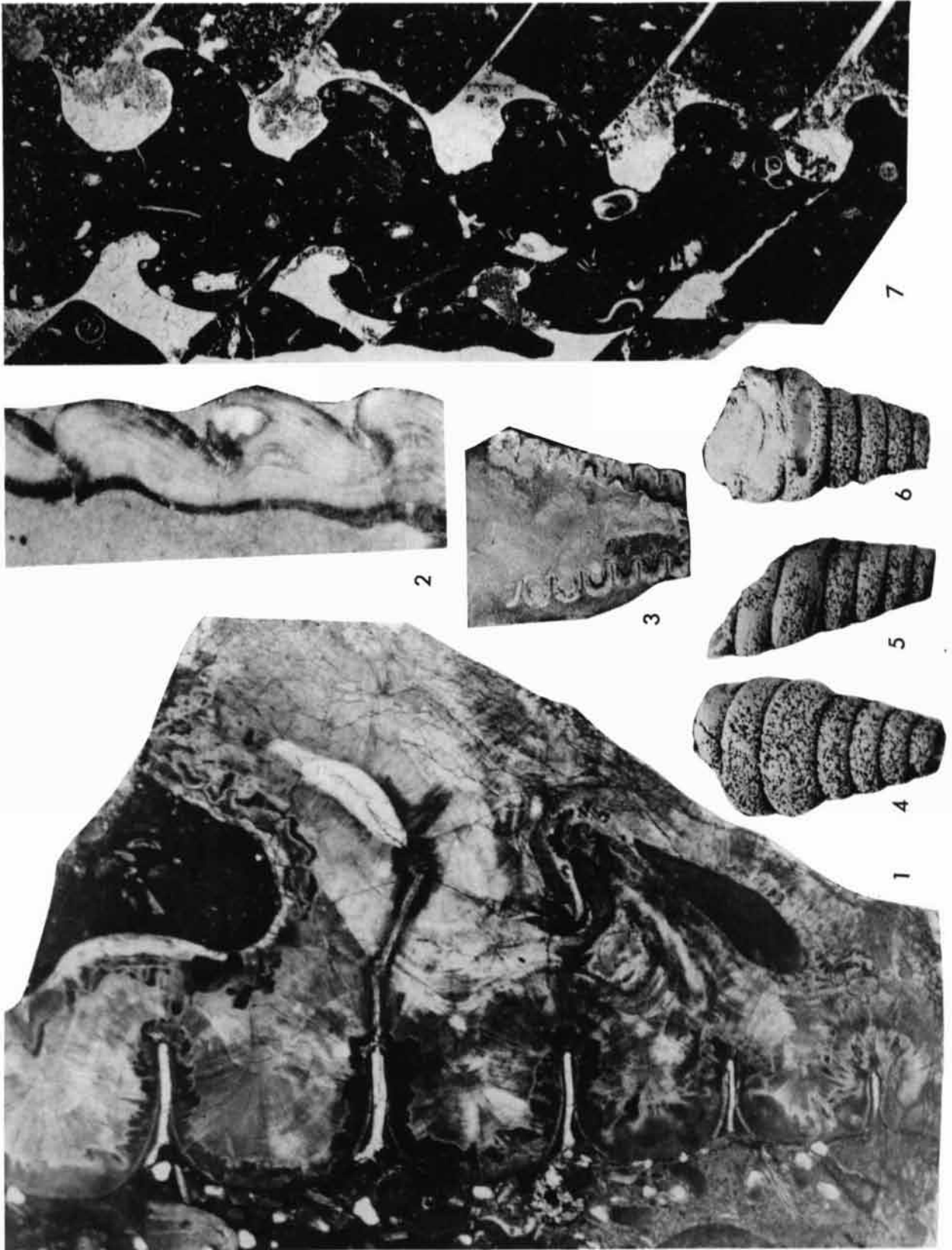
DISCOSORIDAE—*Discosorus*; CYRTOGOMPHOCERATIDAE—*Kiaeroceras*

FIGURE

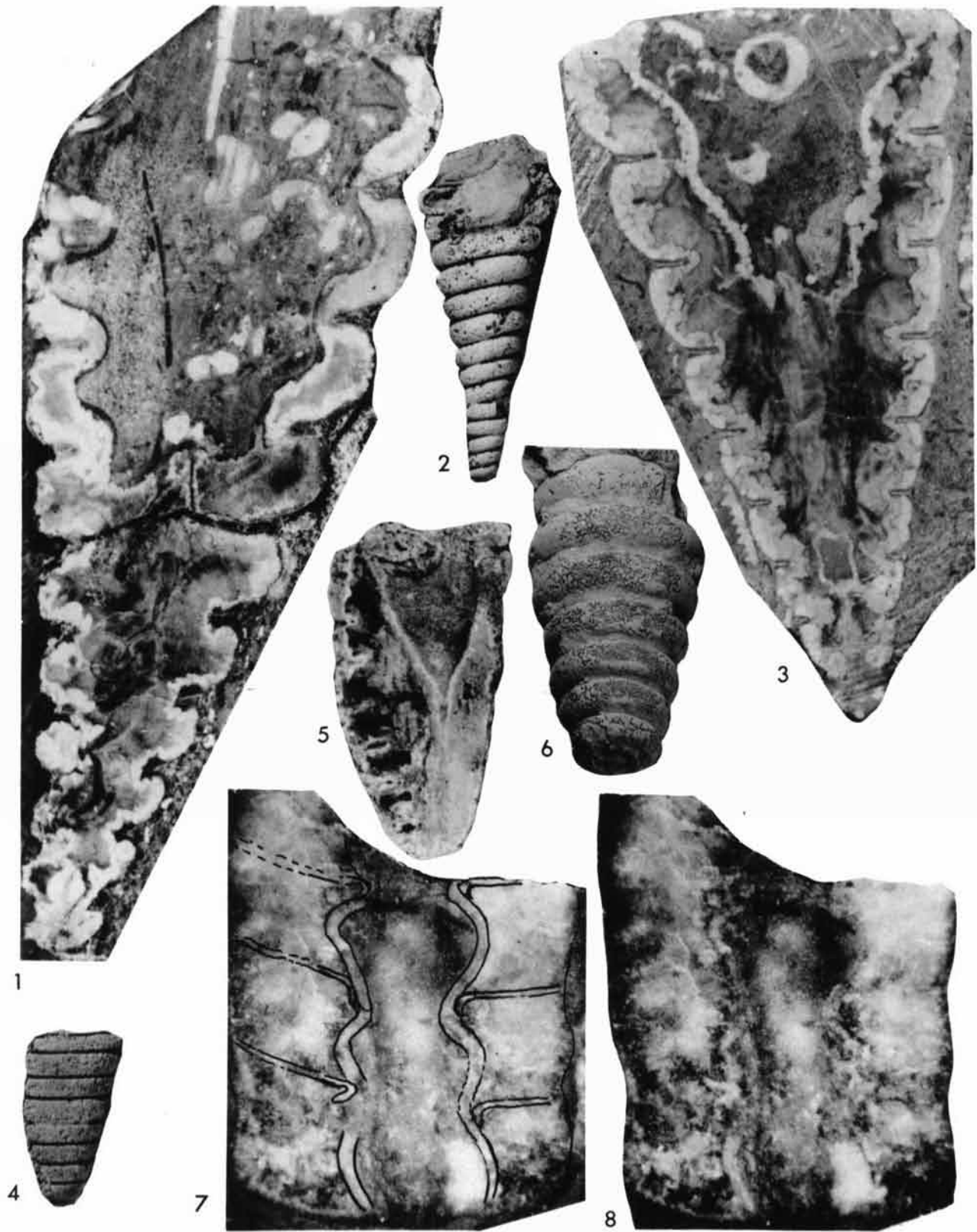
1. *Discosorus* sp., specimen from Thornloe limestone (Middle Silurian), Lake Timiskaming; collection of the writer. Thin section (off center and thus missing central tube) showing recumbent necks, thin rings, and texture of endocones, $\times 7.5$.
2. *Discosorus conoideus* HALL, from lower Clinton shales (Middle Silurian) near Wolcott, N.Y.; collection of the writer. Enlargement of part of siphuncle wall retouched slightly to show short strongly recurved septal necks, enlarged, $\times 5$. (See Pl. 28, fig. 3-5).
3. *Discosorus* sp., from Thornloe limestone (Middle Silurian), Lake Timiskaming; Canada Geol. Survey collection. Longitudinal, horizontal section, showing anterior end of deep anterior conical cavity bounded by endocones, $\times 1$.
- 4-6. *Discosorus* sp. cf. *D. humei* FOERSTE, from Thornloe limestone

(Middle Silurian), Lake Timiskaming; Canada Geol. Survey collection. An isolated siphuncle with the rapid expansion typical of *Discosorus*, but with flattening of expanded parts of segments approaching the condition of typical *Endodiscosorus*, $\times 1$.—4, Ventral view.—5, Lateral view, venter on left.—6, Dorsal view.

7. *Kiaeroceras frognoeyense* STRAND, from Lyckholm formation (bed F) (Ordovician), Piersal, Estonia; Univ. Oslo, Paleont. Mus., no. 12149, photograph courtesy of Dr. TRYGVE STRAND. Vertical section through siphuncle, venter at left, showing well-developed bulleets, their contact with septal necks being largely but not completely obscured by recrystallization, and thick connecting ring which has grown outward into the cameral space, particularly on the ventral side, $\times 6.5$.



FLOWER & TEICHERT—Order Discosorida (Cephalopoda)



the specimen shows that not only the siphuncle but most of the septa have been destroyed.

Holotype. Collection of the writer.

Occurrence. Ordovician, Upper Trenton (Terrebonne or Tetreauville beds), from dam of Jacques Cartier River, Quebec.

Lavaloceras? *perplexum* Flower, n. sp.

Westonoceras? sp. FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 54, pl. 18, fig. 1A, B.

A large exogastric brevicone, fusiform in vertical outline, and gently contracting over not only the living chamber, but also over an appreciable length of the phragmocone, including most of the extant portion. Greatest shell width is attained considerably later on the phragmocone, beyond which the shell tapers, contracting gently to the aperture. Sutures straight on the dorsal surface, but sloping adapically as they approach the venter, a condition which is marked in early stages of the type but decreases adorally. The ventral surface is worn, which evidently increases the apparent obliquity of the sutures; they are truly oblique apically but may have been transverse or very nearly so adorally. Structure of the siphuncle unknown but it is located at some distance from the venter and originally may have been about half way between the venter and center of the shell.

The holotype is a crushed internal mold which in its present condition is considerably wider than high. Though the shell was evidently relatively broad in cross section, it is not evident to what extent crushing has distorted the original condition, though some distortion surely has occurred.

Discussion. FOERSTE & SAVAGE figured this form without proposing a specific name for it. Since it is quite as well known as other species which have been named, a specific name is here proposed, largely to remove it from the large number of figured unnamed forms which call for discussion. FOERSTE & SAVAGE placed this species in *Westonoceras*, largely because there seemed to be no better resting place for it, though they were fully aware that it showed a number of atypical features such as the apparently broad cross section, absence of lateral lobes, and sutures which are straight and transverse over the dorsum, probably essentially transverse in the adoral part of the phragmocone but sloping forward on the dorsum in the early part. Such obliquity can be increased by distortion and this may well apply to the holotype of this species. Subsequently the genus *Lavaloceras* was described and this species seems to be typical of it in the several features by which it is distinguished from true *Westonoceras*.

Sutures which slope forward in the early part of the phragmocone and a similar broad cross section are unknown in *Lavaloceras*, but both of these features, displayed by the holotype, are those to which vertical crushing of the shell has certainly contributed in part at least, and they could be completely due to such distortion.

The holotype is no. 25 HB in the Savage collection, now in the collection of the Illinois Geological Survey, Urbana. It is from horizon 4 of the Nelson limestone, of the Nelson River on the west side of Hudson Bay.

Genus REEDSOCERAS Foerste, 1929

Type species—*Cyrtoceras macrostomum* HALL, 1847

Conradoceras FOERSTE, 1928, Denison Univ. Bull., Sci., Lab., Jour., v. 23, p. 208.

Reedsoceras FOERSTE, 1929, Same, v. 24, p. 233-4.

FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 438.

FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 612.

Reedsoceras comprises large exogastric cyrtocoones, fairly rapidly expanding to the aperture. Sutures straight and transverse, lacking lateral lobes and the tendency to slope forward on the venter so notable in *Faberocheras*. Siphuncle ventral, partially exposed on the holotype of *R. macrostomum*. Segments of siphuncle extremely short, broad, broadly rounded within the camerae, though their rounding is less marked and outline more quadrate in the earlier portion. Nothing is known of details of structure of the siphuncle wall.

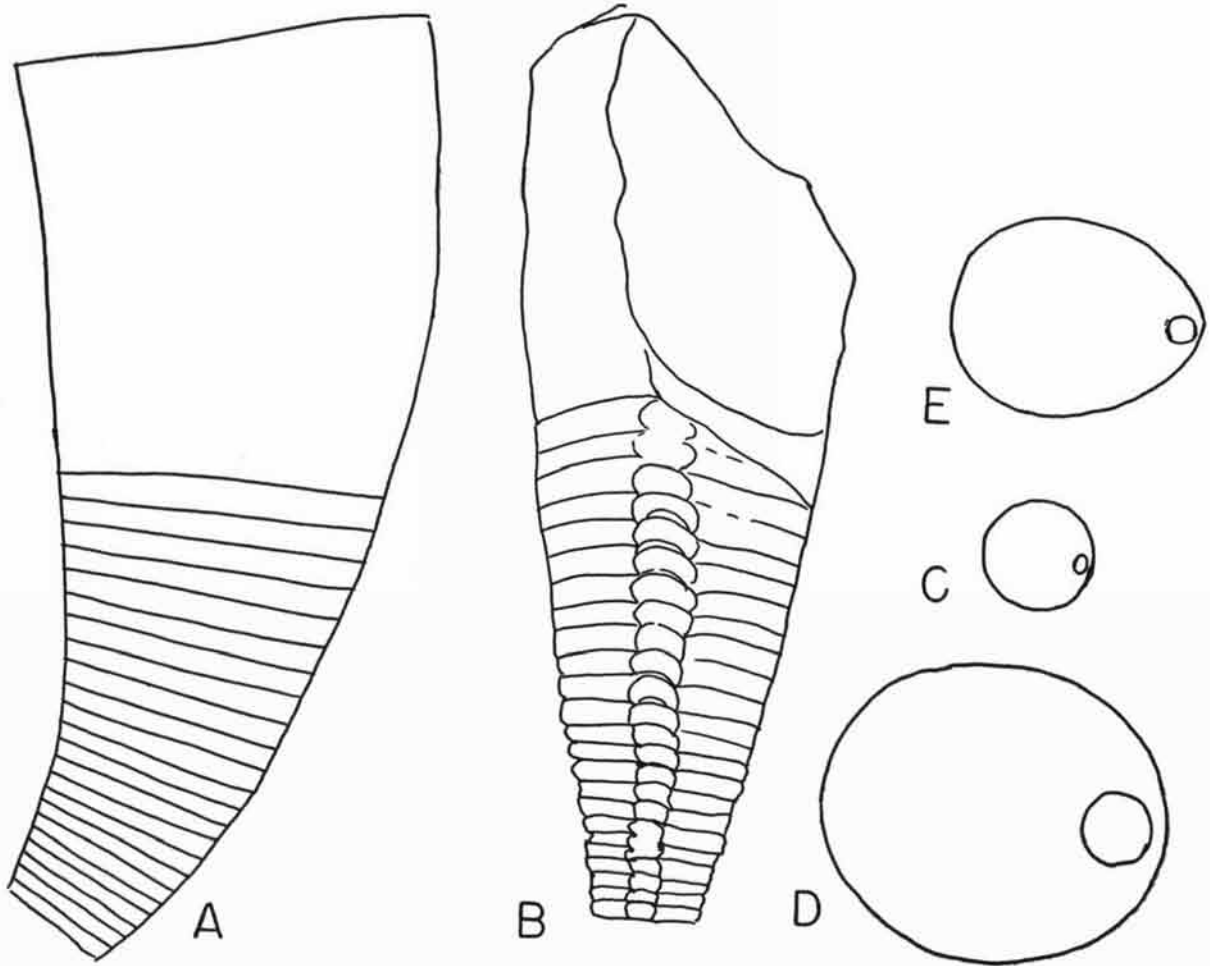
Discussion. In the absence of information concerning the siphuncle other than general shape of the segments, this genus must remain of uncertain affinities. Its present assignment to the *Westonoceratidae* rests upon its large size and short wide siphuncle segments, broadly expanded in the camerae, features which are not known in typical Ordovician *Oncoceratidae*. Further, the known features of this genus are very like those of *Faberocheras*, the Trenton species of which are essentially smooth shells, with a ventral siphuncle. *Reedsoceras* differs in gross features mainly in its somewhat longer living chamber, very shallow camerae with sutures perfectly straight and transverse instead of oblique and sloping forward on the venter. In *R. macrostomum* the venter is as broadly rounded as the

EXPLANATION OF PLATE 30

DISCOSORIDAE—*Stokesoceras*, *Discosorus*; *Endodiscosorus*; APOCRINOCERATIDAE (ELLESROCERATIDA — *Glenisteroceras*

FIGURE

- Stokesoceras* sp. Vertical section showing interior of early stage, possibly retaining initial segment of siphuncle, with recumbent brims at anterior end of dorsal side (at left), short free necks on venter (lower right), $\times 5$. The tube is zigzag and shows traces of small accessory lateral tubes. Thornloe limestone (Middle Silurian), Lake Timiskaming; Canada Geol. Survey collection.
- Discosorus* sp. or *Stokesoceras* sp., from Thornloe limestone (Middle Silurian), Lake Timiskaming; Canada Geol. Survey collection. Siphuncle showing proportions of *Stokesoceras* in the early stage and of *Discosorus* (of the type of *D. halli*) in later stages, $\times 1$.
- Stokesoceras* sp., from Thornloe limestone (Middle Silurian), Lake Timiskaming; Canada Geol. Survey collection. Longitudinal horizontal section through early portion of siphuncle showing long recumbent brims. The section intersects the central tube obliquely in the lower part, $\times 3.5$.
- Endodiscosorus foerstei* TEICHERT, holotype, from Thornloe limestone (Middle Silurian), probably Lake Timiskaming; Canada Geol. Survey collection.—4, Exterior lateral view, venter at right, $\times 1$.—5, Opposite side showing natural weathered section, exhibiting cone and short strongly invaginated necks, $\times 2$.
- Discosorus humei* FOERSTE, from Thornloe limestone (Middle Silurian), Lake Timiskaming; Canada Geol. Survey collection. Ventral view of late portion of siphuncle showing marked contraction of last segment, $\times 1$.
- Glenisteroceras obscurum* FLOWER, holotype, from Ft. Cassin beds (Canadian), on shore of Lake Champlain at Valcour, N.Y.; collection of the writer.—7, Longitudinal section, probably oblique to vertical axis of shell, with outlines of septa and connecting rings strongly retouched, $\times 12$.—8, Same unretouched.

FIGURE 26. General features of *Reedsoceras*.

A-D, *Reedsoceras macrostomum* (HALL); A, lateral view, venter at right; B, ventral view, showing siphuncle segments exposed, with rounding of basal camerae suggestive of impressions of cameral deposits; upper right side incomplete; C, cross

section at base, venter at right; D, cross section at base of living chamber, venter at right.—E, *Reedsoceras mcfarlani* FLOWER, cross section showing narrowly rounded venter. (All figures about $\times 1$; A-D redrawn from FOERSTE, 1928.)

dorsum, but *R. mcfarlani* has a more narrowly rounded venter and thus approaches *Faberoceras* in this feature. As noted in discussion of phylogeny, it is possible that *Faberoceras* is a descendant of *Reedsoceras*. General features of the genus are shown in Figure 26.

Reedsoceras macrostomum (Hall)

Text-fig. 26A-D

Cyrtoceras marginalis CONRAD, 1843 (non PHILLIPS, 1841), Acad. Nat. Sci. Philadelphia, Proc., v. 1, 1843, p. 334.

EMMONS, 1855, American Geology, v. 1, pt. 2, p. 147, fig. 30.
Cyrtoceras macrostomum HALL, 1847, Paleont. New York, v. 1, p. 194 partim, (non pl. 1, 3).

Conradoceras macrostomum FOERSTE, 1928, Denison Univ. Bull., Sci. Lab., Jour., v. 23, p. 208, pl. 44, fig. 1A-C.

Reedsoceras macrostomum FOERSTE, 1929, Same, v. 24, p. 233.

This species seems to be properly confined to the Platteville limestone, and is apparently known only from the holotype (Am. Mus. Nat. Hist. no. 822-3). The type is a dolomite internal mold displaying the ventral side of the siphuncle and showing the form of its segments. It is doubtful whether sectioning would supply

much information concerning details of the structure. HALL (1847) gave the species its present name, that published by CONRAD being preoccupied, and he assigned to the species several specimens from the Trenton limestone of New York. FOERSTE (1928) removed two of these specimens, describing them as *Manitoulinoceras middlevillense* and *Cyrtorizoceras* sp., but the largest one, which resembles *Reedsoceras macrostomum* most closely, seems to have escaped restudy. This specimen I have been unable to locate. Judging from the illustration, it may be a *Reedsoceras* but is almost certainly not conspecific with the holotype. It is not altogether clear from HALL's description whether the specimen in question (original of his Pl. 42, fig. 31b) is from the Platteville of Wisconsin or from the Trenton of Middleville, New York, both Ordovician.

Reedsoceras mcfarlani Flower

Text-fig. 26E

Reedsoceras mcfarlani FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 484, pl. 16, fig. 4-6.

This species, based upon a specimen found in old collections of the Cincinnati Society of Natural History, apparently from the

Cynthiana limestone, has the rapid expansion and close straight septa which place it in *Reedsoceras* rather than *Faberocheras*. The siphuncle is not visible externally and preservation is such that its presence in the interior is most unlikely. Therefore the species contributes little to knowledge of the genus other than an extension of record of its stratigraphic and geographic range. The unique holotype is in the University of Cincinnati Museum.

Genus FABEROCERAS Flower, 1946

Type species—*Faberocheras multicinctum* FLOWER

Faberocheras FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 447.
FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 612.

Faberocheras consists of exogastric cyrtocoines, rather slender, gently enlarging to the aperture, compressed in cross section, venter normally more narrowly rounded than dorsum. Sutures have lateral lobes only faintly developed and tend to slope forward on the venter, slope generally increasing as growth progresses. Siphuncle has thick rings, the structure of which has been discussed at length in Part I of this work. Within the siphuncle are parietal deposits, discrete and segmental in some species, particularly in older ones regarded as more primitive, but in others the deposits extend through a series of segments forming endocoines. The siphuncle segments vary in position; in primitive forms they are close to the venter throughout life; in others, they tend to migrate toward the center of the shell. This trend, occurring as it does in the younger species, is regarded as a specialization. Segments of the siphuncle vary from subquadrate in vertical section, somewhat reminiscent of *Westonoceras* generally in early stages, to those which are much more expanded and broadly rounded in outline. Siphuncle segments are not only highly variable in form from one species to another but show a very appreciable variation when traced through a series of camerae in one individual.

The shell surface is relatively smooth in older members of the genus but younger ones tend to develop transverse costae and may show marked expansions and contractions of the shell in late growth stages.

Discussion. As now delimited, *Faberocheras* is known largely from species of late Trenton and early Cincinnati age in the area of the Nashville and Cincinnati domes. The oldest known species are those of the Catheys limestone of Tennessee and equivalent Cynthiana limestone of Kentucky. The largest assemblage of species is found in the overlying Leipers beds of Maysville age. At Cincinnati one species (*F. magister*) is known in the Eden beds, and another (*F. elegans*) occurs in the Coryville. Outside of this region the genus is not known definitely. Some species from the Bala beds of England suggest *Faberocheras* but are inadequately known internally. Two species from the Lyckholm beds of Estonia are tentatively placed in *Faberocheras* because their known features are more similar to those of species of this genus than to any other. Even the position of the siphuncle is unknown in these forms and their assignment to any genus can only be tentative until they are better known.

The inclusion of species with parietal deposits and species with endocoines in *Faberocheras* seems anomalous in view of the different aspect of sections. However,

endocones are developed from parietal deposits and the species having these structures are evidently closely related; finer generic division would be impractical. The genus is portrayed on Plates 16-23, the illustrations being largely devoted to portrayal of internal structures which have been discussed in Part I of this paper. The genotype is refigured (Pl. 16, fig. 1, 2) and typically early forms with small ventral siphuncles of quadrate segments are shown (Pl. 19, fig. 4-6); *F. elegans* (Pl. 23) exhibits both the subcentral position of the siphuncle and its remarkably short broad segments. This is possibly the youngest species known and though apical parts of the shell showing parietal deposits or endocoines are wanting, the species is specialized in its extremely short and broad siphuncle segments.

The present material suggests that previous descriptions have not by any means exhausted the number of species present in the Leipers formation of southern Kentucky and Tennessee. However, most of the new material is rather fragmentary and only one new species is described from this association.

Faberocheras sonnenbergi Flower

Faberocheras sonnenbergi FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 455, pl. 13, fig. 4-5; pl. 15, fig. 3-4; pl. 16, fig. 7.

A small slender species known largely from portions of phragmocones which are not uncommon in the Cynthiana limestone. Sutures nearly transverse, little lobed. Siphuncle small and ventral, with subquadrate segments resembling those of *Westonoceras* rather more than do those in adult stage of any other species. Anomalously, this species also approaches close to the potentially ancestral *Reedsoceras* in simplicity of its sutures, though not agreeing with it in broad section or rapid expansion.

The species occurs in the Cynthiana limestone of central Kentucky and is known doubtfully from the Catheys limestone of Tennessee, both Middle Ordovician (late Trenton).

Faberocheras saffordi Flower

Compare Pl. 19, fig. 4, 5

Faberocheras saffordi FLOWER, 1946, Bull. Am. Paleont., v. 29, p. 459, pl. 8, fig. 2, 5; pl. 12, fig. 15, fig. 7, 8; text-fig. 21A.

Larger than *Faberocheras sonnenbergi*, rapidly expanding in young, relatively slender in adult. Siphuncle remains fairly close to venter throughout life, its segments subquadrate but relatively broad; large bullettes and thin parietal deposits have been observed. Sutures faintly lobed laterally, inclined slightly forward on venter.

The species is known from the Catheys limestone of Tennessee and Cynthiana limestone of Kentucky, Middle Ordovician (Trenton).

Faberocheras magister (Miller)

Cyrtoceras obscura MILLER, 1875, Cincinnati Quart. Jour. Sci., v. 2, p. 132, fig. 17.

Cyrtoceras magister MILLER, 1875, Same, v. 2, p. 284.
JAMES, 1886, Cincinnati Soc. Nat. Hist., Jour., v. 8, p. 246.
MILLER, 1889, North American Geol. Paleont., p. 434, fig. 729.

BASSLER, 1915, U. S. Natl. Mus., Bull. 92, v. 1, p. 354.
Faberocheras magister FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 461, pl. 13, fig. 3; pl. 14, fig. 5; text-fig. 21F.

This rare form apparently known only from the type, is a much larger shell than *Faberocheras sonnenbergi* and *F. saffordi*. Sutures fairly close-spaced, sloping markedly forward on venter, lateral lobes poorly developed. Siphuncle with short broad rounded segments in adult stage (young unknown), remaining close to

ventral wall of shell. The internal mold shows no trace of surface markings of the shell.

The species is from the Eden beds of Cincinnati, probably from the Economy member, though it is commonly listed as originating in the Southgate member; Upper Ordovician (Cincinnati).

Faberoceras percostatum Flower

Pl. 16, fig. 3-4; Pl. 17, fig. 2; Pl. 18, fig. 1

Faberoceras percostatum FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 463, pl. 8, fig. 4; pl. 11, fig. 3; pl. 13, fig. 2; pl. 14, fig. 9; text-fig. 1C.

A large species, rapidly expanding in young, slender in adult, with coarse prominent transverse markings which are accentuated into low rounded costae on living chamber, with one prominent deep constriction and many narrower shallower ones. Siphuncle remains ventral throughout life, its segments becoming rather broad and rounded; parietal deposits known but they remain thin.

The species occurs in the Leipers beds of the Cumberland River Valley in Kentucky, Upper Ordovician.

Faberoceras transversum Flower

Faberoceras transversum FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 467, pl. 10, fig. 5-6.

Faberoceras transversum resembles *F. sonnenbergi* and other species in having broad but less conspicuous costae on mature parts of the shell. It is notable for its much broader cross section. The species is smaller at maturity and has much more closely spaced septa.

The species is found in Leipers beds of the Cumberland River Valley in Kentucky, Upper Ordovician.

Faberoceras multicinctum Flower

Pl. 16, fig. 1-2; Pl. 18, fig. 2; Pl. 19, fig. 1; Pl. 20, fig. 1

Faberoceras multicinctum FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 468, pl. 8, fig. 1; pl. 9, fig. 2; pl. 12, fig. 3; text-fig. 20A, 21D.

A long slender shell, with surface bearing numerous low angular transverse ridges separated by broad shallow concave interspaces. Siphuncle (presumably ventral in young) lies scarcely adventral from center throughout a considerable adoral part of phragmocone; after a relatively central position is attained, segments broaden rapidly both at septal foramina within camerae, narrow subquadrate profile changing to that of more broadly expanded and strongly rounded segments. Parietal deposits thicken into endocones.

This species is from the Leipers beds of the Cumberland River Valley in southern Kentucky, Upper Ordovician.

Faberoceras shideleri Flower

Faberoceras shideleri FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 471, pl. 11, fig. 6; pl. 16, fig. 1; text-fig. 21B.

A moderate-sized shell with surface bearing only faint rounded costae. Cross section narrowly rounded ventrally, much more so than in *Faberoceras multicinctum*. Siphuncle migrates during growth from ventral to more than halfway to center, segments becoming gradually more rounded in form and tending to broaden as growth progresses. Endocones are developed in this species as in the preceding one.

Faberoceras shideleri occurs in the Leipers beds along Cumberland River in southern Kentucky.

Faberoceras elegans Flower

Pl. 23, fig. 1-4

Faberoceras elegans FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 472, pl. 12, fig. 1, 4; text-fig. 21E.

The unique type represents a late stage of a closely septate large *Faberoceras*. Siphuncle slightly closer to center than venter, its segments broad at septal foramina and remarkably broadly expanded in the camerae. The type shows prominent bullettes but not parietal deposits. Surface with low rounded costae separated by narrow shallow transverse grooves.

The holotype lacks recorded data but bryozoans in the living chamber indicate that it could only have come from Corryville beds of the Cincinnati region. Accordingly, the species may be listed as occurring in the Upper Ordovician (Cincinnati).

Faberoceras gracile Flower, n. sp.

Pl. 10, fig. 6

A distinctive species with rather strongly compressed cross section having greatest width at mid-height of the section, venter not markedly more narrowly rounded than dorsum. Known part of shell extremely slender, with sutures sloping forward strongly on ventral side; siphuncle composed of short broad segments, considerably removed from venter. Holotype is interpreted to represent late growth stage of phragmocone of a species which was rather small, slender, and probably simple externally, for the internal mold is extremely smooth.

The holotype has a length of 70 mm. on the venter, basal length 40 mm. dorsally and 50 mm. ventrally; height increases from 40 to 50 mm. and width from 33 to 45 mm. Septal foramen at base is 7 mm. in diameter, 12 mm. from venter, 22 mm. from dorsum. Adorally, siphuncle is 10 mm. and 12 mm. from venter, 28 mm. from the dorsum. During growth the siphuncle departs from the dorsum more than from the venter. Camerae are extremely shallow, 20 occurring in ventral length of 60 mm.; they vary only slightly in depth, 2.5 to 3.6 mm. Externally the oblique sutures lack lateral lobes. In vertical section, the septa are rather deeply curved, attaining greatest depth twice as close to dorsum as to venter. Obliquity is such that a transverse line crosses at least four camerae.

The siphuncle segments are broad at septal foramina, short and moderately expanded in the camerae. At the base a segment 2.5 mm. long increases in height from 5 to 14 mm.; adorally a segment 3.6 mm. long increases 12 to 15 mm. Rings are thick, their tips inflated into bullettes throughout the type, but the specimen shows no trace of parietal or other deposits within the siphuncle, although these probably were present in more apical portions. The smooth exterior of the internal mold suggests a shell with only faint transverse markings.

Discussion. The rounded siphuncle segments, position of the siphuncle well removed from the venter throughout growth, and shallow camerae of nearly uniform depth all indicate that the holotype represents the mature part of a phragmocone. This species was, then, an unusually small one in contrast to associated forms in the Leipers beds; it is distinctive in cross section and marked by shallow camerae with oblique sutures.

The holotype, in collection of the writer, is from the Leipers beds of the Cumberland River Valley, near Rowena, Kentucky; Upper Ordovician.

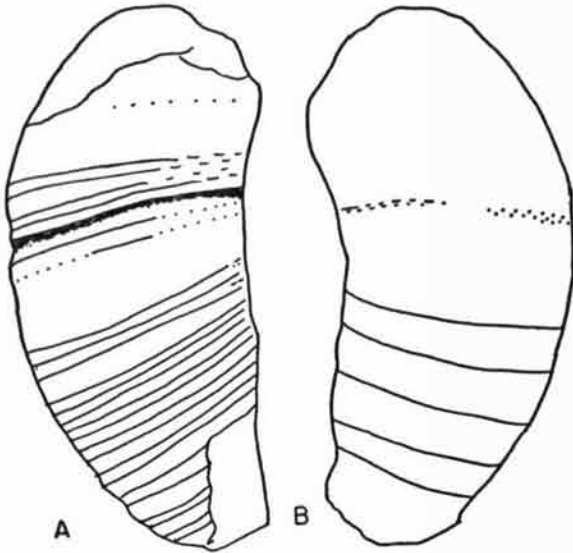
Faberoceras? *troedssoni* (Teichert)

Text-fig. 27

Cyrtogomphoceras? *troedssoni* TEICHERT, 1930, Paläont. Zeitschr., Band 12, p. 296, pl. 9, fig. 32, 33.

Faberoceras troedssoni FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 452.

Under this name TEICHERT described a unique specimen of a rather slender cyrtogonic cephalopod, exogastric, compressed in cross section. The camerae are rather deep, with sutures essentially transverse, showing a slight tendency to slope forward on the venter in anterior parts of the phragmocone. The surface is costate, resembling *Faberoceras multicinctum* and *F. percostatum*.

FIGURE 27. *Faberoceras? troedssoni* (Teichert)

Two lateral views (after TEICHERT, 1930) of holotype, *A*, showing surface features; *B*, an internal mold, exhibiting the sutures; both $\times 0.75$.

Similarity to the latter species is increased by marked constriction of the shell near the middle of the living chamber. Nothing is known of the siphuncle. The original tentative reference to *Cyrtogomphoceras* was suggested because at time of describing the species it seemed more similar to that genus than any other. While the generic position of this form must remain uncertain until the siphuncle is known, it is evidently most similar to some species of *Faberoceras*, described from the Leipers formation of Kentucky. Known features of the species are typical of *Faberoceras* and, as TEICHERT noted, not typical of *Cyrtogomphoceras*, particularly in the costate nature of the shell, constricted living chamber, and absence of any gibbosity on the living chamber. Original illustrations of the species suggests a slightly gibbous shell but the rapid expansion at the base is more apparent than real, and such slight contraction as appears at the anterior end of the living chamber is a feature approached very closely in *Faberoceras percostatum* (FLOWER, 1946, pl. 14, fig. 9). The holotype (only known specimen) from the Lyckholm beds of Estonia, is in the Senckenberg Museum, Frankfurt-a.-M., Germany.

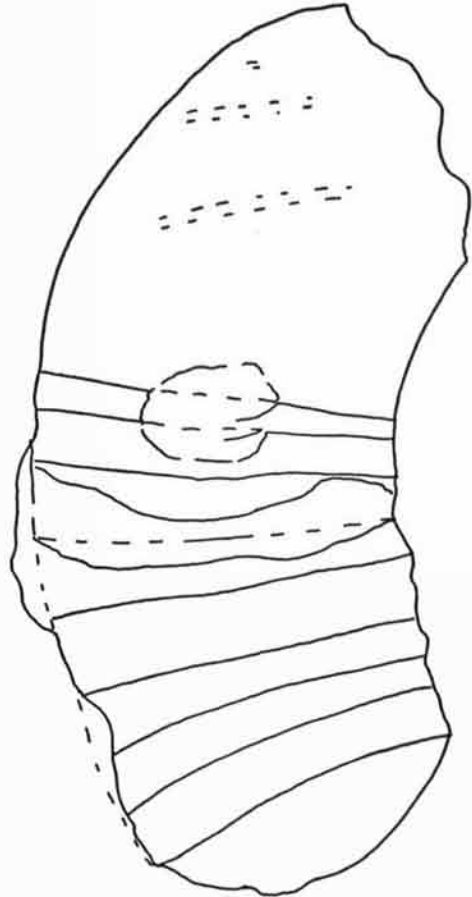
This species is from the Lyckholm beds, Ordovician.

Faberoceras? sp.

Text-fig. 28

Winnipegoceras? sp. TEICHERT, 1930, Paläont. Zeitschr., Band 12, p. 294, pl. 8, fig. 23.

Large exogastric cyrtocone with a long series of rather deep camerae, nearly equal in length, the last shortened, and a considerable portion of the living chamber. In regular curvature and aspect of the camerae, in which lateral lobes are scarcely developed, the species is not typical of *Winnipegoceras* but has very much the aspect of *Faberoceras*. The shell appears to contract slightly vertically along the living chamber, which may be real or due to incompleteness of the specimen. The siphuncle is unknown. Though with some reluctance I suggest changing the generic position of a specimen on which there is so little information, the

FIGURE 28. *Faberoceras? sp.*

Specimen from Lyckholm beds of Estonia, lateral view, slightly restored, $\times 1$ (TEICHERT, 1930).

evidence overwhelmingly suggests assignment to *Faberoceras*, and the species shows features, such as slender form of the phragmocone, lack of a definite gibbous region, and absence of good lateral lobes, which are so foreign to *Winnipegoceras* and so suggestive of *Faberoceras* (a genus not known when the original assignment to *Winnipegoceras* was made) that there seems no other possible course unless to ignore this description and illustration completely. The specimen is from the Lyckholm beds of Estonia; Ordovician.

Faberoceras? cinereum (Blake)

Phragmoceras compressum PORTLOCK, 1843, Rept. Geol. Londonderry, p. 282, pl. 288, fig. 2.

Trochoceras? cinereum BLAKE, 1882, British Fossil Cephalopods (London) p. 216, pl. 20, fig. 2.

Anterior part of the shell (all that is known of this species) exogastric, slender, rather strongly curved, with straight sutures, shell with transverse markings and costae, both sloping gradually to a hyponomic sinus on the venter. Siphuncle not observed. Cross section compressed but greatest width close to venter.

This little-known species recalls *Faberoceras* in general features and possibly the costae are a variation of features known in the more strongly ornamented American species. Atypical characters are position of the greatest shell width close to the venter and strong curvature of the shell. Strong curvature and costae suggest

Glyptodendron, but such assignment is opposed by the character of surface markings.

The species is known only from the type, from the Bala beds of Desertcreat, England; Ordovician.

Faberocheras? *subarcuatum* (Portlock)

Orthocheilus subarcuatum PORTLOCK, 1843, Rept. Geol. Londonderry, p. 374, pl. 28, fig. 9.
Cyrtoceras subarcuatum SALTER, 1865, Cat. Foss. Mus. Practical Geol., p. 32.
 BLAKE, 1882, British Fossil Cephalopods (London), p. 182, pl. 20, fig. 7.

Rather large, moderately rapidly expanding compressed cyrtocone with venter narrower than dorsum in cross section. Sutures essentially straight, surface showing transverse markings reminiscent of those of *F. shideleri*. Siphuncle unknown. Though inadequately known and thus of uncertain generic position, known features of this species suggest *Faberocheras* strongly but are not similar to any other known Ordovician genus. From Bala beds of Desertcreat, England; Ordovician.

Faberocheras? sp.

Cyrtoceras sonax BLAKE, 1882, British Fossil Cephalopods (London, p. 167 (partim), pl. 19, fig. 3 (non fig. 1, 2).

One of the specimens which BLAKE attributed to *C. sonax* is unusually slender and compressed in section, failing to show the endogastric siphuncle of others. It is plainly a different species and the close sutures, sloping forward on the venter, suggest affinities with *Faberocheras*. It is from the Bala beds of Shoeshook, England. It seems unnecessary to propose a new specific name for this form until it is better known. It is noted here as yet another of the cyrtocones in the Bala beds of England which, though inadequately known, have the aspect of *Faberocheras* and are significant as supplying some connection that lessens the geographic gap between the American forms and those of the Lyckholm beds of Estonia.

Genus CLARKESVILLIA Flower, 1946

Type species—*Clarkesvillia halei* FLOWER

Clarkesvillia FLOWER, 1946, Bull. Amer. Paleont., v. 29, no. 116, p. 475.
 FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 612.

Shell a compressed cyrtocone, dorsum rather narrowly rounded, venter flattened, separated from sides by well-defined abdominal angles. Sutures slope adorally from dorsum to venter, rising gradually to the abdominal angles, but without clearly curved lateral lobes and completely transverse on ventral face. Siphuncle about halfway between center and venter, early ephebic segments subquadrate, with free part of ring slightly rounded. Progressing to late ephebic and gerontic stages, rounding of segments increases and they become shorter and broader, in latest stages siphuncle broadly adnate to septa, width of segment twice its length, and free part of ring strongly curved. Apical end of connecting ring strongly inflated into bullettes, more prominent in late than in earlier growth stages and in early ephebic portion parietal deposits are found.

Discussion. This genus erected on the basis of a single species still known only from a single specimen, differs from *Faberocheras* primarily in prominent flattening of the venter, which in *Faberocheras* is typically more narrowly rounded than the dorsum. Internally, the siphuncle shows no marked features by which the genus differs

from *Faberocheras*, though adoral segments are paralleled only by those of *F. elegans*; in other species, adoral segments as short and broad have not been noted. In gross features *Clarkesvillia* approaches very closely to *Glyptodendron* but the siphuncle is more ventrally placed, form of the segments is different (as discussed more fully under that genus) and *Glyptodendron* shows nearly complete reduction of the bullettes; also parietal deposits are either absent or so retarded that they have not yet been observed.

Clarkesvillia halei Flower

Pl. 24, fig. 1-6

Clarkesvillia halei FLOWER, 1946, Bull. Am. Paleont., 29, no. 116, p. 476, pl. 42, fig. 3-4; pl. 43, fig. 1-4.

This species, known only from the holotype, a somewhat crushed shell, retains 17 camerae and the base of a living chamber. It is unnecessary here to repeat the proportions of the specimen, but the form is refigured for comparison with related genera. Early segments of the siphuncle subquadrate, brim recumbent dorsally, narrowly free ventrally, expanding to about twice the diameter of the septal foramen, and maximum height subequal to length of the segment. Apical end of connecting ring broadly adnate to the septum ventrally, essentially free outside of the septal foramen dorsally. Bullettes small but augmented by parietal deposits which are thick, annular and discrete in the apical segments, but in the 4th and 5th segments forming a continuous lining of the siphuncle. In these segments the bullettes, small in earlier ones, are increasing in size; in latest segments, where they have become greatly inflated, thickness of the ring is better shown but no parietal deposits are developed. Here the segment is broadly rounded, maximum width (actually height in the vertical section) being three times that across the septal foramen and twice the length of the segment. Adapically from the septal neck the adoral end of the ring is broadly adnate on both dorsal and ventral sides. The free part of the ring is rounded, so that greatest height of the segment is attained in the anterior half. Adapically the ring is broadly adnate ventrally and less markedly so on the dorsum. Bullettes well developed at the 4th segment from the living chamber but in the 3rd they are smaller, vestigial in the 2nd, and the anterior two septa fail to show the siphuncle in the section.

Holotype. University of Cincinnati Mus.

Occurrence. Waynesville beds (either Ft. Ancient or Clarksville members) at Clarksville, Ohio; Upper Ordovician.

Genus GLYPTODENDRON Claypole, 1878

Type species—*Glyptodendron eatonense* CLAYPOLE

Glyptodendron CLAYPOLE, 1878, Am. Jour. Sci. Arts, ser. 3, v. 15, p. 302.
 CLAYPOLE, 1878, Geol. Mag., dec. 2, v. 8, p. 5.
 S. A. MILLER 1889, North American Geol. Paleont., p. 119.
Cyrtoceras (Glyptodendron) FOERSTER, 1893, Am. Geol., v. 12, p. 139.
Cyrtoceras (Glyptoceras) FOERSTER, 1893, Ohio Geol. Survey, Rept., v. 7, p. 535.
Cyrtoceras BASSLER, 1915, U. S. Natl. Mus., Bull. 92, v. 1, p. 349. (partim).
Glyptodendron FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 432.
 FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 612.

Shell cyrtoconic, compressed in cross section, dorsum narrowly rounded, greatest width adventral of center, venter with a well-defined flattened zone marked by well-defined abdominal angles. Sutures tend to slope adorally from dorsum to abdominal angles but are transverse or describe faint lobes on the ventral face. Siphuncle slightly ventrad of the center, segments sub-spherical in young, equally broad but shorter and more depressed in late stages. Connecting rings thick, but bul-

lettes vestigial and visible only in late growth stages. No parietal or other deposits known in the siphuncle. Shell surface with characteristic scalelike shallow pits arranged in oblique intersecting rows; posterior margin of each pit marked by a narrow raised crescentic line. In addition to these markings *Glyptodendron subcompressum*, at least, shows obscure costae in the adult prominent close to the ventrolateral angles and fading to nothing dorso-laterally. Aperture slopes adapically from dorsum to ventrolateral angles, probably describing a broad sinus over ventral face.

Discussion. This genus was first based on a single specimen of the type species, which FOERSTE (1893) later restudied in the light of additional material which showed that it was not a plant, as CLAYPOLE had supposed, but a fossil showing an impression of some surface marking of a cephalopod shell. FOERSTE'S specimens of *Glyptodendron eatonense* were adequate to show that the shell is a cyrtoconic nautiloid, but because of the crushed and fragmentary nature of the fossils they furnished little more information. However, the presence of similar markings on shells which he identified with *Cyrtoceras subcompressum* BEECHER indicated that this species is congeneric and being represented by better material, it supplies the real basis for revised description of the genus given above.

The internal mold of *Glyptodendron eatonense* is very similar in aspect to that of *Clarkesvillia halei*, so much so, indeed that for some time I considered *Clarkesvillia* as a synonym of *Glyptodendron*. *Clarkesvillia* shows none of the characteristic scarlike surface markings of *Glyptodendron* but this negative evidence has little significance, for the one species and one specimen on which the genus rests fails to preserve any of the shell surface. The suture pattern is more generalized but this difference is not a good basis for generic distinction; in fact, if a real relationship exists between these genera, the older (Richmondian) species should be more generalized than the younger (Brassfield, Medinan) forms. Study of the internal structure reveals profound differences. In *Clarkesvillia* the siphuncle contains well-developed bullettes which persist into adoral parts of the phragmocone close to the living chamber, whereas the bullettes of *Glyptodendron* are vestigial. In addition, the siphuncle of *Clarkesvillia* possesses well-developed parietal deposits which are not developed in segments as close to the living chamber as the bullettes. No such deposits have been observed in *Glyptodendron*, though portions of phragmocones are known reaching far enough adapically from the living chamber to indicate that these structures should be developed if they are present in the genus. It is apparent then that *Glyptodendron* is specialized by simplification of the internal structures. The bullettes are reduced to a vestigial condition or altogether wanting and parietal deposits are either lost completely or so reduced to apical parts of the phragmocone that no specimen has yet been observed in which they are developed. Additional differences are found in the early ephebic segments of the siphuncle, which are elongate and subquadrate in *Clarkesvillia* but rounded and spheroidal in *Glyptoden-*

dron. Late ephebic to gerontic segments in both genera have approximately the same shape, being short, broad in proportion, and fairly well rounded.

The genus *Glyptodendron* is known only from the Brassfield limestone, Lower Silurian of Ohio.

Glyptodendron eatonense Claypole

Glyptodendron eatonense CLAYPOLE, 1878, Am. Jour. Sci. Arts, ser. 3, v. 15, p. 302.

CLAYPOLE, 1878, Geol. Mag., dec. 2, v. 8, p. 5.
S. A. MILLER, 1889, North American Geol. Palcont., p. 119,

fig. 39.
Cyrtoceras (Glyptodendron) eatonense FOERSTE, 1893, Am. Geol., v. 12, p. 139, pl. 7, fig. 1a-d, 2.
Cyrtoceras (Glyptoceras) eatonense FOERSTE, 1893, Ohio Geol. Survey, Rept., v. 7, p. 535, fig. 1a-c, 2.

This species is based on a type which is lost, probably destroyed by a fire at Buchtel College in 1899. However, FOERSTE (1893, 1893a,) had studied the type, which was the impression of the surface markings of a shell; also FOERSTE figured and described better material which showed conclusively that the shell is that of a cyrtoconic cephalopod. His specimens also seem to have been ill-fated, probably lost with other material in a flood at Dayton, Ohio. FOERSTE'S collection included a number of shell fragments which were adequate to show that *Glyptodendron eatonense* is a rather stout, fairly rapidly expanding cyrtocone. The shells were apparently somewhat crushed, as FOERSTE indicated, and so the apparent depressed condition of the cross section is not an original feature. The siphuncle was not clearly shown, though a septum was largely exposed. The surface showed the characteristic scale-like markings of *Glyptodendron*, with raised rounded margins of each depression pointing toward the apex of the shell.

The species is very little known and possibility exists that *Glyptodendron eatonense* and *G. subcompressum* are conspecific. At any rate the present concept of *Glyptodendron* is based on the latter species, since *G. eatonense* shows little more than that the fragment upon which the species and genus are based is a cyrtoconic cephalopod of fairly good size.

The species comes from the Brassfield limestone (Lower Silurian) near Eaton, Ohio, and from the Huffman quarry near Dayton, Ohio.

Glyptodendron subcompressum (Becher)

Pl. 25, fig. 1-5; Pl. 26, fig. 1-3; text-fig. 29 A,B

Cyrtoceras subcompressum BEECHER, 1886, New York State Geologist, 5th Ann. Rept. (for 1885), pl. 14, fig. 2, 3.

HALL, 1888, Palcont. New York, v. 5, pt. 2, Suppl. (in v. 7), p. 35, pl. 129, fig. 2, 3.

FOERSTE, 1889, Boston Soc. Nat. Hist., Proc., v. 24, p. 276, pl. 7, fig. 7.

Cyrtoceras (Glyptodendron) subcompressum FOERSTE, 1893, Am. Geol., v. 12, p. 139, pl. 7, fig. 3.

Cyrtoceras (Glyptoceras) subcompressum FOERSTE, 1893, Ohio Geol. Survey, Rept., v. 7, p. 535, fig. 3, pl. 32, fig. 7a-d.

This shell was a large cyrtocone, when complete, rather rapidly expanding throughout, with cross section compressed, dorsum narrowly rounded and venter flattened. Lateral lobes scarcely developed, but sutures slope slightly forward from dorsum to ventrolateral angles, being transverse or forming a very faint lobe on ventral face. Siphuncle composed of broad rounded, almost spheroidal segments with thick rings, vestigial bullettes, and no accessory deposits, as far as known. The shell surface bears broad rounded pits with raised margins. The posterior margins raised and rounded, and arranged in diagonal rows like chain armor or like the attachment scars of *Lepidodendron*, with which this genus was originally compared. In addition the living chamber shows four low rather obscure lateral costae, strong close to the ventrolateral angles, fading away to nothing as they approach the dorsum. They are curved slightly adapically as they approach the venter, indicating the course of the aperture, which slopes to a broad sinus on the ventral side.

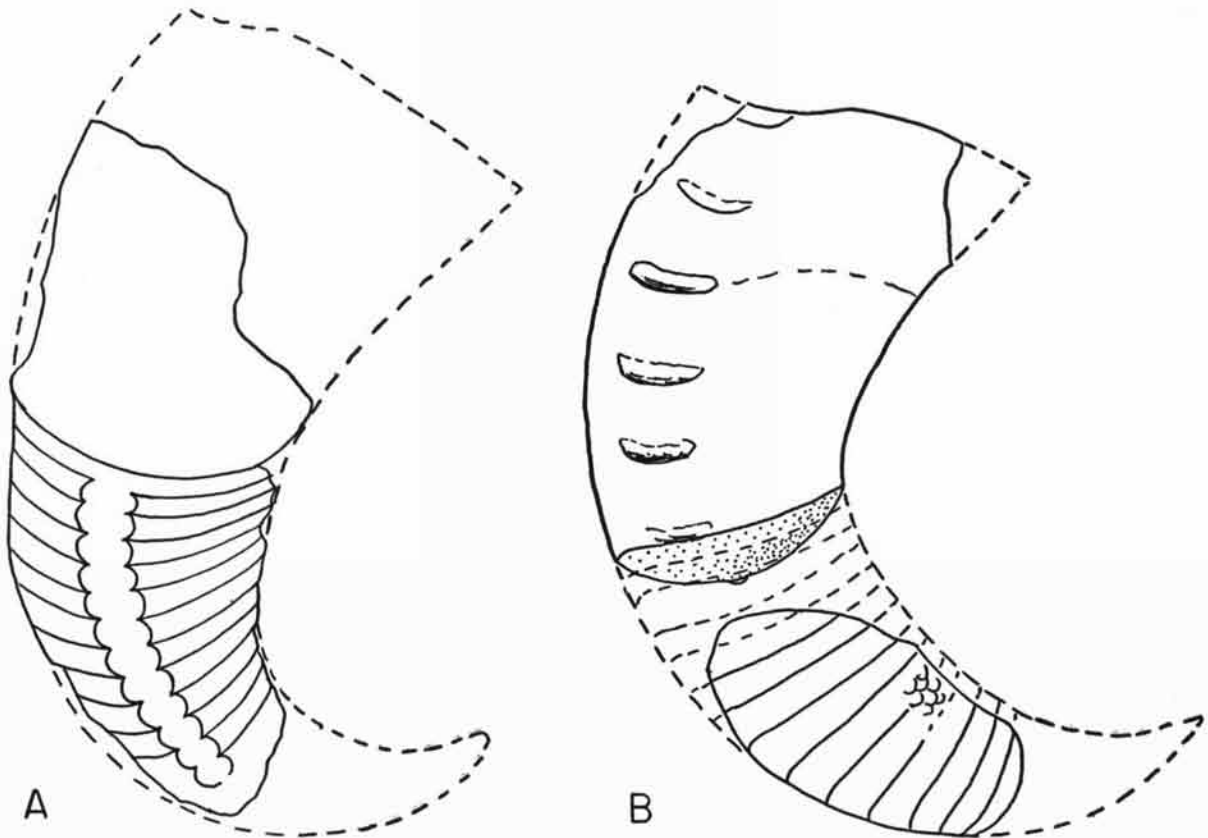


FIGURE 29. Characters of *Glyptodendron subcompressum* (Beecher).

A. Outline of holotype, with restoration of living chamber and apex, based on the original figure, $\times 0.5$.—B. Restoration based on two hypotypes used by FOERSTE, one nearly complete living chamber, another a portion of an obliquely weathered phragmocone with the dorsal part missing, $\times 0.5$.

FOERSTE (1893a, pl. 32, fig. 7a) based a reconstruction of the shell on the two specimens at present available, suggesting that the shell is a gyrocone and a rather slender one. Reexamination of the specimens has led to a very different interpretation, partly by placing the two specimens into closer juxtaposition, and partly by concluding that the living chamber is much more rapidly expanding than FOERSTE's interpretation suggests.

The smaller of the two specimens (U. S. Natl. Mus., no. 125276) preserves a lateral portion of the phragmocone, showing 7 camerae on the exterior. The opposite side, largely filled with calcite, shows 12 camerae. The surface here is oblique, passing so that more than half of the venter is preserved, but the dorso-lateral wall is cut so that the complete height of the shell is not attained. The broken surface was ground slightly to determine details of the structure of the siphuncle. In its present state the specimen is 96 mm. long. The basal septum in the plane of the section is 32 mm. high and the curving venter is 110 mm. long,

describing a curve with a radius which is 90 mm. basally and about 110 mm. adorally. The first camera is 10 mm. deep, the second abnormally shallow (6 mm.), and in fact, there seems to be another incomplete septum within it. Succeeding camerae are rather irregular, being 11 mm. at the deepest and 6 mm. at the least. Except that the last two camerae are shallow, the short ones are erratically spaced between normal long ones of 10 or 11 mm.

The siphuncle is slightly ventrad of the center. At the base the septal foramen 4 mm. high, is 12 mm. from the venter and 21 mm. from the apparent dorsum; near the adoral end a foramen 6 mm. wide is 20 mm. from the venter and 35 mm. from the dorsum. Near the base of the specimen the segments are essentially spheroidal in outline, though the first two appear slightly narrower, the plane of the section being slightly off center. The third visible segment, however, appears circular and was essentially spherical, the outline rounded, the neck short, free, and without an area of adnation. The adoral segments are shorter and broader

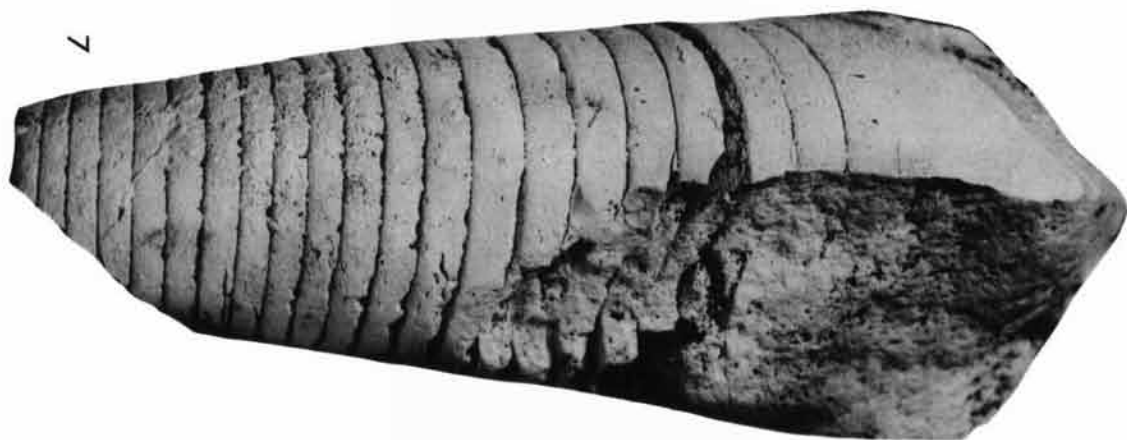
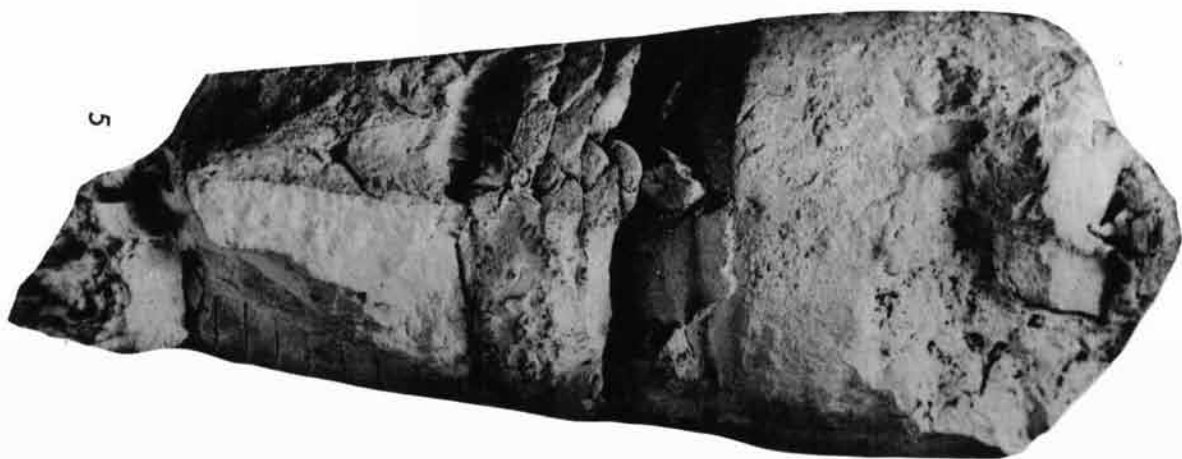
EXPLANATION OF PLATE 31 DISCOSORIDAE—Alpenoceras

FIGURE

1-4. *Alpenoceras ulrichi* FOERSTE, holotype, from Alpena limestone (Middle Devonian) at Alpena, Mich.; Univ. Michigan, Mus. Paleont., no. 10031.—1, Vertical section of siphuncle, venter at right, showing details of septal necks, thick rings, and

endocones, about $\times 12$.—2, Lateral view of apical end of holotype, $\times 3$.—3, Lateral view of complete specimen, venter at right, $\times 1$.—4, Same in ventral view, showing growth lines indicating hyponomic sinus, $\times 1$.





in proportion, expanding from 6 to 12 mm. in a length of only 7 mm. Here the adoral end of the connecting ring appears to be broadly adnate to the septum beyond the recurved neck but the apical end of the ring meets the septum with no area of adnation. Rings are thick, which cannot be attributed completely to the inorganic deposition of fine-grained calcite around it, though such calcite is present and has apparently increased the original thickness. The adapical segments show no trace of bullettes but very small ones are apparent in the adoral segments. These adoral segments are filled with matrix and the adapical ones with calcite, but the calcite is homogeneous, furnishing no reason to believe that it represents replaced organic structures. The dorsolateral part of the shell shows a portion of the surface, with broad pits, each bounded posteriorly by a raised curved line.

The second specimen (U. S. Natl. Mus., no. 125275) represents a lateral portion of a living chamber. At the base the cross section is 68 mm. high, and the passage of the siphuncle (9 mm. high and 7 mm. wide) is 35 mm. from the dorsum and 30 mm. from the venter. The entire width is not displayed but the width is estimated to be 52 mm. at a maximum, which occurs just adventral from the siphuncle; the ventral face, which is slightly narrower, is nearly complete and probably 45 mm. across. The shell height increases to 90 mm. in a length of 105 mm., straight, and 120 mm. on the curving venter, which has a radius of curvature of 140 mm. Farther orad the shell is incomplete but at the adoral end must have had a height of 110 mm. There are obscure costae, four fairly clear, and an adoral fifth which is only faintly suggested. They are well raised ventrolaterally close to the ventrolateral angles, but gradually fade to nothing in the dorsolateral region. Their crests are spaced about 40 mm. apart, curving apicad faintly as they approach the ventrolateral angles, which suggests that the aperture curves to form a broad hyponomic sinus over the ventral face. The typical surface markings of *Glyptodendron* are exhibited on this specimen only on the ventral face, as it is preserved in the basal third of the living chamber.

Discussion. The redescription of this species is based on the two topotypes previously illustrated and described by FOERSTE. The holotype has not been located but the available specimens agree with it much more in proportions than FOERSTE's gyroconic restoration of the shell suggests. This is shown in Figure 29A, in which BEECHER's type is represented, with restoration of the aperture and apex, and a similar restoration (Fig. 29B) is made on the basis of FOERSTE's two specimens. The slight differences in proportion may be due partly to distortion of the specimens, and partly to the latitude involved in tracing such shells either to the aperture or to the apex. BEECHER's type is more rapidly expanding in the adoral part and it shows some slight differences in curvature.

Types. Location of holotype not ascertained. The hypotypes are U. S. Natl. Mus., nos. 12575-6.

Occurrence. Brassfield limestone (Lower Silurian) of Ohio. FOERSTE states that the holotype and his specimens are both from the same quarry. BEECHER's type is reported as from "limestone of the Clinton group, Piqua, Ohio." FOERSTE's specimens are from Brown's quarry, 2 miles west of New Carlisle, Ohio.

Genus HECATOCERAS Teichert & Glenister, 1952

Type species—*Hecatoceras longiquum* TEICHERT & GLENISTER

Hecatoceras TEICHERT & GLENISTER, 1952, Jour. Paleont., v. 26, p. 740.
TEICHERT & GLENISTER, 1953, Bull. Am. Paleont., v. 34, no. 144, p. 43.

The two described species referred to this genus are known only from isolated siphuncles. They are composed of expanded segments, which enlarge only gradually with growth and thus probably belonged to a slender shell. Siphuncles are nearly straight, but show a slight curvature. As septa join the siphuncle more obliquely on the concave side than on the convex one, the siphuncle is regarded as located closer to the concave side of a gently curved shell, assumed to be endogastric. The expanded segments show well-recurved septal necks, length of each neck being about equal to that of the brim. The siphuncles are filled with calcareous deposits, structure of which is somewhat uncertain from published descriptions and illustrations. Heavy endocones outline a central tubular cavity and traces of lamellae parallel to outlines of the segments are believed to represent thick connecting rings of the discosorids. If so, they are anomalous in that bullettes are not swollen.

Discussion. Although *Hecatoceras* is undoubtedly a valid genus, present knowledge of its morphology is inadequate to establish its taxonomic position with certainty in the Discosorida. That the siphuncle is apparently endogastric suggests affinities with the Cyrtogomphoceratidae or older Ruedemannoceratidae but deposits within the siphuncle are foreign to both families, therefore suggesting the Westonoceratidae or its Silurian derivatives, the Lowoceratidae and Discosoridae. Assignment to the Westonoceratidae seems probable in view of the apparent great thickness of the connecting ring. Also, no representatives of the other two families are known in the Ordovician.

Hecatoceras seems to be best interpreted at present as a derivative of *Faberoceras*, in which either a reversal of shell curvature has occurred or, more probably, migration of the siphuncle from venter toward center, already evident in *Faberoceras*, has been carried to such extremes that it becomes dorsally located in an exogastric shell. The internal structure seems to be more similar to that of *Faberoceras* than to *Alpenoceras eifelse*, with which it was previously compared.

The exterior of the siphuncle of the genotype shows a median line (segmental furrow) on the concave side of the siphuncle, suggestive of a radial differentiation in the

EXPLANATION OF PLATE 32

DISCOSORIDAE—*Alpenoceras*

FIGURE

1-4. *Alpenoceras occidentale* (WHITEAVES), from Winnipegosis dolomite (Middle Devonian), Dawson Bay, Lake Winnipegosis, Man.; Canada Geol. Survey, no. 4183.—1, Ventral view, $\times 1$.—2, Lateral view, venter at left (same specimen as shown in Fig. 1), $\times 1$.—3, Portion of another siphuncle representing slightly earlier growth stage, lateral view, venter

at left, $\times 1$.—4, Adoral view of specimen shown in Fig. 3, $\times 1$.

5-7. *Alpenoceras occidentale* (WHITEAVES), holotype, from Winnipegosis dolomite (Middle Devonian) at mouth of Red Deer River, Lake Winnipegosis, Man.; Canada Geol. Survey no. 4181.—5, Ventral view, $\times 1$.—6, Lateral view, venter at right, $\times 1$.—7, Dorsal view, $\times 1$.

rings suspected from variation in the aspect of the rings in thin sections in other genera of the Discosorida.

Hecatoceras is an Ordovician genus now recorded only from Tasmania; probably late Middle or Upper Ordovician.

Hecatoceras longiquum Teichert & Glenister

Pl. 5, fig. 6

Hecatoceras longiquum TEICHERT & GLENISTER, 1952, Jour. Paleont., v. 26, p. 740, pl. 104, fig. 10.

TEICHERT & GLENISTER, 1953, Bull. Am. Paleont., v. 34, no. 144, p. 43, pl. 6, fig. 11, text-fig. 3B.

The species, here refigured occurs in the Ordovician rocks of Tasmania, being known from the Mystery Creek quarry at Ida Bay and Smelter's quarry at Zeehan.

Hecatoceras obliquum Teichert & Glenister

Hecatoceras obliquum TEICHERT & GLENISTER, 1953, Bull. Am. Paleont., v. 34, no. 144, p. 46, Pl. 6, fig. 5-10; text-fig. 3A.

This species is known only from Ordovician strata at Smelter's quarry, Zeehan, Tasmania.

Family LOWOCERATIDAE Flower, 1940

The family Lowoceratidae contains slender exogastric cyrtocones belonging to the Discosorida. Siphuncles are close to the venter. Young shells are characterized by thick connecting rings and swollen bullettes, as in the Westonoceratidae; in adult forms siphuncle segments are more rounded in outline, swelling of the bullettes is suppressed, and connecting rings become relatively thin. Deposits in the siphuncle take the form of endocones. The family as now known contains only two genera, *Lowoceras* and *Tuyloceras*, of the early Middle Silurian of northern North America.

Discussion. When this family group was proposed the internal structure of *Lowoceras* was known, but not that of *Tuyloceras*. Subsequent study has made *Tuyloceras* the better known because specimens showing early growth stages and the shell of *Lowoceras* have not been found. As originally characterized, the family was distinguished from the Discosoridae primarily by slender form of the siphuncle and (by inference) slender rather than breviconic nature of the shell. In these features there is some intergradation between the families. However, the Discosoridae contain shells which exhibit no recapitulation of features of the Westonoceratidae such as thick connecting rings and swollen bullettes in the young. In possessing these features, the Lowoceratidae serve to

connect the Ordovician Westonoceratidae with the Discosoridae and are interpreted as more primitive than the Discosoridae.

Genus TUYLOCERAS Foerste & Savage, 1927

Type species—*Tuyloceras percurvatum* FOERSTE & SAVAGE

Tuyloceras FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 81.

FLOWER, 1940, Geol. Soc. America, Bull., v. 51, p. 1970.

FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 435.

FLOWER & KUMMEL, 1951, Jour. Paleont., v. 24, p. 612.

Shell a strongly compressed exogastric brevicone with venter more narrowly rounded than dorsum in cross section, moderately enlarging to middle of living chamber and nearly tubular beyond, very gently contracting over the mature living chamber to the aperture. Sutures swing strongly adapically from dorsum to venter, so that the siphuncle, which is close to the venter, has the septal foramina transverse instead of sloping orad on the venter in the later portion of the shell. In the early portion, septa are more transverse and here annulations of the siphuncle slope adorally on the ventral side.

The type, in its original condition, showed adoral segments of the siphuncle externally, the venter part of the phragmocone being lost. A small angular section had been ground at the base of the specimen exposing 7 basal segments of the siphuncle. The siphuncle is slender in the early part of the shell, with oblique segments subquadrangle in vertical section, general proportions being reminiscent of a *Westonoceras*. The resemblance to this genus is increased by the presence of small but clearly defined bullettes at the apical ends of obviously thick connecting rings. The interior of the siphuncle is occupied by coarse calcite, evidently recrystallized in the one known specimen. A section taken farther forward shows the anterior end of a series of endocones with which this calcite can be identified. The cones show layers, lamellar structure, and a slight central elevation at their tips, through which the anterior end of a central tube is apparent. Here the siphuncle segments have been greatly widened and septal necks are recumbent or nearly so. Farther adorally, widening of the segments continues a short distance, beyond which their width is nearly constant in the anterior part of the phragmocone. In this interval (Pl. 28, fig. 1) the segments become progressively rounded in outline with loss of flattening of the expanded part and thus they come to resemble segments of typical Discosoridae. It is significant, however, that endocones are considerably retarded in development, be-

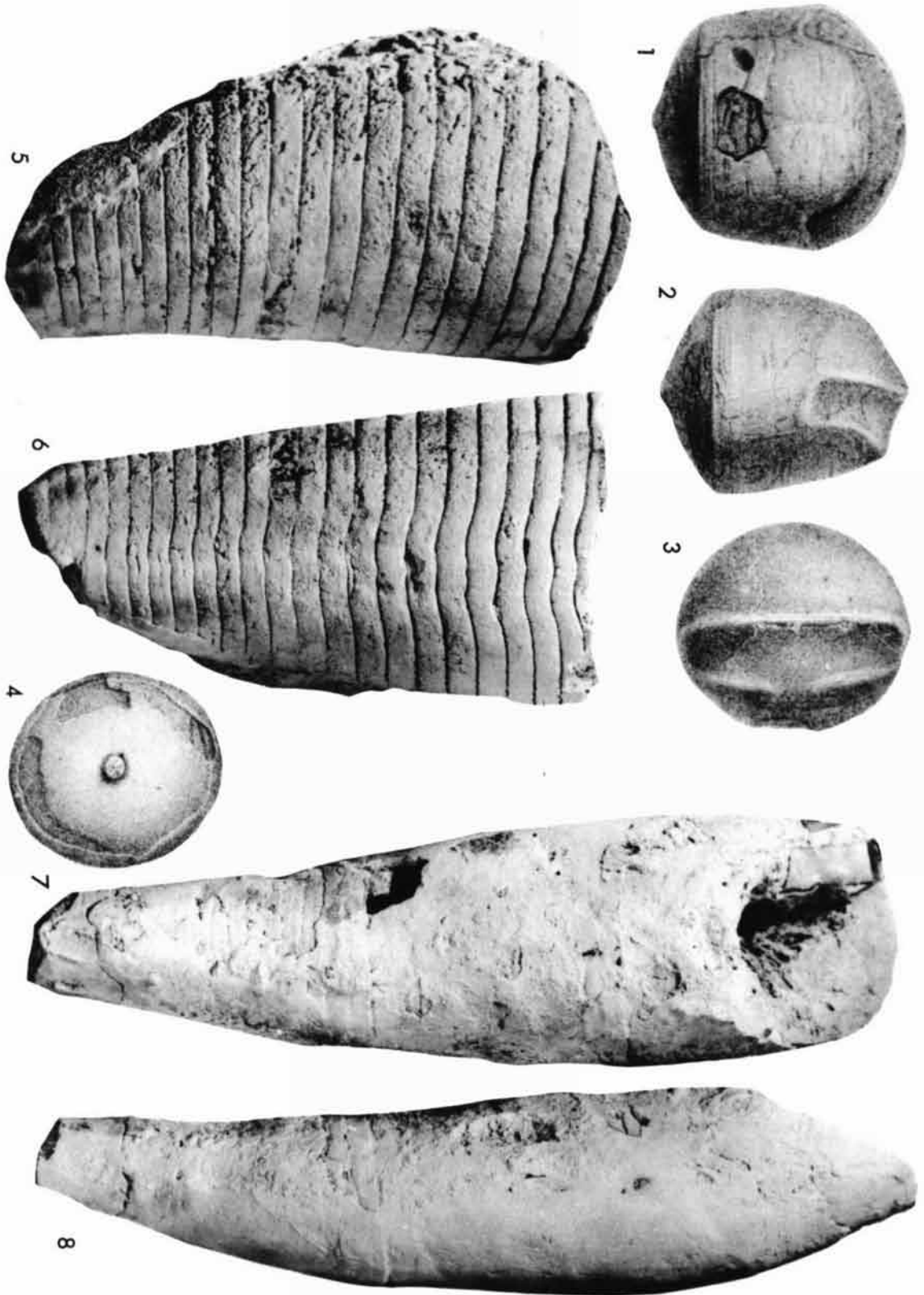
EXPLANATION OF PLATE 33

DISCOSORIDAE—*Alpenoceras*; MESOCERATIDAE—*Mesoceras*

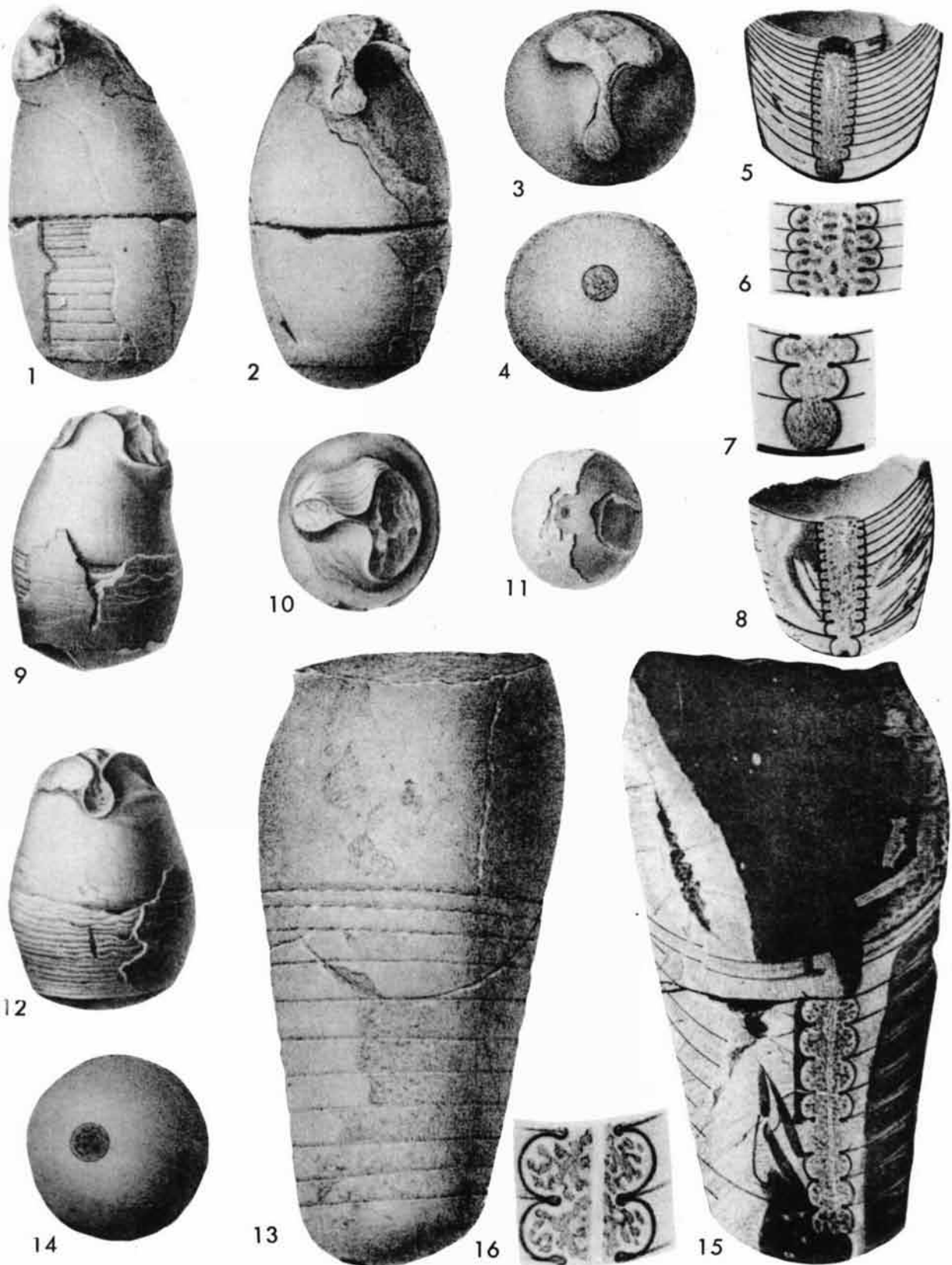
FIGURE

1-4. *Mesoceras bohemicum* BARRANDE, holotype and only known specimen, from Étage E₂ (Middle Silurian), Bohemian basin.
—1, Ventral view.—2-4, Lateral, adoral, and septal views, venter at right. All $\times 1$ (after BARRANDE).
5-6. *Alpenoceras sinuiferum* FLOWER, n. sp., holotype, from Winnipegosis dolomite (Middle Devonian), Dawson Bay, Lake Winnipegosis, Manitoba; Canada Geol. Survey, no. 4165a.

—5, Lateral view, venter at right, showing dorsal part modified by weathering, $\times 1$.—6, Ventral view showing median saddles of sutures, $\times 1$.
7-8. *Alpenoceras occidentale* (WHITEAVES), paratype, from Winnipegosis dolomite (Middle Devonian), Dawson Bay, Lake Winnipegosis, Manitoba; Canada Geol. Survey, no. 4165a.—7, Ventral view, $\times 0.7$.—8, Lateral view, venter at left, smooth dorsum being partly restored with plaster, $\times 0.7$.



FLOWER & TEICHERT—Order Discosomida (Cephalopoda)



ing completely wanting in the 11 adoral camerae, the tip of the last cone being in the 14th camera from the base of the living chamber.

Discussion. *Tuyloceras* is remarkable in the ontogenetic changes from slender subquadrate segments with thick rings and swollen bullettes to more expanded segments of more rounded section in which bullettes are no longer swollen and connecting rings no longer thick.

At the present time only *Tuyloceras percurvatum* is assigned to this genus with certainty. Inspection of the figures of this species shows, however, only a slight difference in gross features between its siphuncle and those of several siphuncles assigned to *Stokesoceras* and *Discosorus*, in which septal markings are strongly oblique and the siphuncle rather gently expanding. Some such fragments may prove to belong to species of *Tuyloceras* rather than other genera but until they can be studied by sections, there is little point in changing generic assignments. *Stokesoceras* sp. cf. *S. perobliquum* FOERSTE & SAVAGE (1927, pl. 13, fig. 4A, B) is quite similar to *Tuyloceras* but clearly distinct specifically from *T. percurvatum*. Other forms, somewhat less suggestive of *Tuyloceras*, suggest a transition in gross features into the Discosoridae by gradual increase in rate of enlargement of the segments, decrease of obliquity of the sutural markings, and gradual replacement of subquadrate segments of the young by segments more rounded in profile. Early portions of some *Stokesoceras*, as *S. perobliquum* (FOERSTE, 1925, pl. 11, fig. 6), show siphuncle segments which are definitely flattened in their expanded portions, very similar to what one would expect of *Tuyloceras* intermediate between the early portion (Pl. 27, fig. 1, 2) and later part (Pl. 28, fig. 1, 2).

Tuyloceras occurs in lower Middle Silurian rocks of northern North America.

Tuyloceras percurvatum Foerste & Savage

Pl. 27, fig. 1, 2, 6, 8; Pl. 28, fig. 1, 2; text-fig. 30.

Tuyloceras percurvatum FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 81.

This species is known only from the holotype, the internal mold of an essentially complete mature shell, 148 mm. long. It is an exogastric cyrtocone with strongly compressed cross section.

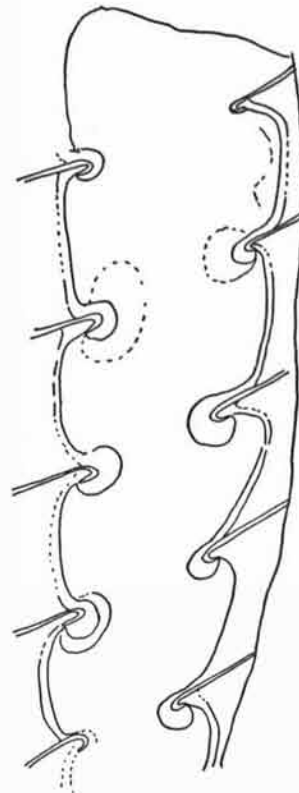


FIGURE 30. Siphuncle of *Tuyloceras percurvatum*.

Vertical section through basal segments of the siphuncle (camera lucida drawing from holotype) showing outline of septal necks, thick rings, and bullettes; $\times 4$.

In the anterior three-fourths of the phragmocone the siphuncle is exposed. Detailed proportions have been given by FOERSTE & SAVAGE and need not be repeated here. In extreme basal portion the siphuncle has been exposed by grinding and though the section is obscure in some features, because the surface is rather rough and further grinding was not attempted lest the critical median section be lost, it is evident that the oblique segments, subquadrate in section, are very similar in general aspect to those of *Westonoceras*, though the long brims are narrowly free from the septa instead of recumbent. Rings are definitely thickened throughout their length, their tips being inflated into definite bullettes. Rather

EXPLANATION OF PLATE 34

MANDALOCERATIDAE—*Pseudogomphoceras*, *Ovocerina*

(Except as otherwise indicated all figures are $\times 1$ and illustrate specimens from Étage E₅, Middle Silurian, Bohemian basin. All figures are after BARRANDE, 1865, fig. 1-8 and 13-16 from his pl. 83 and fig. 9-12 from his pl. 90.)

FIGURE

1-8. *Ovocerina alphaeus* (BARRANDE), holotype (1-6) and hypotype (7-8) from Hinter-Kopenia, Bohemia.—1, Lateral view, venter at right.—2, Ventral view.—3, Adoral view, venter beneath.—4, Septal view, venter beneath, showing large siphuncle slightly on dorsal side of center.—5, Section of phragmocone; orientation not stated.—6, Portion of siphuncle showing form of segments and internal vesicular structure regarded as organic by BARRANDE, $\times 2$.—7, Apex of siphuncle of paratype, $\times 2$, showing detail of early spheroidal segment.—8, Section of phragmocone of same

specimen showing normal condition of small apical siphuncle segment.

9-12. *Ovocerina marsupium* (BARRANDE), holotype and only figured specimen, from Dvoretz, Bohemia.—9-11, Lateral, adoral, and septal views, venter at left.—12, Ventral view.

13-16. *Pseudogomphoceras rigidum* (BARRANDE), holotype and only known specimen, from Hinter-Kopenia, Bohemia.—13, Lateral view, venter at left, similarity with *Ovocerina* in form of anterior end suggesting that complete aperture may have been similar also.—14, Septum at base, venter at left, showing large slightly ventral siphuncle.—15, Longitudinal section, venter at right, showing thick-walled siphuncle, central tube, and thick rings.—16, Part of section, showing thick rings and detail of vesicular structure regarded by BARRANDE as organic, $\times 2$.

coarse and evidently recrystallized solid calcite occupies the entire cavity of the siphuncle in this portion. It is not evident whether absence of a central tube is attributable to this replacement or whether the section lies slightly off center, although the latter seems unlikely. The series of segments is shown in Figure 30.

Although only a small portion of the siphuncle is concealed between the section in the apical part of the specimen and the next (Pl. 28, fig. 1, 2), segments of the siphuncle have already altered markedly in shape. They are much broader, in fact so broad that the recurved brims seem tiny, though actually slightly longer here than in the initial portion of the siphuncle. Segments in this section are enlarging in the lower 8 camerae, their outline becoming more rounded, and the straight condition of the middle of the segment, most evident on the dorsum, becoming lost. The anterior 5 segments have essentially the same form, showing subequal height in the section. The wall of the siphuncle is very poorly preserved here. Throughout this section the rings have become thin and no swollen bullettes are evident. The conformation of endocoines, seen in the 5 basal segments of this section, is essentially similar to that previously known in the Discosoridae. The median elevation penetrated by the central tube is shown in Pl. 28, fig. 2.

Genus *LOWOCERAS* Foerste & Savage, 1927

Type species—*Lowoceras southamptonense* FOERSTE & SAVAGE

Lowoceras FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 77.

—FLOWER, 1940, Geol. Soc. America, Bull., v. 51, p. 1970.

—FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 435.

—FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 612.

The genus *Lowoceras* includes only one known species, *L. southamptonense*, and this species, insofar as I have been able to discover, is known only from the type specimen. The genus was originally defined on the basis of a slender curved siphuncle with very oblique segments, broad septal foramen and segments only slightly expanded within the camerae. By these features alone, it was not evident that *Lowoceras* could be distinguished from isolated siphuncles of a goodly number of slender cyrtocoenic cephalopods. Happily, however, a section of the siphuncle of the type specimen was made for me by the Canada Geological Survey in 1940 and photographs of the section were supplied. The vertical section shows that within the siphuncle of *Lowoceras* are endocoines without bullettes, the structure being essentially that of the Discosoridae. The wall of the siphuncle is missing and neither connecting rings nor septal necks can be seen. No central elevation of the endocone is developed.

Lowoceras occurs in lower Middle Silurian rocks of northern Canada.

Lowoceras southamptonense Foerste & Savage

Pl. 27, fig. 4, 5

Lowoceras southamptonense FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 77, pl. 13, fig. 2A-C.

—FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 435.

This species, known only from the holotype, consists of a portion of 7 segments of a slightly curved siphuncle 67 mm. long. The segments are very slightly expanded within the camerae and the whole siphuncle enlarges scarcely at all in the length of the specimen, suggesting that it is from a mature part of a shell. The strongly oblique septal markings suggest that the siphuncle was probably close to the venter though of course the same appearance can be produced by septa which slope forward very strongly from dorsum to venter. Judging from the outline of the siphuncle, the septal necks must have been only very slightly recurved but a

vertical section fails to show either septal necks or connecting rings. Bullettes clearly are wanting, the anterior of the siphuncle being occupied by simple endocoines terminating in a central tube. The cavity of the last endocone, not quite complete adorally, occupies slightly more than the 3 anterior segments of the holotype.

The holotype (Canada Geol. Survey, no. 7846) is from the Silurian from the southern half of the west side of Southampton Island, Canadian Arctic.

Family DISCOSORIDAE Teichert, 1931

Members of this family are curved more or less breviconic shells; although complete shells are rare and inadequately known for some genera, isolated siphuncles are well known. The siphuncles consist of broadly rounded segments, rather rapidly expanding as they are traced forward through a series of camerae. Septal necks are short, brims long, recumbent or nearly so. Connecting rings are poorly known; they are thin in contrast to those of more primitive Discosorida but retain remnants of the discosorid pattern, in particular, differentiation of the vinculum and two-layered bullette. The bullette is never swollen and rarely can be recognized except by examination of thin sections. Within the siphuncle are endocoines which are typically developed quite far forward in the shell, so that only a relatively short series of adoral siphuncle segments lack these structures. Cones terminate in a central tube, the cone tips being commonly though not invariably elevated slightly around the aperture of the tube. Tubes are commonly empty but may contain diaphragms.

Discussion. TEICHERT (1931) assigned three genera to this family: *Discosorus*, *Stokesoceras* and *Endodiscosorus*. To these are added the Silurian genus *Kayoceras*, which appears to be closely related to *Discosorus*, and *Alpenoceras*, which is thus far exclusively known from Devonian species and differs from other members of the family in being endogastric instead of exogastric. Difference in age and reversal of curvature were considered seriously as a basis for separating *Alpenoceras* into a family of its own, but with no greater differences than are now apparent, it is felt that this would serve no good purpose. On the other hand, retention of *Alpenoceras* in the Discosoridae serves to emphasize its structural similarity with other members of the family in spite of differences in age.

Great difficulty attends interpretation of the shells of the Discosoridae as exogastric or endogastric. SCHINDEWOLF (1942, p. 506, fig. 1-2) has attempted such reconstructions but how uncertain they may be is shown by Figure 31. For three possible interpretations of the orientation of the siphuncle of *Discosorus conoideus*, the siphuncle was traced from FOERSTE's photograph of the holotype. It can be seen that a position close to the convex side, close to the concave side, or even a central position are equally likely. It remains for specimens retaining some parts of the shell wall and septa to indicate that a ventral position of the siphuncle is true for some other species of *Discosorus* and it is therefore a safe inference for this one. SCHINDEWOLF attempted to demonstrate that in one of the species described by him, the siphuncle occurs on the concave side of the shell, where-

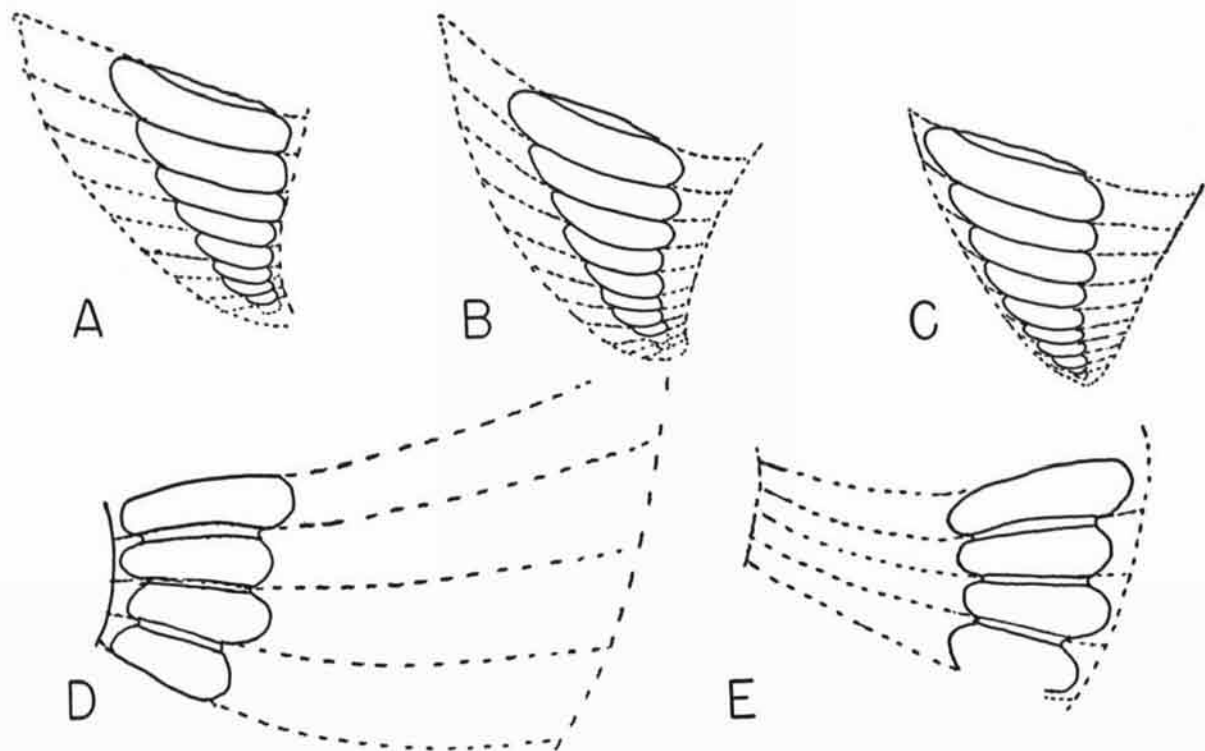


FIGURE 31. Diagram showing uncertainty of establishing position of the siphuncle in discosorids from evidence of the siphuncle alone.

A-C. Three interpretations of *Discosorus conoideus* based on the assumption that the siphuncle is (A) dorsal, (B) central, and (C) ventral.—D,E. Equally logical interpretations of the siphuncle of *Alpenoceras robustum*. All $\times 1$.

as in the other species it is on the convex side. One species certainly is endogastrically curved and thus properly identified as a member of the genus *Alpenoceras*. The other probably is endogastric also (as shown in Fig. 31D) instead of exogastric (as suggested in Fig. 31E) and this is supported by the presence otherwise of only endogastric forms in the Devonian. From morphological evidence either interpretation is possible, as in the case of *Discosorus*. The siphuncle as represented in Figures 31D,E is based on a photograph giving lateral view of *Alpenoceras robustum*, figured by SCHINDEWOLF (1942, p. 35, fig. 11), whose text-figure unfortunately fails to indicate proportions of this siphuncle at all accurately and is particularly misleading in showing segments so abruptly contracted at the septal foramina as to suggest recumbent septal necks, whereas actually the brims are free and a broad concave region occurs between the expanded segments.

Members of the Discosoridae are easily recognized from the aspect of isolated siphuncles. The only forms which could be confused with them are very short portions of actinoceroid siphuncles or short fragments from the anterior end of a *Tuyloceras* siphuncle in which slender form and strong curvature are not evident. Except for the Devonian genus *Alpenoceras*, most members of the Discosoridae are known only from isolated siphuncles. Only a handful of specimens are known which retain enough of the shell to show its external form, the living chamber, or the sutures. Most of the known speci-

mens have been studied on the basis of proportions of the siphuncle alone and it is primarily on the distinction between rapidly expanding and slender siphuncles that *Stokesoceras* and *Discosorus* have been separated. Clearly, however, there is such gradation between these genera that it is very difficult to decide in which genus certain species should be placed. In general, *Discosorus* has a siphuncle which expands quite rapidly initially and the initial chamber must have been relatively large (Pl. 27, fig. 3, 7; Pl. 28, fig. 5). Anterior parts of the siphuncle commonly show a marked reduction in rate of expansion of the segments (Pl. 30, fig. 6; text-fig. 32D,E). However, the holotype of *D. halli* shows a reversal of this condition, for the rate of expansion of siphuncle segments certainly increases rather than decreases in later segments of the siphuncle. An anomalous siphuncle from Timiskaming shows the adapical portion so slender that if it were a separate fragment assignment to *Stokesoceras* probably would be made without question (Pl. 30, fig. 2) and yet the anterior part is typical of *Discosorus* in aspect. *Kayoceras* seems to be little more than a *Discosorus* in which the siphuncle comes to be well removed from the ventral wall of the shell. The anterior segments here are uniform in maximum diameter and on the basis of their form alone could be confused readily with some *Stokesoceras* or even actinoceroid siphuncles. *Endodiscosorus* shows expanded parts of siphuncle segments strongly flattened but species otherwise typical of *Discosorus* and *Stokesoceras* show similar outlines.

Early growth stages (Pl. 30, fig. 1, 3) exhibit rounded siphuncle segments which are broadly expanded and without trace of thick rings or bullettes and it is probable that some of the specimens at hand show the true initial segment of the siphuncle. The present study shows that rather wide variation exists in structure of the cones and tube. Many forms show a median elevation of the endocone material, as noted by TEICHERT (1931), and these appear to be typical in other respects of both *Discosorus* and *Stokesoceras*. However, the type species of *Endodiscosorus* show no such elevation, nor does *Stokesoceras* sp. cf. *S. romingeri* FOERSTE (Fig. 321, J) or *Alpenoceras*. The central tube may be sinuate to zigzag (Pl. 30, fig. 1), sinuate (Pl. 28, fig. 3), or perfectly straight. In one specimen (Pl. 30, fig. 1) there is evidence of short lateral tubes. The central tube is commonly simple and empty. FOERSTE (1924, Pl. 7, fig. 2) has figured a section in which the anterior end of the tube is seen to be annular, resembling short much-expanded siphuncle segments. A similar appearance in *D. conoideus* (Pl. 28, fig. 3) seems to be adventitious and is not in line with the tube. Diaphragms crossing the tube have been observed only in *Alpenoceras eifelse* (SCHINDEWOLF, 1942). Quite evidently much remains to be learned about internal structures of the Discosoridae. Study of such features in relation to individual species has been inhibited by a different problem for species established on the proportions of siphuncles are difficult to determine. Examination of a considerable series of specimens from the Thornloe limestone of Lake Timiskaming has showed such variation that it was impossible to assign them more than tentatively to species which FOERSTE recognized there. Either many species remain undescribed or else there is much wider variation in proportions within the species than is usual in cephalopods. It is evident that only a study of a large suite of specimens can determine which is true. As the purpose of the present work is primarily an investigation of morphology and of relationship, questions of specific identification are here largely by-passed.

Genus DISCOSORUS Hall, 1852 ("1851")

Type species—*Discosorus conoideus* HALL

- Discosorus conoideus* HALL, 1852, (non "1851"), in FOSTER & WHITNEY, Rept. geology of Lake Superior land district, pt. 2, p. 222.
Discosorus HALL, 1852, Paleont. New York, v. 2, p. 99.
 WOODWARD, 1856, Manual Mollusca, p. 3, p. 449.
 HALL, 1859, New York State Cab. Nat. Hist., 12th Ann. Rept., p. 81.
 HYATT, 1884, Boston Soc. Nat. Hist., Proc., v. 22, p. 272.
 FOORD, 1888, Cat. Fossil Cephalopods Brit. Mus., v. 1, p. 194.
 S. A. MILLER, 1889, North American Geol. Paleont., p. 436.
 HYATT, 1900 Cephalopoda, in ZITTEL-EASTMAN Textbook Paleont., v. 1, 1st ed., p. 528 (reprinted with different pagination in later editions).
 FOERSTE, 1924, Michigan Univ., Geol. Mus. Contrib., v. 2, p. 67.
 FOERSTE, 1925, Canada Geol. Survey, Mem. 145, p. 85.
 FOERSTE & SAVAGE, 1927 Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 75.
 TEICHERT, 1931, Am. Mus. Nat. Hist., Novitates, no. 512, p. 2-11.
 TEICHERT, 1933, Palaontographica, Band 78, Abt. A, p. 160, 204 207.
 FOERSTE, 1934, Denison Univ. Bull., Sci. Lab., Jour., v. 29, p. 170.
 FLOWER, 1940, Geol. Soc. America, Bull., v. 51, p. 1970.
 FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 436.
 FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 613.

Discosorus is primarily known from isolated siphuncles composed of broadly rounded segments, which

increase in size very rapidly as traced through a series of camerae. In lateral view the segments are more or less oblique and slope of septal markings suggests that the siphuncle was quite close to the ventral side of the shell.

Septal necks are recumbent, with long brim in contact with the free part of the segment. Connecting rings are poorly known but as noted in Part I, they are relatively thin, as in all Discosoridae, in contrast to more primitive discosorids, but still retain evidence of a vinculum and bullette, though both structures are extremely thin. The interior is occupied by endocones, well described by TEICHERT (1931), the tip of the conical "endosphocone" modified by an elevated protuberance of endocone material surrounding the aperture of the central tube. The tube is essentially straight and no diaphragms are known crossing it.

Some specimens which are known retaining parts of the shell confirm the ventral position of the siphuncle and show that the shell is breviconic and faintly exogastric. The phragmocone is short, rapidly expanding; the mature living chamber is contracted gently as it approaches the aperture. The endocones are typically developed throughout nearly the entire length of the siphuncle, without the usual series of adoral camerae in which siphuncle segments lack cones.

Discosorus is confined to beds of Clinton age. It is most abundant in the Manistique beds of northern Michigan and the equivalent Thornloe limestone of Lake Timiskaming but it has been traced northward to the Ekwan limestone of Hudson Bay and equivalent beds of Southampton Island, east to Anticosti, and southward it extends into the Hopkinton beds of Iowa, Dayton limestone of Ohio, and lower Clinton of New York.

A taxonomic dilemma is posed by publication of a description of *Discosorus conoideus* without definition or diagnosis of the genus in HALL's section of the FOSTER & WHITNEY report dated 1851. This description is a very general one accompanied by illustrations of two specimens from northern Michigan. Specimens from New York referred to this species were described and illustrated by HALL in volume 2 of the *Paleontology of New York*, dated 1852. FOERSTE (1924) retained the name *D. conoideus* for the New York form but excluded the Michigan specimens for which he proposed the new name *D. halli*, for the two are clearly not conspecific. One naturally may conclude that this procedure was incorrect, because according to the Law of Priority the name *D. conoideus* should be retained for the Michigan specimens, as was pointed out by TEICHERT (1931) and SCHINDEWOLF (1942). However, a review of the situation shows that it is complicated by two other factors, in the light of which it seems best to retain the present status of the names.

The description given by HALL in the FOSTER & WHITNEY report is as follows:

DISCOSORUS CONOIDEUS

Plate XXXIV, figures 2, 3

Discosorus conoideus, Paleont. New York, v. 2, p. 99, pl. 28, fig. 13a-c.

A conical body consisting of a series of rings or discs, with rounded outer edges and flattened above and below. Each succeeding ring, or disc, increases in size from the apex to the base.

These discs are composed of a thick crust or shell, having a fibrous structure, which radiates from a small, central, tubular cavity, or space filled by a different kind of material. This cavity may, perhaps, communicate with the internal, conical cavity, formed within the entire series of rings. The structure of the ring, in specimens of this fossil from New York, resembles more nearly that of the Belemnite than anything else with which I am acquainted. The specimens from Lake Michigan afford no new facts regarding the structure of this fossil. One of the specimens has the two broader discs crushed, giving them apparently an abruptly increased diameter; but this appearance is entirely accidental. The oblique direction of the discs and the curved form of the specimens are in like manner, due to pressure. The other specimen has the edges of the discs worn down, the interior being crystallized, leaving only a thin exterior shell. The crystallized interior does not represent the cavity before alluded to, but is the substance of the thick shell or crust, crystallized or partly removed, leaving a cavity.

These fossils were first noticed by Dr. BIGSBY, on Drummond's Island and were figured in the geological transactions before cited, but without a name, and, so far as I know, they have remained without further notice, until the description cited above. *I am unable to find any characters by which to separate the species, now described, from those found in the Clinton group of New York* [italics mine].

Geological position and locality.—The specimens figured were found with *Huronina* at Orthoceras Point, in limestone of the Niagara period; and also in the same rock on Drummond's Island.

The sentence italicized here (but not in the original) should more properly have used the word "specimens" instead of "species," for HALL clearly is describing here a species based primarily upon a specimen from the Clinton of New York and attributing to it two specimens from Michigan which in his estimation differ from it only in features of preservation. On this basis, it would be incorrect to restrict the name *D. conoideus* to the Michigan forms and exclude the New York ones. Yet the two forms are clearly of such different proportions that they are not conspecific, and FOERSTE's proposal of a new name for the Michigan one seems proper.

The situation is further complicated by the fact that the relative dates of appearance of the two publications in question are more apparent than real. Volume 2 of the *Paleontology of New York* was delayed in publication, for HALL states in the preface that the text was largely completed in 1849 but publication was delayed until 1852 awaiting engraving of the plates. In that work, a letter of transmittal to the Governor of New York is dated September 1, 1852, and since Labor Day had not then been heard of, this may safely be taken as the date of publication.

Dr. G. WINSTON SINCLAIR first pointed out to me that a note in the FOSTER & WHITNEY report stated that up to November, 1851, no funds had been appropriated for publication of that work. Inquiry was made to the U.S. Library of Congress for information as to the exact date of appearance of the work. No records of the publication date were found but Miss GRACE H. FULLER, acting chief of the general reference and bibliography division found a deficiency appropriation for "including the cost of superintending and printing of their final geological reports" among other things, which was ap-

proved July 21, 1852. The work certainly must have appeared some time after that date, and with the mechanics of printing and engraving, it is very doubtful whether it could have appeared prior to September of that year.

It is therefore apparent (1) that *Discosorus conoideus*, as published in the FOSTER & WHITNEY report, is based primarily upon the New York specimen rather than the Michigan ones, and (2) that while relative publication dates have not been definitely established, there is valid reason to doubt priority of the FOSTER & WHITNEY report. Accordingly, HALL's 1852 diagnosis of the genus *Discosorus* and accompanying description and illustration of the New York specimen named *D. conoideus* published in the *Paleontology of New York* (v. 2), is accepted as original publication which serves both to establish *D. conoideus* as type species (by monotypy) and fix the type specimen of the species as the New York form illustrated in *Paleontology of New York*, 1852. This confirms the usage of FOERSTE (1924) and serves to stabilize nomenclature, avoiding the confusion that would be entailed by recognizing the Michigan form as *D. conoideus* with consequent suppression of *D. halli* as a junior objective synonym and needed renaming of the New York form.

Discosorus conoideus Hall

Pl. 28, fig. 3-5

Discosorus conoideus HALL, 1852, ("1851") (*partim*), *Paleontology*, in FOSTER & WHITNEY, Rept. Geol. Lake Superior land district, pt. 2, p. 222 (non pl. 34, fig. 2-3; see *D. halli*).

FOERSTE, 1889, Boston Soc. Nat. Hist., Proc., v. 24, p. 286.

FOERSTE, 1893, Ohio Geol. Survey, Paleont., v. 7, p. 546,

pl. 36, fig. 8.

FOERSTE, 1924, Michigan Univ., Geol. Mus., Contrib., v. 2,

p. 68, pl. 7, fig. 1A-C.

TEICHERT, 1931, Am. Mus. Nat. Hist., Novitates, no. 512,

p. 5, fig. 6-7.

Only the siphuncle of this species is known. FOERSTE has refigured the original of HALL's description in the *Paleontology of New York*. It is a specimen consisting of 8 siphuncle segments, increasing in maximum diameter from 5 mm. at the base to 30 mm. at the adoral end. The segments are essentially equal in width and height. The segments double in length in the interval, increasing from 3.2 to 6.5 mm. Septal markings are nearly transverse with reference to the dorsal outline of the siphuncle but strongly inclined to the ventral profile. In lateral view the septal markings are scarcely curved. Analogy with other species suggests that the siphuncle was close to the ventral wall of the shell, but nothing in the present species demonstrates this conclusion definitely.

The holotype has not been sectioned and shows none of the internal features of the siphuncle. Happily, a second specimen was available for sectioning. This is a siphuncle of 9 segments, increasing in maximum height from 7 mm. and width of 6 mm. to a height of 30 mm. and width of 17 mm. The specimen occurred in shale and slight crushing is evidently responsible for compression of the cross section. A vertical section through this specimen (Pl. 28, fig. 3,4) reveals the internal structure. Septal necks are recumbent, developing brims at least three times the length of the neck, longer dorsally than ventrally. Only in the invaginated part of the siphuncle is there any trace of the connecting rings and in the opaque section no differentiation of structure is evident. Endocones are well developed. The conical cavity, filled with matrix, occupies the anterior 5 segments and originally it extended slightly farther forward. On the ventral side part of a 6th segment is preserved in displaced position but still with endocone material. The

endocones show growth lines and lamellae normal to the growth lines. As the endocones thicken, they become simpler and smoother in outline, the annular condition of the outer cones departing more and more from the outline of the outer cones and conforming less and less with expanded segments of the siphuncle. As successive layers are deposited one upon the other, simplification is achieved by evident disconformities which have been accentuated by regions in the expanded portions of the segments by evident recrystallization of part of the material. A broad carbonaceous band lines the cavity of the last endocone. The tip of the conical cavity shows a pointed median elevation. The tube within the endocones is evident but its anterior end is not shown in the plane of the section. Presumably it terminates at one side of this elevation and not in the center. In this respect the species is consistent with the sections shown by TEICHERT (1931). Beyond the tip of the cone, apparent on both sides of the section, are annular structures, somewhat obliquely arranged, the apical one aligned with the convex part of the dorsal wall of one of the connecting rings. Apparently the central tube passes ventrad of them at its anterior end. These structures, superficially resembling cyrtocoanitic segments of the siphuncle, are apparently actually patterns in the endocone structure itself and not a feature of the central tube, though annular structures at the anterior end of the tube have been observed in *Stokesoceras engadinense* (FOERSTE, 1924, pl. 7, fig. 2). In the apical part of the specimen the central tube is seen for only a short distance. Its course is definitely undulating. Calcite immediately surrounding it is white and coarse, and is evidently recrystallized, while the darker outer layers show growth lines and lamellae normal to them.

Discussion. The internal structure made known from this species is essentially similar to that described by TEICHERT (1931) for other species of the genus. The siphuncle is a relatively rapidly expanding one and one in which the septal markings are quite strongly oblique in reference to the ventral profile of the siphuncle. The known portion of the siphuncle must, from the small size of the initial segment, lie close to the true apex of the shell. *Discosorus halli* is, by contrast, a species with a siphuncle which is much more gradually expanded in a corresponding initial portion of the shell, though the rate of expansion increases in later stages.

Of the two specimens figured in v. 2 of the *Paleontology of New York*, FOERSTE has refigured the larger (Am. Mus. Nat. Hist., no. 1580). As no formal designation seems to have been made, that specimen is here selected as the lectotype of *D. conoideus* HALL, 1852 (Paleont. New York, v. 2, p. 99, pl. 28, fig. 13A-C). To remove any further confusion, the same specimen is designated as the type of HALL in FOSTER & WHITNEY, 1852 ("1851"), Rept. Geol. Lake Superior Land District, pt. 2, p. 222 (non pl. 34, fig. 2, 3).

Insofar as I am aware, only three representatives of this species are known. HALL (1952) lists two occurrences, both in the Clinton beds and probably in the lower part of the Clinton group. Matrix surrounding the lectotype contains *Pentamerus*, from which FOERSTE concluded that the specimen came from the Reynales limestone; it is from Lockport, New York. The other specimen is from green shale from near the Ridge Road in the town of Ontario, Wayne County. The shale mentioned is probably the lower Sodus shale. The specimen here figured, in the collection of the writer, came from the bed of a small stream east of Wolcott, less than 0.25 mile above the outcrop of the Wolcott limestone and south of the lane leading east from the highway. Its stratigraphic position is probably the Williamson shale.

Discosorus austini Foerste

Text-fig. 32F,G

Discosorus austini FOERSTE, 1934, Denison Univ. Bull., Sci. Lab., Jour., v. 29, p. 174, pl. 34, fig. 1A,B, 4A-C; pl. 35, fig. 5.

The holotype is the ventral portion of a slightly crushed individual, retaining 9 segments of a siphuncle and the internal mold of one camera and a living chamber. The siphuncle is rapidly enlarging, the septal markings strongly oblique as in *D. conoideus*. FOERSTE attributed 70 mm. of the 100 mm. of the specimen to the phragmocone, and believed only the basal part of the living chamber to be present. In lateral view the living chamber is convex over the basal part but faintly concave adorally, a condition which is commonly found in breviconic cephalopods near the mature aperture. It is believed instead that the entire length of the living chamber is represented here and that it is essentially equal to the phragmocone in length. Nothing is shown of the original cross section of the shell. A second specimen (FOERSTE, 1934, pl. 24, fig. 4A-C) represents three segments of the siphuncle at a relatively late growth stage. They have been sectioned and reveal typical endocones, with the center of the endocone material forming a prominent median elevation. A third specimen, an isolated weathered portion of the siphuncle (FOERSTE, 1934, pl. 38, fig. 4) is doubtfully conspecific. The expanded parts of the siphuncle are strongly flattened and well aligned, to such an extent that this siphuncle approaches that of *Endodiscosorus* in outline. Such flattening is shown in the later but not commensurately early segments of the two other specimens which can be taken as typical.

The species is from the Dayton limestone (Silurian), of southern Ohio, the holotype (U. S. Natl. Mus. no. 89824) from Todd's Fork, near Wilmington, Ohio, and the paratype from Adams County, Ohio (U. S. Natl. Mus., no. 81921A). The more atypical form (U. S. Natl. Mus., no. 81922) is from Osman school, 5 miles east of West Union, Ohio.

Discosorus ehlersi Foerste

Pl. 27, fig. 3, 7

Discosorus conoideus HALL 1852, ("1851") (partim) in FOSTER & WHITNEY, Rept. Geol. Lake Superior land district pt. 2, pl. 34, fig. 3 (non fig. 2, *D. halli*).

Orthoceras? (*Discosorus*) *conoideus* BARRANDE, 1877, Syst. Sil., v. 2, suppl., pl. 437, fig. 19-22.

Discosorus conoideus FOORD, 1888, Cat. Foss. Ceph. Brit. Mus., v. 1, p. 194, fig. 25A-B.

Discosorus ehlersi FOERSTE 1924, (partim), Michigan Univ., Geol. Mus., Contrib., v. 2, p. 69, pl. 7, fig. 5A-B(?); pl. 8, fig. 4(?), 7 (non pl. 13, fig. 1A-B).

FOERSTE, 1925, Canada Geol. Survey, Mem. 145, p. 86, pl. 15, fig. 4, 5.

Beyond the fact that siphuncles attributed to this species by FOERSTE are, from all evidence, typical of *Discosorus*, they seem to have little in common. FOERSTE has designated as a type of this species the rather gently enlarging siphuncle from northern Michigan which FOORD (1888) figured. Another specimen (FOERSTE, 1924, pl. 7) is of interest in that it shows a typical *Discosorus* siphuncle attached to rock, septa (but no shell wall) being preserved at the anterior end. This specimen shows that at least 7 camerae occur between the anterior end of endocone material and base of the living chamber; possibly there are more, for it is not certain that space in front of the last septum represents the living chamber. The specimen unfortunately is doubtfully conspecific with the type of *D. ehlersi*, for segments of its siphuncle are shorter in proportion than those of the type. The siphuncle is obliquely weathered at the anterior end, great contraction of segments there not being natural. However, it is somewhat doubtful that the siphuncle expands uniformly as FOERSTE suggests in his reconstruction, since some species show a decrease in rate of expansion of the anterior segments, whereas others suggest an increase.

One specimen (FOERSTE, 1925, pl. 15, fig. 4) agrees quite closely with the holotype in proportion and I figure here (Pl. 27, fig. 3, 7) another from the Thornloe limestone of Lake Timiskaming, which is quite similar. A second Timiskaming specimen figured by FOERSTE (1925, pl. 15, fig. 5) differs in that the dorsal side of its

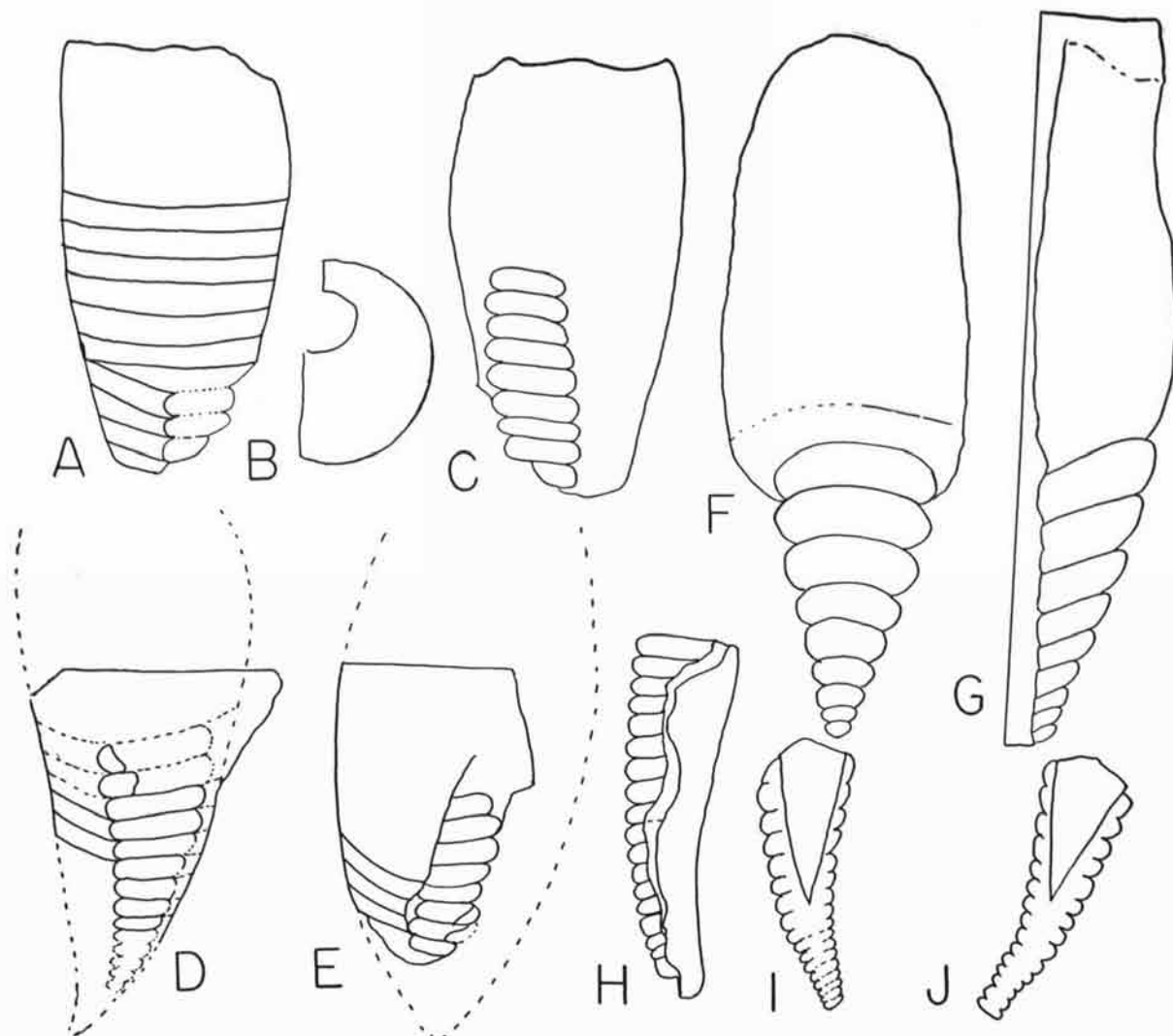


FIGURE 32. Representatives of the Discosoridae.

A-C. *Kayoceras biconoideum* (THOMAS); A, B, opposite lateral views of the holotype; C, part of a septum from the anterior end of a phragmocone of another specimen, showing cross section and position of siphuncle (FOERSTE, 1934).

D-E. *Discosorus* sp. cf. *D. ehlersi* FOERSTE; D, lateral view, venter at right; E, slightly oblique view of mid-ventral region slightly to right of center; dotted lines indicate partial restoration of shell outline (FOERSTE, 1934).

F-G. *Discosorus austini* FOERSTE; specimen evidently somewhat flattened vertically but retaining most, probably all, of the internal

mold of the living chamber; F, ventral view of holotype; G, lateral view, venter at right.

H. *Stokesoceras gracile* (FOORD), lateral view of siphuncle to which part of the dorsal wall of the shell is attached, venter at left (FOERSTE, 1924).

I-J. *Stokesoceras* sp. cf. *S. romingeri*, opposing sides of a vertical section of a siphuncle, showing form of endocone and strongly invaginated septal necks, evidently recumbent as in *Discosorus* (FOERSTE, 1924).

All figures are approximately 0.6.

siphuncle is concave instead of straight; this form shows a new variation in that the siphuncle segments show an atypically rapid increase in length.

The holotype of *Discosorus ehlersi* is from northern Michigan, presumably from the Manistique formation. Other specimens come from the Burnt Bluff and Manistique of the same region and from the equivalent Thornloe limestone (Middle Silurian) of Lake Timiskaming, Ontario.

Discosorus sp. cf. *D. ehlersi* Foerste

Text-fig. 32D,E

Discosorus cf. *ehlersi* FOERSTE, 1934, Denison Univ. Bull., Sci. Lab. Jour., v. 29, p. 176, pl. 42, fig. 2A,B.

Under this name FOERSTE has figured and described a *Discosorus* from Waukesha (lower coral) beds (Middle Silurian) of Ashford, Wis. The siphuncle is more like that of the type of

D. ehlersi than are many specimens assigned to that species. This specimen is particularly significant in that it shows (in addition to 7 siphuncle segments and portions of 2 more at the anterior end) some of the septa and part of the shell wall. The shell expands vertically throughout the length of the specimen moderately and apparently rather uniformly. Laterally the fairly rapid expansion of the initial part of the shell is lost and at the anterior end the walls scarcely diverge anteriorly. The siphuncle is quite close to the ventral wall of the shell.

The figured specimen is in the collection of the Department of Geology of the University of Wisconsin.

Discosorus gunensis Foerste

Discosorus gunensis FOERSTE, 1928, Canada Geol. Survey, Mem. 154, p. 301, pl. 46, fig. 3; pl. 49, fig. 1.

This species is known from two isolated portions of siphuncles from the Gun River beds of Anticosti. They are moderately expanding and thus approach *Stokesoceras*. The larger specimen shows that septal markings slope forward on the concave rather than convex side of the siphuncle. Nothing is known of the internal structure. The difference in septal markings makes this atypical of *Discosorus* and it may be allied to *Stokesoceras* instead.

Discosorus halli Foerste

Discosorus conoides HALL, 1852 ("1851") (*partim*), in FOSTER & WHITNEY, Rept. Geol. Lake Superior land district, p. 2, p. 222, pl. 34, fig. 2, (non fig. 3, = *D. ehlersi*).

Discosorus halli FOERSTE, 1924 (*partim*) Michigan Univ. Geol. Mus., Contrib., v. 2, p. 74, pl. 7, fig. 3, 4 (non pl. 8, fig. 4).

FOERSTE based this species upon a specimen figured by HALL (cited above) but identified with it other forms which show a much more rapid rate of increase in the size of siphuncle segments and it seems hardly possible that these could be conspecific with *Discosorus halli*. The holotype, which FOERSTE refigured, shows a series of 10 camerae, in which, curiously, the rate of enlargement tends to increase toward the anterior end of the specimen. The missing apex probably was slender, as in our Pl. 30, fig. 2. FOERSTE's pl. 7, fig. 4 illustrates a short very rapidly enlarging fragment, in which maximum width of the segments is tripled in the 5 extant camerae. It is close to the specimen figured by BIGSBY (FOERSTE, 1924, pl. 8, fig. 4) but not to the holotype of *D. halli*.

This species occurs in the Manistique dolomite, Middle Silurian of northern Michigan.

Discosorus humei Foerste

Pl. 29, fig. 4-6; Pl. 30, fig. 6

Discosorus humei FOERSTE, 1925, Canada Geol. Survey, Mem. 145, p. 85, pl. 14, fig. 5, 6, (non Pl. 4, fig. 6A-B).
? *Megadiscosorus remotus* FOERSTE, Same, p. 92, pl. 12, fig. 3A,B.

In the siphuncle from which this species is known the venter is strongly oblique to the plane of the septal markings and later growth stages show the expanded parts of the segments well aligned. The specimen here figured seems to supply a connection between the two specimens on which the species is based (with earlier siphuncle segments more rounded in outline) and the Timiskaming specimen which FOERSTE identified as *Megadiscosorus remotus*. The flattening of the siphuncle segments is a feature more typical of *Endodiscosorus*, but no clear generic distinction is possible on this character alone.

Discosorus humei occurs in the Thornloe limestone near Lake Timiskaming, Ontario.

Discosorus infelix (Billings)

Orihoceras infelix BILLINGS, 1866, Cat. Sil. fossils Anticosti, Canada Geol. Survey, p. 87.

— HYATT, 1883, Boston Soc. Nat. Hist., Proc., v. 22, p. 272.
Discosorus? infelix FOERSTE, 1928, Canada Geol. Survey, Mem. 154, p. 302, pl. 40, fig. 8.

The siphuncles from which this species is known are relatively straight and slender. Anterior portions of larger *Stokesoceras* species are quite similar and in absence of knowledge of internal structure, it is possible that *Discosorus? infelix* may actually be an actinoceroid.

The species occurs in the Jupiter formation (Silurian) of Anticosti Island.

Discosorus perexpansus Foerste

Discosorus perexpansum FOERSTE, 1936, Denison Univ. Bull., Sci. Lab., Jour., v. 29, p. 175, pl. 34, fig. 5A,B.

Definition of *Discosorus perexpansus* is based on a fragment consisting of 4 siphuncle segments (and part of a 5th segment) which are crushed and obviously distorted; they are more rapidly expanding than in *D. austini* and somewhat different in shape. Review of the description and illustration leaves the impression, however, that such differences could possibly be produced by distortion of the siphuncle of *D. austini*, and as known from the present single specimen, the species appears to be somewhat doubtful.

The holotype and only known specimen is from the Dayton limestone (Silurian), at Centerville, Ohio. The type is in the U. S. National Museum.

EXPLANATION OF PLATE 35

MANDALOCERATIDAE—Mandaloceras, Ovocerina

(Except as otherwise indicated all figures are $\times 1$ and illustrate specimens from Étage E_a, Middle Silurian, Bohemian basin. All are after BARRANDE, 1865; fig. 1, 2, from his pl. 72, fig. 3-6 from his pl. 71, fig. 7-10 from his pl. 70, and fig. 11-14 from his pl. 74.)

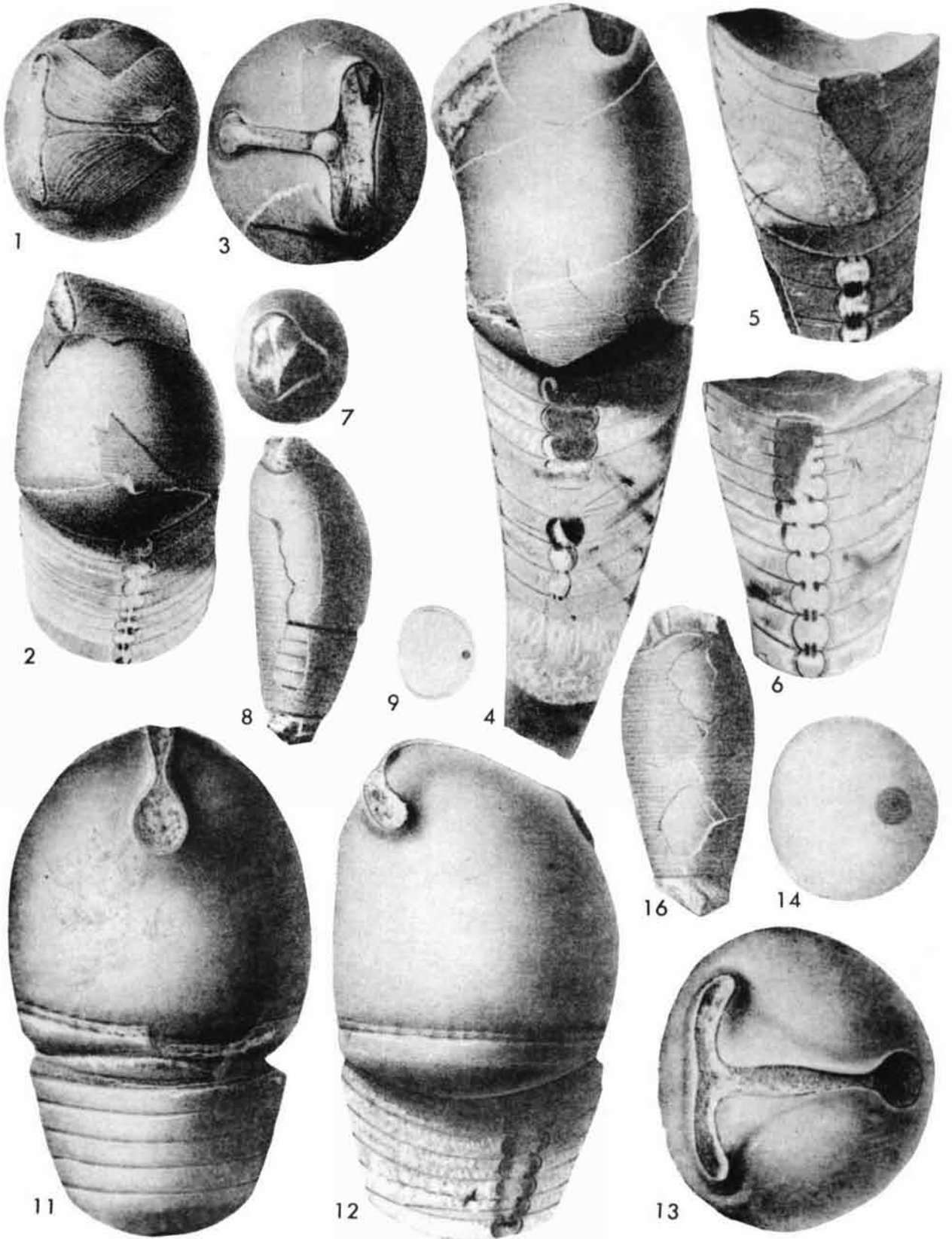
FIGURE

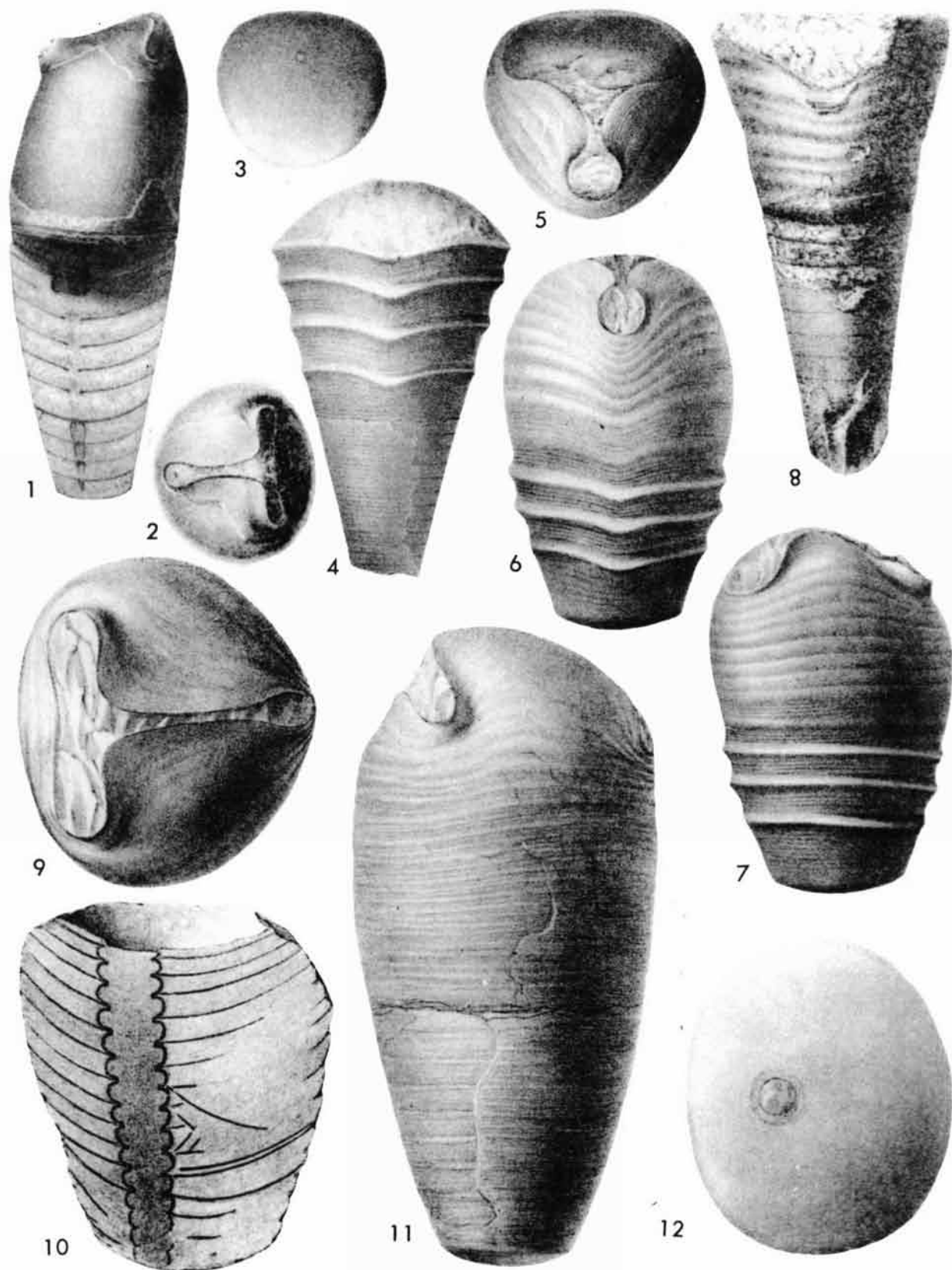
- 1,2. *Mandaloceras haueri* (BARRANDE), specimen from Karlstein, Bohemia.—1,2, Adoral and lateral views, venter at right, the sectioned phragmocone showing rapid increase in size of segments and "obstruction rings" in earlier ones.
3-6. *Mandaloceras verneuili* (BARRANDE), specimens from Lochkov, Bohemia.—3,4, Adoral and lateral views, venter at left, latter showing endogastric curvature and rapid enlargement of siphuncle segments with trace of "obstruction rings" adapically.—5, Another section showing more advanced "obstruction rings" suggestive of actinosiphonate deposits.—6, Section of a third specimen showing enlargement of siphuncle, shortening of anterior segments which approach

those of *Ovocerina alphaeus* in proportions, and "obstruction rings," which are immature above but large and apparently mature in the adapical segment.

- 7-9,16. *Ovocerina mumia* (BARRANDE), lectotype, here selected (from BARRANDE, 1865, pl. 70, fig. 10-13), from Dvoretz, Bohemia; a diminutive species with small ventral siphuncles and generalized apertures which belongs to the group of *O. mumia*. —7-9, Adoral, lateral, and septal views, with venter at right.—16, Dorsal view.

- 11-14. *Mandaloceras bohemicum* (BARRANDE), holotype and only figured specimen, from Dvoretz, Bohemia.—11, Ventral view, showing impression of bryozoans on living chamber.—12, Lateral view, venter at right, sectioned phragmocone showing rapid enlargement of siphuncle segments and (in adapical portion) small "obstruction rings."—13-14, Adoral and septal views, venter at right.





Discosorus parksi Foerste & Savage

Discosorus parksi FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 75, pl. 13, fig. 3A-C; pl. 8, fig. 3; pl. 23, fig. 8.

This species is known only from 3 segments of a siphuncle. Though subequal in size, they are so strongly oblique that their affinities with *Discosorus* are evident; further, the fragment indicates the greatest size known to be attained by the genus.

Discosorus parksi occurs in the Ekwan limestone (Middle Silurian) of Hudson Bay. The type is in the Savage Collection of the University of Illinois.

Discosorus troedssoni Foerste & Savage

Discosorus troedssoni FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 76, pl. 11, fig. 2A,B.
TEICHERT, 1937, Rept 5th Thule Exped., v. 1, no. 5, p. 146, pl. 18, fig. 5, 6.

The two known specimens of this species show a series of siphuncle segments, which are expanded, well rounded, oblique, and only very gently enlarging from the first to last. The portion known is very much smaller than the type of *Discosorus parksi* and the segments are more evenly rounded in their expansion. It is conceivable that the two are conspecific, *D. troedssoni* representing an early stage of *D. parksi*. Both species are anomalous in their straight siphuncles and absence of expansion as segments are traced forward through a considerable series. Such siphuncles are more typical of *Stokesoceras* than *Discosorus*, but it is perfectly possible that this may be a *Discosorus* in which the phragmocone is unusually prolonged, for some true *Discosorus* show marked reduction in rate of expansion of the siphuncle in anterior parts of the phragmocone. Nothing is known of the interior of the siphuncles of either species.

Both the holotype and specimen later figured by TEICHERT are from the Silurian of Southampton Island, in the Canadian Arctic.

Discosorus regularis Lee

Discosorus regularis LEE, 1912, Royal Phys. Soc. Edinburgh, Proc., v. 18, p. 261, p. 259, fig. 1.

This form has a slender conically expanding series of siphuncle segments, essentially straight, with outer walls of the segments strongly flattened. Segments are long in proportion to those of typical *Endodiscosorus*.

From the Silurian of Prince Regent Inlet, Southampton Island, Canadian Arctic.

Discosorus sp. cf. D. regularis Lee

Discosorus? sp. cf. *D. regularis* LEE, TEICHERT, 1937, Rept. 5th Thule Exped., v. 1, no. 5, p. 147, pl. 18, fig. 4.

Under this designation TEICHERT has figured a series of 6 segments of a siphuncle which agree closely with those of *Discosorus regularis* in outline and proportions.

The specimen is from the Silurian of Kûk, Duke of York Bay, Southampton Island, Canadian Arctic.

Discosorus sp. A

Pl. 29, fig. 1

This figured specimen is a thin section in a plane well off center of the siphuncle and probably considerably oblique in its longitudinal axis, for the cavity in the lower part seems to be an oblique section through the central tube. The section shows long recumbent brims at left, which apparently is the dorsal side of the siphuncle. Here also can be seen portions of the connecting ring (this section used in preparing text-fig. 7L) which furnished basis of discussion of the connecting ring of *Discosorus* given in Part I of the present work. The endocone material shows with unusual clarity the growth lines and lamellae normal to them.

The figured specimen, in the collection of the writer, is from an unknown locality, probably Lake Timiskaming, and presumably is from the Thornloe limestone (Middle Silurian).

Discosorus? sp. B

Discosorus? sp. FOERSTE, 1924, Michigan Univ., Geol. Mus., Contrib., v. 2, pl. 5, fig. 2; pl. 13, fig. 1A,B.

This specimen consists of 9 segments of a siphuncle, subequal in diameter, to which a portion of the shell is attached. Both siphuncle and shell are compressed in section, a feature which suggests *Discosorus*, as other shell-bearing siphuncles seem to have a compressed section. The siphuncle alone is suggestive of *Armenoceras*, but no shells of that genus are known in which the cross section is higher than wide. Forms with such large siphuncles are ordinarily broadly depressed in cross section. This specimen is anomalous in slenderness of the shell and siphuncle, in which segments are scarcely oblique to the axis. Nothing is known of the interior of the siphuncle segments. It is probable, but not demonstrable from present evidence, that this is a discosorid, but its form is certainly atypical of *Discosorus* or for that matter, any described discosorid genus.

This fossil occurs in the Burnt Bluff formation (Lower Silurian) of northern Michigan.

Discosorus? sp. C

Pl. 30, fig. 2

Under this rather noncommittal designation is figured a specimen (already noted in discussion of the family) in which early stages are typical of *Stokesoceras* but later more broadly expanding ones typical of *Discosorus*. A similar increase in rate of expansion characterizes *D. halli* but the increase occurs at a considerably later growth stage.

The figured specimen, from the Thornloe limestone (Middle Silurian) of Lake Timiskaming, is in the collection of the Geological Survey of Canada.

EXPLANATION OF PLATE 36

MANDALOCERATIDAE—Mandaloceras, Cinctoceras

(All figures are $\times 1$ and illustrate specimens from Étage E₂ (Middle Silurian, Bohemian basin. All figures are after BARRANDE, 1865; figs. 1, 2 from his pl. 68, figs. 3-7 from his pl. 88, fig. 8 from his pl. 70, and figs. 9-12 from his pl. 86-87.)

FIGURE

- 1,2. *Mandaloceras simplex* (BARRANDE), specimen from Karlstein, Bohemia.—1, Lateral view, venter at left, phragmocone sectioned, adoral segments (nearly hidden by shadow) being typically broad and adapical ones with small "obstruction rings" unusually slender.—2, Adoral view, venter at left.
3-7. *Cinctoceras agassizi* (BARRANDE), lectotype (Figs. 3,5-7), here selected, and paratype (Fig. 4), from Dvoretz, Bohemia.—3,5, Septal and adoral views, venter below.—6, Ventral view.—7, Lateral view, venter at right.—4, Lateral view of immature specimen (paratype).

8. *Cinctoceras singulare* (BARRANDE), holotype and only known specimen, from Kozorz, Bohemia. Ventral view of immature individual with aperture widely open.
9-12. *Cinctoceras imperiale* (BARRANDE), specimens from Dvoretz, Bohemia.—9, Adoral view of shell with well-preserved aperture, venter at right.—10, Vertical section of phragmocone showing large siphuncle segments with thick rings, venter at right.—11, Lateral view of a relatively complete specimen showing characteristic surface.—12, Septum showing flattening of dorsum and slightly dorsal position of siphuncle, venter at right.

Species Formerly Assigned to *Discosorus*

The following three species which have been referred doubtfully to *Discosorus* now are assigned to *Armenoceras* (TEICHERT, 1931): *D.?* *vestustus* FOERSTE, *D.?* *geronticus* FOERSTE, *D.?* *earltonense* FOERSTE.

Now placed in *Endodiscosorus* are *Discosorus?* *lyonense* FOERSTE and *D. remotus* FOERD.

Genus *STOKESOCERAS* Foerste, 1924

Type species—*Stokesoceras romingeri* FOERSTE

- Stokesoceras* FOERSTE 1924, Michigan Univ., Geol. Mus., Contrib., v. 2, p. 76.
 FOERSTE, 1925, Canada Geol. Survey, Mem. 145, p. 81.
 FOERSTE & SAVAGE, 1925, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 72.
 FOERSTE & TEICHERT, 1930, Same, v. 25, p. 214.
 TEICHERT, 1931, Am. Mus. Nat. Hist., Novitates, no. 512, p. 5, 11.
 FLOWER, 1940, Geol. Soc. America, Bull. v. 51, p. 1970.
Discosorus (*Stokesoceras*) SCHINDewolf, 1942, Jahrb. Reichstelle Bodenfor-
 schung, Band 62, p. 509.
Stokesoceras FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 436.
 FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 613.

FOERSTE erected this genus for species, known primarily from isolated siphuncles, which resemble those of *Discosorus* except for being much more slender and relatively straight. The two genera appear to be closely related to the point of intergradation insofar as form of the siphuncle segments is concerned, a matter which has already been noted adequately under the discussion of the *Discosoridae*.

Little is known of *Stokesoceras* except the siphuncle. FOERSTE figured a specimen of *S. gracile* (1924, pl. 8, fig. 2; here reproduced in text-fig. 32H) which retains part of the dorsal concave wall of the shell. From this specimen it is evident that the shell is slender, with siphuncle well removed from the dorsal wall and probably close to the ventral wall, and that the cross section of the shell is compressed. However, in some species the siphuncle is straight or very nearly so. *S. perobliquum* is atypical in the flattening of the expanded parts of the segments.

Two early stages (Pl. 30, fig. 1, 3) show recumbent necks dorsally and laterally but free necks ventrally. The endocones in these forms both exhibit a median elevation like that of *Discosorus*. One shows a zigzag central tube.

In contrast, *Stokesoceras* sp. cf. *S. romingeri* (FOERSTE, 1924, pl. 8, fig. 3; here shown in text-fig. 32I,) suggests recumbent brims on both dorsum and venter and a simple conical anterior end of the endocones. TEICHERT (1931, fig. 4) has illustrated a similar simple condition in *S.* sp. cf. *S. engadinense* with a straight central tube. The most remarkable structures noted in the genus are the annular structures at the anterior end of the tube (text-fig. 33) which FOERSTE (1924, pl. 7, fig. 2) figured for *S. engadinense*. *S.* sp. (Pl. 30, fig. 1) shows evidence of tubules branching from the central tube, a feature not noted in other members of the *Discosoridae*.

TEICHERT (1934) described *Stokesoceras balticum* and compared it with a number of orthoconic cephalopods described by BARRANDE. This comparison is extremely apt in that it opens up the intriguing possibility that *Stokesoceras* might be the origin of yet another deviation from the *Discosorida*, that of long straight cephalopods. While the problem is admittedly complex, this possibility seems

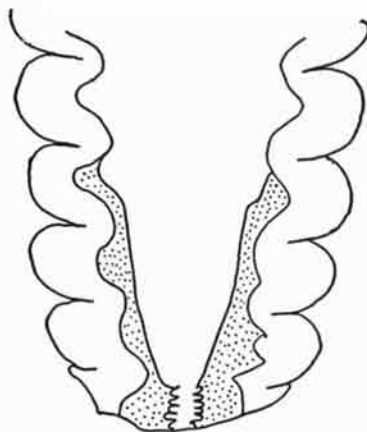


FIGURE 33. *Stokesoceras engadinense* Foerste

Section of siphuncle showing termination of cone in anterior end of tube in which broad annular structures develop, simulating a broadly expanded siphuncle, $\times 2$ (after FOERSTE, 1924, pl. 7, fig. 2).

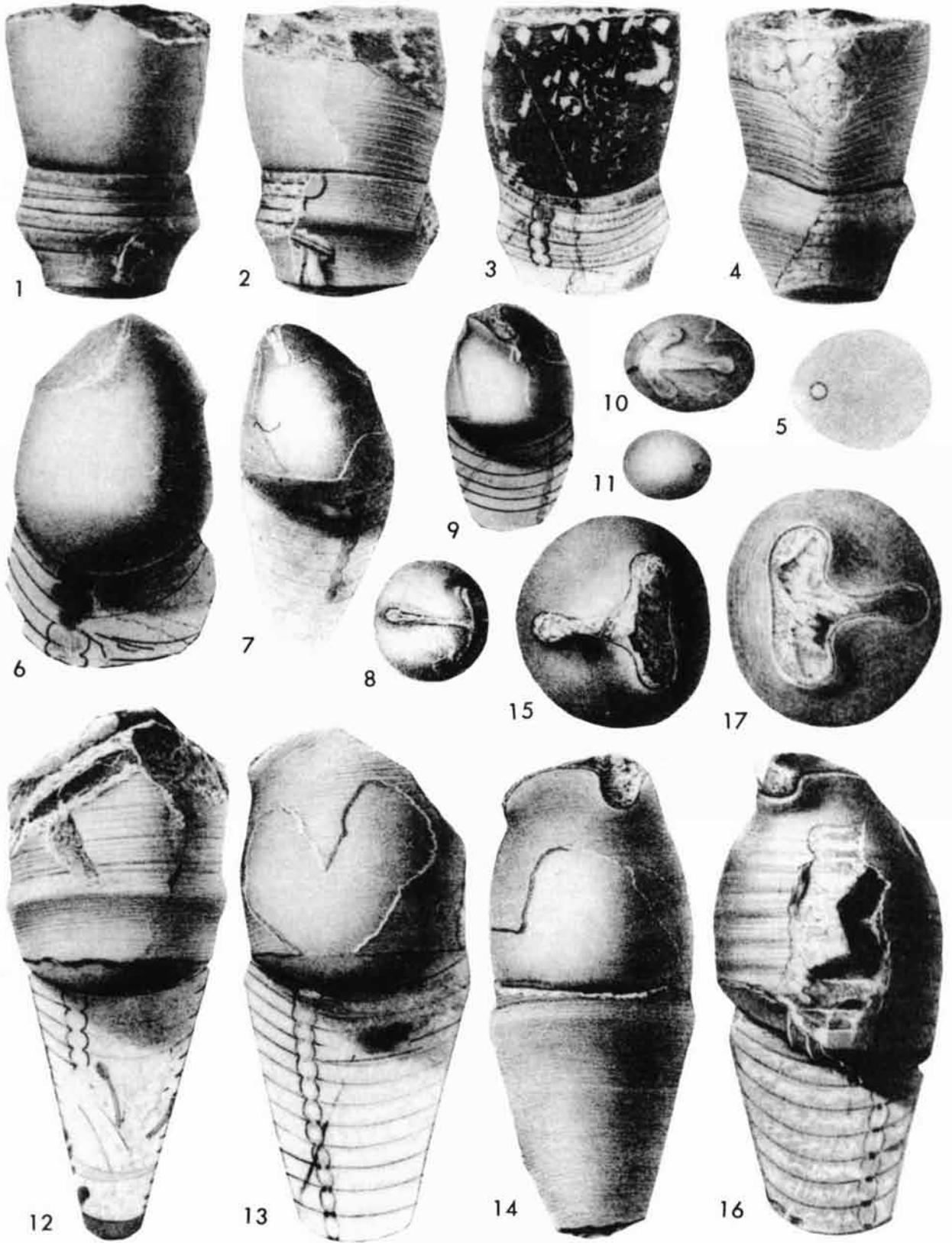
EXPLANATION OF PLATE 37

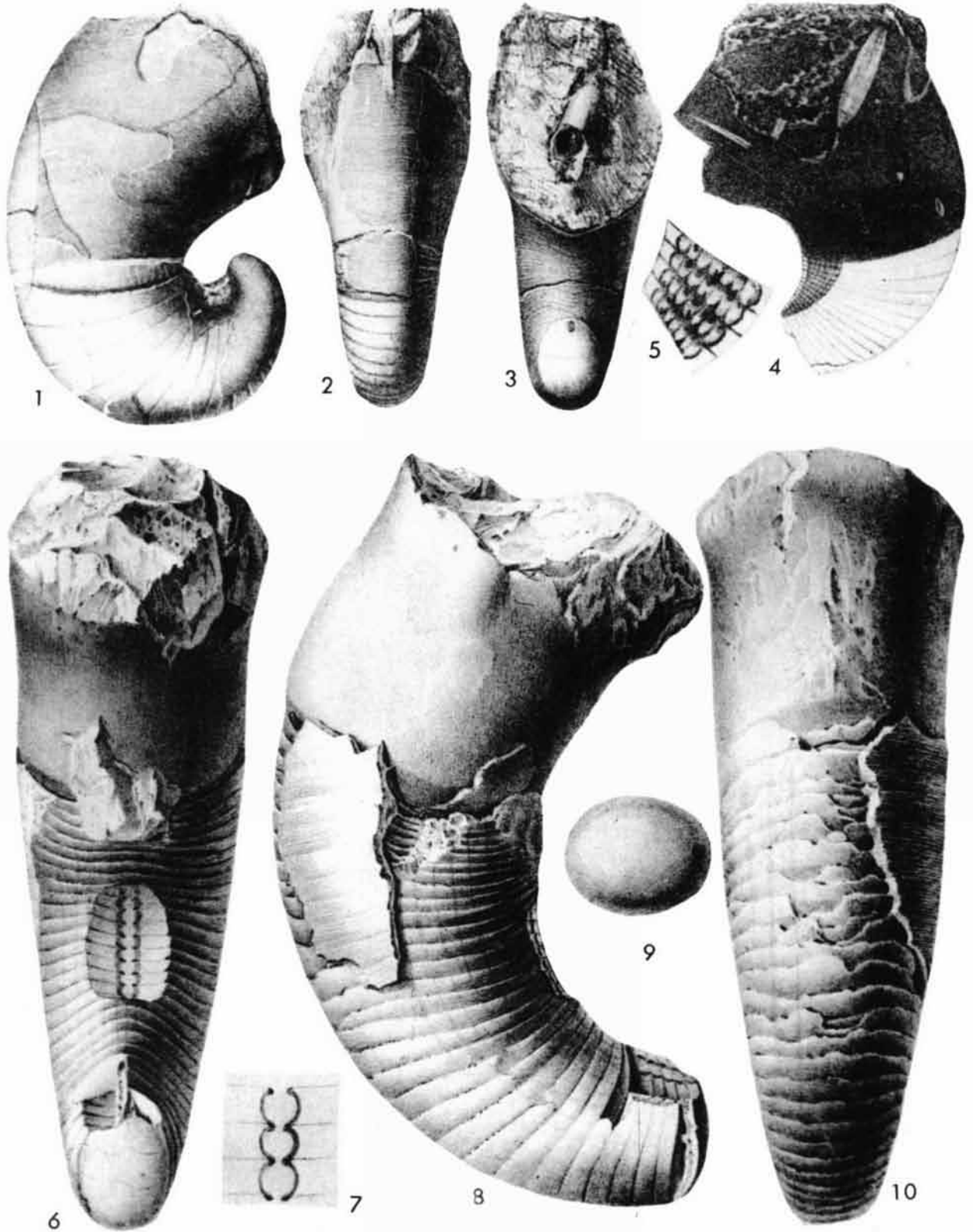
MANDALOCERATIDAE—*Vesporoceras*, *Umbeloceras*, *Cinctoceras*

(All figures are $\times 1$ and illustrate specimens from Étage E₂, Middle Silurian, Bohemian basin. All after BARRANDE, 1865; figs. 1-5 from his pl. 77, fig. 6, 9-11 from his pl. 82, fig. 7, 8 from his pl. 68, fig. 12-15 from his pl. 76, and fig. 16, 17 from his pl. 70.)

FIGURE

- 1-5. *Vesporoceras vespa* (BARRANDE), holotype from Karlstein, Bohemia.—1, Dorsal view.—2, Lateral view, venter at right.—3, Vertical section showing siphuncle segments, venter at left.—4, Ventral view.—5, Cross section with position of siphuncle indicated, venter at left.
6. *Vesporoceras perplexans* FLOWER, n. sp., holotype, from Karlstein, Bohemia. Lateral view, venter at right, showing slightly dorsal siphuncle with broad segments, as in *Ovocerina*.
- 7-8. *Umbeloceras incola* (BARRANDE), specimen from Lochkov, Bohemia.—7, Lateral view, venter at right, phragmocone sectioned, showing ventrally placed siphuncle composed of relatively slender empty segments.—8, Adoral view, venter at left.
- 9-11. *Umbeloceras spei* (BARRANDE), specimen from Lochkov, Bohemia.—9, Lateral view, venter at right, showing siphuncle more slender than in *U. incola*.—10-11, Adoral and septal views, venter at right.
- 12-15. *Vesporoceras cingulatum* (BARRANDE), specimens from Kozorz, Bohemia.—12, Lateral view of immature individual with open aperture, venter at left.—13, Specimen showing slightly later growth stage, with annular expansion on phragmocone and normal contracted living chamber of the adult stage, venter at left.—14, 15, Lateral and adoral views of a similar but slightly smaller individual, venter at right.
- 16-17. *Cinctoceras robustum* (BARRANDE), specimen from Kozorz, Bohemia.—16, 17, Lateral and adoral views, venter at right, phragmocone showing relatively slender siphuncle containing "obstruction rings."





an unlikely one, and indeed, I am inclined to believe that the species in question is not a true *Stokesoceras* but a member of the Michelinoceratidae, possibly assignable to the Stereoplasmoderatidae, in which deposits within the siphuncle join to form endocones. Already two examples of such structure are known in the Ordovician, in *Troedssonella* KOBAYASHI (based on *Polygrammoceras endoceroides* TROEDSSON from the upper gray Orthoceras limestone) and *Striatoceras striatum* and *S. lineatum*, from the Cape Calhoun series of Greenland. The matter is one requiring further investigation and it is hoped that material now on hand but not yet fully prepared for study may shed new light on the problem. The evident fact that orthocones with expanded siphuncle segments may develop endocone-like linings as early as Ordovician weakens the probability that Silurian and Devonian types may be of discosorid origin.

Stokesoceras romingeri Foerste

- ?*Discosorus*—BARRANDE, 1877, Syst. Sil., v. 2, suppl., pl. 474, fig. 9, 10.
 ?*Discosorus gracilis* FOORD, 1888, (partim) Cat. Fossil Ceph. Brit. Mus., v. 1, p. 198, fig. 26B.
Stokesoceras romingeri FOERSTE, 1924, Michigan Univ., Geol. Mus., Contrib., v. 2, p. 77, pl. 9, fig. 3, 4, 6 (non fig. 2).
Stokesoceras cf. romingeri FOERSTE, 1924, Same, pl. 8, fig. 3A,B; pl. 9, fig. 7.
Stokesoceras romingeri FOERSTE, 1925, Canada Geol. Survey, Mem. 145, p. 82, pl. 16, fig. 3.

The holotype is a relatively long portion of a siphuncle showing 26 segments, which are well rounded, scarcely oblique, and very gradually enlarging. Other specimens figured show some variation in rate of expansion of the segments and obliquity of the septal markings. Except for a specimen (FOERSTE, 1924, pl. 9, fig. 2) which TEICHERT (1931) has removed to *Endodiscosorus*, none of the figured fossils shows the typical internal structure. The reassigned specimen just mentioned is singular in showing a very slender apical end in which the annular condition of segments is lost and though the interior is exposed by weathering adorally, no structures are observed. It is evident that *Stokesoceras romingeri* is characterized by wide variation or else the species has been too broadly defined. Unfortunately this type species, the type of the genus, yields no information as to the siphuncle wall or endocones. Such information is yielded only by one specimen (here illustrated in text-fig. 32I), a siphuncle which is much more strongly curved and considerably more rapidly expanding than the holotype, so much so that specific identity of the two seems extremely dubious. The segments suggest long recumbent brims and there is a long endocone with a simple termination.

As at present delimited, *Stokesoceras romingeri* is common to the Burnt Bluff and overlying Manistique dolomites of northern Michigan. A specimen attributed to the species from the Thornloe limestone (Middle Silurian) of Lake Timiskaming is typical and agrees much more closely with the type in proportions than do many of the specimens figured from northern Michigan.

Stokesoceras engadinense Foerste

Text-fig. 33

- Orthoceras (Discosorus) conoides* BARRANDE, 1877, Syst. Sil., v. 2, suppl., pl. 474, fig. 7, 8.
Stokesoceras engadinense FOERSTE, 1924, Michigan Univ., Geol. Mus., Contrib., v. 2, p. 82, pl. 9, fig. 1, 25; pl. 7, fig. 2.
 ——— FOERSTE, 1925, Canada Geol. Survey, Mem. 145, p. 83, pl. 16, fig. 2 (as *S. cf. engadinense* in explanation of plates).
Stokesoceras cf. engadinense TEICHERT, 1931, Am. Mus. Nat. Hist., Novitates, no. 512, p. 9, fig. 4.

Only siphuncles of this species are known. They attain a relatively large size, and increase in width of the segment is not accompanied by a corresponding increase in their lengths. One sectioned specimen (text-fig. 33) is unique in showing a strongly annular anterior end of the tube. In this section the septal necks are plainly developed into long recumbent brims.

Stokesoceras engadinense is known only from the Manistique formation (Middle Silurian) of northern Michigan.

Stokesoceras ekwanense Foerste & Savage

- Stokesoceras ekwanense* FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 73, pl. 6, fig. 2; pl. 7, fig. 6; pl. 11, fig. 6.

This species is based upon three siphuncles, annulated, gently expanding forward, and so large that the latest portion figured could belong to an *Armenoceras*. The internal structure is as yet unknown.

The species is from the Ekwan limestone (Middle Silurian) on the west side of Hudson Bay. Types are in the Savage Collection of the University of Illinois.

Stokesoceras gracile (Foord)

Text-fig. 32H

- Discosorus gracilis* FOORD, 1888, Cat. Fossil Ceph. Brit. Mus., v. 1, p. 198, fig. 26A (non fig. 26B).
Stokesoceras gracile FOERSTE, 1924, Michigan Univ., Geol. Mus., Contrib., v. 2, p. 81, pl. 8, fig. 2.
 ——— FOERSTE, 1925, Canada Geol. Survey, Mem. 145, p. 82, pl. 15, fig. 9A,B.

The holotype and apparently only known specimen consists of a series of siphuncle segments to which part of the concave dorsal part of the shell is attached. In slender form the species is typical of *Stokesoceras* and the shell shows that the siphuncle is far from the dorsum and probably close to the venter and that the cross section of the shell is compressed. The form is atypical however in that the sutures slope forward from venter to dorsum. Possibly *Discosorus gunensis*, which shows this same condition, is related.

The species is from the Manistique formation (Middle Silurian) of Drummond Island, northern Michigan.

Stokesoceras? keewatinense (Whiteaves)

- Actinoceras keewatinense* WHITEAVES, 1904, Canada Geol. Survey, Ann. Rep., new ser., no. 14, App. F, p. 54.
 ——— WHITEAVES, 1906, Canada Geol. Survey, Paleoz. Fossils, v. 3, pt. 4, p. 246, 263, pl. 30, fig. 7, 8.
Stokesoceras? keewatinense FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 74.

EXPLANATION OF PLATE 38 PHRAGMOCERATIDAE—Protophragmoceras

(Except as otherwise indicated all figures are $\times 1$ and illustrate specimens from Étage E₃, Middle Silurian, Bohemian basin. All after BARRANDE, 1865; fig. 1-5 from his pl. 165, fig. 6-10 from his pl. 173.)

FIGURE

1-5. *Protophragmoceras beaumonti* (BARRANDE), from Bohemian basin.—1-3, Lateral, dorsal and ventral views of lecto-holotype.—4, Vertical section of another specimen showing remarkably expanded siphuncle containing festooned deposits.—5, Part of siphuncle from specimen illustrated in Fig. 4, about $\times 2.5$.

6-10. *Protophragmoceras conspicuum* (BARRANDE), holotype, from Bohemian basin.—6, Ventral view, venter partly ground away so as to expose siphuncle.—7, Part of siphuncle, about $\times 2.5$.—8, Lateral view, venter at right.—9, Septum at base, venter at right.—10, Dorsal view, showing faint longitudinal lirae of internal mold of phragmocone and adoral reduction in rate of expansion.

Assignment of this species, based on part of a siphuncle 87 mm. in length, to *Stokesoceras* is doubtful, as FOERSTE & SAVAGE indicate. The internal structure has not been observed.

Stokesoceras? *perobliquum* Foerste

Stokesoceras perobliquum FOERSTE, 1925, Canada Geol. Survey, Mem. 145, p. 84, pl. 11, fig. 6.

(non) *Stokesoceras perobliquum* FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 73, pl. 13, fig. 4A,B.

The holotype, from the Thornloe limestone (Middle Silurian) of Lake Timiskaming, is a slightly curved gently expanding siphuncle with externally flattened segments suggesting *Endodiscosorus*. Segments are slightly oblique, sloping forward on the ventral convex side. Nothing is known of the internal structure.

The specimen from Silurian rocks of Southampton Island, Canadian Arctic, which tentatively is identified with this species has more rounded and more oblique segments. From evidence presented by this specimen alone, it could be part of the siphuncle of an otherwise unknown species of *Tuyloceras*.

Stokesoceras cylindratum Foerste & Savage

Stokesoceras cylindratum FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 72, pl. 18, fig. 4.

This species is known only from a slender straight siphuncle composed of the usual short broadly expanded segments. Externally it is typical of *Stokesoceras* but internally it is unknown.

The type and only known specimen comes from the Ekwan limestone (Middle Silurian) of the Ekwan River; it is in the Savage Collection of the University of Illinois.

Stokesoceras sp. A

Stokesoceras sp. TEICHERT, 1937, Rept. 5th Thule Exped., v. 1, no. 5, p. 147, pl. 18, fig. 7, 8.

Under this designation are figured 4 segments of a siphuncle, typical of *Stokesoceras* in their gradual expansion, slender form, and expanded segments; they are rather long in proportion to their diameter and are moderately oblique. Internal structure is not known.

The fossil comes from the Silurian of Kûk, Duke of York Bay, Southampton Island, Canadian Arctic.

Stokesoceras spp. B and C

Pl. 30, fig. 1, 3

Under this designation are noted two sections showing the early stages of discosorids. The first, *Stokesoceras* sp. B (Pl. 30, fig. 1), represents a small siphuncle 23 mm. long, showing 10 segments, with an apical angle of 25 degrees. The segments are more broadly rounded in outline basally than adorally; at the anterior end on the venter the segments are slightly flattened, but not enough so to suggest *Endodiscosorus* closely. At the anterior end of the specimen on the dorsum the septal neck is recumbent but the fourth septal neck on the ventral side is narrowly free. Structures within the endocone material are obscured by replacement, the material being largely silicified. The conical outline of the anterior end of the deposit is modified by a median elevation through which pass two tubes. Farther adapically the central tube can be seen to follow a zigzag course and at one point a portion of the tube is plainly bifurcated, suggesting existence of some branching. Probably the section does not show the anterior opening of the main tube but some lateral accessory tubes instead. This section is of particular interest as the only one thus far observed showing such branching of the central tube, which is straight in some species. Though endocone material is replaced, it is quite evident from this section that segments of the siphuncle are rounded to the apex and there is no evidence of thick rings which might be destroyed here or of bullettes which could not have been

lost similarly. The figured specimen, from the Thornloe limestone (Middle Silurian) of Lake Timiskaming, is in the collection of the Geological Survey of Canada.

A second specimen, designated as *Stokesoceras* sp. C (Pl. 30, fig. 3), in collections of the Canada Geological Survey from the same locality and horizon as *S.* sp. B, is a tiny siphuncle with apex much smaller than that of any true *Discosorus*. It is considerably more rapidly expanding and the expanded portions of the segments are slightly flattened so that the aspect approaches that of *Endodiscosorus* to some extent. The section is a horizontal longitudinal one showing the septa recurved on both sides forming very long recumbent brims. The last endocone has a faintly sinuous outline and bears an unusually slender strongly elevated median protuberance. The plane of the section shows the central tube only as a small subquadrate cavity in the 3rd and 4th segments from the apex; the section is oblique to the plane of the tube. The apical segments are scarcely more rounded in outline than anterior ones. Absence of bullettes is evident and there is no trace of a thickened connecting ring. Replacement is responsible for coarse white material, largely silica, on the outside of the siphuncle and forming a thinner band outlining the last endocone. Longitudinal fibrous material in the center of the section is probably a replacement phenomenon also; through it growth lines of the endocones can be seen, though they are faint.

Discussion. Though the specific affinities of these two specimens are uncertain, they are of particular interest in that they show adapical portions of discosorid siphuncles not previously observed or figured. It is probable that they represent the initial parts of siphuncles though from isolated specimens which are slightly abraded externally this cannot be proved. Assignment to *Stokesoceras* rather than to *Discosorus* rests upon the fact that typical *Discosorus* has early portions of siphuncles much more rapidly expanded and all evidence indicates that initial siphuncle segments are about three times the size of those shown in the present specimens. The genotype of *Endodiscosorus* appears to have a singularly large blunt siphuncle apex also. The central elevation of the endocone material is a feature not previously noted in *Stokesoceras*, and suggestion of lateral branching of the central tube shown by *S.* sp. B have not been observed elsewhere in the Discosoridae.

Genus ENDODISCOSORUS Teichert, 1931

Type species—*Endodiscosorus foerstei* TEICHERT

Endodiscosorus TEICHERT, 1931, Am. Mus. Nat. Hist., Novitates, no. 512, p. 10.

Discosorus (*Endodiscosorus*) SCHINDEWOLF, 1942, Jahrb. Reichstelle f. Bodenforschung, Band 62, p. 509.

Only the siphuncle of this genus is known. It is composed of annular segments that enlarge rapidly initially and are more slender adorally. Expanded portions of the segments are strongly flattened and well aligned, with flattening more pronounced on the basal part of the convex side, which is apparently ventral. The endocones are particularly massive and leave a smooth anterior cavity without the median elevation found in *Discosorus*.

Discussion. Only the type species has been assigned to this species previously, though TEICHERT noted that one of the specimens figured by BARRANDE appears to belong here. Several species of both *Discosorus* and *Stokesoceras* approach *Endodiscosorus* in the characteristic external flattening of the expanded segments. On this basis it is extremely difficult to draw definite generic boundaries but rejection of *Endodiscosorus* as a junior synonym is not to be recommended, especially since there is doubt whether it should be allied to *Discosorus* or *Stokesoceras*; further, any reduction would attain stability only

when a single genus remained in the family Discosoridae. The internal differences are real enough to justify recognition of *Endodiscosorus*. Unfortunately, species currently assigned to *Stokesoceras* and *Discosorus* which approach *Endodiscosorus* in aspect of the siphuncle exterior furnish no information of the interior of the siphuncle.

Endodiscosorus foerstei Teichert

Pl. 30, fig. 4, 5

Endodiscosorus foerstei TEICHERT, 1931, Am. Mus. Nat. Hist., Novitates, no. 512, p. 10, fig. 8, 9.

The holotype of the species is a small siphuncle 30 mm. long that enlarges from a blunt apex 17 mm. high to 21 mm., most of the expansion occurring in the adapical half of the specimen. The supposed ventral side is convex, with basal segments more flattened than anterior ones; the opposite side is nearly straight. Septa are so nearly transverse that orientation is uncertain, but convexity of the venter is suggested by those species of *Discosorus* which approach *E. foerstei* most closely in proportions.

The weathered side of the siphuncle shows strongly invaginated septa at the base on the venter; on the dorsum they are less evident, which is possibly more a matter of preservation than a real difference. The cone is smooth, terminating in a tube placed slightly addorsal from the center but running straight to the middle of the apex. Though the surface of the cone approaches the siphuncle wall at its anterior end, it is smooth and fails to show the usual annular form found in true *Discosorus*.

The holotype, from the Timiskaming region of Canada, is evidently from the Thornloe limestone (Middle Silurian). Originally in the collection of Dr. CURT TEICHERT, it is being deposited in the collection of the Geological Survey of Canada, no. 12,392.

Endodiscosorus sp.

Orthoceras? (*Discosorus*) sp. BARRANDE, 1877, Syst. Sil., v. 2, suppl., pl. 474, fig. 9, 10.

Stokesoceras romingeri FOERSTE, 1924, Michigan Univ., Geol. Mus., Contrib., v. 2, p. 77 (partim) pl. 9, fig. 2.

Endodiscosorus sp. TEICHERT, 1931, Am. Mus. Nat. Hist., Novitates, no. 512, p. 2, fig. 1.

This form is known only from a small straight siphuncle of annular type with a well-defined anterior margin of the endocones forming a narrow cone, rounded slightly at its base. The specimen calls attention to the occurrence of *Endodiscosorus* in the Silurian of northern Michigan and suggests that in part this genus is very close to typical *Stokesoceras*, to which FOERSTE assigned this fossil.

Endodiscosorus remotus (Foord)

Discosorus remotus FOORD, 1888, Cat. Fossil Ceph. Brit. Mus., v. 1, p. 197.

Discosorus? *remotus* FOERSTE, 1924, Michigan Univ., Geol. Mus., Contrib., v. 2, p. 75, pl. 4, fig. 6A, B.

In refiguring this species FOERSTE noted that it is not a typical *Discosorus*. The flattening of the expanded portions of the segments, vertical in profile of the dorsum, and oblique profile of the venter in reference to the septa show definite affinities between this form and *Endodiscosorus foerstei*. However, *E. remotus* has much longer siphuncle segments which enlarge slightly more rapidly. Both species show an adoral decrease in rate of enlargement of the segments.

The holotype is in the British Museum of Natural History. It is from Drummond Island, Lake Huron, occurring probably in the Manistique formation (Middle Silurian).

Endodiscosorus lyonensis (Foerste)

Discosorus? *lyonense* FOERSTE, 1936, Denison Univ. Bull., Sci. Lab., Jour., v. 29, p. 178, pl. 34, fig. 2A, B.

The holotype consists of 7 segments of a siphuncle, blunt apically, enlarging rapidly in the first 4 segments, then becoming extremely slender. The expanded parts of the segments are strongly flattened, the supposed ventral side being expanded and the opposite side straight in reference to the septal markings. In form the siphuncle is perfectly typical of *Endodiscosorus*, approaching *E. foerstei* in the shortness of segments in proportion to their diameters. It is, however, a giant as compared with *E. foerstei* and the expansion of the siphuncle on the ventral side is much more pronounced in *E. lyonense*.

This species is from the Hopkinton dolomite (Middle Silurian) of Iowa. Only the holotype (U. S. Natl. Mus., no. 7786) is known.

Genus KAYOCERAS Foerste, 1934

Type species— *Discosorus?* *biconoideum* THOMAS

Kayoceras FOERSTE, 1934, Denison Univ. Bull., Sci. Lab., Jour., v. 29, p. 183.

This genus was erected for reception of two species with broadly expanded siphuncles of evidently discosorid type and septal markings nearly normal to the axis of the siphuncle instead of markedly oblique. A nearly complete anterior portion of the shell is known. The cross section is slightly broader than high, dorsum and venter being so nearly equal in small convexity of profile as to leave some doubt as to whether the shell is slightly endogastric or exogastric. The siphuncle lies between the center and presumed ventral wall of the shell, the expanded segments being separated from this wall by about half their maximum diameter. Sutures are transverse and exhibit shallow lateral lobes. A good part of the living chamber is known, but features of the aperture are unknown.

Discussion. FOERSTE compared this genus with *Discosorus*. Isolated siphuncles differ from those of *Discosorus* by very faint obliquity of the septal markings, which indicates position of the siphuncle to be relatively close to the center of the shell. However, segments in the known portion of the shell show scarcely any adoral expansion, and indeed, the last few segments show a very slight decrease in diameter. On this basis, the genus is more readily confused with *Stokesoceras* than *Discosorus*. The matter is not of great importance, for these two genera are very closely related.

Internal features of the siphuncle have not been observed in *Kayoceras*. The breviconic shell indicates that it is a discosorid and not a relative of *Armenoceras* of the Actinoceratidae.

The two known species are both from the Hopkinton, lower Clintonian (Middle Silurian), of Iowa.

Kayoceras biconoideum (Thomas)

Text-fig. 32A-C

Discosorus? *biconoideum* THOMAS, 1915, Iowa Acad. Sci., Proc., v. 22, p. 298 (partim), pl. 34, fig. 2 (non fig. 1).

Kayoceras biconoideum FOERSTE, 1934, Denison Univ. Bull., Sci. Lab., Jour., v. 29, p. 183, pl. 31, fig. 1A-C; pl. 41, fig. 2.

Kayoceras thomasi Foerste

Discosorus biconoideum THOMAS, 1915, Iowa Acad. Sci., Proc., v. 22, p. 298 (partim), pl. 34, fig. 1 (non fig. 2).

Kayoceras thomasi FOERSTE, 1934, Denison Univ. Bull., Sci. Lab., Jour., v. 29, p. 186, pl. 41, fig. 3

Genus *ALPENOCERAS* Foerste, 1927Type species—*Alpenoceras ulrichi* FOERSTE

- Alpenoceras* FOERSTE, 1927, Michigan Univ., Geol. Mus., Contrib., v. 2, p. 205.
 FLOWER, 1945, Am. Midland Naturalist, v. 33, p. 698.
 FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 613.
Endodiscosorus (*Endostokesoceras*) SCHINDEWOLF, 1942, Jahrb. Reichstelle f. Bodenforschung, Band 62, p. 509.
Discosorus (*Neodiscosorus*) SCHINDEWOLF, 1942, Same, p. 509.

Shell cyrtoconic, endogastric, moderately breviconic, expanding fairly rapidly to the middle of the mature living chamber which contracts faintly at the aperture. Cross section originally slightly depressed, sutures essentially straight and transverse. Surface with growth lines showing moderately developed hyponomic sinus on the concave ventral side throughout life. Siphuncles close to concave ventral side of the shell, its segments nummuloidal and reported by FOERSTE to have continuous lining within. Restudy of the type species shows that the siphuncle has subquadrate slightly rounded segments, the siphuncle being broadly adnate to septa on the dorsum at the anterior end and more narrowly adnate on the venter at the adapical end. The connecting rings are originally thick and supplemented by a secondary thickening on the outside, which extends a short distance along the surface of the septum at the anterior end of each camera. Deposits within the siphuncle of the type species are identical with those of the Discosoridae and differ from those figured by SCHINDEWOLF representing species from the Middle Devonian of the Eifel region, Germany, only in that diaphragms crossing the central canal are not evident in our material.

The siphuncle segments broaden and become more rounded in outline as they are traced adorally in the shell. The fullest expression of this development is indicated in the adoral end of the sectioned part of the type of *A. ulrichi* but not fully shown, as the anterior end of the phragmocone was not sectioned.

Originally only *Alpenoceras ulrichi* was assigned to this genus. Restudy of the type material of *Cyrtoceras occidentale* WHITEAVES revealed not one but two additional species which are described below. Later SCHINDEWOLF (1942) described as *Endodiscosorus* (*Endostokesoceras*) *eifelsenis* and *Discosorus* (*Neodiscosorus*) *robustus* forms from the Eifel (Devonian) of Germany which are clearly nothing more than specimens (mostly isolated siphuncles) of typical *Alpenoceras*. Unfortunately, SCHINDEWOLF ignored the genus *Alpenoceras* in making his comparisons and in the process of making generic assignments has so revised the genera of Discosoridae that, by definition, the type species of *Endodiscosorus* is excluded from that genus. The slight differences shown by the European species, consisting of more rounded segments of the siphuncle and the presence of diaphragms crossing the central canal, are not deemed worthy of recognition by the erection of a new genus. The first character varies with the growth stage, adoral segments being more rounded than adapical ones. Also, the faintly quadrate condition of the early segments is more prominent in a section than in an isolated siphuncle. While no diaphragms are observed in the American species, it must be remembered that only the adapical part of the one known specimen of *A. ulrichi* has been sectioned and only one portion of *A. occidentale*, where the

preservation is very unfavorable for the preservation of such details, has been studied.

The interpretation of the genus as endogastric could conceivably be incorrect, in spite of a sinus on the concave side of *Alpenoceras ulrichi*. It is not impossible that the shell may be exogastric, with a dorsal siphuncle. No sinus on the concave side is indicated for *A. eifelsenis*, though one good exterior of the shell is figured by SCHINDEWOLF (1942, pl. 1), on the basis of which affinities of that species with *Alpenoceras* are obvious.

Alpenoceras ulrichi Foerste

Pl. 31, fig. 1-4

- Alpenoceras ulrichi* FOERSTE, 1927, Michigan Univ., Geol. Mus., Contrib., v. 2, p. 206, pl. 1, fig. 2a-g; pl. 5, fig. 2.

The shell, 100 mm. in length, is slightly curved, expanding from a height of 14 mm. and width of 18 mm. to 45 and 32 mm., respectively, the adoral end being definitely crushed vertically. The anterior end of the shell is poorly preserved but it is evident that the shell contracted slightly as it approached the aperture. Growth lines of the surface are fine, faint, and closely spaced. The figures accompanying FOERSTE's description are retouched and do not give a correct idea of this feature.

The apical part of the specimen, 25 mm. long on the venter, contains 9.5 camerae. FOERSTE ground away a region here, removing material and making a cavity at an acute angle. It is evident that the siphuncle structure thus exposed, is that of a discosorid, but unfortunately it was necessary to remove some of the lateral portion of the type in order to photograph the siphuncle. Permission for this was given by Dr. EHLERS of the University of Michigan.

The section exposes 9.5 camerae, the apical segment being incomplete; the next is 2.75 mm. long, expanding from 1.5 mm. to 2.7 mm. The segments widen adorally more rapidly than they increase in length, so that the last complete segment is 4 mm. long, expanding from 3 mm. to 5 mm. Septal necks are very short, strongly recurved, and, in the only available section, are presumably not quite in contact with the free part of the septum, though as can be seen, the margins of the septal necks are not very clear. The segments are more strongly inflated on the dorsum than venter. On the dorsal side the adoral end of the connecting ring lies in contact with the free part of the septum; there is no such area on this side at the adapical end. On the dorsal side, the segment is less strongly inflated; no real area of adnation exists at the adoral end of the segment and only a very slight one at the adapical end. The greatest width of the segment is on the adoral side of its mid-length.

The connecting rings are relatively thick. Longitudinal lamellae are present but faint and rather variable. It is evident that the anterior end of the ring forms a broad vinculum, as in *Faberoceras*. A suggestion of textural differentiation is seen here but, as may be expected from an opaque section, it is obscure and variable from one segment to another. The upper left of Pl. 31, fig. 1, shows most clearly a differentiation of the adapical end of the ring, the bullette, indicating that structural differentiation of this part of the ring persists even though its swollen condition is lost.

Deposits within the siphuncle occupy the 7 adapical camerae of the 9.5 in the sectioned portion of the type. Clearly no annular deposits, such as characterize the Westonoceratidae, occur and a simple system of endocones comparable to those in *Discosorus* is found instead. Where the irregular endocone reaches its tip and becomes a tube, there is no evidence of irregularities at the base of the cone such as are found in some discosorids. The tube, however, appears to be a real structure, as textural differences can be seen which distinguish its rather narrow walls from the lamellar structure of the endocones. Growth lines in the endocones are not apparent in this specimen. The structure consists mainly of lamellae normal to the inner surface of the cones. The apical part

of the tube, which is slightly and irregularly inflated near the middle of each segment of the siphuncle, contains some calcite, which is probably not organic. No trace of diaphragms crossing the tube can be seen in the type. In outline the adapical segments of the siphuncle are faintly quadrangular and trapezoidal, with greatest width at the anterior end of the segment. Farther adorally, the more mature segments are both wider at the septal foramen in proportion to their length and outlines of the segments become more evenly rounded.

On two points the type is ambiguous. Septation is scarcely evident from the exterior. It is uncertain whether the adoral 50 mm. is the living chamber, or whether it may contain some camerae. The point is not important as regards recognition of the species, because congeners of *A. ulrichi* are very different in proportions. The original cross section is questionable. FOERSTE considered it nearly circular, with perhaps slight lateral compression. The type, which is least distorted at the base, shows there a slightly depressed cross section that is definitely wider than high. This depressed condition I believe to be original, a view which receives some support from the depressed cross section of the only congeneric American species, *A. occidentale* and *A. sinuiferum*.

The holotype is University of Michigan, Museum of Paleontology, no. 10031. No other specimens are yet known.

This species is from the Alpena limestone, at a quarry of the Michigan Alkali Company, Alpena, Mich.

Alpenoceras occidentale (Whiteaves)

Pl. 32, fig. 1-7; Pl. 33, fig. 7, 8

Cyrtoceras occidentale WHITEAVES, 1890, Royal Soc. Canada, Trans., v. 8, sec. 4, p. 103-4, pl. 7, fig. 5, 6.

WHITEAVES, 1892, Canada Geol. Survey, Contrib. Canadian Paleont., v. 1, pt. 4, p. 345.

TYRRELL, 1892, Canadian Geol. Survey, Ann. Rept. 5, Sec. E, p. 163.

KINDLE, 1912, Ottawa Naturalist, v. 26, p. 110.

MCLERNAN, 1913, International Geol. Congr., no. 12, Guide Book 8, p. 365.

KINDLE, 1914, Canada Geol. Survey, Summ. Rept. for 1912, p. 255.

Nephriticeras occidentalis KINDLE & MILLER, 1939, Geol. Soc. America, Special Paper no. 23, p. 96.

Alpenoceras occidentale FLOWER, 1945, Am. Midland Naturalist, v. 33, p. 698.

This is a large rather slender breviconic shell, endogastric, and faintly contracted at the aperture. The greatest diameters are attained somewhat below the base of the mature living chamber, beyond which point the shell contracts very gently to the aperture, all outlines becoming slightly convex. The holotype is an incomplete, apparently immature individual with a dorsal length of 130 mm., expanding from 25 by 25 mm. at the base to a width of 52 mm. and height of 47 mm. in a length of 100 mm. A hypotype representing a more complete individual shows more clearly the circular section at the apex and the gradual contraction of the shell toward the aperture. It expands from 22 by 22 mm. to 45 by 54 mm. in the basal 150 mm. and contracts to 50 by 45 mm. in the remaining 57 mm. The contraction continues still farther but the shell is too incomplete for measurement in the adoral region. The sutures are markedly oblique, sloping adorally on the convex dorsal side, but they are unlobed. Obliquity is such that a line normal to the shell axis cuts three septa. The septum has a depth of 6 mm. where the shell height is 44 mm. The camerae are very shallow, 7 occurring in a length equal to the adoral height of 35 mm. and 8 in a length equal to an adoral shell height of 45 mm.

The siphuncle is slightly removed from the concave ventral wall of the shell, being 5 mm. in diameter at the setpal foramen and 3 mm. from the venter. Segments are slightly depressed in section and broadly expanded, the largest observed being 5 mm. in length and expanding from 7 to 15 mm. transversely and to 14 mm. vertically. A section reveals short septal necks, recumbent or very nearly so, and a continuous internal lining which first led me to believe that *Alpenoceras* is properly a discosorid. Although

preservation of fossils from the Winnipegosis region is inadequate for study of fine details of the deposits, subsequent comparison of this form with better-preserved specimens of *A. ulrichi* has served to confirm this interpretation.

The most complete living chamber is found on the hypotype already mentioned. At the base it is 50 mm. wide and 47 mm. high. In a dorsal length of 75 mm. (estimated) the height and width are both decreased to about 40 mm. The aperture is incomplete and its form cannot therefore be determined. Probably there is a ventral hyponomic sinus but evidence of it is not clear.

Discussion. This species is larger and much more slender than *Alpenoceras ulrichi*. The next-described species, *A. sinuiferum*, though incompletely known, has a still larger shell that is readily differentiated by the presence of ventral saddles of the sutures as well as by its markedly different proportions.

Reference of this species to *Nephriticeras* by KINDLE & MILLER seems to have no justification. The species is not rapidly enough expanded or strongly enough curved, the siphuncle is too close to the venter, and there are no longitudinal markings on the surface. In all features, it is quite typical of *Alpenoceras*.

Type specimens are the holotype (Canada Geol. Survey, no. 4181) and paratypes (no. 4182) consisting of three isolated siphuncles, one of which was figured with the original description of the species. The hypotype here figured is no. 4165a.

This species is recorded from the Winnipegosis dolomite (Middle Devonian) at various localities on Lake Winnipegosis. The holotype is from the mouth of the Red Deer River; other specimens are from Dawson Bay, including Island 53 in Dawson Bay, by TYRRELL's designation.

Alpenoceras sinuiferum Flower, n. sp.

Pl. 33, fig. 5, 6

Among fossils from Lake Winnipegosis is one specimen of *Alpenoceras* that is clearly distinct from *A. occidentale*. Not only is it a much larger shell when complete and more rapidly expanding but it is readily differentiated by the presence of small saddles on sutures on the ventral side of the shell. The holotype and only known specimen is a portion of phragmocone 103 mm. long, slightly broader than high in cross section, expanding from 24 by 27 mm. to 52 mm. and an estimated width of 58 mm. in a length of 85 mm. on the siphonal side. The septa slope adorally on the convex dorsal side of the shell but are less oblique than in *A. occidentale*. Ten camerae occur in a length equal to the adoral shell height of 52 mm. There the extreme adoral camerae are slightly shorter than others, indicating that the mature part of the phragmocone is encountered here. Farther apicad, 9 camerae occur in a similar length. The mid-ventral part of the sutures shows a slight median saddle. The siphuncle (as exposed) is circular in section, a segment at the adoral end 3 mm. from the ventral wall expanding from 6 mm. to 11 mm. in the camera. The form of the segments has not been fully observed but the siphuncle appears to differ from that of *A. occidentale* only in the absence of flattening on the ventral side.

Discussion. Although known only from a portion of phragmocone, this species is distinctive both in its proportions and the small mid-ventral saddles of the sutures. The type indicates by shortening of the latest camerae that it belonged to a mature individual. Presumably there is a slight adoral contraction of the shell, though poor preservation of the convex dorsum produces an effect here which, in lateral view, is perhaps more apparent than real. From analogy with *A. occidentale* we may assume that the living chamber was not more than 60 mm. long and the entire shell probably not more than 180 mm. It is a shorter and more gibbous form than *A. occidentale* and attains much greater height and width of the shell.

The holotype is in collections of the Geological Survey of Canada (no. 4165a).

This new species comes from the Winnipegosis dolomite (Middle Devonian) at Sta. 774, Dawson Bay, Lake Winnipegosis, Man.; collected by TYRRELL.

Alpenoceras eifelense (Schindewolf)

Endoscosorus (Endostokesoceras) eifelense SCHINDEWOLF, 1942, Jahrb. Reichstelle f. Bodenforschung, Band 62, p. 510-521, pl. 34, fig. 1-3; pl. 35, fig. 1-10, pl. 36, fig. 1-3; pl. 37, fig. 1-3; pl. 38, fig. 1-2; pl. 39, fig. 1-3; pl. 40, fig. 1-3; pl. 41, fig. 1-3; pl. 42, fig. 1; text-fig. 3-13.

It is not necessary to duplicate SCHINDEWOLF's detailed description or fine illustrations of this species. The shell is rapidly expanding and slightly curved (SCHINDEWOLF, 1942, pl. 34, fig. 1) and contracts gently adorally (SCHINDEWOLF, 1942, text-fig. 3). The siphuncle, as in *A. ulrichi*, is close to the venter. The early segments (SCHINDEWOLF, 1942, text-fig. 5a) are slightly more expanded than in *A. ulrichi* but reminiscent of that species in form, particularly in flattening of the connecting ring on the ventral side of the shell, where it is nearly in contact with the shell wall. The siphuncle broadens rapidly when traced orad in the phragmocone, by expansion of the septal foramina more than by increase of expansion of the segments within the camerae. With this expansion the segments become more rounded in outline and their expansion in the camerae is slightly increased. As a result, the later segments of the siphuncle look quite unlike those of *A. ulrichi*, which, it must be remembered, is known internally only from an early part of the shell, but I have found no good criteria by which the segments can be distinguished from those of the larger *A. occidentale*.

The interior of the siphuncle shows some features different from those of other species of *Alpenoceras*. The early stages (SCHINDEWOLF, 1942, text-fig. 7; pl. 36, fig. 2) show annular structures which might be compared to true annuli; on the other hand, invaginations in the deposit might be compared to radial canals of the actinoceroids. That they are not true radial canals is indicated by the fact that apparently they do not penetrate marginal parts of the siphuncle deposits. The differentiation between outer dark deposits of the siphuncle and inner deposits consisting of lighter calcite is probably not original but due to changes introduced by replacement. The boundaries between the two regions, shown in most of the material, are far from uniform. The outer layers subjected to slower replacement show original lamellar structures, which have been lost in the more strongly recrystallized inner portions.

One feature which is well shown by SCHINDEWOLF's figures, is a marked discordance between the original deposits, which at first seem to form a continuous lining within the siphuncle, and the later-formed deposits which form the apex of the endocoines. Clearly, it is as though there are two distinct structures here, one lying upon the other in marked unconformity. In part, this appearance is adventitious. In SCHINDEWOLF's pl. 38, fig. 2, there is what appears to be a clear growth line of the deposit on the right of the endocone which penetrates the middle of the figure. Yet as this line is traced adapically it appears that the deposit which it bounds becomes thinner instead of thicker, a feature which is known to be contrary to the growth of such structures and one which we may definitely distinguish as adventitious, but I am inclined to consider this a gerontic variation and not a typical or normal structure. However, a real discordance between the growth lines in the endocoines and first deposits is clearly seen (SCHINDEWOLF, 1942, pl. 39, fig. 2; pl. 40, fig. 3) and is indicated less conclusively in several other illustrations. In contrast, a simpler structure that is more in keeping with the normal endocone growth in discosorids also is seen (*loc. cit.*, pl. 36, fig. 1; pl. 37, fig. 3; pl. 38, fig. 1a,b). The last-cited illustration (pl. 38, fig. 1b) shows conclusively that the peripheral structure is to be expected from an arrangement of endocoines, somewhat modified in later growth stages, rather than a true lining of the siphuncle such as is to be found in *Striatoceras striatum* (TROEDSSON, 1926). It is therefore nec-

essary to conclude that the structures in this species are actually normal discosorid endocoines but that in late stages of growth shortening of the cone produces striking and perplexing disconformities of the first and latest deposits, introducing the deceptive effect of two distinct structures. If true, they would to some extent be analogous to those found in *Fabroceras*, where endocoines rest on an original pattern of annuli.

Another feature which deserves mention is the clear presence of dissepiments crossing the central canal in this species. These have not been known previously in discosorids, although comparable structures cross the whole siphuncle in the Ellesmeroceratidae and are known in the central canal of some Piloceratidae, including *Cassinoceras amplum* (DAWSON), as well as on the remote fringe of true piloceroids, for they are encountered in *Manchuroceras*. Similar structures have been figured also in *Narthecoceras crassisiphonatum* (WHITEAVES).

Modification of the endocoines in late growth stages, together with partitioning of the siphuncular canal seem to be the only features by which this species can be differentiated from other representatives of *Alpenoceras*. The practical difficulties involved in study of these structures, which require good sections of really well-preserved fossils, cause me to be reluctant to accept them as good generic criteria. Further, our knowledge of other species of *Alpenoceras* is not sufficient to prove that the distinction is real. We know the internal structure of *A. ulrichi* only from a section of the adapical part of the phragmocone of a single known specimen. Material of *A. occidentale* and *A. sinuiferum* is more abundant but dolomitization has caused a loss of fine structural detail in the one section that has been made. The Winnipegosis area is not very accessible for collecting and improbability that available specimens would yield any better results caused me to refrain from making additional sections. Therefore it seems that extant evidence does not justify the generic separation of this species from *Alpenoceras*.

According to SCHINDEWOLF, all types of this species are in the Geologisches Landesmuseum, Berlin.

Alpenoceras eifelense comes from the Stringocephalus limestone, upper Middle Devonian, at Sötenich in the Eifel region, Germany.

Alpenoceras? robustum (Schindewolf)

Text-fig. 31D,E

Discosorus (Neodiscosorus) robustum SCHINDEWOLF, 1942, Reichstelle Bodenforschung, Band 62, p. 521, pl. 35, fig. 11; pl. 42, fig. 3; text-fig. 14.

This species rests upon two specimens, both of which consist of a few segments of siphuncles without any trace of the surrounding shell. Judging from size of the segments, they came from the adoral part of a phragmocone of a rather large cephalopod, for the largest segment is 11 mm. long and expands vertically from 19 to 29 mm. Although more abundant sections are desirable, the published illustrations and descriptions contain nothing to oppose SCHINDEWOLF's conclusion that the siphuncles belong to shells which should be classed as discosorids. However, they are described as a new species belonging to a new subgenus (*Neodiscosorus*), which is defined as an exogastric shell with siphuncle on the convex side and differentiated from *Discosorus* by more gradual enlargement of the siphuncle and higher segments, and from *Stokesoceras* by the higher (or longer) segments and somewhat more rapid expansion of the siphuncle as it is traced adorally in the phragmocone.

The specimens supply no evidence demonstrating the position of the siphuncle in the shell, for this could be exogastric, central, or endogastric. The species cannot be placed definitely in any genus and it cannot be differentiated with certainty from several already described. If exogastric in position, the siphuncle should be compared with *Tuyloceras* FOERSTE & SAVAGE. However, the rapid change in direction of the three segments figured by SCHINDE-

WOLF (pl. 35, fig. 11) is such that interpretation of them as part of an exogastric siphuncle is impossible. Considered as an endogastric siphuncle, nothing is evident in the descriptions or illustrations to distinguish this form from an *Alpenoceras*, though if it belongs to this genus it denotes a larger species than any yet known from relatively complete shells. Further, *Alpenoceras*, being known from the Devonian, is a much more likely assignment for this inadequately known species than any other genus.

According to SCHINDEWOLF, the types are in the Geologisches Landesmuseum, Berlin.

This species occurs in high Upper Devonian beds (Orthoelymeniastufe) at Ense bei Wildungen (Kellerwald), Germany.

Family PHRAGMOCERATIDAE Hyatt, 1900

The family Phragmoceratidae here is revised to include a series of Silurian endogastric shells in which the broadly expanded siphuncles retain thick rings and possess small to vestigial bullettes. *Phragmoceras* has a strongly contracted aperture. With it are tentatively placed three genera (*Tubiferoceras*, *Priesteroceras*, *Phragmocerina*) with contracted apertures but poorly known or completely unknown siphuncles. *Tubiferoceras* approaches *Phragmoceras* in gross features to the point of intergrading with it; *Priesteroceras* is only slightly removed from these genera in the specialized crenulate margin of the aperture; and *Phragmocerina*, which is slightly younger (persisting to the close of the Silurian), is regarded as a modification probably stemming from some of the smaller, more generalized species of *Phragmoceras*. The entire group of species seems to be allied, ranging from Middle into Upper Silurian.

Phragmoceras possesses a siphuncle with broadly expanded segments, thick rings, and small bullettes developed at tips of the rings. The pattern of the siphuncle is generally simpler than that of the older Cyrtogomphoceratidae, differentiation in the ring being less marked, bullettes uniformly smaller, and ring less thickened, never showing the addition of material to its outer surface such as often is found in the Cyrtogomphoceratidae.

Several Silurian genera with uncontracted apertures appear to agree more closely with *Phragmoceras* than with the Cyrtogomphoceratidae and therefore are assigned to the Phragmoceratidae. They are *Protophragmoceras*, *Endoplectoceras*, and *Sthenoceras*.

Some published illustrations suggest that parietal deposits may be developed in the siphuncle of genera belonging to the Phragmoceratidae and that they may even be thickened into endocones. Some deposits with remarkably crenulated patterns in *Protophragmoceras* were figured by BARRANDE and some *Phragmoceras* siphuncles noted more fully in discussion of the genus, show structures suggesting endocones not unlike those of *Fabero-ceras*. No specimens have been available for reinvestigation of these matters. If the structures are real, plainly the deposits have developed independently in this group and no affinities with the more specialized Westonoceratidae are indicated.

Of the genera included in the Phragmoceratidae by HYATT (1900) only *Phragmoceras* and *Protophragmoceras* remain. *Codoceras* is actinosiphonate and thus removed to the oncoceroids, while uncertainty as to the

aperture and internal structure leave *Gomphoceras* as a genus of such uncertain structure that its affinities are doubtful.

Genus PROTOPHRAGMOCERAS Hyatt, 1900

Type species—*Cyrtoceras purchisoni* BARRANDE

- Protophragmoceras* HYATT, 1900, in ZITTEL-EASTMANN Textb. Palacont., ed. 1, v. 1, p. 532 (reprinted in later editions with different pagination).
 _____ FORREST, 1926, DENISON Univ. Bull., Sci. Lab., Jour., v. 21, p. 334, pl. 17, fig. 1A-D.
 _____ FORREST & SAVAGE, 1927, Same, v. 22, p. 89.
 _____ TEICHERT 1930, Paläont. Zeitschr., Band 12, p. 298.
 _____ STRAND, 1934, Norsk. Geol. Tidsskr., v. 13, p. 92.
 _____ FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 434.
 _____ FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 613.

This genus was erected for compressed cyrtocoones, endogastric, resembling a *Phragmoceras* with open, uncontracted aperture. The sutures swing forward on the convex dorsum, exhibiting lateral lobes which vary with extent of compression of the cross section. The growth lines slope strongly adapically on the dorsum, forming a sinus which is remarkably deep and sharp in some species. The siphuncle is close to the venter, its segments short, broad, and widely expanded. The connecting ring is thick but not known to expand into bullettes at the septal foramina. Aside from extreme thickness of the ring, the fine structure of which, from lack of material for study by thin sections, remains unknown, rare traces of a thickening or differentiation of materials are observed at the septal foramen, suggesting incipient bullettes. One species (actually one specimen) (Pl. 38, fig. 4, 5) shows a siphuncle that expands with remarkable rapidity in the anterior camerae, within which are organic deposits that display a peculiar festooning which is not closely comparable to any structures seen in other cephalopods. This section may be slightly tangential to the center of the siphuncle, so as to intersect extremely thick deposits which perhaps are comparable to parietal deposits and endocones of *Fabero-ceras*; nowhere else in the Discosorida, however, have closely comparable festooned structures been observed.

Segments of the siphuncle vary in outline. Some forms including the type species, have segments which in section show even and equal rounding of both ends (Pl. 39, fig. 6; Pl. 38, fig. 7). Others have segments characterized by slightly greater expansion in the anterior half; this is scarcely developed in *P. purchisoni* (Pl. 39, fig. 13), better developed in *P. neutrum* (Pl. 39, fig. 14), and most fully expressed in the form described below as *P. barrandei* (Pl. 39, fig. 1, 2), which BARRANDE included in *P. purchisoni* but which differs materially from typical specimens of that species in a number of features.

The shells vary considerably in proportions, some expanding quite rapidly and others being relatively slender. *P. beaumonti* exhibits rapid expansion in the youngest stages, whereas corresponding portions of *P. virgula* and *P. obliquum* are much more slender. *P. conspicuum* (Pl. 38, fig. 6-10) is an example of a very large species in which the usual adoral reduction in the rate of expansion is carried to extremes. *P. eremita* shows a similar tendency at an earlier growth stage and much smaller shell diameter. Here the septa are unusually closely spaced (Pl. 40, fig. 9-12).

Typical and adequately known species of *Protophragmoceras* are confined to Middle Silurian rocks of Bohemia. Ordovician species formerly placed in the genus now are removed to *Strandoceras* (FLOWER, 1946). Some inadequately known forms from the Silurian of North America have been assigned to the genus but some are not well enough known for determination of generic position and others are definitely assignable to other genera.

Protophragmoceras? boreale FOERSTE & SAVAGE is atypical in its slight curvature and gentle rate of expansion. It has a relatively slender siphuncle, the structure of which is not adequately known. Available evidence favors assigning this species to *Danoceras*, though its affinities might be instead with some similar Bohemian endogastric shells, the generic position of which still is perplexing. The species is from the Attawapiskat limestone (Silurian) of Hudson Bay.

Protophragmoceras? sp. FOERSTE & SAVAGE (1927, pl. 5, fig. 9), from the Attawapiskat limestone (Silurian) of Hudson Bay, is a nearly straight slender shell known only from a small fragment. It could represent the anterior part of a *Phragmoceras* but is not adequate to prove generic relationship.

Protophragmoceras? sp. FOERSTE & SAVAGE (1927, pl. 23, fig. 3, 4) is based on an essentially complete living chamber which is not atypical of *Protophragmoceras* in form. The shell expands fairly rapidly, the siphuncle being close to the concave side of the shell but tiny at the septal foramen; therefore it is possible that the species may belong instead to some of the endogastric genera of the Oncoceratidae. This fossil occurs in the Ekwan or Attawapiskat limestone at rapids on Severn River west of Hudson Bay.

Protophragmoceras patronus CLARKE & RUEDEMANN (1903, p. 97, pl. 19, fig. 1, 2), from the Lower Shelby bed (Racine equivalent, Middle Silurian) at Oak Orchard Creek, New York, is clearly a portion of a large compressed rapidly expanding curved shell and belongs to the genus *Uranoceras*, being atypical only in the rather unusually broad cross section of the whorl. The widely

spaced septa are totally at variance with anything known in *Protophragmoceras*.

As pointed out elsewhere, the prominence of bullettes and complexity of the siphuncle of *P. sphynx* (SCHMIDT) and *P. tyriense* STRAND of the Baltic Ordovician require the erection of a separate genus, *Strandoceras* for these species (FLOWER, 1946).

Protophragmoceras murchisoni (Barrande)

Cyrtoceras murchisoni BARRANDE, 1866-67 (*partim*) Syst. Sil., p. 687, pl. 148 fig. 7-9; pl. 160, fig. 10-19; pl. 165, fig. 8-18 (*non* 19-30); pl. 176, fig. 5-12; pl. 200, fig. 9-12 [all plates, 1866; text, 1867].
Protophragmoceras murchisoni HYATT, 1900, in ZITTEL-EASTMAN Textb. Palaeont. ed. 1, v. 1, p. 532, fig. 1086.
FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 344, pl. 37, fig. 1A,B.

This is a fairly large species, rapidly expanding initially, more slender adorally, attaining a shell height of 45 mm. at the base of the living chamber, which may have a ventral length of 45 mm. and attain a height of 48 mm. at the aperture. Cross section strongly compressed, venter as broadly rounded as dorsum, siphuncle with rounded segments, expansion only slightly concentrated in the adoral half of the segments. Rings are thick and no expansion of the bullettes has been noted. The initial portion is rapidly expanding and closely septate (Pl. 39, fig. 12) contrasting in this respect with the less closely septate corresponding stages of the smaller species *P. neutrum* and *P. beaumonti*.

Étage E₂ (Middle Silurian) at various localities in the Bohemian Basin.

Protophragmoceras barrandei Flower, n. sp.

Pl. 39, fig. 1, 2

Cyrtoceras murchisoni BARRANDE, 1866, Syst. Sil., pl. 165, fig. 19-20.

One specimen which BARRANDE figured as *Cyrtoceras murchisoni* is really more slender and sparsely septate than that species and is particularly distinctive in the subtrapezoidal, nearly heart-shaped segments of the siphuncle. The type expands from 8 to 30 mm. in the 65 mm. of the dorsal part of the phragmocone and continues to a height of 36 mm. in 44 mm. of the living chamber. The rate of expansion is uniform throughout the length of the specimen. The camerae are deeper in proportion to height than those of typical *C. murchisoni*, three camerae occupying 13 mm.

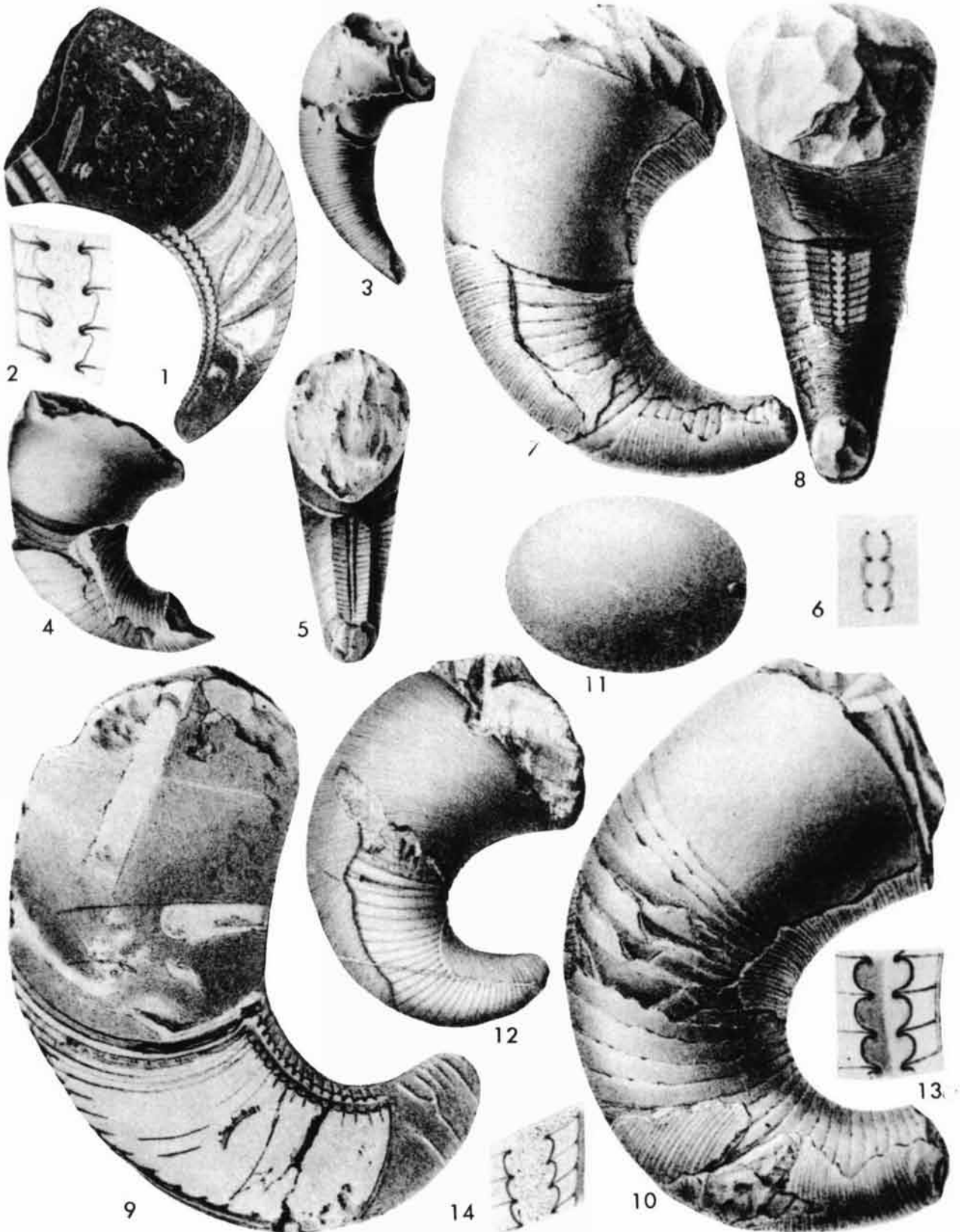
EXPLANATION OF PLATE 39

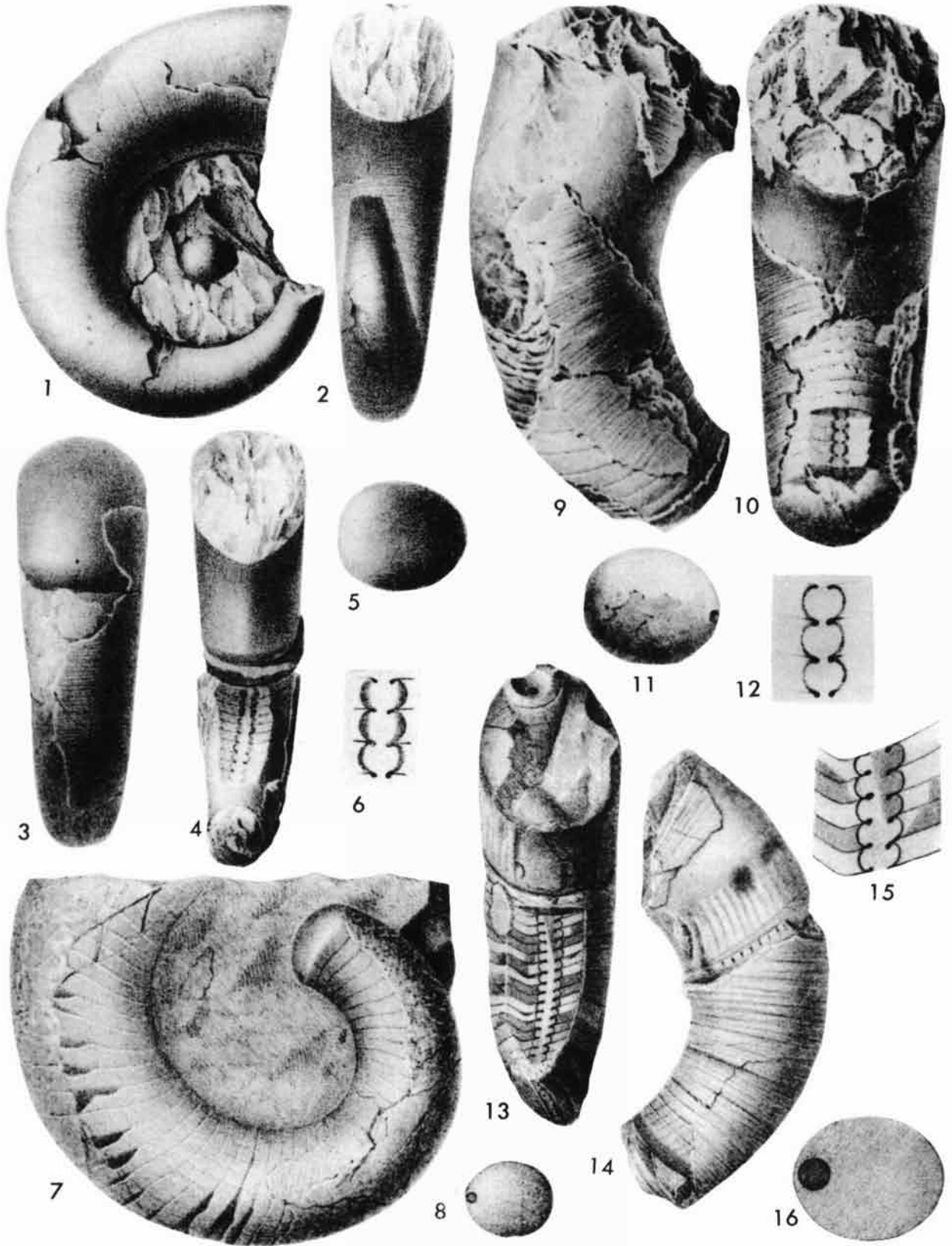
PHRAGMOCERATIDAE—*Protophragmoceras*

(Except as otherwise indicated all figures are $\times 1$ and illustrate specimens from Étage E₂, Middle Silurian, Bohemian basin. All after BARRANDE, 1865; fig. 1, 2, 14, from his pl. 165, fig. 3-6 from his pl. 173, and fig. 7-13 from his pl. 165 and 176.)

FIGURE

- 1,2. *Protophragmoceras barrandei* FLOWER, n. sp., holotype, from Lochkov, Bohemian basin.—1, Vertical section, venter at left, showing difference in proportions as compared with commensurate parts of *P. murchisoni* (Fig. 12).—2, Part of siphuncle from anterior end of phragmocone of fig. 1, showing marked expansion of heart-shaped to subquadrate segments near adoral end, enlarged, about $\times 4$.
3. *Protophragmoceras virgula* (BARRANDE), specimen from Bohemian basin. Lateral view, showing slight inclination of growth lines and evidence of maturity in faint constriction at the aperture.
- 4-6. *Protophragmoceras obliquum* FLOWER, n. sp., holotype, from Bohemian basin.—4, Lateral view, venter at right.—5, Ventral view, showing rapid expansion of shell and strong inclination of growth lines.—6, Part of siphuncle showing subspherical segments and possibly of bullette from connecting ring.
- 7-13. *Protophragmoceras murchisoni* (BARRANDE), specimens from Bohemian basin.—7,8, Lateral and ventral views of moderate-sized typical specimen with part of mid-ventral region cut away to expose siphuncle.—9, Vertical section of large individual which is slender adorally.—10, Lateral view of internal mold of large specimen comparable to that illustrated in Fig. 9.—11, Septum at base of living chamber of specimen shown in Fig. 10, venter at right.—12, Small immature specimen, comparable with preceding forms in proportions.—13, Portion of siphuncle, about $\times 2.5$.
14. *Protophragmoceras neutrum* (BARRANDE), from Bohemian basin. Part of siphuncle in vertical section, showing segments slightly swollen at anterior end, about $\times 2.5$.





at the adoral end of the phragmocone where the shell height is 30 mm. In an equivalent part of *C. murchisoni*, 4.5 to 5 camerae occupy an equal length. As can be seen from the figure, segments of the siphuncle differ markedly in form, expanding abruptly from the septal necks so that greatest width, nearly twice the diameter at the septal foramen, is attained in the adoral quarter, the sides converging adapically from there, only slightly convex, until close to the adapical septum where the rate of contraction is greatly increased. The apical end of the connecting ring is broadly adnate on the ventral but narrowly so on the dorsal side.

Location of type presumably in the Narodny Museum of Prague. From Étage E₂ (Middle Silurian), Lochkov, Bohemia.

Protophragmoceras virgula (Barrande)

Pl. 39, fig. 3

Cyrtoceras virgula BARRANDE, 1866-67 (*parim*) Syst. Sil., p. 694, pl. 173, fig. 8-11 (non fig. 13-16) [plate, 1866; text, 1867].

This is a small, relatively slender species. The type is a shell attaining an aperture of 20 mm. in height and 17 mm. in width, the entire shell being less than 50 mm. in length. The growth lines slope only gently adapically from venter to dorsum, expansion being relatively gentle, uniform, and increasing from 8 to 15 mm. in 20 mm.

A faint constriction of the internal mold near the aperture indicates that the shell is mature. The siphuncle has not been observed in section.

BARRANDE cites this species as from "notre calcaire inférieur E," but later lists it not from E₁ but E₂. Presumably the meaning of the earlier statement is that it lies low in E₂.

Protophragmoceras obliquum Flower, n. sp.

Pl. 39, fig. 4-6

Cyrtoceras virgula BARRANDE, 1866-67, Syst. Sil., p. 694, pl. 173, fig. 13-16 non fig. 8-12) [plate, 1866; text, 1867].

This name is introduced for a species which BARRANDE figured as *Cyrtoceras virgula* but which differs from other representatives of that species taken as typical largely on the basis of their numerical precedence on the plate, in being larger and more rapidly expanding, but mainly in that growth lines slope remarkably strongly apical from the dorsum to the venter, all features being at marked variance with other specimens figured.

The living chamber increases from 25 to 32 mm. in height, with a dorsal length of 22 mm. and a ventral length of 16 mm. Faint apertural modifications indicate that the specimen is mature. The profile of the aperture flares slightly on the ventral side, the phragmocone—indeed, the whole shell—expanding much more

rapidly than in *C. virgula* (BARRANDE, 1867, pl. 173, fig. 8-11), increasing from 11 to 18 mm. in 20 mm. As can be seen from the illustration, the growth lines slope strongly apical from dorsum to venter, curving, convex on the anterior side, with slope particularly prominent in the dorsolateral regions.

From Étage E₂, Middle Silurian, Bohemian Basin.

Protophragmoceras beaumonti (Barrande)

Pl. 38, fig. 1-5

Cyrtoceras beaumonti BARRANDE, 1866-67, Syst. Sil., p. 685, pl. 165, fig. 21-26 [plate, 1866, text, 1867].

This is a small species, rapidly expanding in the young with living chamber showing great reduction in rate of expansion. The siphuncle, as shown in BARRANDE's figure reproduced here, is remarkable for rapid increase in diameter in the adoral camerae and for the peculiar festooned calcareous deposit within it, the nature of which is not properly understood.

BARRANDE cites this species as coming from both horizons E₁ and E₂ at Butovitz, Lochkov, and several other localities.

Protophragmoceras neutrum (Barrande)

Pl. 39, fig. 14

Cyrtoceras neutrum BARRANDE, 1866-67, Syst. Sil., p. 679, pl. 165, fig. 1-7; pl. 200, fig. 5-8 [plates, 1866; text, 1867].

This species, slightly larger and less rapidly expanding than *P. beaumonti*, is refigured here only to show outline of siphuncle segments which are only slightly more expanded in the anterior than posterior end. They lack the subtrapezoidal form of *P. barrandei*, which is a larger, more gently and more uniformly expanding species.

From Étage E₂, Lochkov, Kororz, of the Bohemian Basin.

Protophragmoceras conspicuum (Barrande)

Pl. 38, fig. 6-10

Cyrtoceras conspicuum BARRANDE, 1866-67, Syst. Sil., v. 1, p. 675, pl. 173, fig. 16-20 [plate, 1866; text, 1867].

This species is refigured as an example of the size which the genus is known to attain. The form is typical in being relatively slender adorally and moderately expanding in the earlier portion. Faint longitudinal markings are visible on the internal mold of the phragmocone, structures regarded as indicative of incipient cameral deposits and found in many breviconic shells. The siphuncle segments are equally rounded at both ends with the connecting ring appreciably thick.

From Étage E₂, Lochkov, Bohemia.

EXPLANATION OF PLATE 40

PHRAGMOCERATIDAE—Protophragmoceras, Endoplectoceras

(Except as otherwise indicated all figures are $\times 1$ and illustrate specimens from Étage E₂, Middle Silurian, Bohemian basin. All after BARRANDE, 1865-87; fig. 1-6 from his pl. 30, fig. 7, 8, from his pl. 491, fig. 9-12 from his pl. 174, fig. 13-16 from his pl. 510.)

FIGURE

- 1-6. *Endoplectoceras secula* (BARRANDE), specimens from Lochkov, Bohemian basin.—1, 2, Lateral and ventral views of a relatively complete shell showing form, surface markings, and particularly the slight asymmetric coiling.—3, 4, Dorsal and ventral views of less complete shell, venter partially removed to expose siphuncle.—5, Cross section at base of living chamber of specimen illustrated in Figs. 3, 4, venter at right.—6, Part of siphuncle of same specimen shown in Figs. 3-5, about $\times 2.5$.
- 7-8. *Endoplectoceras inexpectans* (BARRANDE), specimen from Kuchelbad, Bohemian basin, retaining only part of phragmocone.—7, 8, Lateral view and septum at base, venter at left.
- 9-12. *Protophragmoceras eremita* (BARRANDE), holotype from Bo-

- hemian basin.—9-11, Lateral, ventral, and septal views, venter removed to show siphuncle in horizontal longitudinal section.—12, Part of siphuncle showing subspherical segments, $\times 2.5$.
- 13-16. *Endoplectoceras secula* (BARRANDE), specimen from Vallon de Slivenetz, Bohemia.—13, Ventral view, with part of phragmocone ground to expose siphuncle.—14, Lateral view of specimen shown in Fig. 13 prior to removal of venter; well defined are longitudinal markings on the internal mold of lower part of living chamber, apparently indicating a remarkably extended basal zone.—15, Part of siphuncle, $\times 2.5$.—16, Cross section at base of living chamber, venter at left, showing equal rounding of dorsum and venter and size and position of siphuncle.

Protophragmoceras eremita (Barrande)

Pl. 40, fig. 9-12

Cyrtoceras eremita BARRANDE, 1866-67, Syst. Sil., p. 676, pl. 174, fig. 9-12 [plates 1866; text, 1867].

This species is of particular interest in that the known portion of the shell is slender, the slender form not being confined to the living chamber, but appearing at an early stage of the phragmocone. The septa are unusually closely spaced. In both features the species, more than any other of the genus, approaches the proportions of *Endoplectoceras secula*, and yet is clearly assignable to *Protophragmoceras*, for the coiling is in the plane of symmetry of the shell. The siphuncle segments are equally rounded at both ends and essentially subspherical in outline.

From Étage E₂ (Middle Silurian), Konieprusse, Bohemia.**Genus ENDOPLECTOCERAS Foerste, 1926**Type species—*Trochoceras secula* BARRANDE*Endoplectoceras* FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 345, pl. 34, fig. 4A-D.

FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 613.

Shell compressed, venter a little more narrowly rounded than dorsum or both subequally rounded, curved endogastrically, gently expanding and strongly curved, with a slight trace of dextral coiling which is believed to be original. The sutures show very faint lateral lobes, sloping forward on the convex dorsal side of the shell. Ventral siphuncle composed of broad short segments, strongly expanded within the camerae, with thick connecting rings of the discosorids, expanded very faintly into bullettes at the septal foramina. The siphuncle is otherwise empty. The surface bears rugose transverse markings which fail to indicate any trace of a hyponomic sinus.

Discussion. This genus agrees with *Protophragmoceras* in section and internal structure, differing from it mainly in greater slenderness of the shell, particularly in the adoral portion, and very faintly trochoceroïd coiling. The only known species are *Endoplectoceras secula* and *E. inexpectandum*, the latter assigned tentatively to the genus by FOERSTE, since its internal structure is not known, but on present evidence not possibly referable to any other described genus.

The faint trochoceroïd nature of the shell was not noted by FOERSTE in his description, who cited *Cyrtoceras secula* as the type species. BARRANDE originally placed it in *Trochoceras*. The two species are both from Étage E₂ (Middle Silurian) of the Bohemian basin.

Endoplectoceras secula (Barrande)

Pl. 40, fig. 1-5, 13-16

Trochoceras secula BARRANDE, 1865-77, Syst. Sil., pl. 30, fig. 1-6 (1865); p. 127 (1867); suppl., p. 239, pl. 510, fig. 1-5 (1877).
Endoplectoceras secula FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 345, pl. 34, fig. 4A-D.

This remarkable species is refigured here to show its salient features. Plate 40, figures 1, 2, represents a slightly immature shell retaining most of the surface and showing clearly the slight asymmetry of the coiling. Plate 40, figures 3-6, represents the late portion of another immature shell, on which the venter has been ground away, exposing the siphuncle in which the thickness of the connecting ring is quite evident. Plate 40, figures 13-16, shows a specimen not figured by BARRANDE until later (1877). It represents an apparently mature individual, the apical part of which is missing. The segments of the siphuncle are broader, shorter, and more strongly inflated, as may be expected at a later growth stage. Thickening of the rings is less evident. The internal mold of the living chamber bears longitudinal markings on its basal portion, evidently representing a rather remarkable basal zone, a clear indication of maturity. The larger size of the siphuncle as shown in cross section is partly due to the later growth stage represented, but is largely due to the fact that it cuts through the expanded portion of a segment. The cross section of the other specimen (Pl. 40, fig. 5) shows the siphuncle at the smallest diameter of a segment, at the septal foramen.

Étage E₂ (Middle Silurian), Lochkov and Vallon de Silvenetz, Bohemia.**Endoplectoceras inexpectandum (Barrande)**

Pl. 40, fig. 7-8

Trochoceras inexpectandum BARRANDE, 1877, Syst. Sil., suppl., pl. 491.
FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 345.

This species is known only from a portion of phragmocone comprising about three-fourths a volution. The shell is endogastric, faintly asymmetric in coiling and gently expanding. The compressed cross section, scarcely more narrowly rounded ventrally than dorsally and adoral slope of sutures on the convex dorsal side indicate that the species belongs to *Endoplectoceras*, even without the knowledge of the interior of the siphuncle. FOERSTE suggested this generic assignment tentatively. A more thorough study of the species and possible relatives leaves no doubt as to affinities of this form with *E. secula*.

Étage E₂ (Middle Silurian), Kuchelbad, Bohemia.**Genus STHENOCERAS Flower, n. gen.**Type species—*Cyrtoceras aduncum* BARRANDE

Large endogastric cyrtocoones with early part moderately rapidly expanding, curvature and rate of expansion both reduced in late stages, the mature living chamber tending to become nearly straight with slightly convex sides and aperture very slightly contracted. The cross section is variable but typically broad, with dorsal side slightly flattened. Sutures are generally straight and

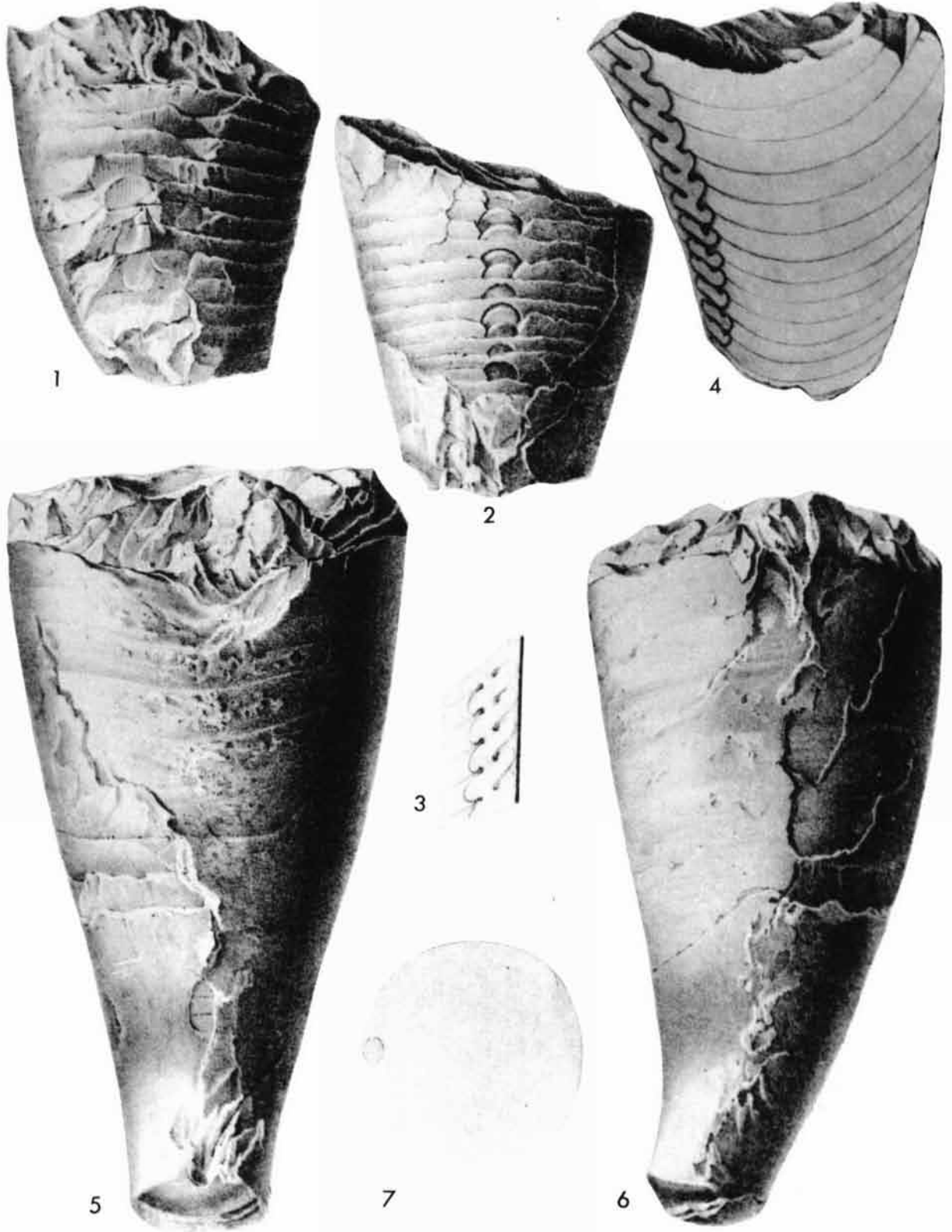
EXPLANATION OF PLATE 41**PHRAGMOCERATIDAE—Sthenoceras**(All figures are $\times 1$ and illustrate specimens from Étage E₂, Middle Silurian, Bohemian basin. All after BARRANDE, 1865, pl. 169.)**FIGURE**1-3. *Sthenoceras fractum* (BARRANDE), from Bohemian basin.—

1, Lateral view, venter at right.—2, Ventral view, —

3, Section of siphuncle showing small bullettes.

4-7. *Sthenoceras aduncum* (BARRANDE), from Bohemian basin.

—4, Vertical section of phragmocone, venter at left, showing broadly expanded thick-walled siphuncle.—5,6 Ventral and lateral views of relatively complete specimen.—7, Cross section, venter at left, showing position and size of siphuncle.





1



4



5



2



3



6

transverse but may slope forward slightly on the dorsum in late stages; and slight lateral lobes may develop. The siphuncle is close to the venter, segments being typically short and broadly expanded with thick rings and usually small bullettes. Shells are smooth or with transverse markings. A slight hyponomic sinus generally occurs on the ventral side.

Discussion. This genus is erected for a group of shells which in their slight curvature and faintly gibbous living chamber have a strong resemblance to *Danoceras*. Their internal structure, notably broadly expanded siphuncle segments with thick rings and small bullettes, indicates that the genus is related instead to the Phragmoceratidae, and in particular to *Protophragmoceras*.

The nucleus of the genus is a well-defined group of species with internal structure of discosorid pattern. Of these forms, *Sthenoceras aduncum* and *S. fractum* are essentially circular in section, while *S. nobile* is a more slender shell, slightly wider than high, and *S. moestum* is slender but compressed in section. All have short broadly expanded siphuncle segments. The section of *S. aduncum* shows thick connecting rings and structures which may well fit BARRANDE's interpretation of bullettes. The interior of the siphuncle of *S. fractum* is not known. The two remaining species (siphuncles represented by drawings) have thin rings, possibly a matter of interpretation, and small annular deposits, which quite clearly are bullettes.

Other species that show less certain affinities to this genus seemingly include (1) large shells typical of the genus in general aspect but departing in one way or another from the postulated pattern of the siphuncle, and (2) generally smaller and more slender species in which segments of the siphuncle are an obvious departure from that of the small group of typical species noted above. Inspection of BARRANDE's illustrations, which are the only available basis for an attempt to evaluate relationships of these species, suggests a homogeneity in this stock which may be more apparent than real. It is suspected that a considerable part of the group may be of oncoceroid origin. Certainly, in view of the apparent discontinuity of actinosiphonate deposits in other oncoceroids, notably in

Manitoulinoceras (FLOWER, 1946) where only two specimens out of about 30 from the Cincinnatian show any such deposits, it is quite likely that these species with slender siphuncles but without actinosiphonate deposits should be placed in *Danoceras* or in a closely allied generic group and that the absence of actinosiphonate rays is not a feature of great taxonomic significance. All known species are from Middle Silurian (Étage E₂) of the Bohemian basin.

Tentatively the following species are placed in *Sthenoceras*:

(1) *Orthoceras conjugatum* BARRANDE (1866, pl. 195, fig. 1-7), an essentially straight shell, rapidly expanding in young, sides becoming convex and less expanding in the adult. Section very slightly compressed, dorsum slightly flattened, siphuncle with short broad segments, essentially spheroidal and apparently with thick rings.

(2) *O. appellans* BARRANDE (1877, pl. 526, fig. 7-11), so closely allied to the preceding form that illustrations suggest that they may be conspecific. It is known only from a portion of phragmocone showing crowded camerae comparable to those in anterior part of the phragmocone of *O. conjugatum*.

(3) *Cyrtoceras crumea* BARRANDE (1877, pl. 529, fig. 12-17), a large gibbous form with slightly compressed section and relatively small thick-walled siphuncle segments.

(4) *Orthoceras karreri* BARRANDE (1877, pl. 523, fig. 6-13; pl. 524, fig. 13-17), a nearly straight form with circular section, ventral siphuncle of short broad segments, and apparently thick connecting rings.

(5) *Cyrtoceras speciosum* BARRANDE (1866, pl. 17c, fig. 1-4; lectotype, here selected), a gibbous endogastric large cyrtocone with section broader than high, dorsum flattened, siphuncle with short segments that broaden rapidly with growth. A larger shell (BARRANDE, 1867, pl. 178, fig. 1), representing a more mature individual, is regarded as conspecific. Plainly a different species (BARRANDE, 1867, pl. 178, fig. 5, 6) has a siphuncle more angular in outline and shell showing reduction of expansion at an earlier stage; probably this is an appreciably smaller species. A distorted specimen (BARRANDE, 1867, pl. 217, fig. 5) cannot be identified certainly.

(6) *Cyrtoceras dolium* BARRANDE (1866, pl. 178, fig. 8-11) is nearly straight, with cross section slightly higher than wide and dorsum strongly flattened. The siphuncle has segments which are broad in the adult but angular in outline; another specimen figured by BARRANDE (1866, pl. 178, fig. 5-7) is clearly more closely related to this form than to true *C. speciosum*.

EXPLANATION OF PLATE 42 PHRAGMOCERATIDAE—Phragmoceras

(All figures are from thin sections of specifically unidentified phragmocones from the Middle Silurian of Gotland. Specimens are in the Naturhistoriska Riksmuseet, Stockholm, Sweden.)

- 1,2,5. *Phragmoceras* sp. A (illustrated by parts of a single thin section, no. 1).—1, Basal part of section showing recumbent necks, outline of connecting rings, bullettes, larger dorsally and showing differentiation of layers, dark band marking inner surface of free part of ring; toward venter (at right) the sharply curved anterior boundary of ring apparently represents the second amorphous band; noteworthy is marked thickness of ring on dorsum of anterior segment, $\times 22$.—2, Same section showing longer series of siphuncle segments showing calcite (apparently inorganic) which has affected original structures by replacement and recrystallization, $\times 14$.—5, Septal neck, from anterior part of section (not included in Fig. 2) showing recumbent brim; white calcite bounding the neck is inorganic and the bullette is missing, $\times 18$.
- 3,4. *Phragmoceras* sp. B (illustrated by a single thin section, no. 2).

- 3, Entire section showing form of siphuncle segments at a late growth stage, with apparently inorganic vesicular material inside siphuncle and inorganic material lining segments of the siphuncle, $\times 5$.—4, Anterior septal neck from anterodorsal part of siphuncle, neck retouched by strengthening its outline; bullette present, with anterior end of connecting ring below it but free part of ring (above) not preserved, $\times 10$.
6. *Phragmoceras* sp. C. Thin section (no. 3) showing series of

siphuncle segments with siphuncle and camerae filled by inorganic calcite, but showing less extensive replacement of original structures; dark bullettes are outlined by light inorganic calcite; connecting rings largely preserved as dark calcite but destroyed in anterior portion; anterior ovoid bodies are probably algal; $\times 8$. (See Pl. 43.)

(7) *Cyrtoceras ramseyi* BARRANDE (1866, pl. 179, fig. 4-8), a large gibbous endogastric shell with subcircular section and ventral siphuncle with segments slightly more slender than in the preceding but still short and obscurely heart-shaped.

(8) *Cyrtoceras custos* BARRANDE (1877, pl. 525, fig. 15-17), a large form with circular cross section similar to the preceding species, but siphuncle unknown.

(9) *Cyrtoceras conturbatum* BARRANDE (1877, pl. 530, fig. 15-17), similarly a large gibbous shell with section apparently flattened markedly on the dorsum.

(10) *Orthoceras discors* BARRANDE (1866, pl. 194, fig. 1-10), a large nearly straight shell, very rapidly expanding in the young, mature part more slender, cross section slightly wider than high, and dorsum markedly flattened in cross section. The siphuncle segments are slender but thick-walled in the young, attaining in the adult short broad segments with thick rings typical of the Phragmoceraidae. This species is of interest in that simplification of the segments in the young stages could, if it replaced the typical adult condition, lead to other forms which on different evidence appear to be allied to *Danoceras* and of oncoceroid origin.

Sthenoceras aduncum (Barrande)

Pl. 41, fig. 4-7

Cyrtoceras aduncum BARRANDE, 1866, Syst. Sil., pl. 169, fig. 9-13; pl. 181, fig. 10-11.

Shell circular in cross section, endogastric, slender in young, rapidly expanding over middle of phragmocone, then more slender, with a marked reduction in rate of expansion near the mature aperture which slopes to a broad shallow ventral sinus. Sutures are straight and transverse and siphuncle close to the venter, with segments broadly expanded as in *Phragmoceras*. BARRANDE'S illustrated section shows short broadly expanded segments with apparently a thick connecting ring and structures which, judging from other figures showing the same phenomenon, doubtless represent small bullettes.

Sthenoceras fractum (Barrande)

Pl. 41, fig. 1-3

Cyrtoceras fractum BARRANDE, 1866, Syst. Sil., pl. 169, fig. 5-8.

This species is smaller than *Sthenoceras aduncum* but similar to it in general features. BARRANDE'S illustrations include a vertical section of the siphuncle showing definite, if small, bullettes.

Sthenoceras nobile (Barrande)

Cyrtoceras nobile BARRANDE, 1866, Syst. Sil., pl. 172, fig. 1-11.

This species has a depressed cross section. It is more slender than the preceding forms and the siphuncle smaller but it contains definite bullettes.

Sthenoceras moestum (Barrande)

Cyrtoceras moestum BARRANDE, 1866, Syst. Sil., pl. 171, fig. 1-5.

This species is slender and of moderate size like the preceding one but differs in that the cross section is compressed, with dorsum and venter about equally rounded rather broadly. The siphuncle, though relatively small, has bullettes. This species is of interest in that it serves as possible connection between forms with broader whorls and the compressed *Protophragmoceras*. Indeed, this species differs from *Protophragmoceras* primarily in its greatly reduced shell curvature.

Genus PHRAGMOCERAS Broderip, 1839

Type species—*Phragmoceras arcuatum* J. SOWERBY

- Phragmoceras* BRODERIP, in MURCHISON, 1839, Silurian System, p. 621.
 PORTLOCK, 1843, Rept. Geology Londonderry, p. 381.
 MCCOY, 1884, Synopsis Carb. Fossils, Ireland, p. 11.
 WOODWARD, 1851, Manual Mollusca, pt. 1, p. 90.
 SAEMANN, 1852, Palaeontographica, Band 3, p. 139.
 MCCOY, 1854, British Paleozoic Rocks, Fossils, p. 322.
 BARRANDE, 1854, Neues Jahrb. Mineral., p. 10, pl. 1, fig. 12.
 1855, Soc. Géol. France, Bull., sér. 2 tome, 12, p. 158, pl. 5, fig. 5.
 BILLINGS, 1857, Canadian Naturalist, Geol., v. 2, p. 136, pl. 2, fig. 4.
 CHAPMAN, 1863, Canadian Journal, new ser., p. 22.
 CHAPMAN 1864, Expos. Min. Geol. Canada, p. 130.
 BARRANDE, 1867, Syst. Sil., p. 187.
 BLAKE, 1882, Monograph British Fossil Cephalopods, p. 59.
 ZITTEL, 1884, Handb. Paläont., Band 2, p. 375.
 MILLER, 1889, North American Geol. Paleont., p. 452.
 WHIDBORNE, 1890, Mon. Dev. Fauna South England, I, Palaeontograph. Soc. (London), p. 111.
 KOKEN, 1896, Die Leitfossilien, Leipzig, p. 49.
 HYATT, 1900, in ZITTEL-EASTMAN Textb. Palaeont., ed. 1, v. 1, p. 532 (reprinted with different pagination in later editions).
 JAEKEL, 1902, Deutsch Geol. Gesell., Zeitschr., Band 54, Protok., p. 8, 68, 80.
 JAEKEL, in RUEDEMANN, 1903, Am. Geologist, v. 31, p. 200.
 GRABAU & SHIMER, 1910, North American Index Fossils, v. 2, p. 131.
 FRELL, 1921, Centralblatt f. Mineral., 1921, p. 305-315.
 FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 350.
 FOERSTE & SAVAGE, 1927, Same, v. 22, p. 92.
 FOERSTE, 1929, Same, v. 24, p. 326.
 FOERSTE, 1930, Same, v. 25, p. 97.
 FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 613.

Phragmoceras is an endogastric shell, usually rapidly expanding, strongly compressed in cross section, with aperture greatly constricted, main part being compressed oval to subtriangular and lesser part being produced on ventral side as a narrow long slit that widens at its tip into a narrow ovate lobe, the hyponomic sinus. Sutures have lateral lobes but are in general normal to curvature of the shell and not strikingly oblique. Siphuncle close to concave ventral side of shell, with segments invariably broadly expanded; connecting rings relatively thick, as is common to most Discosorida, and lacking accessory deposits. The surface bears growth lines which, in the early part of the shell, slope strongly apically from the ventral to dorsal side; near the aperture growth lines are modified in accordance with the pattern of the aperture.

The described features, especially those relating to the aperture pose an interesting problem. Did *Phragmoceras* attain its characteristic aperture only upon reaching maturity? Or did it resorb early but typical apertural portions of the shell before growing farther? Two facts suggest the latter interpretation. (1) To my knowledge, no immature specimens of *Phragmoceras* have been found or illustrated possessing the open strongly oblique aperture which early growth lines suggest. (2) It is possible also that the great number of species described may be based in large part upon mature and immature representatives of the same species, as size and proportions have long been accepted as primary criteria for recognition of species in this and other breviconic genera. The extremely large number of species already named suggests that this possibility is a very real one.

Nearly all American specimens of *Phragmoceras* are found in dolomite, a matrix unfavorable for the study of details of the siphuncle. It is evident from inspection of Bohemian materials in the collection of the Harvard Museum of Comparative Zoology that the connecting

ring is uniformly thickened. HEDSTRÖM (1917, pl. 4, fig. 5; pl. 5, fig. 8; pl. 6, fig. 10-12; pl. 8, fig. 13; pl. 9, fig. 6-8; pl. 11, fig. 6; pl. 14, fig. 1, 2; pl. 15, fig. 1, 2; pl. 18, fig. 7; pl. 19, fig. 8) has presented figures showing thick ring that may be inflated at the septal foramen. Unfortunately, at the time of HEDSTRÖM's work the complexity of these siphuncles was not recognized and the structures were not described or illustrated in detail adequate for comparison with other discosorids. It is evident that the septal necks are short and recurved, probably recumbent or in some narrowly free. The segments are obscurely heart-shaped, being strongly expanding at their anterior ends and narrowing gradually toward their adapical ends. Annular thickening of calcareous materials at the septal foramen is a common phenomenon. Available figures are not adequate to show whether the septal foramen is constricted by thickening of the connecting ring alone or whether accessory annular deposits are developed. It is quite probable, however, that a bullette, comprised only of a thickened connecting ring, will account for the known phenomena and there is reason to believe that the structure here is analogous to that of *Cyrtogomphoceras* and *Strandoceras*. It is not possible to state definitely that accessory annulosiphonate deposits may not be present within the siphuncle but they are not clearly indicated and it is unnecessary to postulate them. The question can be decided only by examination of specimens in which work on thin sections is desirable or perhaps necessary, using better material than has been available for the present study.

The genus *Phragmoceras* is characteristic of the Middle Silurian of both Europe and North America. Because of the large number of species, full bibliographic citations are not given here but instead, species are listed in relation to geographic realms where they occur.

Species of *Phragmoceras* from Bohemia

Phragmoceras broderipi BARRANDE

Phragmoceras broderipi BARRANDE, 1847, HAIDINGER's Berichte, Band 3, p. 269. BARRANDE, 1865-67 (*partim*), Syst. Sil., p. 207, pl. 56, fig. 1-3; pl. 57, fig. 1-8; pl. 58, fig. 1-8; pl. 99, fig. 1-7; (*non* pl. 65, fig. 3) [plates, 1865; text, 1867]. BARRANDE, 1877, Syst. Sil., suppl., pl. 486, fig. 1-4; pl. 488, fig. 1-3.
Étage E₂ (Middle Silurian).

Phragmoceras biimpressum BARRANDE

Phragmoceras biimpressum BARRANDE, 1865-67, Syst. Sil., p. 206, pl. 60, fig. 1-4 [plates, 1865; text 1867].
Étage E₂ (Middle Silurian).

Phragmoceras broderipi sublaevis BARRANDE

Phragmoceras broderipi var. *sublaevis* BARRANDE, 1865-67, Syst. Sil., p. 216, pl. 98, fig. 1-4 [plate, 1865; text, 1867].
Étage E₂ (Middle Silurian).

Phragmoceras imbricatum BARRANDE

Phragmoceras imbricatum BARRANDE, 1847, HAIDINGER's Berichte, Band 3, p. 269. BARRANDE, 1848, Same, Band 4, p. 208. BARRANDE, 1865-67, Syst. Sil., p. 212, pl. 46, fig. 1-12; pl. 175, fig. 1-15 [plates, 1865-66; text 1867].
Étage E₂ (Middle Silurian).

Phragmoceras labiosum BARRANDE

Phragmoceras labiosum BARRANDE, 1847, HAIDINGER's Berichte, Band 3, p. 218. BARRANDE, 1865-67, Syst. Sil., p. 218, pl. 50, fig. 1-6 [plate 1865; text 1867].
Étage E₂ (Middle Silurian).

Phragmoceras longum BARRANDE

Phragmoceras longum BARRANDE, 1847, HAIDINGER's Berichte, Band 3, p. 269. BARRANDE, 1865-67, Syst. Sil., p. 213, pl. 59, fig. 1-4 [plate, 1865; text 1867].
Étage E₂ (Middle Silurian).

Bohemian Species Transferred from *Phragmoceras* to Other Genera

Other Bohemian species previously included in *Phragmoceras* are now assigned to other genera. Particularly worthy of notice are Devonian forms which resemble *Phragmoceras* externally but differ in having concave siphuncle segments containing actinosiphonate deposits. Although not all siphuncles of Devonian species are known (probably owing to poor preservation of internal structures of nautiloids from the Devonian of Bohemia), it seems safe to place these species in *Bolloceras*. Of 38 species assigned by BARRANDE to *Phragmoceras*, most are now placed in other genera.

Bolloceras dux (BARRANDE)

Phragmoceras dux BARRANDE, 1877, Syst. Sil., suppl. pl. 531, fig. 1-3; pl. 532, fig. 9, 10; pl. 533, fig. 1, 2.
Étage G₂ (Devonian).

Bolloceras forbesi (BARRANDE)

Phragmoceras forbesi BARRANDE, 1865, Syst. Sil., pl. 65, fig. 4-6.
Étage G₂ (Devonian).

Bolloceras guttersum (BARRANDE)

Phragmoceras guttersum BARRANDE, 1865, Syst. Sil., pl. 100, fig. 4, 5; pl. 244, fig. 14, 15.
Étage G₂ (Devonian).

Bolloceras hospes (BARRANDE)

Phragmoceras hospes BARRANDE, 1877, Syst. Sil., suppl. pl. 536, fig. 1-3; pl. 543, fig. 4-7.
Étage G₂ (Devonian).

Bolloceras inflexum (BARRANDE)

Phragmoceras inflexum BARRANDE, 1877, Syst. Sil., suppl., pl. 540, fig. 1-4.
Étage G₂ (Devonian).

Bolloceras? murale (BARRANDE)

Phragmoceras murale BARRANDE, 1877, Syst. Sil., suppl., pl. 537, fig. 6, 7; pl. 543, fig. 1-3 (may represent new genus).
Étage G₂ (Devonian).

Bolloceras adequatum (BARRANDE)

Phragmoceras adequatum BARRANDE, 1877, Syst. Sil., suppl., pl. 472, fig. 5-9.
Étage G₂ (Devonian).

Bolloceras angustum (BARRANDE)

Phragmoceras angustum BARRANDE, 1877, Syst. Sil., suppl., pl. 578, fig. 5-7.
Étage G₂ (Devonian).

Bolloceras baro (BARRANDE)

Phragmoceras baro BARRANDE, 1877, Syst. Sil., suppl., pl. 454, fig. 4-6.
Étage G₂ (Devonian).

Bolloceras clypeatum (BARRANDE)

Phragmoceras clypeatum BARRANDE, 1877, Syst. Sil., suppl., pl. 536, fig. 4-6; pl. 537, fig. 1-5; pl. 538, fig. 1-4.
Étage G₂ (Devonian).

Bolloceras comes (BARRANDE)

Phragmoceras comes BARRANDE, 1865, Syst. Sil., pl. 63, fig. 1-4; pl. 244, fig. 3. BARRANDE, 1877, Syst. Sil., suppl., pl. 455, fig. —; pl. 456, fig. —; pl. 491, fig. 15-17.
Étage G₂ (Devonian).

Bolloceras pigrum (BARRANDE)

Phragmoceras pigrum BARRANDE 1865, Syst. Sil., pl. 64, fig. 1-7; pl. 65, fig. 1, 2. BARRANDE, 1877, Syst. Sil., suppl., pl. 426, fig. 14, 15.
Étage G₂ (Devonian).

Bolloceras princeps (BARRANDE)

Phragmoceras princeps BARRANDE, 1877, Syst. Sil., suppl., pl. 475, fig. 5-7.
Étage G₃ (Devonian).

Bolloceras raptor (BARRANDE)

Phragmoceras raptor BARRANDE, 1877, Syst. Sil., suppl., pl. 535, fig. 1-3.
Étage G₃ (Devonian).

Bolloceras rex BARRANDE

Phragmoceras rex BARRANDE, 1865, Syst. Sil., pl. 61, fig. 1; pl. 62, fig. 1-6; pl. 101, fig. 1-5.
Étage G₃ (Devonian).

Bolloceras suessi (BARRANDE)

Phragmoceras suessi BARRANDE, 1865, Syst. Sil., pl. 67, fig. 1, 2.
Étage G₃ (Devonian).

? *Bolloceras* sp. (BARRANDE)

Phragmoceras broderipi BARRANDE, 1865-67, Syst. Sil., p. 207, (partim), pl. 65, fig. 3 [plate, 1865; text, 1867].
Étage G₃ (Devonian).

Mandaloceras? *globulosum* (BARRANDE)

Phragmoceras globulosum BARRANDE, 1865, Syst. Sil., pl. 52, fig. 10-13.
Étage ?E₂ (Middle Silurian)

Tetrameroceras infaustum (BARRANDE)

Phragmoceras infaustum BARRANDE, 1865, Syst. Sil., pl. 55, fig. 1-12. (non BARRANDE, 1877, Syst. Sil., suppl., pl. 482, fig. 4, 5 (appears to represent a different species).
Étage E₂ (Middle Silurian).

Tetrameroceras insolitum (BARRANDE)

Phragmoceras insolitum BARRANDE, 1865, Syst. Sil., pl. 52, fig. 14-18.
Étage E₂ (Middle Silurian).

Tetrameroceras loveni (BARRANDE)

Phragmoceras loveni BARRANDE, 1865, Syst. Sil., pl. 48, fig. 8-11; pl. 49, fig. 16-19; pl. 99, fig. 8-11.
Étage G₃ (Devonian).

Tetrameroceras bicinctum (BARRANDE)

Phragmoceras bicinctum BARRANDE, 1865, Syst. Sil., pl. 51, fig. 1-4.
Étage E₂ (Middle Silurian).

Tetrameroceras callistoma (BARRANDE)

Phragmoceras callistoma BARRANDE, 1865, Syst. Sil., pl. 47, fig. 1-7 (non pl. 67, fig. 3-8, = *Hexameroceras* sp.).
Étage E₁, E₂ (Middle Silurian).

Tetrameroceras discrepans (BARRANDE)

Phragmoceras discrepans BARRANDE, 1865, Syst. Sil., pl. 49, fig. 12-15.
Étage E₂ (Middle Silurian).

Tetrameroceras problematicum (BARRANDE)

Phragmoceras problematicum BARRANDE, 1865, Syst. Sil., pl. 54, fig. 10-12.
Étage E₂ (Middle Silurian).

Tetrameroceras rimosum (BARRANDE)

Phragmoceras rimosum BARRANDE, 1865, Syst. Sil., pl. 48, fig. 1-7.
Étage E₂ (Middle Silurian).

Tetrameroceras vetus (BARRANDE)

Phragmoceras vetus BARRANDE, 1865, Syst. Sil., pl. 54, fig. 1-9.
Étage E₂ (Middle Silurian).

Hexameroceras panderi (BARRANDE)

Phragmoceras panderi BARRANDE, 1865, Syst. Sil., pl. 48, fig. 12-15; pl. 50, fig. 7-15.
BARRANDE, 1877, Syst. Sil., suppl., pl. 428, fig. 14-20.
Étage E₂ (Middle Silurian).

Metaphragmoceras bohemicum (BARRANDE)

Phragmoceras bohemicum BARRANDE, 1877, Syst. Sil., suppl., pl. 533, fig. 3, 4; pl. 534, fig. 1.
Étage G₃ (Devonian).

Metaphragmoceras verneuili (BARRANDE)

Phragmoceras verneuili BARRANDE, 1865, Syst. Sil., pl. 66, fig. 1-3.
Étage G₃ (Devonian).

Conradoceras conradi (BARRANDE)

Phragmoceras conradi BARRANDE, 1865, Syst. Sil., pl. 49, fig. 1-11.
Étage E₂ (Middle Silurian).

Paraclitoceras devonicans (BARRANDE)

Phragmoceras devonicans BARRANDE, 1865, Syst. Sil., pl. 107, fig. 1-3.
Étage G₃ (Devonian).

Hemiphragmoceras pavidum (BARRANDE)

Phragmoceras pavidum BARRANDE, 1865, Syst. Sil., pl. 51, fig. 8-15.
Étage E₂ (Middle Silurian).

Hemiphragmoceras pusillum (BARRANDE)

Phragmoceras pusillum BARRANDE, 1865, Syst. Sil., pl. 52, fig. 1-9.
Étage E₂ (Middle Silurian).

Pentameroceras rimosum (BARRANDE)

Phragmoceras rimosum BARRANDE, 1865, Syst. Sil., pl. 48, fig. 1-7.
Étage E₂ (Middle Silurian).

Clathroceras sulcatum (BARRANDE)

Phragmoceras sulcatum BARRANDE, 1865, Syst. Sil., pl. 47, fig. 8-13.
Étage E₂ (Middle Silurian).

Inversoceras perversum (BARRANDE)

Phragmoceras sulcatum BARRANDE, 1865, Syst. Sil., pl. 53, fig. 1-33; pl. 100, fig. 6-9.
Étage E₂ (Middle Silurian).

Inversoceras perversum falciforme (BARRANDE)

Phragmoceras perversum var. *falciferum* BARRANDE, 1865, Syst. Sil., pl. 100, fig. 6-9.
Étage E₂ (Middle Silurian).

Mandaloceras? *saturnum* (BARRANDE)

Phragmoceras saturnum BARRANDE, 1870, Syst. Sil., pl. 428, fig. 16-19.
Étage E₂ (Middle Silurian).

"Phragmoceras" *desideratum* (BARRANDE)

Phragmoceras desideratum BARRANDE, 1865, Syst. Sil., pl. 53, fig. 34, 35 (based on fragment inadequate for generic determination).
Étage E₂ (Middle Silurian).

Species of *Phragmoceras* from Sweden

All true species of *Phragmoceras* from Sweden occur in Middle Silurian (Gotlandian) deposits. Forms not precisely located stratigraphically are *P. angelini* BARRANDE (1867, Syst. Sil., p. 187, 191) and *P. hisingeri* D'ORBIGNY (= *Nautilus complanatus* HISINGER, non SOWERBY, 1820). Other species, described by HEDSTRÖM (1917), are recognized as occurring in successive zones which are numbered in upward order: (1) *P. costatum*, *P. munthei*, *P. fasciatum*, *P. convolutum*; (2) *P. eurystoma*, *P. eurystoma flexible*, *P. fasciatum*; (3) *P. eurystoma*; (4) no species recorded; (5) *P. re-tortum?*, *P. brevidomicilium*, *P. hedstroemi* FOERSTE, 1929 (= *P. ellipticum* HEDSTRÖM, 1917, non HALL & WHITFIELD, 1875), *P. incertum*; (6) *P. inflexum*, *P. limbatum?*; (7) *P. dentatum*, *P. obesum*, *P. fuscimen*, *P. dubium*, *P. praecurvum*, *P. transversale*, *P. undulatum*, *P. gradatum*, *P. liljevalli*, *P. parvulum*, *P. discoidium*, *P. gigas*, *P. simile*, *P. sigmoideum*, *P. inflexum*, *P. mobergi*.

The following species, originally assigned to *Phragmoceras*, now are referred to the genus *Tuberiferoceras*: *T. proboscoideum*, *T. prominens*, *T. prominens minus*; all occur in the Silurian of Gotland.

Species of *Phragmoceras* from Great Britain

The following species of *Phragmoceras* recorded from Great Britain all occur in the Wenlock (Middle Silurian), the first-mentioned occurring also in lower Ludlow beds and the second in lower and upper Ludlow; *P. arcuatum* SOWERBY, *P. ventricosum* SOWERBY, *P. obliquum* BLAKE, *P. subexternum* BLAKE, *P. externum* BLAKE.

Phragmoceras prius BLAKE is too poorly preserved to be placed with certainty but it is not a *Phragmoceras*; probably it belongs to *Beloitoceras* or *Oncoceras*.

Species of *Phragmoceras* from North America

Phragmoceras appears to have entered North America from the north in early Clinton time. It is significantly absent in the Clinton of New York and regions south and east of the Cataract axis. In the east central region it occurs in the Liston Creek limestone of northern Indiana but is unknown in southern Indiana or equivalent strata around the Nashville dome and Hatchitigbee anticline of western Tennessee. The genus is much more abundant and widespread in the later half of the Middle Silurian in beds of Racine and Guelph age. Possibly the oldest species is *P. severnense* of the Severn limestone of Hudson Bay. Clinton forms in the east are confined to the maritime region and are best known in the section at Port Daniel, Quebec. They are less prominent in Anticosti, and unknown in Nova Scotia.

Clinton species. Following are bibliographic citations and records of the occurrence of species of *Phragmoceras* found in rocks of Clinton age (Middle Silurian) in North America.

Phragmoceras altum FOERSTE

Phragmoceras altum FOERSTE, 1936, Denison Univ. Bull., Sci. Lab., Jour., v. 31, p. 89, pl. 20, fig. 3.
Gascons formation, Pt. Daniel, Quebec.

Phragmoceras angustum (NEWELL)

Gomphoceras angustum NEWELL, 1888, Boston Soc. Nat. Hist., Proc., v. 23, p. 475, fig. —.
Phragmoceras angustum KINDLE & BREGER, 1904, Indiana Dept. Geol., Nat. Res., 28th Ann. Rept., p. 477, pl. 18, fig. 1.
GRABAU & SHIMER, 1910, North American Index Fossils, v. 2, p. 132, fig. 1383.
FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 330, pl. 56, fig. 1.
Liston Creek limestone, northern Indiana.

Phragmoceras anticostiense FOERSTE

Phragmoceras anticostiense FOERSTE, in TWENHOFFEL, 1927, Canada Geol. Survey, Mem. 154, p. 320, pl. 58, fig. 1.
FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 332.
Chicotte formation, Anticosti.

Phragmoceras northropi FOERSTE

Phragmoceras northropi FOERSTE, 1936, Denison Univ. Bull., Sci. Lab. Jour., v. 31, p. 90, pl. 21, fig. 2.
?Gascons formation, Pt. Daniel, Quebec.

Phragmoceras severnense FOERSTE & SAVAGE

Phragmoceras severnense FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 93, pl. 19, fig. 2A,B.
FOERSTE, 1929, Same, v. 24, p. 356.
Severn limestone, Hudson Bay region.

Phragmoceras nelsonense PARKS

Phragmoceras nelsonense PARKS, 1915, Royal Canadian Inst., Trans., v. 11, p. 83, pl. 1, fig. 7; pl. 3, fig. 1-2.
FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab. Jour., v. 22, p. 93, pl. 19, fig. 3-6.
FOERSTE, 1929, Same, v. 24, p. 348.

From drift of Hudson Bay region, regarded as from the Ekwan limestone.

Phragmoceras lineolatum WHITEAVES

Phragmoceras lineolatum WHITEAVES, 1904, Canada Geol. Survey, Ann. Rept., new ser., v. 14, App. F, p. 57.
WHITEAVES, 1906, Canada Geol. Survey, Paleoz. Fossils, v. 3, pt. 4, p. 265 (partim), pl. 34, fig. 2 (non fig. 1, 3).
FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 97, pl. 20, fig. 1, 3A,B.
FOERSTE, 1929, Same, v. 24, p. 347.
Attawapiskat limestone, Hudson Bay region.

Phragmoceras parksi FOERSTE & SAVAGE

Phragmoceras parksi FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 95, pl. 21, fig. 1A,B.
FOERSTE, 1929, Same, v. 24, p. 350.
Attawapiskat limestone, Hudson Bay region.

Phragmoceras vantuyli FOERSTE & SAVAGE

Phragmoceras vantuyli FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 100, pl. 21, fig. 2A,B.
FOERSTE, 1929, Same, v. 24, p. 358.
Attawapiskat limestone, Hudson Bay region.

Phragmoceras whiteavesi FOERSTE & SAVAGE

Phragmoceras lineolatum WHITEAVES, 1906, Canada Geol. Survey, Paleoz. Fossils, v. 3, pt. 4, p. 265 (partim), pl. 34, fig. 1, (non fig. 2, 3).
Phragmoceras whiteavesi FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 98, pl. 20, fig. 2.
FOERSTE, 1929, Same, v. 24, p. 358.
Attawapiskat limestone, Hudson Bay region.

Phragmoceras whitneyi PARKS

Phragmoceras whitneyi PARKS, 1915, Royal Canadian Inst., Trans., v. 11, p. 77, pl. 3 fig. 5; pl. 6 fig. 2.
FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 99, pl. 22, fig. 1.
FOERSTE, 1929, Same, v. 24, p. 359.
Ekwan or Attawapiskat limestone, Hudson Bay region.

Phragmoceras sp.

Phragmoceras lineolatum PARKS, 1915, Royal Canadian Inst., Trans., v. 11, p. 78.
Phragmoceras sp. FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 94, pl. 20, fig. 4.
Ekwan or Attawapiskat limestone, Hudson Bay region.

Phragmoceras sp.

Phragmoceras sp. FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 100, pl. 16, fig. 3A,B.
Attawapiskat limestone, Hudson Bay region.

Phragmoceras slocomi FOERSTE

Phragmoceras slocomi FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 336, pl. 60, fig. 1.
?Waukesha beds, Wisconsin.

Racine (Niagaran) species. The next group of species are those recorded from Niagaran (Middle Silurian) rocks of Racine age.

Phragmoceras hoyi WHITFIELD

Phragmoceras hoyi WHITFIELD, 1878, Wisconsin Geol. Survey, Rept. for 1877, p. 86.
WHITFIELD, 1882, Geol. Wisconsin, v. 4, p. 301, pl. 19, fig. 4, 5.
CHAMBERLIN, 1883, Same, v. 5, p. 194.
FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 346.
Racine dolomite, Wisconsin.

Phragmoceras hoyi compressum WHITFIELD

Phragmoceras hoyi var. *compressum* WHITFIELD, 1877, Wisconsin Geol. Survey, Ann. Rept. for 1877, p. 86.
WHITFIELD, 1882, Geol. Wisconsin, v. 4, p. 301, pl. 20, fig. 3.
Phragmoceras hoyi compressum FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 346.
Racine dolomite, Wisconsin.

Phragmoceras nestor HALL

- Phragmoceras nestor* HALL, 1868 (adv. sheets, 1865), New York St. Cab. Nat. Hist., 20th Ann. Rept., p. 347, 363, fig. 7, 8.
 HALL, 1870, Same, revised ed., p. 405, fig. 3, 4.
 DAY, 1879, Wisconsin Acad. Sci., Arts, Letters, v. 4, p. 115.
 WHITFIELD, 1882, Geol. Wisconsin, v. 4, p. 301, pl. 19, fig. 3.
 GRABAU & SHIMER, 1910, North American Index Fossils, v. 2, p. 132, fig. 1380-1381.
 FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 348, pl. 51, fig. 3A,B.
 Racine dolomite, Wisconsin.

Phragmoceras altdorsatum FOERSTE

- Phragmoceras altdorsatum* FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 329, pl. 57, fig. 3.
 Cedarville dolomite, Cedarville, Ohio.

Phragmoceras colliciare FOERSTE

- Phragmoceras colliciare* FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 339, pl. 52, fig. 1-3
 Cedarville dolomite, Cedarville, Ohio.

Phragmoceras cuneiforme FOERSTE

- Phragmoceras cuneiforme*, FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 342, pl. 50, fig. 2, 3.
 Cedarville dolomite, Cedarville, Ohio.

Phragmoceras carmani FOERSTE

- Phragmoceras carmani* FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 337, pl. 55, fig. 1
 Cedarville dolomite, ?Green Co., Ohio.

Phragmoceras northropi FOERSTE

- Phragmoceras northropi* FOERSTE, 1936, Denison Univ. Bull., Sci. Lab., Jour., v. 31, p. 90, pl. 21, fig. 2.
 ?Gascons formation, Pt. Daniel, Quebec.

Phragmoceras chicagoense FOERSTE

- Phragmoceras chicagoense* FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 339, pl. 63, fig. 3A,B.
 Racine dolomite, Chicago, Ill.

Phragmoceras parvum HALL & WHITFIELD

- Phragmoceras parvum* HALL & WHITFIELD, 1875, Ohio Geol. Survey, Paleont., v. 2, p. 151, pl. 8, fig. 10.
 ? LESLEY, 1889, Pennsylvania Geol. Survey, Rept. Progr., 4, p. 639, fig. —.
 KINDLE & BRUGER, 1904, Indiana Dept. Geol., Nat. Res., 28th Ann. Rept., p. 477, pl. 25, fig. 3, 4.
 GRABAU & SHIMER, 1910, North American Index Fossils, v. 2, p. 132, fig. 1382.
 FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 351, pl. 50, fig. 5A,B; pl. 55, fig. 2.
 Cedarville dolomite, Ohio.

Phragmoceras ruedemanni FOERSTE

- Phragmoceras parvum* CLARKE & RUEDEMANN, 1903, New York State Mus., Mem. 5, p. 99, pl. 21, fig. 1-8.
Phragmoceras ruedemanni FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 355.
 Lower Shelby dolomite, Rochester, New York.

Phragmoceras sp.

- Phragmoceras* sp. FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 347, pl. 61, fig. 3
 Cedarville dolomite, Ohio.

Phragmoceras projectum (NEWELL)

- Gomphoceras projectum* NEWELL, 1888, Boston Soc. Nat. Hist., Proc., v. 23, p. 476, text-fig.
Phragmoceras projectum FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 354.
 Huntington dolomite, Delphi, Ind.

Species of Guelph (Niagaran) age. Some difficulty attends the separation of beds of Racine age from those of the Guelph in the late Middle Silurian. Certainly it is in the latest Middle Silurian in America that one finds the culmination of cyroconic and breviconic cephalopods, many of which are indigenous types, although many others mark the inception of genera in America characteristic of BAR-

RANDE's Étage E₂ of Bohemia. As noted above, the lower Shelby beds of CLARKE & RUEDEMANN appear to contain a typical Racine assemblage, whereas the upper Shelby beds contain a more advanced association that clearly is of Guelph age. Some greater difficulty attends recognition of the Racine-Guelph boundary in Ohio and Indiana. In general, the beds characterized by *Megalomus* have been considered to be those of Guelph age. However, when visiting the Silurian quarries at Monon, Ind., where an association is found which has long been considered Racine, a fine large *Megalomus* was found which plainly must have come from the lower layers exposed there. It may well be that the Racine-Guelph interval was one in which no serious interruption of deposition occurred and where no hard and fast boundary can be drawn. The differences on which the division was first drawn may prove to be the result of local concentration of faunas, in part comprising assemblages of fossils around local reefs and in part representing extremely local conditions which caused the fossils to be preserved in dolomite in one locality but destroyed in another.

With these reservations, I have attempted to separate the species of *Phragmoceras* from beds of Guelph age (listed below) from those of the underlying Racine equivalents (listed above).

Phragmoceras arcanum FOERSTE

- Phragmoceras arcanum* FOERSTE, 1930, Denison Univ. Bull., Sci. Lab., Jour., v. 25, p. 100, pl. 19, fig. 7.
 Port Byron dolomite, Illinois.

Phragmoceras auroraense FOERSTE

- Phragmoceras auroraense* FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 333, pl. 53, fig. 1A,B, 2A,B, 3.
 Guelph dolomite, Rising Sun, Ohio.

Phragmoceras byronense WORTHEN

- Phragmoceras byronense* WORTHEN, 1875, Illinois Geol. Survey, v. 8, pl. 24, fig. 6.
 FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 335, pl. 61, fig. 1A,B.
 FOERSTE, 1930, Same, v. 25, p. 98.
 Port Byron dolomite, Illinois.

Phragmoceras ellipticum HALL & WHITFIELD

- Phragmoceras ellipticum* HALL & WHITFIELD, 1875, Ohio Geol. Survey, Paleont., v. 2, p. 152, pl. 8, fig. 11.
 ? LESLEY, 1889, Pennsylvania Geol. Survey, Rept. Progr., no. 4, p. 637, fig. —.
 GRABAU & SHIMER, 1910, North American Index Fossils, v. 2, p. 133, fig. 1384.
 FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 343, pl. 50, fig. 4
 ?Guelph dolomite, Highland County, Ohio.

Phragmoceras hillsboroense FOERSTE

- Phragmoceras hillsboroense* FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 345, pl. 51, fig. 1A,B.
 Pebbles dolomite, Highland Co., Ohio.

Phragmoceras hespelerense FOERSTE

- Phragmoceras nestor canadense* WHITEAVES, 1884, Canada Geol. Survey, Paleoz. Fossils, v. 3, pt. 1, p. 39 (*partim*), pl. 7, fig. 1a,b, (*non* fig. 1, which is *P. canadense*).
Phragmoceras hespelerense FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 345, pl. 58, fig. 3; pl. 60, fig. 3.
 Guelph dolomite, Hespeler, Ontario.

Phragmoceras canadense WHITEAVES

- Phragmoceras nestor var. canadense* WHITEAVES, 1884, Canada Geol. Survey, Paleoz. Fossils, v. 3, pt. 1, p. 39 (*partim*), pl. 7, fig. 1, (*non* fig. 1a, 1b).
 WHITEAVES, 1895, Same, v. 3, pt. 2, p. 105.
Phragmoceras canadense FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 336, pl. 54, fig. 1A,B.
 Guelph dolomite, southern Ontario.

Phragmoceras ontarioense FOERSTE

- Phragmoceras parvum* WHITEAVES, 1884, Canada Geol. Survey, Paleoz. Fossils, v. 3, pt. 1, p. 41, pl. 7, fig. 2.
 WHITEAVES, 1895, Same, v. 3, pt. 2, p. 108.
 ? KINDLE & BRUGER, 1954, Indiana Dept. Geol. Nat. Res., 28th Ann. Rept., p. 477, pl. 25, fig. 3, 4.

Phragmoceras ontarioense FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 349, pl. 58, fig. 2A,B.

FOERSTE, 1930, Same, v. 25, p. 101, pl. 19, fig. 3-6.

Guelph dolomite, southern Ontario.

Phragmoceras vicinum FOERSTE

Phragmoceras vicinum FOERSTE, 1930, Denison Univ. Bull., Sci. Lab., Jour., v. 25, p. 99, pl. 20, fig. 4

Port Byron dolomite, Illinois.

Phragmoceras wortheni FOERSTE

Phragmoceras wortheni FOERSTE, 1930, Denison Univ. Bull., Sci. Lab., Jour., v. 25, p. 98, pl. 19, fig. 1, 2; pl. 28, fig. 5.

Port Byron dolomite, Port Bryon, Illinois.

Phragmoceras sp.

Phragmoceras sp. FOERSTE, 1930, Denison Univ. Bull., Sci. Lab., Jour., v. 25, p. 98, pl. 21, fig. 7; pl. 28, fig. 4.

Port Byron dolomite, Illinois.

Phragmoceras sp.

Phragmoceras sp. FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 334, pl. 54, fig. 2A,B.

Pebbles dolomite, Adams Co., Ohio.

Species Doubtfully or Erroneously Assigned

Phragmoceras ventricosum OWEN

Phragmoceras ventricosum OWEN, 1844, Geol. Expl. Iowa, Wisconsin and Illinois, ed. 2, p. 76, pl. 13, fig. 9.

Niagaran, Iowa and Wisconsin; Not recognizable.

The following species formerly assigned to *Phragmoceras* now are placed in other genera as indicated below.

Phragmoceras accola (RUEDEMANN).

Gomphoceras ruedemanni (FOERSTE).

Gomphoceras camerani (FOERSTE & SAVAGE).

Oncoceras constrictum HALL (= *Phragmoceras constrictum* CHAPMAN).

Tetramoceras corallophilum (CLARKE).

Gomphoceras hector (BILLINGS).

Tubiferoceras labiatum (WHITFIELD).

Barrandoceras nator (LESLEY).

Beloitoceras clochense (in part).

Maelonoceras praematurum (BILLINGS).

Genus TUBIFEROCERAS Hedström, 1917

Type species—*Phragmoceras proboscoideum* HEDSTRÖM

Tubiferoceras HEDSTRÖM, 1917, Sveriges Geol. Undersökning, Ser. C:A, No. 15, p. 11.

FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 352, pl. 48, fig. 2A-C.

FOERSTE, 1929, Same, v. 24, p. 360.

FLOWER & KUMMEL, 1950, Jour. Paleont., v. 24, p. 612.

Compressed endogastric brevicones, differing from *Phragmoceras* primarily in that the dorsal sinus of the aperture is projected adorsally and then forward in a tubular extension of the aperture. The ventral hyponomic sinus is characteristic, being a long narrow slit that is rounded at its ventral extremity. In form the shells of this genus differ from those of typical *Phragmoceras* in being straighter and quite rapidly expanding. The dorsal profile is uniformly convex; the ventral profile may be straight or slightly convex over the living chamber, but straight or very faintly concave adapically. The marked curvature and the accompanying obliquity of the adoral sutures found in typical *Phragmoceras* is not developed here. The structure of the siphuncle has not been made known for any of the species placed in this genus.

Discussion. The fact that some species of this genus appear relatively early, before *Phragmoceras* is well developed, may raise some question as to whether *Tubifero-*

ceras is actually related to *Phragmoceras*. That its aperture is more specialized is anomalous when the early appearance of the genus is considered. Some intergradation in the characters of the aperture between *Tubiferoceras* and typical *Phragmoceras* does seem to occur—indeed it is so marked that one can, in surveying the species, sympathize with HEDSTRÖM's doubts concerning generic distinctness of the group for he introduced the name *Tubiferoceras* conditionally. From the available evidence, while the relationship of the genus to *Phragmoceras* may be taken with some reservation, no better solution can now be offered, and objections to accepting inferences as to affinities of the two genera are not by any means unsurmountable. Therefore it seems best to retain *Tubiferoceras* in the Phragmoceratidae, regarding it as a remarkable but an extremely early specialization of the simpler *Phragmoceras*. If this assumption is correct, it follows that the Phragmoceratidae were already well established and well differentiated by the time of their appearance in North America in strata of late Clinton age. While there are some difficulties in correlation, *Tubiferoceras* and *Phragmoceras* seem to appear first in beds of late Clintonian age in Europe also.

Tubiferoceras proboscoideum (Hedström)

Phragmoceras proboscoideum HEDSTRÖM, 1917, Sveriges Geol. Undersök. Ser. C:A, no. 15, p. 8-9, pl. 1, fig. 1-10.

Tubiferoceras proboscoideum FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 352, pl. 48, fig. 2A-C.

Middle Silurian, Gotland (Horizon 1 of HEDSTRÖM); Stricklandia beds (?late Clinton equivalent).

Tubiferoceras prominens (Hedström)

Phragmoceras prominens HEDSTRÖM, 1917, Sveriges Geol. Undersök., Ser. C:A, no. 15, p. 9, pl. 2, fig. 1-8; pl. 3, fig. 1.

Tubiferoceras prominens FOERSTE, 1921, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 352.

Middle Silurian, Gotland (HEDSTRÖM's horizons 6 and 7); late Middle Silurian (probably Guelph equivalent).

Tubiferoceras prominens minus (Hedström)

Phragmoceras prominens var. *minus* HEDSTRÖM, 1917, Sveriges Geol. Undersök., Ser. C:A, no. 15, p. 10, pl. 3, fig. 2-9.

Tubiferoceras prominens var. *minus* FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 352.

Tubiferoceras prominens minus FOERSTE, 1929, Same, v. 24, p. 361.

Megalomus beds (division 7 of HEDSTRÖM), late Middle Silurian, Gotland.

Tubiferoceras gilberti (Kindle & Breger)

Trimeroceras gilberti KINDLE & BERGER, 1904, Indiana Dept. Geol., Nat. Res., 28th Ann. Rept., p. 475, pl. 15, fig. 1.

GRABAU & SHIMER, 1010, North American Index Fossils, v. 2, p. 130.

Tubiferoceras gilberti FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 353.

FOERSTE, 1929, Same, v. 24, p. 361, pl. 60, fig. 2.

Liston Creek limestone (Middle Silurian), Wabash, Ind.

Tubiferoceras? lineare (Newell)

Gomphoceras linearis NEWELL, 1888, Boston Soc. Nat. Hist., Proc., v. 23, p. 473, 2 figs.

Tubiferoceras? lineare FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 363.

Liston Creek limestone (Middle Silurian), Wabash, Ind.

Tubiferoceras labiatum (Whitfield)

- Phragmoceras labiatum* WHITFIELD, 1878, Wisconsin Geol. Survey, Ann. Rept. for 1877, p. 86.
 ——— WHITFIELD, 1882, Geol. Wisconsin, v. 4, p. 302, pl. 20. f-1, 2.
 ——— HEDSTRÖM, 1917, Sveriges Geol. Undersök., Ser. C:A, no. 15, p. 11.
Tubiferoceras labiatum FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 353.
 ——— FOERSTE, 1919, Same, v. 24, p. 362.

Waukesha beds, late Clintonian (Middle Silurian), Wisconsin.

Genus PRISTEROCERAS Ruedemann, 1925

Type species—*Pristeroceras timidum* RUEDEMANN

- Pristeroceras* RUEDEMANN, 1925, New York State Mus., Bull. 265, p. 57, pl. 18, fig. 1-7, text-fig. 34-37.
 ——— FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 363.

This genus was erected for endogastric brevicones essentially similar to *Phragmoceras* in form and appearance but differing in the strongly crenulate margin of the aperture, which is particularly marked at the narrow slit of the hyponomic sinus. The cross section was originally compressed, the siphuncle on the concave ventral side. RUEDEMANN (1925, fig. 37) has figured a structure interpreted as a series of siphuncle segments. They are flattened and perhaps somewhat doubtful, for isolated siphuncle segments are otherwise unknown. They are generally too fragile to be preserved in this way and similar segments are known only in cephalopods having a siphuncle that is greatly strengthened by internal deposits such as we have no reason to expect here. If the structure is correctly interpreted, it indicates that the siphuncle segments are expanded and broadened markedly at their adoral ends, as in *Phragmoceras*. The drawing shows segments of unusually angular outline, instead of broadly rounded.

Discussion. RUEDEMANN described together the new genus and species named *Pristeroceras timidum*. No other species of the genus is known. *P. timidum* is represented by a considerable series of flattened shells from the Bertie waterlime, Upper Silurian, near Buffalo, New York. Preservation of the Bertie fossils is such as to indicate improbability that any better specimens will be found. As consequence, though we know more about the species than can usually be learned from such material, its relationships are expected to remain somewhat uncertain. The aperture is logically one which can be developed from that of *Phragmoceras*. The siphuncle structures, if real, suggest affinities with the Phragmoceratidae. Such crushed siphuncles would be expected to show traces of actinosiphonate rays if they belonged to a member of the Hemiphragmoceratidae, which seems the only alternate possibility of relationship for the

genus. Reference of *Pristeroceras* to the Phragmoceratidae, though inferential, is consistent with all known evidence.

Pristeroceras timidum Ruedemann

- Pristeroceras timidum* RUEDEMANN, 1925, New York State Mus., Bull. 265, p. 57, pl. 18, fig. 1-7; text-fig. 34-37.

Bertie waterlime (Upper Silurian), Buffalo, N.Y.

Genus PHRAGMOCERINA Flower, 1948

Type species—*Gomphoceras osculum* RUEDEMANN

- Phragmocerina* FLOWER, 1948, Bull. Am. Paleont., v. 32, no. 129, p. 8.

Slightly compressed brevicones, endogastric apically, essentially straight adorally, the apertural plane being essentially parallel to the last septum, instead of strongly inclined to it, as in typical *Phragmoceras*. The adoral septa are subparallel and transverse, instead of becoming increasingly oblique. Aperture consists of a rounded faintly transverse main aperture on the dorsal side, a long narrow hyponomic sinus which is inflated at the tip. The siphuncle is small; its structure has not been observed.

Discussion. The relationships of this genus present a dilemma in absence of knowledge of the siphuncle structure, for this cannot be obtained from any available specimen. On the basis of general similarity to *Phragmoceras* and lacking any conflicting evidence, the genus is placed tentatively in the Phragmoceratidae. It must be pointed out, however, that possibly resemblances may be due to homeomorphy rather than genetic relationships, for shells of the aspect of *Phragmoceras* are known to appear in the Ellesmoceratidae (lower Canadian), Hemiphragmoceratidae (Silurian), and *Bolloceras* (Devonian). Homeomorphy is conclusively indicated by the very different siphuncle patterns found in these groups, as well as by the erratic spacing in geological time of the groups involved. There is little support placing *Phragmocerina* in the Hemiphragmoceratidae, the only Silurian stock other than Phragmoceratidae in which shells of *Phragmoceras* type are known to develop. In the Hemiphragmoceratidae siphuncles contain actinosiphonate deposits and the shells tend to be exogastric.

The genus is represented only by two described species, both from Upper Silurian rocks.

Phragmocerina osculum (Ruedemann)

- Gomphoceras osculum* RUEDEMANN, 1916, New York State Mus., Bull. 189, p. 76, pl. 27, fig. 10-11.

- Phragmocerina oscula* FLOWER, 1948, Bull. Am. Paleont., v. 32, no. 129, p. 8.

Cobleskill limestone, Morganville, N.Y.

EXPLANATION OF PLATE 43**PHRAGMOCERATIDAE—Phragmoceras**

Phragmoceras sp. C, from Middle Silurian of Gotland. Further enlargement ($\times 22$) of basal part of thin section (no. 3) illustrated on Pl. 42, fig. 6. Layers of bullettes are only faintly indicated. Recumbent septal necks, longer dorsally (toward right) than ventrally, terminate in connecting ring in which the

vinculum is almost completely suppressed. Free part of ring, thicker dorsally than ventrally, shows obscure layering but no further differentiation. Small but indistinctly outlined masses of amorphous material at anterior end of the rings represent vestigial remnants of the vinculum, venter on left.



FLOWER & TEICHERT—Order Discosorida (Cephalopoda)

Phragmocerina litchfieldensis Flower

Phragmocerina litchfieldensis Flower, 1948, Bull. Am. Paleont., v. 32, no. 129, p. 9, pl. 2, fig. 1-3.

Manlius limestone, Litchfield, Herkimer Co., N.Y.

**Family MANDALOCERATIDAE Flower,
n. fam.**

The family Mandaloceratidae is here erected for essentially straight breviconic shells showing faint exogastric affinities which are apparent largely in profile of the contracted living chamber, though a few species are endogastric. Apertures vary from T-shaped to those with a rounded main aperture but possessing a narrow, very long hyponomic sinus on the ventral side. The siphuncles range from those with short broad, broadly rounded, strongly expanded segments and thick connecting ring to those with slender segments in which the connecting ring is thinned. Forms with such siphuncles approach the Trimeroceratidae in internal features but are distinguished by absence of a mid-dorsal sinus on the aperture. The Hemiphragmoceratidae are distinguished as endogastric shells with complexly symmetrically lobed aperture and siphuncle containing actinosiphonate deposits which are continuous, or apparently continuous, from one segment to the next.

The visored Silurian brevicones, of which this family forms a part, have long presented taxonomic difficulties owing to uncertainty as to their affinities. HYATT (1900) recognized two families, Phragmoceratidae and Trimeroceratidae, which he placed in the division Actinosiphonata of the Cyrtocoanites. FOERSTE (1926) concluded that the true Phragmoceratidae had little in common with other forms which he placed in the Trimeroceratidae and new family Hemiphragmoceratidae. The Hemiphragmoceratidae contains dominantly endogastric shells with aperture lacking an azygous dorsal sinus and siphuncle with well-developed actinosiphonate deposits which apparently are continuous from segment to segment. The Trimeroceratidae contain small, dominantly exogastric forms with small, generally slender siphuncles which lack actinosiphonate deposits. *Mandaloceras* was placed by FOERSTE in the Hemiphragmoceratidae but was recognized as a genus atypical in several respects, particularly in structure of the siphuncle.

Both Hemiphragmoceratidae and Trimeroceratidae were referred by FLOWER & KUMMEL (1950) to the Oncoceratida, although admittedly their affinities with simpler and more typical oncoceroids were not clearly established; at that time no other possible origin was suggested by the available evidence.

Review of the genera here assigned to the Mandaloceratidae has brought to light previously unsuspected indications of affinity with Discosorida, largely found in the new genus *Pseudogomphoceras*. In this genus the internal structure is strikingly similar to that of *Madiganella*, especially in the form of siphuncle segments, apparently thick rings, preservation of the central tube, and position of the siphuncle close to the center. Typical *Ovocerina* proves to have quite similar internal structure, though lacking the central tube, abundant

species of this genus showing some variation in the position of the siphuncle, degree of inflation of the segments, and some variation in form and aperture. Nevertheless, these shells exhibit thick rings as in discosorids and their remarkable similarity to *Madiganella* indicates a quite probable connection of the Mandaloceratidae with the Ruedemannoceratidae. Further examination of the stock demonstrated the existence of wide variations, ranging from remarkable brevicones with a constriction at mid-length (here recognizable as belonging to the genus *Vespoceras*) to elaborately costate forms (separated as *Cinctoceras*). At first it was believed that genera assigned to the Mandaloceratidae might be contemporaneously converging homeomorphs, partly of discosorid and partly of oncoceroid derivation. Discosorid affinities were suggested by forms with large broadly expanded siphuncle segments and thick rings. Oncoceroid affinities were suggested by forms with small ventral siphuncles and thin rings, and by some others, including typical *Mandaloceras*, in which the siphuncle segments increase markedly in size during ontogeny, but early segments exhibit structures which BARRANDE called "obstruction rings" and which seem to be a type of actinosiphonate deposit.

Three distinct types of siphuncles are discernible and yet these seem to vary among the species in manner so independent of variations in features of the aperture, form and ornamentation as to indicate that the Mandaloceratidae constitute a single group which is not separable into two groups, one of oncoceroid and the other of discosorid origin. The types of siphuncles mentioned are characterized respectively by (1) broad segments with thick rings, (2) narrow segments with thin rings, and (3) so-called obstruction rings in a siphuncle that is small apically but broad adorally. The numerous gradations among these types suggest variation within a genetic group rather than two distinct convergent stocks.

Former assignment of these shells to the Oncoceratida rested primarily on the apparently actinosiphonate nature of the "obstruction rings." Similar actinosiphonate deposits are seen in the Devonian family Brevioceratidae and are closely approached in Chazyan *Valcouroceras*. That such similar structures could be developed in a stock quite removed from the Oncoceratidae seemed incredible. Regrettably, no material was available for investigation of the "obstruction rings" at first hand. It became apparent however that these structures might have had either of two possible origins: (1) by specializations stemming from the bullette which here becomes inflated and produces irregular actinosiphonate deposits; or (2) by deposits within the siphuncle forming structures which are distinct from connecting rings and which here simulate actinosiphonate deposits. Acceptance of either explanation accompanied by rejection of the other, is not possible at the present time. True actinosiphonate deposits are actually developments from the connecting rings and not deposits within the siphuncle that differ from the ring in origin and composition. For this reason origin in the connecting ring seems likely. On the other hand the obstruction rings are developed fully only in adapical portions of the phragmocones and show the

pattern of growth characteristic of deposits within the siphuncle which is common to the actinoceroids, Michelino-ceratidae, and such discosorids as exhibit these structures.

As pointed out in Part I, inclusion of the Mandaloceratidae in the Discosorida provides some interesting implications. It is one of several stocks in which there is demonstrable simplification of the internal structures, producing small ventral siphuncles with apparently thin rings and no internal deposits. Such siphuncles are particularly characteristic of the species here segregated in the genus *Umbeloceras* but appear to be found also in a group of small species retained at least temporarily in *Ovocerina*. If such simplification can occur as a specialization, it is possible that further specialization may have been carried to even greater lengths, and indeed it is from these forms that the family Trimeroceratidae could well be derived. Evidence connecting the family with the Oncoceratidae was not strong. No close connection with the oncoceroids could be demonstrated and it may be that this family also should be placed with the Discosorida.

In restudying species assigned to the Mandaloceratidae, it was found that too much had sometimes been included under a single specific name. A striking example is *Gomphoceras contrarium* BARRANDE, which contains one species now assigned to *Vesporoceras*, a species of *Cinctoceras*, a smooth generalized mandaloceroid, and a gibbous form with a large ventral siphuncle. In some other species some variations in proportion of the adult shells are evident, possibly representing natural variation within a species. However, BARRANDE seems to have accepted the postulate that immature shells could develop contracted apertures, not differing widely from those which he regarded as adults, which were twice to four times the size of small individuals. Such a series can be accepted as belonging to a single species only by adopting the hypothesis that contracted apertures were periodically resorbed before the shell grew further. With only fossil material at hand, such a hypothesis is not readily disproved but seemingly it should not be adopted unless very strong evidence is found. The fact that some obviously immature shells show uncontracted apertures opposes the above interpretation. That they are no more widely known than they are is attributable to several circumstances. Such shells, which one would be likely to regard as incomplete, generally are passed over in seeking material for illustration and they may be more common than published evidence leads one to believe. The scarcity of such shells is real however, indicating that probably growth of the shells was quite rapid until the contracted aperture and form characteristic of a given genus and species was attained. What variations would further growth produce? Clearly, one should expect further constriction of the aperture, possibly with modification of its original pattern. Yet shape of the aperture has been widely accepted as perhaps the most important criterion for recognition of the species. Careful reexamination of BARRANDE's illustrations indicates that variation of the aperture does occur among specimens which one would otherwise group together in a single species. Additions to the shell material of brevicones would tend to pro-

duce internal thickening near the aperture, development of a basal zone, and possibly further incipient cameral deposits.

Unfortunately no studies on possible variation within species of breviconic nautiloids have been made and lacking these, the only guide is common sense in using the rather meager evidence available.

Genus PSEUDOGOMPHOCERAS Flower, n. gen.

Type species—*Gomphoceras rigidum* BARRANDE

Shell straight, circular in section, with transverse sutures, essentially a generalized orthocone in the young but showing marked contraction of the living chamber as the aperture is approached. Aperture incomplete but with indication of more marked contraction on the siphonal ventral side than on the dorsum, and with suggestion that a part of the aperture is attained ventrally. There can be little doubt that the aperture when complete resembles those of *Ovocerina* and *Mandaloceras*, with which BARRANDE originally grouped this species.

The siphuncle is remarkable in almost exactly resembling that of the Ordovician genus *Madiganella*, both in its short broad segments, broadly expanded in the camerae and rounded in outline, and in possession of a well-defined central tube, which is here surrounded by vesicular material regarded by BARRANDE as organic.

Discussion. Early portions of the shell belonging to this singular genus and the one species assigned to it are distinguishable from *Madiganella* only by the absence of any curvature, circular nature of the cross section, and extreme simplicity of the sutures. In all of these features some species of *Madiganella* approach, if they do not attain this simple condition (GLENISTER, *vide litt.*). Yet the living chamber of *Pseudogomphoceras rigidum* is contracted. Though no specimen has been recognized which retains a complete aperture, the living chamber must have had the general conformation of species of *Ovocerina* and *Mandaloceras*. In view of this, the temptation is strong to place *P. rigidum* in *Ovocerina*, which it resembles most closely internally. Perhaps in future the two genera may be united but at the present time it seems necessary to keep them separate, for even though the apertures are similar, other evidence is insufficient to support belief that they belong together. The only features by which *Pseudogomphoceras* and *Ovocerina* as now understood, can be separated with certainty pertain to the siphuncle. *Pseudogomphoceras* alone is known to possess a central tube; its siphuncle segments are uniform in size and rate of expansion over all of the known phragmocone, a feature which is certainly not true of the closely related *Ovocerina alpheus*.

Pseudogomphoceras rigidum (Barrande)

Pl. 34, fig. 13-16

Gomphoceras rigidum BARRANDE, 1865-67, Syst. Sil., v. 2, pl. 83, fig. 10-14 (1865); p. 326 (1867).

Étage E₂ (Middle Silurian), Hinter-Kopania, Bohemia.

Genus *OVOCERINA* Flower, 1947Type species—*Gomphoceras marsupium* BARRANDE*Ovocerina* Flower, 1947, *Am. Midland Naturalist*, v. 37, p. 253.

Shell breviconic, early portion straight, contraction of the aperture producing a faintly exogastric aspect due to greater convexity on the ventral than dorsal side. Smaller species are more definitely curved and exogastric. The cross section is typically a little broader than high. Sutures are essentially straight and transverse. The aperture bears a prominent hyponomic sinus, sharply outlined, with tip rounded, in some broadly joined to the main part of the aperture but in others with connection reduced to a relatively narrow slit. Typical species show the main aperture as a broad rounded opening, but others may show the opening transversely extended, approaching the T-shaped aperture of *Mandaloceras*; still others may exhibit apertures extended into lateral sinuses with a mid-dorsal sinus as well, such species suggesting a trend toward *Eotrimeroceras* and the Trimeroceratidae.

Siphuncles vary widely, in typical forms being located slightly on the dorsal or ventral side of the center. The septal foramen is large. Those species for which the siphuncle is known in section, show short broad segments very much like those of *Pseudogomphoceras*. In *Ovocerina alphaeus* similar vesicular structure occurs within the siphuncle but no central tube; vesicular structure has not been observed in other species. *O. alphaeus* shows good evidence, as noted by BARRANDE, of natural truncation of the shell. Review of the species indicates that some others show suggestion of similar truncation, whereas some species certainly lack it. In smaller species the siphuncle tends to be more ventral in location, with slender segments and thickening of the connecting ring apparently lost. Evidence suggests that *Ovocerina*, as now understood, may be subdivided when the genus is studied more thoroughly. Present available information, which is largely that supplied by BARRANDE's descriptions and figures, is inadequate to show a really clear separation of the known species into smaller divisions of potential generic rank. Therefore, the genus is left for the present as a very comprehensive one. Gradation among the various species groups (summarized below) is sufficient to suggest that forms included in *Ovocerina* constitute a single phyletic stock, rather than contemporaneously convergent homeomorphs. All of the species so far known are of Middle Silurian age, from Étage E₂ of the Bohemian basin.

Forms with more open and more generalized apertures approach the Devonian genus *Ovoceras* in form. That genus has a small ventral siphuncle composed of very slender segments and is probably a member of the Brevicoceratidae of the Oncoceratida, indicating that resemblance between it and *Ovocerina* is homeomorphic.

Species of *Ovocerina* are rather readily divisible to well-defined groups as follows.

A. Group of *Ovocerina alphaeus*. Shells with broad siphuncle on dorsal side of center, with expanded segments and thick rings, septal foramen generally large. Truncation of the apex well

demonstrated only in *O. alphaeus*, but furnishing logical explanation for the unknown apical portions of the phragmocones of most, if not all, other species.

B. Group of *Ovocerina sphaerosoma*. Living chambers, and in some adoral camerae also, tending to have spheroidal outlines. Truncation is suspected but not clearly demonstrated. Siphuncles large, located slightly ventrad of center; little is known of the form and structure of the segments.

C. Group of *Ovocerina magna*. Shells with siphuncle on ventral side of center; septal foramen generally small. Siphuncle segments, where known, generally less expanded than in group A. In general form and appearance shells of this species group approach typical *Mandaloceras*.

D. Group of *Ovocerina mumia*. Relatively slender, small shells characterized by a rather large aperture with relatively simple outline in which the dorsal opening is wide and the hyponomic sinus commonly not sharply set off from it by a narrow slit as in most species of groups A-C. Siphuncle small, with segments, where known, relatively slender, thin-walled, and empty.

GROUP OF *OVOCERINA* ALPHAEUS*Ovocerina alphaeus* (Barrande)

Pl. 34, fig. 1-8

Gomphoceras alphaeus BARRANDE, 1860, *Soc. Geol. France, Bull.*, v. 17, p. 588, pl. 9.BARRANDE, 1865-67, *Syst. Sil.*, v. 2, pl. 83, fig. 1-8 (1865); p. 271 (1867).

This species, here refigured because of its importance, has a short phragmocone with sides slightly convex but not rapidly diverging, composed of about 15 camerae. Segments are short and broad except at the extreme base where a first segment twice the length of later segments is essentially spherical and a second one is transitional in proportions. One of the sections (Pl. 34, fig. 5-7) fails to penetrate the apical septal foramen; a second section (Pl. 34, fig. 8) shows the foramen closed by some dark shell material. Clearly the interpretation which BARRANDE offered, of natural truncation of the shell at this point, is based on a phenomenon for which no other explanation appears at all adequate. Vexingly, there is no indication of what the earlier portion of the shell was like in this species.

The living chamber shows greater convexity on the venter than dorsum, giving the whole shell a definitely exogastric aspect. The aperture has an elongated ventral sinus, well rounded and slightly expanded at its tip. The dorsal part of the aperture is a transverse oval, the dorsum slightly convex, the ventral part transverse on either side of the narrow slit leading to the hyponomic sinus, with lateral terminations strongly rounded. The interior of the siphuncle contains vesicular material comparable only to that portrayed for *Pseudogomphoceras rigidum* but showing no trace of a central tube.

Discussion. This species is well known internally. The short broad adult segments of the siphuncle shows an outline which is only a slight modification of that of *Pseudogomphoceras* and the sort of modification which would be expected with septa much more closely spaced; the segments are much shorter but the outline of the connecting ring and expansion of the segments is somewhat comparable to those of *Pseudogomphoceras* having equivalent distance across the septal foramen. Nothing like the vesicular tissue reported by BARRANDE as occurring in this species and *P. rigidum* has been observed anywhere else. Unless the figures are widely at variance with others which I have been able

to compare with originals, appearance of materials in BARRANDE's sections has been rendered with remarkable fidelity. It is hard to see how inorganic deposits could have produced this effect and certainly in examination of numerous sections I have encountered nothing similar. Therefore it seems probably that BARRANDE's explanation of the structure as organic is highly probable, even though the function and manner of secreting the vesicular tissue remain problematical.

Comparison with *Pseudogomphoceras* suggests that the siphuncle of *Ovocerina alphasus* lies on the dorsal side of the center and on the ventral side in *P. rigidum*.

Ovocerina marsupium (Barrande)

Pl. 34, fig. 9-12

Gomphoceras marsupium BARRANDE, 1865, Syst. Sil., v. 2, pl. 90, g. 1-5.
Ovocerina marsupia FLOWER, 1947, Am. Midland Naturalist, v. 37, p. 253.

A small markedly exogastric species with very closely spaced septa and siphuncle relatively small at base located on dorsal side of center. Dorsal aperture nearly transverse on either side of slit leading to ventral sinus, strongly convex over dorsal side.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina halli (Barrande)

Gomphoceras Halli BARRANDE, 1865, Syst. Sil., v. 2, pl. 74, fig. 7-11.

Shell slender in mature part, aperture large, with dorsal aperture broadly convex on both dorsum and venter. Siphuncle large on dorsal side of center, septa extremely close. Internal structure unknown.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina billingsi (Barrande)

Gomphoceras billingsi BARRANDE, 1865-67, Syst. Sil., pl. 105, fig. 8-11 (1865); p. 276 (1867).

A strongly inflated shell with septum at base of the extant part circular and a siphuncle on dorsal side of center. Septa slope forward from dorsum to venter, the cross section becoming slightly broader than high at the point of maximum size and the transverse dorsal aperture being faintly divided by a median emargination so that it is faintly concave mid-dorsally.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina gracilis (Barrande)

Gomphoceras gracile BARRANDE 1865-67, Syst. Sil., pl. 105, fig. 1-4 (1865); v. 1, p. 286, (1867).

This is an essentially straight slender species with rather deep camerae as in *Ovocerina transversa*, but the cross section is circular, the dorsal aperture flattened dorsolaterally and ventrolaterally, so that it is subtrapezoidal in form.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina centralis (Barrande)

Gomphoceras centrale BARRANDE 1865-67, Syst. Sil., pl. 74, fig. 1-5 (1865); p. 308 (1867).

A relatively slender species, enlarging gently to middle of the rather long living chamber. Septal foramen unusually large even for this genus and located slightly on dorsal side of the center. The aperture is T-shaped, but the narrow lateral limbs widen centrally, the dorsum being convex here and the hyponomic sinus widening as it approaches the lateral limbs.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina transversa (Barrande)

Gomphoceras transversum BARRANDE, 1865-67, Syst. Sil., pl. 106, fig. 1-4 (1865); p. 306 (1867).

Shell is broadly transverse in section. The septum shows a large foramen on dorsal side of center. The main aperture is well rounded both dorsally and ventrally, forming a transverse ellipse, from the base of which springs the usual prominent ventral hyponomic sinus.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina transgadiens (Barrande)

Gomphoceras contrarium BARRANDE, 1865, Syst. Sil., pl. 105, fig. 5-7 (partim).
Gomphoceras transgadiens BARRANDE, 1867, Same, p. 305.

This species is known from a smooth living chamber, differing from the costate *Gomphoceras contrarium*, in which the dorsal aperture is bilobed. The septal foramen lies well on the dorsal side of the center. The cross section of the shell is circular and lacks the dorsal flattening of typical *G. contrarium*, with which this species was first identified by BARRANDE.

Étage E₂ (Middle Silurian), Bohemian basin.

GROUP OF OVOCERINA SPHAEROSOMA

Ovocerina microstoma (Barrande)

Gomphoceras microstoma BARRANDE, 1865 (partim), Syst. Sil., pl. 72, fig. 14-17 (non pl. 72, fig. 7-13; pl. 92, fig. 16-20).

This is a straight fusiform shell with aperture greatly restricted, dorsal part not widely extended laterally, but high, transverse dorsally, the ventral sinus merging into the remainder of the aperture. One of the specimens illustrated by BARRANDE (p. 72, fig. 14-17) represents a large species slightly produced adorally and resembling *Ovocerina ovum*. Another (pl. 72, fig. 13) is given as a "middle-aged specimen" and a third (pl. 72, fig. 7-10) as "a young individual." Almost certainly these belong to different species. Another shell (pl. 92, fig. 16-20) is comparable in size with the lectotype (original shown in pl. 72, fig. 14-17, here selected) but has the aperture concave on the dorsum and obscurely Y-shaped. The several forms included by BARRANDE in this species all seem to belong to the group of *O. sphaerosoma* ranging from simple forms with a ventral siphuncle to those with more spheroidal living chambers.

All are from Étage E₂ (Middle Silurian), of the Bohemian basin.

Ovocerina nuciformis (Barrande)

Gomphoceras nuciforme BARRANDE, 1865-67, Syst. Sil., pl. 75, fig. 5-9 (1865); p. 294 (1867).

This is a small species with relatively small siphuncle located adventral of center. The aperture is a broad transverse ellipse dorsally. The living chamber and anterior camerae form an almost perfect sphere.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina stigmata (Barrande)

Gomphoceras stigmatum BARRANDE, 1865-67, Syst. Sil., pl. 75, fig. 18-21 (1865); p. 302 (1867).

Only the living chamber is known. This is large and circular in section. A rather large siphuncle occurs well on the ventral side of the center. The aperture, distinctly elevated on the internal mold, has the dorsal aperture elliptical and not as strongly produced laterally as in most species.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina sphaerosoma (Barrande)

Gomphoceras sphaerosoma BARRANDE, 1865-67, Syst. Sil., pl. 104, fig. 10-12 (1865); p. 302 (1867).

The isolated living chamber from which this species is known is almost perfectly rounded, the septum at its base merging with the shell outline. The cross section is slightly wider than high with dorsal aperture a transverse ellipse, slightly flattened dorsally.

The remarkable rounding of this specimen makes one wonder whether the natural truncation of the shell has actually removed all of the phragmocone. Such a development is suggested for there is striking similarity between this species and some of the Ascoceratida in intergradation of the septum with the contour of the external shell. The single specimen from which the septum is known cannot, of course, prove or disprove this suggestion.

Étage E₂ (Middle Silurian), Bohemian basin.

GROUP OF OVOCERINA MAGNA

Ovocerina magna (Barrande)

Gomphoceras magnum BARRANDE, 1865-67, Syst. Sil., pl. 89, fig. 7-10 (1865); p. 289 (1867).

This is a very large species, slightly depressed in cross section, siphuncle ventral, septal foramen rather large, aperture with dorsal portion a transverse oval, more transverse dorsally, less so ventrally, the sides sloping into the hyponomic sinus which is at first narrow, then broadly rounded terminally.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina? manca (Barrande)

Gomphoceras mancum BARRANDE, 1865-67, Syst. Sil., pl. 70, fig. 14-16 (1865); p. 324 (1867).

The apertural end of this shell is unknown. The siphuncle is composed of short broadly expanded segments that in manner typical of *Ovocerina* scarcely enlarge as they are traced forward in the phragmocone. Some uncertainty attends orientation of the specimen. The siphuncle lies closer to the side which is noted as dorsal, yet in the diagrammatic cross section it is regarded as closer to the venter, which is less flattened than the dorsum in cross section.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina fera (Barrande)

Gomphoceras ferum BARRANDE, 1865-67, Syst. Sil., pl. 80, fig. 18-22 (1865); p. 285 (1867).

A typical straight *Ovocerina* with large ventrally placed siphuncle composed of short rather broadly expanded segments, in the apical part of which are some "obstruction rings." The dorsal aperture is large and subtrapezoidal, slightly flattened ventrolaterally and more strongly flattened dorsolaterally.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina amygdala (Barrande)

Gomphoceras amygdala BARRANDE, 1865-67, Syst. Sil., pl. 77, fig. 23-26; pl. 80, fig. 1-17 (1865); p. 273 (1867).

A moderate-sized exogastric mandaloceroïd shell, with aperture a thick T-shaped structure, lateral limbs strongly rounded at tips, mid-dorsal area slightly convex. A portion of a siphuncle (BARRANDE, 1865, pl. 80, fig. 13) shows broad and short segments but not strongly expanded. No organic deposits are evident.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina tenera (Barrande)

Gomphoceras tenerum BARRANDE, 1865-67, Syst. Sil., pl. 81, fig. 13-17 (1865); p. 304 (1867).

A moderately small species, circular in section, dorsal aperture bilobed, rounded at sides, dorsum slightly concave in middle. Siphuncle slightly ventrad of center, composed of short broad segments typical of the genus.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina ovum (Barrande)

Gomphoceras ovum BARRANDE, 1865 (*partim*), Syst. Sil., pl. 84, fig. 1-9, pl. 105, fig. 12-14 (*non* pl. 75, fig. 10-12).

The specimens included under this species by BARRANDE are probably not conspecific, but aside from the removal of one tiny species, the proposal of new names seems pointless. The species are closely related, and are, with the exception mentioned, large and gibbous forms of *Ovocerina*. The original of BARRANDE's pl. 84, fig. 1-4, is a large fusiform shell, tapering at the aperture and at the apical end of the known part. The dorsal aperture is perfectly straight dorsally. Figures 6-8 of the same plate represent a smaller form, not attenuated at the aperture, which is convex mid-dorsally. Neither are probably identical with the form illustrated in pl. 105, fig. 12-14, which is typical, with the aperture transverse dorsally, but otherwise unlike the original of pl. 84, fig. 1-4; it lacks the spindle-shaped profile. Segments of the siphuncle are large and broadly rounded, the rings are thick, and there are traces of small structures which appear to be incipient bullettes.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina recta (Barrande)

Gomphoceras rectum BARRANDE, 1865-67, Syst. Sil., pl. 69, fig. 16-19; pl. 106, fig. 9-11; pl. 81, fig. 1-6 (?) (1865); p. 314 (1867).

The original of BARRANDE's pl. 69 is a moderate-sized faintly exogastric shell with segments of the siphuncle narrower than usual, essentially spheroidal and the main aperture a broad transverse band, straight dorsally and ventrally. The siphuncle is on the ventral side of the center. The larger specimen (BARRANDE, 1865, pl. 106) is not dissimilar in outline or aperture to that shown in pl. 69 and may be conspecific. The specimen shown in pl. 81 is quite probably not even congeneric, and that originally figured as this species was reassigned by BARRANDE to *Gomphoceras conicum* on pl. 104.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina? belloti (Barrande)

Gomphoceras Belloti BARRANDE, 1865-67 (*partim*), Syst. Sil., pl. 82, fig. 1-6 (*non* pl. 72, fig. 4-6) (1865); p. 275 (1867).

The lectotype (BARRANDE, 1865, pl. 82, fig. 1-5) is a compressed shell with ventral siphuncle, the dorsal lobe of the aperture a compressed ellipse from which the hyponomic sinus is sharply differentiated. BARRANDE's pl. 82, fig. 6, shows a larger form which in section shows rather broad short but only slightly expanded siphuncle segments. Relationship of this form is uncertain. Further modification of the aperture would produce something very close to *Umbeloceras spei* and BARRANDE assigned to *Ovocerina belloti* a small specimen with an aperture restored to conform with the high narrow T-shaped aperture of some other species. *O. recta* (in part *O. belloti*) seems to be best grouped with the generalized forms with ventral siphuncles and suggests a direct connection between such forms and *Umbeloceras*.

Étage E₂ (Middle Silurian), Bohemian basin.

GROUP OF OVOCERINA MUMIA

Ovocerina mumia (Barrande)

Gomphoceras mumia BARRANDE, 1865-67, Syst. Sil., pl. 70, fig. 10-13; pl. 92, fig. 4-7 (1865); p. 292 (1867).

Shell slender, exogastric, dorsum nearly straight, venter convex in profile, aperture with broadly oval dorsal aperture merging into a short round hyponomic sinus. Siphuncle small, near venter, its structure not observed.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerna extenuata (Barrande)

Gomphoceras extenuatum BARRANDE, 1865-67, Syst. Sil., pl. 88, fig. 9-11 (1865); p. 285 (1867).

This is a moderate-sized slender species with aperture poorly known. The cross section is subquadrate, the siphuncle small and ventrad of the center.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina myrmidio (Barrande)

Gomphoceras myrmidio BARRANDE, 1865-67, Syst. Sil., pl. 69, fig. 11-14; pl. 92, fig. 8-9 (1865); p. 293 (1867).

Gomphoceras porrecta BARRANDE, Samec, 1865, pl. 81, fig. 9-12.

The two specimens figured are not conspecific. The smaller one seems to be a miniature edition of *Ovocerina halli* with aperture having narrower limbs; the specimen on BARRANDE's pl. 81 is clearly a slightly more gibbous edition of *O. mumia*.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina nana (Barrande)

Gomphoceras nanum BARRANDE, 1865-67, Syst. Sil., pl. 71, fig. 14-18 (1865); p. 293 (1867).

This is a very small species, as the name implies. The siphuncle is small and ventral, the aperture strongly concave dorsally, broad, with dorsal aperture and hyponomic sinus not sharply separated.

Étage E₂ (Middle Silurian), Bohemian basin.

Ovocerina porrecta (Barrande)

Gomphoceras porrectum BARRANDE, 1865-67 (*partim*), Syst. Sil., pl. 89, fig. 1-6; (*non* pl. 81, fig. 9-12) (1865); p. 296 (1867).

In dimensions this species is slightly larger than *Ovocerina extenuata* but circular in section. The aperture is broadly elliptical dorsally and not sharply set off from the hyponomic sinus. The specimen which BARRANDE originally attributed to this species (1865, pl. 81) he later (1867, p. 296) referred to *O. myrmidio*.

Étage E₂ (Middle Silurian), Bohemian basin.

Genus CINCTOCERAS Flower, n. gen.

Type species—*Gomphoceras imperiale* BARRANDE

This genus consists of large, essentially straight brevicones, some slightly exogastric, others straight. The aperture is closed and T-shaped but the transverse limbs are broad and in this respect the genus resembles *Ovocerina* rather than *Mandaloceras*. It is set apart from *Ovocerina* by the strongly costate shell, the costae being numerous, low, and usually sharp on the exterior, though they may be only broadly rounded internally. In typical forms the cross section is broad, tending to be flattened somewhat on the dorsum, and the siphuncle consists of short broadly expanded segments, as in *Ovocerina*, with thick walls and without organic deposits. Some forms, notably *C. contrarium*, and *C. robustum*, have smaller siphuncles located on the ventral side of the center, segments being less broadly expanded and with minute obstruction rings. After much perplexity, these species are included in the genus, entailing assumption that the siphuncle becomes smaller and develops rings within this stock, rather than that these two species are convergent homeomorphs from another smooth-shelled stock.

All known species are from Étage E₂, Middle Silurian, Bohemian basin.

Cinctoceras imperiale Barrande

Pl. 36, fig. 9-12

Gomphoceras imperiale BARRANDE, 1865-67, Syst. Sil., pl. 86, fig. 1-8; pl. 87, fig. 1-5 (1865); p. 288 (1867).

This species, here reillustrated, is a very large closely costate form with depressed section that is flattened dorsally, with siphuncle on dorsal side of center, composed of short broad segments, apparently thick-walled, and without internal deposits. The aperture is T-shaped, the transverse limbs being thick and broadly rounded.

Étage E₂ (Middle Silurian), Bohemian basin.

Cinctoceras agassizi (Barrande)

Pl. 36, fig. 3-7

Gomphoceras agassizi BARRANDE, 1865-67, Syst. Sil., pl. 88, fig. 1-8 (1865); p. 269 (1867).

This is a small strongly costate species, agreeing with *Cinctoceras imperiale* in broad cross section, flattened dorsum, and dorsal siphuncle. The aperture, as illustrated, is more open dorsally and more similar to that of *Ovocerina*, for the dorsal lobe is not reduced to a pair of lateral limbs but is a transverse oval, merging gradually into a narrow slit that separates it from the rounded hyponomic sinus.

Étage E₂ (Middle Silurian), Bohemian basin.

Cinctoceras robustum (Barrande)

Gomphoceras robustum BARRANDE, 1865-67, Syst. Sil., pl. 70, fig. 1-6 (1865); p. 298 (1867).

This species is a brevicone which contracts more gently toward the aperture than do the preceding species. The aperture is wide, T-shaped, with arms broad as in the ventral sinus. The lectotype (BARRANDE, 1865, pl. 70, fig. 1-3) is a rather small mature shell, with siphuncle ventrad of the center, its segments rather more slender than those of *Cinctoceras imperiale* and containing obstruction rings. The specimen shown on figs. 5-6 is similar in proportions, but that shown in BARRANDE's pl. 70, fig. 4, is considerably larger and may be a distinct species.

Étage E₂ (Middle Silurian), Bohemian basin.

Cinctoceras contrarium (Barrande)

Gomphoceras contrarium BARRANDE, 1865-67 (*partim*), Syst. Sil., pl. 87, fig. 7-10 (*non* fig. 6, pl. 82, 105 (1865); p. 282 (1867)).

This species is restricted here to include only costate shells. The internal mold of the living chamber which is the lectotype (original of pl. 87, fig. 7-9, here selected) is large, exogastric, the dorsum slightly flattened, and in this respect resembling *Cinctoceras imperiale* and *C. agassizi*, while in its siphuncle, placed slightly on the dorsal side of the center, it also agrees with these species. The sectioned phragmocone (BARRANDE, 1865, pl. 87, fig. 10) may be conspecific but there is little by which one can judge, since the species was originally too broadly drawn. If so, the segments are short and broad and is *C. imperiale*.

The original of BARRANDE's pl. 105 is here renamed *Ovocerina bilobata*. It belongs to the group of species with a ventral siphuncle. I do not propose a new name for the original of his pl. 87, fig. 6, as only one view of the species is shown, which is not adequate to determine its affinities. The specimen assigned to *Gomphoceras contrarium* with question on pl. 82, is here renamed *Vesporoceras perplexans* and discussed under that genus. With species so broadly drawn, it is small wonder that without very critical work they appear to intergrade.

Étage E₂ (Middle Silurian), Bohemian basin.

Cinctoceras rugosum Barrande

Gomphoceras rugosum BARRANDE, 1865-67, Syst. Sil., pl. 69, fig. 1-5 (1865); p. 299 (1867).

This is a relatively small species, known from an internal mold on which rugose markings of the surface are somewhat smoothed out. The aperture is produced, probably by internal thickening of the shell, the limbs broad, T-shaped, slightly curving toward the venter, suggesting *Umbeloceras*. The siphuncle is relatively small and ventral, its structure not known. This form may be considered a small edition of *C. robustum*, by which it is connected with more typical forms. The cross section is slightly broader than high here, but the dorsum is not obviously flattened.

Étage E₂ (Middle Silurian), Bohemian basin.

Cinctoceras singulare (Barrande)

Pl. 36, fig. 8

Gomphoceras singulare BARRANDE, 1865-67, Syst. Sil., pl. 70, fig. 7-9 (1865); p. 327 (1867).

This species is based upon two immature specimens which expand to the aperture and show their generic affinities by the costae which increase in strength and prominence with growth of the shell. The types could be immature stages of rather large individuals of *Cinctoceras robustum* but hardly of those species with a marked flattening of the dorsum or with a dorsally placed siphuncle.

Étage E₂ (Middle Silurian), Bohemian basin.

Genus VESPOCERAS Flower, n. gen.

Type species—*Gomphoceras vespa* BARRANDE

This genus is erected for a remarkable group of essentially straight brevicones which, in part, appear to merge into *Ovocerina*, differing at first in a broad annular expansion of the shell, followed by a marked constriction, after which growth of the shell follows its usual course to a contracted living chamber with an aperture varying like that of *Ovocerina* or *Mandaloceras*. In some species the contracted aperture is not attained, and a form of this sort has been selected as type of the genus. The siphuncles are broadly expanded, as in typical *Ovocerina* but more slender in others and some show a trace of "obstruction rings." It should be noted that one form, *Gomphoceras clava* of BARRANDE, shows a faint constriction comparable to that of *Vesporoceras* but by its apertural features shows closer affinities to *Umbeloceras* and is placed in that genus.

Vesporoceras vespa (Barrande)

Pl. 37, fig. 1-5

Gomphoceras vespa BARRANDE, 1865-67, Syst. Sil., pl. 77, fig. 1-5 (1865); p. 328 (1867).

Shell compressed in cross section, venter narrowly rounded, dorsum broad and more smoothly rounded. The known part of the shell, essentially straight shows rapid expansion to a sharp annular expansion, contraction, then more gradual expansion over a rather long living chamber which is slightly convex in profile. The siphuncle, about midway between venter and center, is composed of rather short broad spheroidal segments which fail to show any organic deposit. BARRANDE believed that the aperture was not attained in the type. If not, the living chamber is one of unusual length and instead the species is here regarded as one with an open aperture and prominent hyponomic sinus.

Étage E₂ (Middle Silurian), Bohemian basin.

Vesporoceras cingulatum (Barrande)

Pl. 37, fig. 12-15

Gomphoceras cingulatum BARRANDE, 1865, Syst. Sil., pl. 69, fig. 20; pl. 76, fig. 1-17; pl. 106, fig. 5-8.

This species may be too broadly defined. BARRANDE's pl. 76, fig. 1-4, shows a specimen with open aperture not dissimilar to the type species. The prominent annular expansion lies low on the living chamber. Pl. 76, fig. 5-7, is similar, showing a comparable growth stage, but fig. 8-10 represent a later stage, for the annulus lies on the phragmocone. This specimen shows the attainment of a contracted *Mandaloceras*-like aperture, though the aperture is broken and its form is not plainly shown. Obstruction rings occur in basal segments of the siphuncle. An essentially complete mature specimen is illustrated in pl. 76, fig. 12-14, showing a T-shaped aperture with rather broad lateral limbs. The specimen in pl. 76, fig. 15-17, is slightly smaller and more slender, but differs mainly in the mid-dorsal convexity of the aperture. A similar apertural pattern is shown in a considerably larger specimen in pl. 106, fig. 5-8. If these specimens are conspecific, an interesting case of variation within the species is presented as to proportion and apertural features of the mature shells, and also some examples of immature shells with uncontracted apertures.

Étage E₂ (Middle Silurian), Bohemian basin.

Vesporoceras perplexans Flower, n. sp.

Pl. 37, fig. 6

Gomphoceras contrarium BARRANDE, 1865 (*partim*), Syst. Sil., v. 2, pl. 82, fig. 10-12.

This is a straight brevicone with strongly depressed cross section. The siphuncle, like that of typical *Ovocerina*, lies on the dorsal side of the center and the short segments are very broadly expanded and without known deposits. The aperture has a prominent hyponomic sinus, the dorsal portion being incomplete. The anterior part of the phragmocone is broadly expanded but into a broad rounded annulation rather than a narrow sharp one, as in the preceding species.

Étage E₂ (Middle Silurian), Bohemian basin.

Vesporoceras striatum (Barrande)

Gomphoceras striatum BARRANDE, 1865-67, Syst. Sil., pl. 71, fig. 10-13 (1865); p. 303 (1867).

This shell has a dorsal aperture shaped as a broad transverse ellipse, as in *Ovocerina*, and a short narrow hyponomic sinus that is broadly rounded terminally. The siphuncle is large at the foramen but located on the ventral side of the center of the shell. Its structure is not known. The shell is slightly expanded and then rather strongly contracted, the contraction occurring at about the base of the living chamber, beyond which the usual breviconic living chamber is developed. The species serves, in the smaller and more ventral siphuncle, as a transition from *V. perplexans* to more typical species of the genus.

Étage E₂ (Middle Silurian), Bohemian basin.

Vesporoceras aegrum (Barrande)

Gomphoceras aegrum BARRANDE, 1865-67, Syst. Sil., pl. 79, fig. 24-26 (1865); p. 269 (1867).

This species is similar to the preceding in the rounded nature of the early annular expansion but here it is larger and greater in diameter than any subsequent part of the shell. The cross section is circular, the siphuncle smaller and more ventrally placed, the aperture is more rounded and less transverse dorsally.

Étage E₂ (Middle Silurian), Bohemian basin.

Vesloceras atrophum (Barrande)

Gomphoceras atrophum BARRANDE, 1865-67, Syst. Sil., pl. 79, fig. 18-23 (1865); p. 274 (1867).

This is a species of circular section, the siphuncle somewhat ventrad of the center and larger than in the preceding form. The aperture is almost a dorsal semicircle connected to the usual hyponomic sinus. As in *Vesloceras aegrum*, the annular expansion attains the maximum diameter of the shell but it is narrower and more sharply defined. A section of the siphuncle reveals short broad segments such as are found in typical species of *Ovocerina*.

Étage E₂ (Middle Silurian), Bohemian basin.

Genus MANDALOCERAS Hyatt, 1900

Type species—*Gomphoceras bohemicum* BARRANDE

Mandaloceras HYATT, 1900 in ZITTEL-EASTMAN Textb. Palaeont., v. 1, ed. 1, p. 531.

FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 359, pl. 48, fig. 5A-C.

FOERSTE, 1929, Same, v. 24, p. 369.

Mandaloceras was erected for essentially straight visored brevicones with a T-shaped aperture but the genus has subsequently undergone some restrictions. FOERSTE (1924) removed actinosiphonate shells of somewhat similar form and aperture to the genus *Hemiphragmoceras*. Later the genus *Eotrimeroceras* was introduced to include some forms older than the main group of species from Anticosti.

In reviewing species having the aspect of *Mandaloceras*, it has been necessary to restrict the genus even further. There are many Middle Silurian species which have apertures like those of the Devonian genus *Ovoceras* in which a prominent hyponomic sinus extends from a broad rounded aperture. These forms are set apart as the genus *Ovocerina*. Study of the species showed that relationships are more complex than separation simply on apertural features would suggest, and many forms were finally placed in *Ovocerina* which originally had been retained in *Mandaloceras* on the basis of the T-shaped aperture.

Some small species having the aspect of *Mandaloceras* show only relatively slender siphuncle segments. In general, these are characterized by apertures in which the lateral limbs curve adventrally and such species are segregated in the genus *Umbeloceras*.

Mandaloceras, as here restricted, consists of shells with a T-shaped aperture and a siphuncle in which segments expand rapidly from early to late growth stages. Early segments contain a deposit which, though confined to the septal foramina, appears to be an abortive type of actinosiphonate deposit. Under this definition, only a relatively few species can be placed in *Mandaloceras* with certainty. There remain some inadequately known Bohemian species so that generic disposal of them among above-mentioned groups is problematical. The problem becomes much more serious when the less well-preserved species described from other regions are considered, for there is little or often, no information whatsoever concerning the internal structure of these species.

Mandaloceras bohemicum (Barrande)

Pl. 35, fig. 11-14

Gomphoceras bohemicum BARRANDE, 1865-67, Syst. Sil., pl. 74, fig. 12-16 (1865); p. 306 (1867).

Mandaloceras bohemicum HYATT, 1900, in ZITTEL-EASTMAN Textb. Palaeont., v. 1, ed. 1, p. 531, fig. 1084.

FOERSTE, 1924, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 359, pl. 48, fig. 5A-C.

This is a large gibbous species which has been refigured several times as the type species of *Mandaloceras*. The siphuncle is large, adventral from the center, composed of short broadly expanded segments. Small annular dark "obstruction rings" are present, of which the lowermost in the type appears to be irregular and shows the projections which characterize actinosiphonate deposits. The aperture is T-shaped, with lobes curved faintly toward the venter, concave mid-dorsally, the hyponomic sinus widened at its tip and at mid-length. The shell is more convex in ventral than dorsal profile and is evidently slightly exogastric.

Étage E₂ (Middle Silurian), Bohemian basin.

Mandaloceras simplex (Barrande)

Pl. 36, fig. 1, 2

Gomphoceras simplex BARRANDE, 1865-67, Syst. Sil., pl. 68, fig. 1-8 (1865); p. 315 (1867).

A more slender species but agreeing closely with *Mandaloceras bohemicum* in the T-shaped aperture and in conformation of the siphuncle segments and presence of small "obstruction rings" within the slender apical segments.

Étage E₂ (Middle Silurian), Bohemian basin.

Mandaloceras haueri (Barrande)

Gomphoceras Haueri BARRANDE, 1865-67, Syst. Sil., pl. 72, fig. 1-3 (1865); p. 312 (1867).

A straight breviconic shell, with shallow anterior camerae, segments of the siphuncle enlarging rapidly from the apical to adoral region, and located only slightly on ventral side of the center. Typical deposits are presented in apical segments.

Étage E₂ (Middle Silurian), Bohemian basin.

Mandaloceras verneuili (Barrande)

Pl. 35, fig. 3-6

Gomphoceras Verneuili BARRANDE, 1865-67, Syst. Sil., pl. 71, figs. 1-9 (1865); p. 330 (1867).

This species is distinctive in its endogastric curvature. The aperture, gradually enlarging segments of the siphuncle, and obstruction rings showing better than in any other species obviously actinosiphonate structure, prove that in spite of reversal of curvature, it is closely allied to the type species of *Mandaloceras*.

Étage E₂ (Middle Silurian), Bohemian basin.

Inadequately Known Bohemian Species Here Assigned to Mandaloceras

The following species, cited only in terms of BARRANDE's illustrations, are tentatively placed in *Mandaloceras*, though they are either inadequately known or, as noted, anomalous in some respects.

Mandaloceras probum (BARRANDE), pl. 72, fig. 18-20.

Mandaloceras obscurum (BARRANDE), pl. 72, fig. 21-22.

Mandaloceras conicum (BARRANDE), pl. 75, fig. 1-4; pl. 104, fig. 1-4 (as *Gomphoceras rectum* in explanation of plate).

Mandaloceras crassiventre (BARRANDE), pl. 85, fig. 10-11. A large species, inadequately known.

Mandaloceras consobrinum (BARRANDE), pl. 69, fig. 6-10. A slender form with a slender siphuncle which tends to be dorsad of the center. The adoral 4 camerae are not sectioned; it is likely that there the siphuncle expands as in typical *Mandaloceras*.

Mandaloceras decurtatum (BARRANDE), pl. 75, fig. 13; pl. 92, fig. 1-3. A small gibbous form, with the siphuncle of broad subquadrate segments containing small "obstruction rings."

Mandaloceras solidum (BARRANDE), pl. 508, fig. 14-17.

Mandaloceras surgens (BARRANDE), pl. 515, fig. 14-15.

Mandaloceras vellerosum (BARRANDE), pl. 85, fig. 7-9.

Species of *Mandaloceras* from Silurian of England

The following species from England have been assigned to *Mandaloceras* but available information does not permit close analysis which is necessary to distinguish true members of the genus. Some species possibly are assignable to *Ovocerina*. No representatives of *Umbeloceras*, *Vesporoceras*, or *Cinctoceras* are recognized.

Mandaloceras ellipticum M'COY. A relatively large typical species. Silurian (lower Ludlow).

Mandaloceras eta (BLAKE). Characterized by a Y-shaped aperture and compressed section; larger than any Bohemian species showing these features. Silurian (lower Ludlow).

Mandaloceras neglectum (BLAKE). A smaller compressed form with Y-shaped aperture. Silurian (lower Ludlow).

Mandaloceras cinctum (BLAKE). Aperture apparently transverse dorsally, not clearly preserved; more probably a *Mandaloceras* than any other genus. Silurian (lower Ludlow).

Mandaloceras? crater (BLAKE). Main part of aperture relatively broad and short but too transverse for *Ovocerina*. Silurian (Wenlock).

Mandaloceras amygdala (BARRANDE). A single specimen has been identified with this species by BLAKE. Silurian (lower Ludlow).

Mandaloceras aequale (BLAKE). A small ovate compact species. Middle Silurian (Wenlock).

Mandaloceras? corona (BLAKE). A small compressed species with aperture so convex dorsally as to approach *Trimeroceras*. Middle Silurian (Wenlock).

Species of *Mandaloceras* from Silurian of North America

Mandaloceras austini FOERSTE. Relatively large, form typical, aperture not clearly shown. Cedarville dolomite, Ohio.

Mandaloceras diminuens FOERSTE. Aperture relatively open, shell small, compressed. Port Byron dolomite, Illinois.

Mandaloceras erectum FOERSTE. A relatively slender form with aperture incompletely known. Gascons formation, Port Daniel, Quebec.

Mandaloceras hawthornense FOERSTE. Typical of genus in form and aperture. Racine dolomite, Illinois.

Mandaloceras marcyae (WINCHELL & MARCY). Racine dolomite, Illinois.

Mandaloceras parvulum (WHITEAVES). Type cannot be located, identification dubious. "Niagaran, Manitoba."

Mandaloceras subgracile (WHITEAVES). Compressed, with Y-shaped aperture. Gascons or Bouleaux formation Port Daniel, Quebec.

Mandaloceras scrinum (HALL). A typical species with Y-shaped aperture. Racine dolomite, Illinois.

Mandaloceras wabashense (NEWELL). A large but typical species. Liston Creek or Huntington dolomite, Wabash, Ind.

Mandaloceras chaceae FLOWER. Irondequoit limestone, late Clinton, New York.

Genus *UMBELOCERAS* Flower, n. gen.

Type species—*Gomphoceras spei* BARRANDE

This genus is erected for essentially straight brevicones showing slight exogastric tendencies in that the

ventral profile is usually a little more convex than the dorsal one. Aperture with a prominent hyponomic sinus, dorsal aperture being prolonged into two lateral branches which curve gradually toward the venter. Shells are variable in cross section, ranging from slightly compressed in the type species to circular or even slightly depressed. Siphuncles are composed of slender elongate-ovate segments, only slightly expanded in the camerae, and located usually very near ventral wall of shell; no deposits observed within the siphuncles.

Étage E₂ (Middle Silurian), Bohemia.

Umbeloceras spei (Barrande)

Pl. 37, fig. 9-11

Gomphoceras spei BARRANDE, 1865-67, Syst. Sil., pl. 82, fig. 7-9 (1865); p. 316 (1867).

A small compressed shell with arms of the aperture curving toward venter; siphuncle composed of slender biconvex segments.

Étage E₂ (Middle Silurian), Lochkov, Bohemia.

Umbeloceras capitatum (Barrande)

Gomphoceras capitatum BARRANDE, 1865-67, Syst. Sil., pl. 75, fig. 14-17 (1865); p. 307 (1867).

This is a small essentially straight species, fusiform, bulbous, with aperture strongly elevated on the internal mold, part of which is result of internal thickening of the shell near the aperture. Lateral arms of the aperture are narrow, rather short, and curve toward the venter at their tips. The siphuncle has not been observed.

Étage E₂ (Middle Silurian), Hinter-Kopania, Bohemia.

Umbeloceras clavulinum Flower, n. sp.

Gomphoceras clava BARRANDE, 1865-67 (*partim*), Syst. Sil., pl. 77, fig. 6-12 (non pl. 77, fig. 13-22, of pl. 92, fig. 10-13) (1865); p. 278 (1867).

This name is proposed for the small slender species represented by specimens which BARRANDE regarded as young individuals of *Gomphoceras clava*. Shells circular in section, gently enlarging, then more rapidly contracting to an aperture with a strong hyponomic sinus and two lateral slits curving ventrad near their ends. The siphuncle is ventral and small at the septal foramen but its structure has not been observed.

Étage E₂ (Middle Silurian), Lochkov, Bohemia.

Umbeloceras clava (Barrande)

Gomphoceras clava BARRANDE, 1865-67 (*partim*), Syst. Sil., pl. 77, fig. 14-22; (non pl. 77, fig. 1-13 or pl. 92, fig. 10-13) (1865); p. 278 (1867).

This species, even as restricted, shows considerable variation in size of individuals. The shell bears a faint constriction located at or just below the base of the living chamber following a markedly expanded ring, both of these features being quite inconstant. One sectioned specimen shows siphuncle segments which are atypical in being subquadrate and slightly scalariform, with faint annular deposits at the septal foramina. The aperture is typical of *Umbeloceras*, as is the position of the siphuncle.

The specimen which BARRANDE (1865) figured on pl. 92, fig. 10-13, is atypical of *Umbeloceras clava* in dorsal emargination of the aperture and transverse position of the lateral limbs. Also, it bears only a vestigial constriction near the base of the living chamber.

Étage E₂ (Middle Silurian), various localities in Bohemia.

Umbeloceras incola (Barrande)

Pl. 37, fig. 7-8

Gomphoceras incola BARRANDE, 1865, (partim), Syst. Sil., pl. 68, fig. 9-19 (non pl. 81, fig. 7-8, or pl. 92, fig. 15).

Shell strongly exogastric, with the ventral profile much more strongly curved than the dorsal one. BARRANDE figured five specimens. The largest (his pl. 68, fig. 8-12) was apparently interpreted by him as typical and is therefore here designated as lectotype. Successively smaller than this specimen are others illustrated in pl. 68, fig. 14, 15, and 13. Two of these specimens are sectioned, showing siphuncles typical of the genus. BARRANDE's pl. 68, fig. 16-19, depicts a much smaller shell, which, though similar in aperture, seems so much more gibbous than others that its specific identity is questionable. On the other hand, the specimen figured in pl. 81, fig. 7-8, is not only smaller, but much more slender, and is certainly not to be included in this species. It is more comparable with a small mature shell which BARRANDE figured (pl. 104, fig. 5-9) as *Gomphoceras cylindricum*. All of the forms show an aperture with narrow, gently and uniformly curved lateral limbs. No deposits are apparent in the siphuncle. The immature specimen figured on pl. 92 is an essentially straight shell with open aperture and thick-walled siphuncle which appears essentially tubular. It is almost certainly allied to the group of *Rizoceras* and not to the species here under consideration.

Étage E₂ (Middle Silurian), Bohemian basin.**Umbeloceras cylindricum (Barrande)***Gomphoceras cylindricum* BARRANDE, 1865-67 (partim), Syst. Sil., pl. 79, fig. 1-17 (non pl. 104, fig. 5-9) (1865); p. 308 (1867).

This is a small rather slender species, with aperture similar to that of *Umbeloceras incola* in pattern but the shell is slender, with convexity of venter and dorsum more nearly equal. The figured specimens show variation in size and emargination of the aperture on the internal mold. The siphuncle is composed of slender segments, which contain small annular deposits showing none of the features of actinosiphonate deposits.

Étage E₂ (Middle Silurian), from various localities in the Bohemian basin.**Umbeloceras minor Flower, n. sp.***Gomphoceras cylindricum?* BARRANDE, 1865, Syst. Sil., v. 2, pl. 104, gf. 5-9. *Gomphoceras incola* BARRANDE, 1865, Syst. Sil., pl. 81, fig. 7-8.

This species is erected for small slender specimens which BARRANDE regarded as the young individuals of *Gomphoceras cylindricum* and *G. incola*. They resemble *Umbeloceras clavulinum* but tend to be slightly less slender, with limbs of the aperture broader and less curved adventrally at their tips. In *U. minor* the siphuncle is very slender, approaching the orthochoanitic condition in the earliest stage observed.

Étage E₂ (Middle Silurian) from various localities in the Bohemian basin.**Umbeloceras? accedens (Barrande)***Gomphoceras accedens* BARRANDE, 1865-67 (partim), Syst. Sil., pl. 78, fig. 5-9 (non pl. 92, fig. 14) (1865); p. 268 (1867).

This species is less adequately known than others. The shell is markedly exogastric, and could be considered a more gibbous, markedly exogastric edition of *Umbeloceras incola* and on this basis is related to *Umbeloceras*. The structure of the siphuncle is not known. The aperture has lateral limbs curved adventrally but is less constricted than other species of the genus, and thus approaches *Ovocerina*.

Étage E₂ (Middle Silurian), Bohemian basin.**Umbeloceras tumescens (Barrande)***Gomphoceras tumescens* BARRANDE, 1865-67, Syst. Sil., pl. 81, fig. 18-30 (1865); p. 316 (1867).

Shell nearly straight, venter only slightly more convex than dorsum, shell relatively slender, living chamber with long hyponomic sinus, aperture widened at middle of dorsum, limbs little curved, but pointing obliquely adventrally. Siphuncle small and slightly removed from venter, even close to living chamber. The small size of the ventral siphuncle suggests that this is an *Umbeloceras*, as also indicated by the limbs of the aperture, though median widening of the aperture is not typical. Both typical *Ovocerina* and true *Mandaloceras* have a much larger septal foramen in parts of the siphuncle close to the mature living chamber.

Étage E₂ (Middle Silurian), Bohemian basin.**Umbeloceras amphora (Barrande)***Gomphoceras amphora* BARRANDE, 1865-67, Syst. Sil., pl. 78, fig. 10-15; pl. 104, fig. 15-17 (1865); p. 272 (1867).

Two specimens assigned to this species were figured by BARRANDE. That shown on his pl. 78 has a bilobed aperture only faintly curved adventrally at the end of the limbs, so much so that its affinities may be questioned. The second specimen (BARRANDE's pl. 104) is somewhat different in proportions and has an aperture more typical of *Umbeloceras*, the limbs being unusual only in their breadth and shortness. Quite probably both specimens are related to *Umbeloceras* rather than to *Ovocerina* or to *Mandaloceras*.

Étage E₂ (Middle Silurian), Bohemian basin.**Umbeloceras trilobatum Flower, n. sp.***Gomphoceras rectum* BARRANDE 1865, (partim), Syst. Sil., pl. 104, fig. 1-4 (non pl. 69, fig. 15-19, of pl. 106, fig. 9-11).

This is a small slender form with aperture having three nearly equal rather broad lobes, each rather broadly rounded at the tip. The shell is more rapidly expanding and more gibbous than *Umbeloceras minor* but the two are quite similar.

Étage E₂ (Middle Silurian), Bohemian basin.**Genus INVERSOCERAS Hedström, 1917**Type species—*Phragmoceras perversum* BARRANDE*Inversoceras* HEDSTRÖM, 1917, Sveriges Geol. Undersök., ser. C:A, no. 15, p. 7. FOERSTE, 1926, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 355, pl. 35, fig. 4A-D. FOERSTE, 1930, Samec, v. 25, p. 102.

This genus resembles *Phragmoceras* externally except for reversed curvature of the shell, *Inversoceras* being exogastric, whereas *Phragmoceras* is endogastric. Section compressed, siphuncle small, marginal, its segments slender, faintly nummuloidal organic deposits unknown. Sutures with moderate lateral lobes. Aperture with a long hyponomic sinus, the dorsal portion varying from a transverse oval to T-shaped, very much as in *Phragmoceras*.

From *Mandaloceras* the genus differs in that greatest height of the shell is attained well orad of the base of the living chamber and the aperture is not bounded by a domelike contraction of the living chamber. Nevertheless, there is reason to believe that *Inversoceras* is more closely related to *Mandaloceras* than to *Phragmoceras*. It agrees with the smaller species of *Mandaloceras* and differs from *Phragmoceras* in its small slender faintly nummuloidal siphuncle. Further, several species of *Mandaloceras* approach rather close to the form of *Inversoceras*, though not to such extent that confusion as to generic disposition

of the species might develop. This is shown particularly by *Mandaloceras clava* (BARRANDE, 1865, pl. 77, fig. 6-13) and more markedly in *M. incola* (*op. cit.*, pl. 81, fig. 1-6). Larger species such as *M. verneuili* and *M. simplex*, also approach the pattern of *Inversoceras* but may have no real connection, since they are larger forms with broad siphuncles which come to lie dorsad of the center of the shell.

Middle Silurian, Bohemia and North America.

Species of *Inversoceras*

The described species of *Inversoceras* are listed below.

Inversoceras barrandei FOERSTE, 1926, Bohemia, E₂.

I. constrictum FOERSTE, 1926, Bohemia, E₂.

I. dayi FOERSTE, 1930, Racine dolomite, Illinois.

I. jalciforme BARRANDE, 1865, Bohemia, E₂.

I. percurvatum FOERSTE, 1926, Bohemia, E₂.

I. perversum (BARRANDE), 1865, Bohemia, E₂.

I. sp. cf. I. perversum (BARRANDE), 1865, Bohemia, E₂.

I. subrectum (BARRANDE), 1865, Bohemia, E₂.

FOERSTE (1926) subdivided the Bohemian species, but noted that the differences might prove to be sexual rather than specific, a possibility in Paleozoic nautiloids which can hardly be assessed except in terms of reasonableness. Such a hypothesis would be greatly strengthened by a study aimed at showing whether the specimens occur in assorted pairs, but even this would not be conclusive.

Family MESOCERATIDAE Hyatt, 1884

BARRANDE (1877) erected the genus *Mesoceras* for reception of a single anomalous species known only from a single living chamber. This was done because BARRANDE was uncertain whether the specimen is more closely allied to *Orthoceras* or to *Gomphoceras*. HYATT (1884) proposed the family Mesoceratidae, placing in it *Mesoceras* and *Billingsites*. He later (1900) assigned the family to the Mixochoanites. MILLER (1932) pointed out that *Billingsites* belongs in the Mixochoanites (later changed by FLOWER & KUMMEL, 1950, to the order Asoceratida) but that *Mesoceras* shows no such affinities. *Billingsites* was removed from the family, leaving *Mesoceras* as its sole representative, and the family was regarded as uncertain in affinities.

Strangely, BARRANDE'S question as to whether *Mesoceras* is more related to orthoconic stocks or to breviconic ones (*Orthoceras* or *Gomphoceras* in the old broad sense of these genera) is a valid one. A shell (*Cryptorthoceras*) with very similar aperture has been described by FLOWER (1939), who assigned it to the dominantly orthoconic Pseudorthoceratidae, showing that such an aperture could develop in a stock which is fundamentally orthoconic. However, the similarity of apertures does not indicate a relationship between *Mesoceras* and *Cryptorthoceras*. The orthoconic affinities of *Cryptorthoceras* are shown by the relatively great length of the living chamber. The shell was obviously a long, slender, rather large orthocone. Its internal structure shows that it belongs to the Pseudorthoceratidae, whereas no such relationship is suggested for *Mesoceras*. The shortness of the living chamber points to affinities with a stock which is dominantly breviconic rather than longiconic and the large

septal foramen of *Mesoceras* is foreign to anything known in the Pseudorthoceratidae. Further, no undoubted members of this family have been found below the base of the Devonian, though some Silurian and even Ordovician forms have been placed in the family. These earlier forms belong instead to the family Stereoplasmoceratidae, as will be shown at another time.

Mesoceras has long remained without any suitable resting place in the taxonomic scheme of cephalopods. In conversations between TEICHERT and FLOWER in 1951, in which complete assignment of nautiloid genera to families and orders was attempted, neither of us had any good suggestions as to affinities of *Mesoceras* and the Mesoceratidae.

In reviewing brevicones of the Middle Silurian of Bohemia, it became evident that *Mesoceras* agrees closely with some of the forms, notably species of *Ovocerina* and *Mandaloceras*, here placed in the Mandaloceratidae. Similarity is found in the short living chamber with the shell contracting and forming an incomplete dome over the anterior end, the broad cross section, and the unusually large septal foramen which is centrally located. These features most strongly suggest a real relationship. *Mesoceras* is logically interpreted as a derivative of the Mandaloceratidae in which form of the living chamber is modified slightly and the hyponomic sinus of the aperture is almost completely suppressed.

It is pertinent to raise question as to whether *Mesoceras bohemicum* may be founded on a specimen which is abnormal. If so, the abnormalities have produced such a marked change in form of aperture that an attempt to identify it with any species of *Ovocerina* or *Mandaloceras* is hopeless. The existence of abnormality in this specimen can only be a supposition. It would explain why this remarkable form, brought to prominence in paleontological literature, remains without a duplicate.

So strong are the similarities of *Mesoceras* with the Mandaloceratidae that the temptation was strong to suppress the name Mandaloceratidae and recognize the family Mesoceratidae as including *Mandaloceras* and allied genera. This course was rejected. In the absence of the phragmocone of a good specimen of *Mesoceras*, its affinities must always remain a matter of inference. Retention of the Mandaloceratidae is desirable, since definition of the family and recognition of its discosorid affinities rest on a good series of species which are quite adequately known internally as well as externally. Therefore, it seems best to retain the Mesoceratidae for reception of *Mesoceras* alone, and to point out here its quite obvious similarities to contemporaneous *Ovocerina* and *Mandaloceras*, by which its probable affinities with the Discosorida are convincingly, if not irrefutably, demonstrated.

The Mesoceratidae may be defined as follows. Shell known only from the living chamber which is straight, short, strongly contracted over the anterior end, leaving an aperture consisting of broad long transverse slit, straight dorsally, slightly emarginate ventrally, the emargination probably representing a vestigial hyponomic sinus. The cross section is slightly depressed. The septum is deeply curved, the suture simple and transverse. The si-

siphuncle produces a large central perforation in the septum. Contraction of the shell over the aperture suggests a faintly exogastric condition, the dorsum being more convex than the venter. The family differs from the Mandaloceratidae only in reduction of the hyponomic sinus to a vestigial condition. Nothing is known of the phragmocone or the siphuncle other than the straight transverse last septum and the evidently large size of the siphuncle at the base of the living chamber.

Middle Silurian, Bohemian basin.

Genus MESOCERAS Barrande, 1877

Type species—*Mesoceras bohemicum* BARRANDE

- Mesoceras* BARRANDE, 1877, Syst. Sil., suppl., p. 198-200.
 — HYATT, 1884, Boston Soc. Nat. Hist., Proc., v. 22, p. 278.
 — HYATT, 1900, in ZITTEL-EASTMAN Textb. Palaeont., v. 1, ed. 1, p. 516.
 — MILLER, 1932, State Univ. Iowa Studies Nat. Hist., v. 14, p. 19.

Genus known only from the type species which in turn is known only from a single isolated living chamber. It is essentially straight, with cross section broader than high, dorsum and venter equally rounded, septal foramen large and subcentral. Shell contracts over adoral end, leaving an aperture which consists of a broad transverse slit with a slight ventral emargination representing a rather reduced hyponomic sinus. In lateral profile, the dorsum is more convex than venter as it curves over the adoral end of the shell, the aperture then faces slightly toward the ventral side. The ventral profile approaches the dorsum gently, but is only very slightly convex in profile.

Previous uncertainties and diverse opinions as to affinities of *Mesoceras* have been discussed under the family Mesoceratidae. It remains here only to emphasize features indicating affinities with the Mandaloceratidae.

The only shells with which *Mesoceras* agrees in the short living chamber, rather deeply curved septum at its base, and unusually large subcentral perforation for the siphuncle, are found in species of *Ovocerina* and *Man-*

daloceras. This is shown by comparison of illustrations of *Mesoceras* (Pl. 33, fig. 1-3) with those of representatives of the Mandaloceratidae (Pl. 34-37). In *Ovocerina* the septum is similarly deep and in many species the septal perforation is large. In some it is slightly on the dorsal side of the center but in others slightly on the ventral side. *Mandaloceras* is quite different internally but the siphuncle is large as it passes through the anterior septa and relatively central in position, particularly in the later growth stages. In *M. verneuli*, the siphuncle is very nearly central at the base of the living chamber (Pl. 35, fig. 4) and the same is true in *M. haueri* (Pl. 37, fig. 2), considerably more ventral in the type species (Pl. 35, fig. 12). Between species of *Mandaloceras* and *Ovocerina* one cannot choose in this respect but indication of affinities with either is significant. In *Ovocerina* the dorsal part of the aperture is typically rounded but it is widened transversely in several species, and in this feature no sharp demarcation is found between *Ovocerina* and the narrow transverse dorsal aperture of *Mandaloceras*. The aperture of *Mesoceras*, likewise, is transverse. It is rather broad in relation to *Mandaloceras* and rather narrow as compared with *Ovocerina*. It differs from both genera in that the hyponomic sinus, strongly developed in all Mandaloceratidae, is here reduced to a mere notch on the ventral side.

That the features in which *Mesoceras* differs from the Mandaloceratidae may be abnormal has been discussed. This possibility seems a real one.

Mesoceras bohemicum Barrande

Pl. 33, fig. 1-4

- Mesoceras bohemicum* BARRANDE, 1877, Syst. Sil., suppl., p. 198-200, pl. 508, fig. 1-4.
 — MILLER, 1932, State Univ. Iowa, Studies Nat. Hist., v. 14, no. 4, p. 19, pl. 2, fig. 8-12.

BARRANDE'S illustration of the unique type of this species is reproduced here. It is from Étage E₂ (Middle Silurian), Bohemian basin.

APPENDIX TO SYSTEMATIC DESCRIPTIONS

In the course of investigating the Discosorida, considerable attention was given to a number of cephalopods which, it was found, should be excluded from this order. They vary from *Apocrinoceras*, originally assigned to the Westonoceratidae, through species which have been erroneously referred to discosorid genera. For the most part, mention of these forms in the systematic part has been confined to simple notice of their reassignment. Rather than leave the basis for this procedure obscure for the present, it seems best to discuss these forms in an appendix, thereby avoiding confusion by presenting reasons for changes which have been made.

Two of the forms studied are so inadequately known that although clearly they are not typical of any described genera, any new genus based upon them would be inadequately known morphologically and of uncertain position. We have already more than enough generic

groups of this sort. Instead of creating more genera, these species are retained in the genus to which they have been assigned, though the impropriety of this is indicated by the use of quotation marks.

Order ELLESMEROCERATIDA

Flower in Flower & Kummel, 1950

Family APOCRINOCERATIDAE Flower, n. fam.

The Apocrinoceratidae are small annulated orthocones having siphuncles with short necks and thick rings, differing from the Protocycloceratidae, from which they are descended, by a tendency for the siphuncle to expand within the camerae, so that in specialized genera the septal necks are recurved. *Apocrinoceras*, originally re-

ferred to the Westonoceratidae, is most advanced of the three genera now assigned to the family in this respect. Reasons for regarding the Apocrinoceratidae as a specialized group derived from the Protocycloceratidae and unrelated to families of the Discosorida have been given in Part I of this work (chapter on history of investigation and discussion of origin of the Discosorida).

Shells are tiny, with low rather closely spaced annuli. Sutures are relatively simple. The size and position of the siphuncle are variable, ranging from small marginal siphuncles to those which are relatively large and well removed from the ventral wall of the shell. The family is known only in beds of later Canadian age and genera thus far described are each based on a single known species. One is from Australia, another from Argentina, and a third from eastern New York.

Essential features of the siphuncle wall of apocrinoceratid genera are shown in Text-fig. 34. It can be seen that *Desioceras* and *Glenisteroceras* supply something of a transition from the markedly cyrtochoanitic *Apocrinoceras* to the more tubular siphuncles which prevail in the Protocycloceratidae. It may be that when the internal structure of more cephalopods currently attributed to genera of the Protocycloceratidae have been examined, additional representatives of the Apocrinoceratidae will be found.

Lower Ordovician (Upper Canadian).

Genus DESIOCERAS Cecioni, 1953

Type species—*Desioceras floweri* CECIONI

Desioceras CECIONI, 1953, Bol. Museo Nac. Hist. Nat. (Santiago de Chile), tomo 26, no. 2, p. 93.

Shell a small slender orthocone with low regular annuli; sutures with rounded ventral saddles, siphuncle

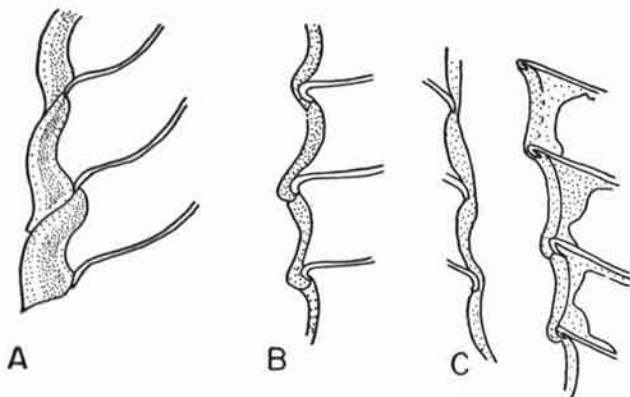


FIGURE 34. Structure of siphuncle wall in the Apocrinoceratidae.

A. *Desioceras floweri* (modified from CECIONI, 1953, to compensate for slight obliquity of plane of section to axis of siphuncle), showing necks scarcely recurved, rings thick, layered, and sigmoidal in profile. Plane of section essentially horizontal.

B. *Glenisteroceras obscurum*, based on holotype (Pl. 30, fig. 7-8), exact orientation of section not known but probably oblique and more nearly horizontal than vertical.

C. *Apocrinoceras talboti*, vertical section through siphuncle based on TEICHERT & GLENISTER (1954, pl. 1, fig. 7), venter at left.

close to venter, its diameter about one-third that of shell, necks achoanitic, rings thick, outlining segments which are expanded primarily in their anterior half, sinuate, the curvature being reversed in the adapical part. A trace of layers within the rings is indicated by different textures.

Dr. CECIONI has kindly supplied photographs of the type species of this genus which show the structures more clearly than do his published figures, in which unfortunately coarse half tones with little contrast were employed. As noted in discussion of the family, this genus seems to serve as connection between shells with more markedly expanded siphuncles (*Apocrinoceras*, *Glenisteroceras*) and the essentially tubular ones of the Protocycloceratidae.

Desioceras floweri Cecioni

Text-fig. 34A

Desioceras floweri CECIONI, 1953, Bol. Mus. Nac. Hist. Nat. (Santiago de Chile), tomo 26, no. 2, p. 94, pl. 3, fig. 1, 2; text-fig. 19.

Erratic, from Canadian beds, Rio San Lorenzo, near Jujuy, Argentina.

Genus GLENISTEROCERAS Flower, n. gen.

Type species—*Glenisteroceras obscurum* FLOWER, n. sp.

Shell small, orthoconic, subcircular in section, sutures not fully observed but essentially transverse. Siphuncle relatively large, with short broad segments expanded most in the anterior third of their length, their outline subtrapezoidal. Connecting rings thick, septal necks scarcely recurved. Owing to central location of the siphuncle, no dorsoventral differentiation appears in outline of the segments. Organic deposits not recognized in the camerae or within the siphuncle.

Discussion. This genus is erected for a single small species which differs from *Apocrinoceras* in its large subcentral siphuncle, less recurved septal necks, and slightly more expanded subquadrate form of the siphuncle segments.

Lower Ordovician (Canadian).

Glenisteroceras obscurum Flower, n. sp.

Pl. 30, fig. 7, 8; text-fig. 34B

This is a small faintly annulated orthocone, sutures not observed from exterior but evidently essentially straight and transverse. The siphuncle is large, about one-third of the entire shell in diameter, with broad, subtrapezoidal segments and septal necks only very slightly recurved, connecting rings thick.

The holotype is a tiny fragment embedded in matrix, the structure being exposed by a section. Owing to the subcentral position of the siphuncle, the relationship of the plane of the section to the plane of symmetry of the shell is not evident. In section, three perfect segments of the siphuncle occur in the basal 4 mm. of the specimen which has a length of 6 mm. In that length the width of the shell, clearly very close to the maximum, increases from 4 to 5 mm. A segment expands from 1 mm. at the septal foramen to a maximum width of 2 mm. in the anterior third of the segment. The septal necks point obliquely adapically and slightly outward. Beyond their tips, the segments expand rapidly to the maximum width in the anterior third, then contract gently, the profiles becoming straight or even slightly concave, and joining the next

adapical septum with no area of adnation. The ring is remarkably thick but shows no differentiation of structure, a matter which may or may not be the result of crystallization.

Calcite occupies the camerae, largely obscuring the septa, but fails to show any indication of original organic structures. The interior of the siphuncle also is occupied by calcite which is darker near the connecting ring but otherwise shows no differentiation. There is no evidence that this calcite is original or organic.

Discussion. The single fragmentary specimen on which this species is based was collected by me in 1934 during my first visit to the Fort Cassin beds of the Champlain Valley. In size and calcite replacement the fossil suggested a few segments of a cystid stem, but a section ground parallel to a natural break showed a siphuncle complete with septal necks. It was recognized that this is a form completely unlike any previously known Canadian cephalopod but description was delayed in the hope of obtaining more complete specimens. This hope has remained unfulfilled. In the meantime TEICHERT & GLENISTER (1954) have described as *Apocrinoceras talboti* the only other Canadian cephalopod which is at all closely similar to this one. The importance of both, as the only Canadian cephalopods with the expanding segments and thick rings like those of the discosorids, now makes the description of even this small fragment desirable.

The holotype, in collection of the writer, comes from limestone of the Fort Cassin formation (Lower Ordovician), on the shore of Lake Champlain at Valcour, N.Y.

Genus APOCRINOCERAS Teichert & Glenister, 1954

Type species—*Apocrinoceras talboti* TEICHERT & GLENISTER
Apocrinoceras TEICHERT & GLENISTER, 1954, Bull. Am. Paleont., v. 35, no. 150, p. 75.

Shell orthoconic slender, circular in section, internal mold nearly smooth, with faint low annuli. Sutures transverse, slightly sinuate, with ventral saddle, ventrolateral lobes, dorsolateral saddles and median dorsal lobe. Siphuncle close to venter, necks slightly recurved, rings outlining segments which expand moderately beyond tip of the neck, attaining greatest width of the segment in its anterior third, contract more gently in the adapical half, passing within the preceding septum with no area of adnation dorsally and a slight one ventrally. Dorsal necks moderately recurved, ventral necks scarcely at all. Segments are short and subquadrate in outline. The connecting ring is definitely thickened. The only available figure shows the interior of the siphuncle filled with calcite in which no organic structures can be recognized. Calcite has also been deposited outside the ring and extends a little way along the septa.

Discussion. This genus is known at present from the single species listed below, which in turn is known only from a single specimen. There is no point in reproducing here the photographs given by TEICHERT & GLENISTER, which are the only illustrations of the genus and species. The siphuncle is relatively small in diameter in relation to diameter of the shell. Its marginal position, small size, and form of the segments give it the aspect of a *Westonoceras* in which the outline of the siphuncle is greatly simplified.

The one species occurs in horizon 3 of the Emanuel limestone, Upper Canadian (lower Ordovician), from Emanuel Creek, Kimberly division, western Australia.

Apocrinoceras talboti Teichert & Glenister

Text-fig. 34C

Apocrinoceras talboti TEICHERT & GLENISTER, 1954, Bull. Am. Paleont., v. 35, no. 150, p. 76, pl. 1, fig. 7-9.

Order ACTINOCERATIDA Teichert, 1933

[Actinoceroida]

Family ARMENOCERATIDAE Foerste & Teichert, 1930

Genus ELRODOCERAS Foerste, 1924

Elrodocus? rallsense (Foerste & Teichert)

Westonoceras? rallsense FOERSTE & TEICHERT, 1930, Denison Univ. Bull., Sci. Lab., Jour., v. 25, p. 285, pl. 47, fig. 4.

This perplexing species is probably the oldest recorded *Westonoceras*. However, the anomalously large siphuncle and the presence of apparent central and radial canals proclaim it to be an actinoceroid and not a relative of *Westonoceras*. FOERSTE & TEICHERT compared the species both with *Westonoceras* and *Elrodocus*, assigning it to the former genus because the siphuncle is relatively central, though they noted that it is abnormally large. From the present material it is impossible to say where the species should be placed, except that it is obviously an actinoceroid. The form of the segments and pattern of the canals suggests *Elrodocus*, but *Elrodocus* is a Silurian genus, and if these affinities are correctly interpreted, this species, based on a single specimen, is the only forerunner of the *Elrodocus* stock thus far recognized in the Ordovician. Quite probably a new genus will be required for this species. At the present time it can hardly be left in *Westonoceras* and a tentative assignment to *Elrodocus* is made.

The holotype (U. S. Natl. Mus., no. 82234) is from the Kimmswick limestone (Middle Ordovician) from Sanders Forks, Ralls County, Missouri. The Kimmswick limestone, which generally is regarded as equivalent to the Hull (lower Trenton), may be as young as the Cobourg or Red River beds.

Order ONCOCERATIDA Flower in Flower & Kummel, 1950

This order is here emended slightly to include the family Graciloceratidae and thus contains dominantly compressed exogastric cyrtocoones and brevicones with ventral siphuncles. Primitively, segments are tubular, a condition found only in the small family Graciloceratidae. In all others adult segments are expanded, though early stages of the oldest forms (Chazyan) may approach or even attain a tubular outline. Rings are primitively thin and homogeneous, but later specialization produces a thickening of the rings, which, when most fully developed, produces actinosiphonate structure. Curiously, the order, when it first appears in the Chazyan, shows differentiation of three families: (1) Graciloceratidae, with tubular siphuncles; (2) Oncoceratidae, with a narrow cross section, slightly expanded segments, but without development of thickened rings or actinosiphonate deposits; and (3) Valcouroceratidae, broader in cross section and with actinosiphonate deposits developing in larger species but not the smaller ones. The Valcouroceratidae are contemporaneous with the Oncoceratidae and though obviously more specialized, are regarded as derived from them.

At the urging of my colleagues, who seem to agree in wishing a reduction in the number of nautiloid orders, I have consented to suppress the Bassleroceratida, a change which has some advantages and some disadvantages. The only possible disposal of this order, conceived to include the first exogastric cyrtocoines with ventral tubular siphuncles, is inclusion of the Bassleroceratidae as a primitive family of the Tarphyceratida and the Graciloceratidae as primitive family of the Oncoceratida. As thus revised, division of the orders takes special account of suppression of the primitively thick connecting ring. No change in interpretation of the phyletic relationships (FLOWER, 1954, p. 35, fig. 7) is involved but simply a redefinition of ordinal boundaries.

Family ONCOCERATIDAE Hyatt, 1883

The first oncoceroids (Chazyan) are exogastric shells with faintly contracted apertures. The ventral siphuncles are tubular in the young and only slightly expanded in the adult. Relatively slight expansion is not uncommon in later Ordovician types. As yet, no good basis has been found for separation of the Ordovician forms, which are relatively simple, from the Silurian ones, which exhibit great diversification in form and internal structures. As yet, no Ordovician species are known to develop actinosiphonate deposits such as are developed in Silurian members of the family. Ordovician actinosiphonate cephalopods are, as far as known, confined to the families Valcouceratidae and Diestoceratidae. As previously noted, the position of the Diestoceratidae as an oncoceroid or as a discosorid family seems very uncertain.

Fuller discussion of the Oncoceratida is planned for another time and it suffices here to point out its position and note specifically forms referred to genera of the Oncoceratidae. The problem of oncoceroid genera concerned has already been outlined (FLOWER, 1946).

Neumatoceras FOERSTE is an oncoceroid, judging by its internal structure, as noted in discussion of *Westonoceras*, and the suggestion that it is synonymous with *Westonoceras* (MILLER, YOUNGQUIST & COLLINSON, 1954) is therefore rejected.

Genus BELOITOCERAS Foerste, 1924

Beloitoceras? baffinense (Schuchert)

Cyrtoceras baffinense SCHUCHERT, 1900, U. S. Natl. Mus., Proc., v. 22, p. 151, 171, pl. 14, fig. 11-13.
Thuloceras? baffinense TROEDSSON, 1926, Meddel. om Grønland, Bind 71, p. 95, 117.
Beloitoceras? baffinense FOERSTE, 1928, Denison Univ. Bull., Sci. Lab., Jour., v. 23, p. 12, 45-46, pl. 8, fig. 1; pl. 23, fig. 3A-B.
 ——— FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 236, 270.
Westonoceras? baffinense MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 85, pl. 18, fig. 5.

This species is still known only from the holotype, a fairly gently expanding cyrtocoine portion of a phragmocone. Available information concerning its form and aspect is consistent with regarding this specimen as the early portion of a *Beloitoceras* shell, possibly of the *B. amoenum* group, but there are no known structural features which justify transfer of this species to *Westonoceras*. MILLER, YOUNGQUIST & COLLINSON state: "FOERSTE referred it with question to *Beloitoceras*, but no undoubted representatives of that genus are known from the Upper Ordovician of Baffin Land." This

slender reason no longer exists, for several very typical species of *Beloitoceras* occur in the Mt. Silliman fauna, though they have mistakenly been placed in *Westonoceras*.

Beloitoceras cornulum (Schuchert)

Cyrtoceras cornulum SCHUCHERT, 1900, U. S. Natl. Mus., Proc., v. 22, p. 151, 170-171, pl. 14, fig. 8-10.
Beloitoceras? cornulum FOERSTE, 1928, Denison Univ. Bull., Sci. Lab., Jour., v. 23, p. 44, pl. 8, fig. 8A,B; pl. 23, fig. 7.
 ——— FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 236, 270.
Westonoceras? cornulum MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 87 (partim), pl. 45, fig. 10-11, pl. 46, fig. 6-7 (non pl. 44, fig. 17-18; pl. 47, fig. 1-8; pl. 48, fig. 1-3; pl. 49, fig. 1, 2; text-fig. 11).

This species is based on a portion of phragmocone, rather strongly curved, slender apically, enlarging more rapidly in the adoral part. The cross section is compressed but with dorsum and venter about equally rounded. Structure of the siphuncle in the type has not been observed. The species has all the characteristics of an early growth stage of *Beloitoceras* or *Oncoceras* and alone supplies no basis for removing the species from the oncoceroid group.

Among specimens figured and described under this name by MILLER, YOUNGQUIST & COLLINSON, one (pl. 46, fig. 6, 7) appears to be conspecific with *B. cornulum*. It is a compressed shell with convex venter and concave dorsum which might possibly be considered a *Neumatoceras*, but appears to be more appropriately placed in *Beloitoceras*. The specimen illustrated in their pl. 45, fig. 10, 11, also is accepted as belonging to *B. cornulum*, but as indicated in following paragraphs, other specimens figured by these authors are doubtful.

(1) The original of pl. 44, fig. 17-18, is a slightly flattened and crushed specimen uniformly expanding to the aperture but not displaying any such adoral increase in rate of vertical expansion as the type shows. Growth lines are prominent, close, and indicate a relatively low shallow hyponomic sinus. This specimen could be an immature individual of a species of *Oncoceras* but its form much more convincingly suggests a small, essentially mature species of *Cyrtorizoceras*.

(2) The originals of pl. 47, fig. 1, 2, are subannular shells, cyrtocoine, fairly rapidly expanding. They are the only cephalopods illustrated which seem at all similar to a form now in my hands for description from Middle Trenton beds of Quebec. It is an oncoceroid for which recognition of a new genus is required.

(3) The original of pl. 47, fig. 3, 4, is a strongly compressed rapidly expanding shell that is best assigned to *Cyrtorizoceras*.

(4) The original of pl. 47, fig. 5-8, is a typical *Neumatoceras* showing characteristic form of the genus both as to profile and shape of living chamber.

(5) The original of pl. 48, fig. 1-3, also is a *Neumatoceras* but quite obviously different from that cited in the preceding paragraph. This specimen is notable for its broad cross section at the base, a little below the end of the phragmocone, and the marked lateral contraction of the anterior part of the phragmocone and entire living chamber.

(6) The original of pl. 49, fig. 1, 2, is quite different from other specimens, being a slender, rather gently contracting living chamber. From what can be seen, the remainder of the shell could have been relatively slender, only slightly gibbous, and thus typical of *Beloitoceras*, or strongly gibbous and arched, and therefore a *Neumatoceras*. The profile of the living chamber is only faintly suggestive of *Westonoceras* but the broad smoothly rounded cross section is an oncoceroid feature not known in *Westonoceras*.

(7) The portion of a phragmocone shown in MILLER, YOUNGQUIST & COLLINSON's text-fig. 11 is perfectly typical of an oncoceroid and absolutely foreign to a *Westonoceras* or any discosorid.

Beloitoceras thompsoni (Miller, Youngquist & Collinson)

Westonoceras thompsoni MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 93, (partim), pl. 50, fig. 5-7.

The specimen comprising the holotype of the species called *Westonoceras thompsoni* (by original designation) is a *Beloitoceras* of the *B. amoenum* group, judging by all that can be determined from the description and illustrations. Two fragments of true *Westonoceras* were assigned to the species, however, and a third specimen comprises a fragment of living chamber and a few adoral camerae. This last-mentioned fossil may belong to a *Westonoceras* but it is inadequate for generic assignment. Clearly it is not conspecific with the holotype of *B. thompsoni*. Mt. Silliman beds (Ordovician), Baffin Island.

Beloitoceras wilsonae (Miller, Youngquist & Collinson)

Westonoceras wilsonae MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 96, pl. 49, fig. 4-6.

The shape of this shell and the small ventral siphuncle indicate that it represents a species of *Beloitoceras*, and clearly of the species group of *B. amoenum* (FLOWER, 1946, p. 270). The species is based on a single specimen from the Mt. Silliman beds (Ordovician) of Baffin Island.

Genus ONCOCERAS Hall, 1847**Oncoceras washburni (Miller, Youngquist & Collinson)**

Westonoceras washburni MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 95, pl. 47, fig. 9, 10.

This is a small slender shell with costate surface and internal features not clearly shown. The form is distinctive and shared by relatively few known species. Among them are *Oncoceras duncaniae*, which has shown traces of similar surface markings, *O. exile*, and, less closely similar, *O. madisonense* (FLOWER, 1946). Rather surprisingly, forms of similar aspect are either absent in Mohawkian faunas or else have escaped notice and description. Somewhat comparable forms are encountered in the Chazyan but they are not as closely similar and regrettably they have lain in my collection some years undescribed.

Genus NEUMATOCERAS Foerste, 1935**Neumatoceras? tumidum (Schuchert)**

Oncoceras tumidum SCHUCHERT, 1900, U. S. Natl. Mus., Proc., v. 22, p. 172, pl. 14, fig. 1-3

Westonoceras? tumidum FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 55.

Westonoceras? tumidum FOERSTE, 1928, Same, v. 23, p. 102, pl. 8, fig. 7A,B.

Winnipegoceras? tumidum FOERSTE, 1929, Same, v. 24, p. 216.

Neumatoceras? tumidum FOERSTE, 1935, Same, v. 30, p. 32.

ROY, 1940, Field Mus. Nat. Hist., Geol. Mem., v. 2, p. 146, (partim), (non fig. 106 a-d).

FLOWER, 1946, Bull. Am. Paleont., v. 29, no. 116, p. 239, 294, 295.

Westonoceras tumidum FLOWER, 1946, Same, p. 441.

Westonoceras? tumidum MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 94, pl. 18, fig. 6, 7.

This is a vexingly inadequately known but highly characteristic species. The known part of the holotype consists of a living chamber and some adoral camerae of an exogastric brevicone. The known part is contracting rather strongly from its base to the aperture and is unusually broad in cross section for either a member of the *Oncoceratidae* or *Westonoceratidae*. It is not comparable to any species of *Westonoceras*. What is known of the shell suggests two possibilities: (1) that it is a relatively broad *Neumatoceras*, rather less gibbous than most species, and (2) that it is a member of the *Beloitoceras amoenum* group, again anomalously broad in cross section. Neither possibility can be proved and the other definitely rejected. The fact that other species assignable to *Neumatoceras*

show a similar broad cross section over the gibbous region, followed by marked adoral lateral contraction of the shell, suggests that *Neumatoceras* is the more reasonable of the possible relationships.

The species is known only from the holotype, found in the Mt. Silliman beds (Ordovician) of Baffin Island. The type is no. 2b120 in the U. S. Natl. Museum. Clearly MILLER, YOUNGQUIST & COLLINSON were correct in regarding as a distinct species the much larger form which ROY (1941) assigned to *Neumatoceras? tumidum*.

Neumatoceras medium Flower, n. sp.

Westonoceras? cf. W.? breviposticum MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 86, pl. 48, fig. 4-5.

Neumatoceras breviposticum (MILLER, 1932) is a relatively small species having a venter with convexity strongly increased and then greatly reduced as it passes over the anterior end of the phragmocone where greatest shell height is attained. The dorsal profile is slightly convex over the anterior part of the phragmocone and base of the living chamber, becoming strikingly concave in the anterior half of the living chamber. It is possible that the specimen figured by FOERSTE (1935, p. 9, 34, pl. 7, fig. 5) belongs to a different species, for it shows growth lines suggesting a very strongly excavated hyponomic sinus, a feature definitely not developed in the series of specimens figured by MILLER on which the species is based. The two species are, however, somewhat similar in size and closely spaced septa, and the proposal of a new species for the specimen figured by FOERSTE is left for further study. However, the specimen from Baffin Island assigned to this species is so different in proportions that either a new specific name must be proposed for it or else the species must be regarded as so variable that it will approach, is not attain, definition of the genus *Neumatoceras*. This form has a ventral profile which is strongly and uniformly convex, except possibly in the missing early part of the shell; there is not the usual marked increase in convexity where greatest height of the shell is attained. The sutures have strongly lateral lobes but curvature of the lobes is nearly uniform throughout the length; in *N. breviposticum* the lobes of the last few sutures are greatly exaggerated. The dorsal profile is essentially straight and there is only the faintest suggestion of convexity in its outline at the base of the living chamber. The siphuncle, which is removed from the venter by a distance equal to its own height, is made up of slender elongate segments, which are apparently contracted at the septal foramina, though the exact extent of the contraction is not clearly indicated. This is a relatively slender siphuncle for an oncoceroid; it is completely outside the known limits of variation of the siphuncles of *Westonoceras*.

The holotype, (specimen figured by MILLER, YOUNGQUIST & COLLINSON), is in the U. S. Natl. Museum. It is from the Mt. Silliman beds (Ordovician) of Frobisher Bay, Baffin Island.

Neumatoceras? contractum Foerste & Savage

Westonoceras? contractum FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 55, pl. 16, fig. 2A,B.

FOERSTE, 1935, Same, v. 30, p. 32.

Westonoceras? cornulum MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 87 (partim), pl. 48, fig. 1-3.

This is a species known only from living chambers with a few adoral camerae. It is distinctive in rapid lateral contraction of the shell, concave dorsal and strongly convex ventral profiles, and rather deep adoral camerae, except where gerontic contraction has set in. The internal structure is most inadequately known but the small size of the siphuncle at the septal foramina indicates that this species is properly assigned to *Neumatoceras* and belongs with the oncoceroids, rather than *Westonoceras*. The shell is one which, prior to the adoral contraction, attains a width proportionately large in relation to height as compared with species of oncoceroids and the *Westonoceratidae*.

Neumatoceras? contractum has been known from a single specimen from the Shamattawa limestone (Ordovician) of Hudson Bay. I here assign to it also a somewhat smaller form previously figured at *Westonoceras? cornulum* from the Mt. Silliman beds of Baffin Island. This specimen agrees strikingly with the type in proportions but is slightly smaller and shows gerontic camerae which the type does not. It is a little more gibbous and may well prove to be a distinct species. However, its affinities are clearly with this species and not with *Beloitoceras cornulum*.

Neumatoceras sp.

Winnipegoceras? sp. FOERSTE, 1929, Denison Univ. Bull., Sci. Lab., Jour., v. 24, p. 217, pl. 16, fig. 6.

This is a small species comparable in proportions and shape to *Neumatoceras*, the resemblance being strong enough and contrast with the much larger *Winnipegoceras* great enough to allow little doubt but that change in generic assignment is necessary. It should be noted that the Cat Head fauna is strikingly different from that of both the underlying Dog Head, and the overlying Selkirk, although the Dog Head and the Selkirk have many species in common. The present specimen appears to be somewhat flattened and only one side of the shell is preserved. Mt. Silliman beds (Ordovician), Baffin Island.

Genus OONOCERAS Hyatt, 1884

Oonoceras humei (Miller, Youngquist & Collinson)

Winnipegoceras humei MILLER, YOUNGQUIST & COLLINSON, 1954, Geol. Soc. America, Mem. 62, p. 101, pl. 22, fig. 5, 6.

This is a slender compressed cyrtocone, the shell contracting toward the aperture very gently—indeed, so much so that the apparent contraction might possibly be a result of weathering rather than an original condition. The sutures show lateral lobes, the siphuncle is unknown. In form this species stands quite apart from *Winnipegoceras*, to which it was originally assigned, but it is generically quite indistinguishable from a considerable group of Ordovician species which FOERSTE placed in *Richardsonoceras* and which FLOWER (1946) united with *Oonoceras*. The present form seems quite closely comparable with several forms described from the Cynthiana limestone, in particular *O. triangulatum cylindratum*, and to a lesser extent with the Whitewater species *O. shideleri* and *O. jennemani* (FLOWER, 1946). Without knowledge that internal structure may contradict these obvious affinities and with only the external aspect of a weathered internal mold as evidence, this species cannot be considered as firmly identified. The species, known from a single specimen, is from the Mt. Silliman beds (Ordovician) of Baffin Island.

Family DIESTOCERATIDAE Foerste, 1926

Genus DANOCERAS Troedsson, 1928

Danoceras? askerense Strand

Westonoceras? askerense STRAND, 1933, Norsk Geol. Tidsskr., Bind 14, p. 74, pl. 3, fig. 12.

STRAND was very dubious as to affinities of this species with *Westonoceras*. The shell is fusiform, compressed, without definite curvature, and appears to be more closely allied with small species assigned to *Danoceras* than to *Westonoceras*. Nothing is known of the siphuncle. The only known specimen is from the Gastropod limestone, Ordovician, in Asker, near Oslo, Norway.

Order BARRANDEOCERATIDA Flower in Flower & Kummel, 1950

Here are placed dominantly coiled shells having tubular siphuncles with thin homogeneous connecting rings. The group must have been derived from the Canadian Tarphyceratida, in which the rings are thick and complex, a feature which is a primitive one of the cephalopods. The Barrandoceratida is not a large group; it is one that becomes specialized in the Silurian and is represented only by a single highly specialized family in the Devonian. Subsequent investigations have shown that the Devonian Rutoceratida stem not from the Barrandoceratida but from the Oncoceratida. Probably the Centroceratida were derived from the Rutoceratida. It is significant that the coiled cephalopods are not a phyletically homogeneous group. Rather, the Tarphyceratida and Barrandoceratida together constitute an early Paleozoic group which declined in the Silurian and is represented only by some extremely specialized forms in the Devonian. The Devonian Rutoceratida will probably prove to be the ancestral radicle from which developed the coiled stocks that dominate Devonian to Recent faunas.

Family BARRANDEOCERATIDAE Foerste, 1925

Genus LAURELOCERAS Flower, 1943

Laureloceras? septentrionale Foerste & Savage

Westonoceras? septentrionale FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 56, pl. 5, fig. 8.

All that is known of this species is a portion of quite slender exogastric phragmocone, compressed in cross section, with rather distant septa which have faint lateral lobes and slope slightly forward on the venter, particularly at the adoral end of the specimen. The ventral siphuncle is made up of nearly cylindrical segments, scarcely enlarging in the camerae.

Discussion. FOERSTE & SAVAGE were not at all convinced that this species was a *Westonoceras* and say "It is placed in *Westonoceras* merely to avoid the erection of a new genus on such insufficient material." The species, from horizon 7, in the Attawapiskat limestone, is Middle Silurian and far outside the range of true *Westonoceras*. Although somewhat generalized in the faint development of lateral lobes of the sutures and occurring in beds which show no other cephalopods of Laurel affinities, this species seems to be better placed in *Laureloceras* FLOWER, being typical in the essentially tubular siphuncle slightly removed from the venter.

Family URANOCERATIDAE Hyatt, 1900

Genus CLIFTONOCERAS Flower, n. gen.

Type species—*Cliftonoceras quadratum* FLOWER, n. sp.

Shell gyroconic, compressed in cross section, venter flattened, dorsum rounded, greatest shell width ventrad of center and between it and the abdominal angles. Sutures with well-defined lateral lobes, a broad dorsal saddle, and venter either with sutures transverse or forming slight lobes but in either case the forward course of the sutures as they rise from the lateral lobes is quite abruptly

modified at the abdominal angles. The siphuncle lies well ventrad of the center but it is separated by more than the diameter of the septal foramen from the ventral wall. Segments are subparallel-sided in the middle but contract as they approach the septal foramen. Neck straight on venter, recumbent on dorsum; ring adnate dorsally at anterior end and ventrally at its apical end. Rings apparently homogeneous in structure. Surface apparently smooth but not adequately known. The shells were probably large gyrocones.

Discussion. This genus is based on a species which, judging from its flattened venter and general aspect, seemed to have an internal mold which could be regarded as a rather specialized *Glyptodendron*. The siphuncle is very different from that of *Glyptodendron*, being more ventral and the segments are quite different in form. Therefore, no real relationship to this genus is believed to exist, but instead, *Cliftonoceras* is regarded as belonging to the Uranoceratidae. In other genera of this family the siphuncle, generally more centrally placed, is not dissimilar from that of *Cliftonoceras* in outline but its orthochoanitic condition is regarded as primitive. Expansion of the siphuncle segments is at first gentle, with hardly more than a faint inflation of the connecting ring. Curiously, the apical end of the connecting ring in such forms may seem to pass within the adapical septal neck so as to touch it in some specimens but contracting without touching it in others. This contraction at the end of the ring seems to precede the condition in which inflation becomes broader and the neck becomes recurved, more so dorsally than ventrally, so as to accommodate it and the present genus shows an advanced stage of such expansion. An extreme case (FOERSTE, 1925, pl. 8, fig. 1) is illustrated by *Uranoceras hercules* but the Bohemian species, *U. uranium* (BARRANDE), shows only gentle inflation of the ring without definitely recurved necks.

Cliftonoceras quadratum Flower, n. sp.

Pl. 26, fig. 4-8

The type is a portion of a rather strongly curved shell, probably originally gyroconic, 90 mm. in length, with a radius of curvature increasing from 70 to 80 mm. and comprising less than a quarter revolution. It preserves 6 camerae and a maximum (ventral) basal 30 mm. of a living chamber. Cross section subquadrate, dorsum rather broadly rounded, sides slightly convex, and prominent ventral face rather broad. The shell is compressed, being 30 mm. wide and 38 mm. high at the apical end, increasing to 43 and 50 mm. in a ventral length of 70 mm. The greatest width of the cross section is found essentially at mid-height of the section, rather than at the abdominal angles, owing to the slight convexity of the lateral faces. In the ventral length of 70 mm. and dorsal length of 25 mm. are 6 camerae, which range in depth from 11 to 13 mm., the last one shorter, indicating maturity. The sutures form a broad dorsal saddle, broad shallow lateral lobes, faint saddles on the abdominal angles, and are very nearly transverse, but forming a very slight lobe on the ventral face.

At the base of the type the septal foramen is 5 mm. high, 10 mm. from the venter and 25 mm. from the dorsum. Segments of the siphuncle are much longer than wide, with free part nearly straight dorsally but convex ventrally, more curved and more expanded in the anterior than adapical end. The ventral septal neck is slightly recurved and free but dorsally it is recumbent. The ad-

apical end of the ring meets the septum with a broad area of adnation ventrally and a much slighter one dorsally. A section of the siphuncle shows the connecting rings only incompletely. They seem unusually thick but lack any trace of a bullette and the thickness seems highly variable.

The type exhibits slight pitting of the internal mold, a condition which appears to be the result of solution of the limestone and not original. A fragment of the shell shows an essentially smooth surface.

Discussion. The holotype was studied at this time because it was received from the U. S. National Museum bearing a label (evidently written by FOERSTE) identifying it as a new species of *Glyptodendron*. Differences in cross section, suture pattern, position, and outline of the siphuncle, indicate that this species is not a *Glyptodendron* but in fact, is closely related only to *Nautilus oceanus* HALL, here referred to *Cliftonoceras*. The present species is much smaller than *C. oceanus*, and contraction of the anterior camera indicates that it is essentially mature, this difference being a significant one. It agrees with HALL's species quite closely in curvature and rate of expansion, so it must have attained maturity between a half and a quarter of a whorl earlier. Probably *C. quadratum* attained one revolution when complete; *C. oceanus* must have attained about one and one half revolutions. The sutures of *C. oceanus* show deeper lateral and clearer ventral lobes, in contrast to the shallow lateral lobes and nearly transverse ventral sutures of *C. quadratum* but its abdominal angles are much less sharply defined and the ventral face is more convex and less clearly separated from the lateral faces. *C. oceanus* is more specialized in sutures but more smoothly rounded in cross section.

This new species occurs in limestone identified as Brassfield, Silurian, near Clifton, Tenn. Because the related *C. oceanus* is from the Laurel limestone and the Clifton locality yielded also a *Cummingsoceras* (probably *C. elrodi*), this genus being known also from the Laurel and the essentially equivalent Joliet but not from the Brassfield, it is suggested that the limestone near Clifton may be of Clintonian age (Middle Silurian) rather than actual Lower Silurian Brassfield limestone. It is a yellowish sparsely crinoidal limestone with pinkish hues.

The holotype is deposited in the U. S. National Museum, no. 67236.

Cliftonoceras oceanus (Hall)

Nautilus oceanus HALL, 1882, Indiana Dept. Geol., Nat. Res., 5th Ann Rept., p. 325.

HALL, 1883, Albany Inst., Trans., v. 10, p. 75.

"*Nautilus*" *oceanus* HALL, FOERSTE, 1925, Denison Univ. Bull., Sci. Lab., Jour., v. 21, p. 35, pl. 3, fig. 2; pl. 9, fig. 1; pl. 17, fig. 1.

FOERSTE (1925) pointed out that this species did not belong in any genus then described but he refrained from making a new genus for its reception because the siphuncle of the holotype and only known specimen was not known. The type, in the New York State Museum, is from the Laurel limestone (Middle Silurian) (not Waldron shale as stated) of Waldron, Ind. Though the siphuncle is still unknown, evident affinities with the smaller but better known *C. quadratum* allow reference of this species to *Cliftonoceras*.

NAUTILOIDEA OF UNCERTAIN AFFINITIES

"*Cyrtogomphoceras*" *shamattawaense* Foerste & Savage

Cyrtogomphoceras? shamattawaense FOERSTE & SAVAGE, 1927, Denison Univ. Bull., Sci. Lab., Jour., v. 22, p. 88, pl. 19, fig. 1A,B.

This is a nearly straight brevicone, broadly depressed in cross section, with sutures essentially straight and transverse, the siphuncle close to the side which is essentially straight in profile, the opposite side being slightly more convex. Expansion is gentle and the shell contracts with moderate rapidity laterally over the adoral half of the living chamber, which ends in a moderate constriction, be-

yond which the shell is extended to the rather obscure aperture. The species has somewhat the aspect of an unusually straight *Cyrtogomphoceras*. The siphuncle is atypical of this genus in that it is unexpectedly small at the septal foramen. A transverse longitudinal section was made through the lower part of the phragmocone at the level of the siphuncle but internal structure proved to be completely destroyed. FOERSTE & SAVAGE state of the siphuncle: "Where the dorso-ventral diameter, in the present depressed condition, is 35 mm., the center of the siphuncle is 3 mm. from the ventral wall of the conch. The diameter of the septal neck is 5 mm. laterally, the area of contact of the septum with the overlying segment of the siphuncle equalling 8 mm. laterally, the segment being enlarged within the camerae, though its exact form remains unknown." The present specimen, which is obviously all that was originally figured of the holotype, fails to show any such features. Either this description was based upon another specimen, not otherwise noted in description of the species, or upon an adapical portion, not mentioned and not included in the original figure of the species.

Discussion. The taxonomic position of this species is highly uncertain. In form it is faintly suggestive of *Cyrtogomphoceras* but is too straight, the sutures are transverse, and the siphuncle is small. However, there is no other genus in which it can be placed, and though it might be described as representative of a new genus, its position would remain uncertain.

The unique holotype is no. 43 HB in the SAVAGE collection, of the Illinois Geological Survey. It is from horizon 1 in the Shamattawa limestone (Ordovician), 4 miles upstream from the mouth of the Shamattawa River, near Hudson Bay.

"Stokesoceras" balticum Teichert

Stokesoceras balticum TEICHERT, 1934, Meddel. fra Dansk Geol. Forening, Bind 8, Hæfte 4, p. 387, pl. 8, fig. 3.

This species is from the drift of Denmark. It comprises a part of a phragmocone of 5 camerae of a straight cephalopod. The large siphuncle has segments which are expanded very much as in *Ormoceras*, short necks and short brims but it contains a lining

which thickens rapidly from anterior to adapical segments suggesting the endocones of a *Stokesoceras*. That the apical increase in thickness of the material is very gradual and that the siphuncle segments are well rounded and not strongly appressed where one is in contact with the other, suggest that this may not be a true *Stokesoceras* at all. TEICHERT has very significantly compared this specimen with several orthoconic cephalopods with expanded siphuncles, which seem to contain similar linings. While the question of placement of these forms is too great for discussion here, it has been evident that such linings are present in orthoconic cephalopods with expanded siphuncle segments ever since TROEDSSON (1926) described such structures in shells which were, externally, kionoceroids. However, such forms are not common and none have been studied in enough detail to permit conclusions as to their affinities with reasonable certainty. Actinoceroids can develop deposits of this aspect when radial canals are not evident but the disappearance of the radial canals is a phenomenon of preservation lacking real biological significance. *Striatoceras*, the generic repository of TROEDSSON's species, was regarded by FLOWER (in FLOWER & KUMMEL, 1950) as a member of the Stereoplasmoderata. However, these shells require much more study and good material seems to be extremely scarce.

Shells of this general type range sparingly through Ordovician as well as Silurian and Devonian. If the group is not polyphyletic, which is perfectly possible, it could be a stock of orthocones developed from *Stokesoceras* of the Silurian, thus comprising yet another strange offshoot of the order Discosorida. The fact that these shells are dominantly orthoconic leads me to believe that they are not true *Stokesoceras*. Certainly there is such gradation in form between *Stokesoceras* and *Discosorus* and *Endodiscoceras* that it is often hard to decide in which generic group certain species are best placed. Further, some *Stokesoceras* are known showing endocones having essentially the pattern of those seen in other Discosoridae. Gradation indicates actual relationship. Regrettably, *S. balticum* is so remote from typical *Stokesoceras* that it seems unlikely that it is a true member of the genus. Yet at present no better suggestion is offered as to proper generic assignment.

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