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Cambrian Cephalopods

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Contents

Illustrations

FIGURES *Page*

PLATES

Abstract

The description and classification of new material from the Upper Cambrian of the Llano uplift in Texas has provided the basis for a review of the whole problem of the oldest cephalopods. In the light of these discoveries it is possible to evaluate more critically the Cambrian fossils that have formerly been assigned to the cephalopods. These fossils may be grouped as follows:

The new genus and species *Palaeoceras mutabile* exhibits siphuncular bulbs, previously reported only in material from eastern Asia. From this new evidence, the bulbs are accepted as a feature of the family Plectronoceratidae, which is redefined accordingly. The other genera, *Plectronoceras* of the Cambrian and *Multicameroceras* and *Sinoeremoceras* of the early Ordovician, are briefly reviewed.

Data concerning three Cambrian genera which are certainly cephalopods, but whose extant descriptions and illustrations are insufficient to determine their precise morphology and taxonomic position, are analyzed in detail. *Shantungendoceras,* which has been reviewed elsewhere, is probably Ordovician and not Cambrian in age. *Angaroceras* is regarded as a synonym of *Ruthenoceras.* What can be learned concerning the genera in this group is sufficient to determine that they may belong either to the Ellesmeroceratidae or Plectronoceratidae, but could not be members of any more advanced families.

New material of *Shelbyoceras* shows clear septa, but no siphuncle, and an aperture with a sinus on the convex side. If a siphuncle is present, it is tiny and close to the same side. Either *Shelbyoceras is* an exogastric cephalopod without close relatives, or it is a septate shell without a siphuncle, and therefore not a cephalopod. The second interpretation is regarded as probably the correct one.

Some Cambrian shells formerly assigned to the cephalopods have proved to be aseptate. One such form is described as *Kygmaeoceras perplexum.* Such fossils, which include the Hyolithidae and Tentaculitidae, are of uncertain position, because the shell offers no good evidence of the nature of the animal of which it was once a part.

A stratigraphic survey shows that as cephalopods are traced from the Chazyan to older strata, the uniformity of form and structure increases. It is evident that a general structural pattern, based upon the combined features of the oldest families, the Ellesmeroceratidae, and Plectronoceratidae, can be accepted as archaic. Within this general pattern it is possible to select more specific features as reasonable primitive ones. The siphuncular bulbs of the Plectronoceratidae are regarded as truly archaic cephalopod features.

In the light of this summary, it is evident that the cephalopods converge in the lower Canadian and Upper Cambrian to a reasonable uniform structural pattern. This pattern is so remote from that of the Lower Cambrian genera *Volborthella* and *Salterella,* that it is quite evident that these tiny shells have no close relationship with the oldest fossils which can be called cephalopods with certainty. They well may be included with the invertebrates of uncertain position.

Foreword

This paper is essentially a prelude to the description of the cephalopods of the El Paso limestone of New Mexico in which these fossils, by reason of their large size, are particularly conspicuous. Owing to their silicification, the cephalopods stand out more strikingly in the outcrop than do representatives of most other groups; also, they can be removed and studied with relative ease and to good advantage in terms of regional correlation.

The El Paso group, which has been considered until very recently as a single formation, embraces the entire Canadian interval of Ordovician time. The lower part, of Gasconade age, contains the first beds in which the cephalopods are conspicuous and important contributors to the general faunal content. Most of the lower Canadian or Gasconade cephalopods belong to a single prolific family, the Ellesmeroceratidae, which by middle Canadian time had declined suddenly. Their place was taken by three new orders, the Endoceratida, Bassleroceratida, and Tarphyceratida. These orders, with a few specialized surviving families of the Ellesmeroceratida, constituted the cephalopod contribution to later Canadian faunas, which persisted in America until Chazyan time, when they were joined by the Michelinoceratida, Ascoceratida, Actinoceratida, Discosorida, Oncoceratida, and Barrandeoceratida.

This study of Cambrian cephalopods is designed to clear up some confusion which has surrounded the nature of the oldest known cephalopods, those to which we must look for some idea of the nature of the primitive features of the group.

The study is concerned with several interrelated problems. First, what are the characteristics of those Cambrian fossils which are true cephalopods? Second, what may be the classification of those forms which have been described as cephalopods but which, from our present evidence, cannot properly be retained in that group? Third, what forms attributed to the Cambrian now appear restricted to post-Cambrian strata? From consideration of these problems, it is possible to pass to a question of more general interest, namely, what was the nature of the most primitive of the true cephalopods?

The student of the cephalopods is particularly fortunate in this regard, for the Cambrian types are very primitive indeed and diversification did not begin until Ordovician time. In most other groups wide diversification took place prior to the Cambrian. However, until the present study was undertaken, it was not clear that the Cambrian cephalopods could be accepted as truly archaic.

Although the material basis of this study is a collection of only seven specimens from the Upper Cambrian of the Llano uplift in Texas, it required such a radical revision of current views that it seemed pertinent to incorporate with the description a review of the previously reported cephalopods of the Cambrian and a discussion of the general problems involved.

In published reports, Cambrian cephalopods have been placed in the Endoceratida, the Ascoceratida (Mixochoanites), and the Protochoanites. A few others were regarded as allied to endogastric cyrtocones of the lower Canadian, assigned first to the Cyrtendoceratidae, and currently to the Ellesmeroceratidae. In the following pages these conclusions are replaced by a different and simpler interpretation.

The conclusions reached are summarized in the abstract. It will suffice here to point out that the oldest true cephalopods are Upper Cambrian, and that the two adequately known genera are assignable to the family Plectronoceratidae. One inadequately known genus could belong either to this family or to the Ellesmeroceratidae. Reasons are advanced for regarding the Plectronoceratidae as the most primitive of the true families, and the archaic stock of the cephalopod line.

Acknowledgments

The new material upon which this investigation is based was submitted for study by Dr. J. L. Wilson, of the University of Texas, and Dr. Virgil Barnes and Mr. Horace Ellinwood, of the Texas Bureau of Economic Geology, with the permission of the director, Dr. John Lonsdale. The locality and stratigraphic data are the contributions of Dr. Barnes and Mr. Ellinwood, and not of the writer, who has no firsthand knowledge of the region. The first draft of this study was completed at the New York State Museum, where Mr. Howard Heller and the writer took most of the photographs. I wish particularly to acknowledge the valuable aid of Mr. Heller in relation to the extremely difficult task of photographing the minute specimens of *Palaeoceras mutabile*. Subsequent photographic work was done by Mr. Charles Treseder, and the figures accompanying the report were redrawn largely by Mr. David Moneypenny. Dr. G. Winston Sinclair called my attention to Kordes report of Mixochoanites in the Cambrian, which otherwise I would have overlooked, and Mrs. Helen Valentine kindly supplied a translation of the Russian text. For additional suggestions, assistance, and discussion of many of the problems encountered in this work I am indebted to the late Dr. Josiah Bridge, Dr. B. F. Howell, Dr. Christina Lochman, and Dr. Curt Teichert.

Previous Reports of Cambrian Cephalopods

The first Cambrian fossils to be attributed to the Cephalopoda are the tiny, conical, septate shells of the Lower Cambrian assigned to the genera *Volborthella* and *Salterella*. Grabau and Shimer (1910, p 41) regarded them as the most primitive of the nautiloids, and erected for them the order Protochoanites. Opinion has since been divided as to whether these shells have anything to do with the primitive cephalopods (Schindewolf, 1934; Kobayashi, 1935; Miller, 1943).

Walcott (1905) described *Cyrtoceras cambria* from the Upper Cambrian of China. This species later became the type of the genus *Plectronoceras* Ulrich and Foerste (1933). Kobayashi (1935) described a second species, *P. liaotungense,* in which he found in only one camera a connecting ring outlining an inflated portion of the siphuncle between the short septal necks. This he called a siphuncular bulb. Kobayashi (1933) previously had found similar structures in the Wanwanian (Lowermost Ordovician) genera *Multicameroceras* and *Sinoeremoceras.* These, together with the little known *Wanwanoceras,* were placed by Kobayashi (1935) in the family Plectronoceratidae, which he regarded as characterized by unstable siphuncles, but commonly showing siphuncular bulbs at some growth stage. This interpretation was accepted originally by the writer (Flower, 1941-a). Miller sectioned additional material of *Plectronoceras cambria* and failed to find any connecting rings whatsoever. He suggested (Miller, 1943), therefore, that the single connecting ring reported by Kobayashi, and represented only by a heavily retouched photograph, might be adventitious. Ulrich, Foerste, Miller, and Unklesbay (1944) regarded *Plectronoceras* as probably orthochoanitic, and as such the family Plectronoceratidae could be regarded as a possible synonym of the Cyrtendoceratidae as employed by them. They pointed out further that their upper Canadian genus *Clelandoceras* might eventually prove to be a synonym of the Upper Cambrian *Plectronoceras,* if, as they suspected, the siphuncle of *Plectronoceras* proved to be tubular and orthochoanitic. This suggestion is logical. It would, however, be remarkable to find a single cephalopod genus having such a large vertical range. Flower (1947; and Flower and Kummel, 1950) accepted the interpretation of the bulb of *Plectronoceras* as adventitious, but regarded the family Plectronoceratidae as a valid receptacle for the genus *Plectronoceras* alone, in which connecting rings were either absent or so poorly calcified that they had not yet been found preserved. The Wanwanian genera in which siphuncular bulbs had been reported, were removed tentatively to the Ellesmeroceratidae. Perplexity also surrounded the reality of the bulbs in those genera. The illustrated sections showed only faint color contrast. As published, the siphuncles were outlined so heavily in ink that a critical reevaluation of the structures proved impossible. Much of the perplexity arose from the fact that no one except Kobayashi had seen cephalopods showing siphuncular bulbs, and his illustrations were all heavily retouched. The new evidence supplied by *Palaeoceras mutabile* indicates that Kobayashi was fundamentally correct in his interpretation of the Plectronoceratidae.

Sun (1937) described the genus *Shantungendoceras* from the Upper Cambrian of China. The problems presented by this genus have been reviewed previously by the writer (Flower, 1951). Sun's views were influenced largely by Grabau's (1919) opinions as to the antiquity of the endoceroid, which are no longer tenable. Sun made several morphological assumptions not supported by his material. The structure which he regarded as a central siphuncle appears to be adventitious; there is no evidence of endocones nor of a holochoanitic siphuncle wall. The siphuncle is not central, but small and marginal.

Meanwhile, in the Upper Cambrian of North America, Butts (1926) had reported cephalopods in the Copper Ridge dolomite of Alabama. These specimens later formed the nucleus of the genus *Shelbyoceras* (Ulrich and Foerste, 1931) which subsequently received fuller treatment, species being recognized in the Cambrian of both Alabama and Missouri (Ulrich, Foerste, and Miller, 1943). The genus is rare; in all, seven specimens were known at that time. When these fossils were first reported, their Cambrian origin was received with some doubt (E. R. Cumings, in conversation, 1938). The basis for this doubt was the reasonable assumption that regions yielding Upper Cambrian cherts also might yield some few cherts from overlying Ordovician strata which otherwise had been removed by erosion. Subsequent investigations yielded no forms congeneric with *Shelbyoceras* in the overlying Ordovician strata, and *Shelbyoceras* has come to be accepted as the only North American Cambrian cephalopod. Anomalously, the present findings require a sharp reversal of this opinion. Though *Shelbyoceras* is certainly Cambrian, its cephalopod nature is very dubious.

On the basis of two cephalopods known only from chance-oriented sections, Korde (1949) described two species, two genera, and a new family which he attributed, amazingly, to the Mixochoanites.

Ulrich, Foerste, Miller, and Unklesbay (1944) described as *Walcottoceras?* sp. a portion of a small, straight, annulated shell from the Upper Cambrian of Oklahoma.

Rusconi (1952) described as a Cambrian cephalopod a curved, annulated fossil which he named *Cycloceras? salagasterensis*. This is dismissed as irrelevant to the present problem, since his Cambrian certainly contains Ordovician elements. Further, the nature of the fossil as a cephalopod requires substantiation.

Something of a confusion of tongues has resulted from changing concepts of cephalopod classification in the last twenty years, in which interval most of the above discoveries were reported. Kobayashi (1935) proposed a phyletic succession starting with the Plectronoceratidae, passing to the Ellesmeroceratidae, and thence to such diverse groups as the endoceroids and the "Orthoceratidae" (Michelinoceratidae). Flower (1941-a) accepted this classification for the most part, but found that several morphological assumptions on which it was based (in particular, the early appearance of holochoanitic structure) would have to be abandoned in the light of new evidence, mainly supplied by thinsection study of siphuncle walls. Confusion resulted from the fact that the studies of the American Ozarkian and Canadian cephalopods (Ulrich, Foerste, and Miller, 1943; Ulrich, Foerste, Miller, and Unklesbay, 1944) were based largely upon chert-replaced steinkerns of cephalopods. Such material does not permit a proper investigation of shell structure. Though some notable morphological discoveries were recorded, in the main the classification employed was a rather primitive one. Flower (1947) later reemphasized the secondary nature of the holochoanitic siphuncle walls in endoceroids, and presented the skeleton of the current classification of the earlier cephalopods. This was published later in summary form (Flower and Kummel, 1950) with a drastic revision of the major divisions of the Nautiloidea. Subsequently detailed studies of the problem have been continued. Thus far, however, publication of the results, in detail, has been delayed, largely in order that they might incorporate the evidence supplied by the rich cephalopod faunas of the El Paso limestone.

Palaeoceras Flower, n. gen.

Genotype: *Palaeoceras mutabile* Flower, n. sp.

Shells very small, slender, straight, compressed in cross-section, venter slightly more narrowly rounded than dorsum. Sutures with prominent lateral lobes in the young, high ventral and low dorsal saddles, but more nearly transverse in late growth stages. Siphuncle close to the venter. In the young stages septal necks are relatively short, one-third to one-fourth the length of the segment. The remainder of the segment is outlined by a thick connecting ring in which evidence of layering is apparent. This part of the segment is greatly expanded in the camerae, forming a siphuncular bulb. Connecting rings are incompletely preserved, and were quite probably fragile and poorly calcified structures. From the young to the adult the septal necks lengthen, becoming nearly holochoanitic in the latest known stages. The siphuncular bulbs become necessarily shorter and less strongly expanded—first vestigial, and finally completely lost. Diaphragms traverse the cavity of the siphuncle.

The shell surface bears only faint lines of growth. No hyponomic sinus is evident.

Discussion. The above brief general description of the genus is supplemented by a detailed description of the genotype and only known species, described below. Superficially, *Palaeoceras* could be mistaken for the lower Canadian genus *Ectenoceras,* which it resembles in cross-section, sutures, general form, and relatively small size. However, it is separated not only from *Ectenoceras* but from all genera of the Ellesmeroceratidae, to which *Ectenoceras* belongs, by the remarkable structure of the siphuncle. Similar structures have been reported previously only in three genera. Of these, *Plectronoceras is at* once differentiated as a tiny compressed cyrtocone. Further, it apparently retains siphuncular bulbs throughout life, whereas later growth stages of *Palaeoceras* show a gradual lengthening of the septal necks and reduction and ultimate loss of the siphuncular bulbs. Two other genera agree with *Palaeoceras* in this ontogenetic progression. Both are much larger shells, very closely septate, and faintly endogastric. *Sinoeremoceras* expands at a moderate rate to the aperture; the adoral part of *Multicameroceras is* faintly gibbous and contracted slightly adorally.

Palaeoceras is known thus far only from the genotype from the late Trempealeauan of the Llano uplift of Texas.

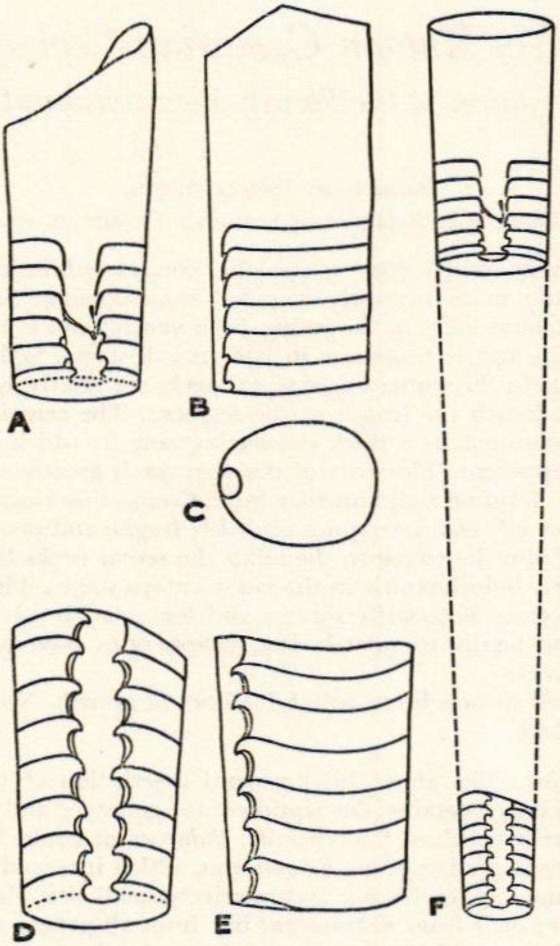


Figure 1

Palaeoceras mutabile.

A-C. Paratype, representing late growth stage: (A) ventral view; (B) lateral view, venter on left; (C) cross-section, oriented as in B. About × 4.

D-E. Holotype, showing early growth stage: (D) ventral view; (E) lateral view, venter on left. About × 6.

F. Restoration of shell, in ventral view, showing estimated length of the unknown interval between the two known specimens, and indicating the ontogenetic changes in the siphuncle. About × 2½.

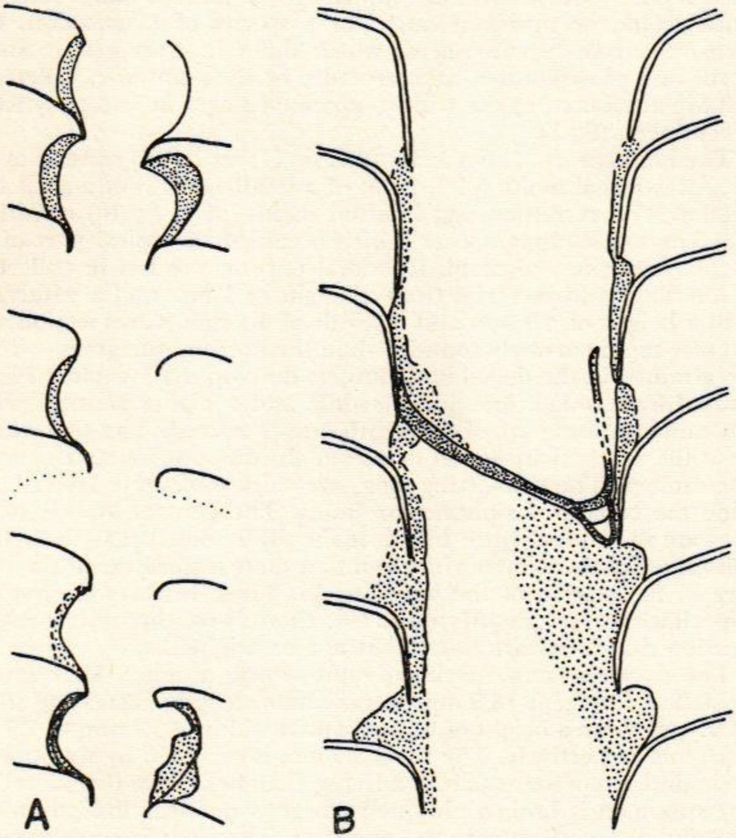


Figure 2

DETAILS OF THE STRUCTURE OF THE SIPHUNCLE OF *Palaeoceras mutabile,* AS SEEN FROM THE VENTRAL SIDE.

A. Siphuncle of holotype. About × 20.

B. Siphuncle from basal part of paratype, showing latest known growth stage. About × 22.

Palaeoceras mutabile Flower, n. sp.

(pl 1, figs 5, 9-10; p12, fig 11; p1 3; figs 1 A-F,'2 A-B)

General description. This is a tiny, slender, straight shell of compressed section which, without knowledge of the structure of the siphuncle, could be mistaken easily for a species of *Ectenoceras. It* is known only from two fragments which differ in cross-section, suture pattern, rate of expansion, and structure of the siphuncle, differences which are attributed to the widely separated stages in ontogeny which they represent (fig 1).

The holotype (pl 1, figs 5, 10; pl 2, fig 11; fig 1 D-E) consists of two parts. An external mold (pl 1, fig 5) of a small portion of a shell is 12 mm long. The corresponding internal mold (p1 1, fig 10) consists of only 6.5 mm of a phragmocone which occupied the apical part of the corresponding external mold; its adoral portion was lost in collecting. The internal mold increases from a height of 4 mm and a width of 3 mm to a height of 4.3 mm and a width of 4.4 mm. Cross-section with the venter more narrowly rounded than the dorsum, the greatest width being attained in the dorsal half. Sutures develop shallow lateral lobes, separated by a broad, low dorsal saddle and a higher ventral saddle. Seven camerae, and part of an eighth, are preserved. The siphuncle is close to the venter, with septal necks one-third to one-fourth the length of the camera. The connecting rings are thick, obscurely layered, and outline the expanded siphuncular bulbs. The general aspects of the species are shown in Figure 1 D-E. It should be noted that the ventral saddles are slightly asymmetrical, and that there is some variation in the degree of inclination of the septal necks. These features suggest that the specimen is very slightly distorted; there is on the other hand no indication that such variation might not be original.

The paratype is a specimen representing a much later growth stage. It is a fragment 13.5 mm in maximum length, increasing in the basal 12 mm from a height of 6.5 mm and a width of 5.5 mm to 7.5 mm and 6.5 mm respectively. The basal 5.5 mm is occupied by six camerae; the remainder represents part of a living chamber. Since the adoral end of the specimen is broken obliquely, there is no clear indication that its maximum length attains the aperture. The shell is compressed in cross-section, the venter more narrowly rounded than the dorsum, but the greatest width is attained at midheight of the shell, and not in the dorsal portion as in the holotype. The sutures show only the faintest development of lateral lobes, a slight ventral saddle, but no clear dorsal saddle. The siphuncle is ventral, circular in section, the segments nearly tubular and about one-fifth the width of the shell in diameter. Septal necks are long and parallel to the shell axis. In adapical segments the necks are slightly more than half the length of the camerae. In later segments the length of the neck is gradually increased until it reaches the level of the preceding septum, though it is still rather widely separated from contact with it, because of the gentle curvature of the septa into the septal necks. Thick connecting rings are present, and in adapical segments their outer surfaces are definitely expanded into the camerae, outlining vestigial siphuncular bulbs. In later segments the expansion of the connecting ring becomes progressively reduced and is eventually lost. The middle of the phragmocone of the paratype shows the siphuncle crossed by a conspicuous diaphragm. The general aspects of this specimen are shown in Figure 1 A-C.

The marked differences shown by these two specimens are of a magnitude sufficient to justify placing them in different species and different genera. Indeed, in the light of past usage, once they might have been considered members of different divisions within the Nautiloidea. Yet there is reason to believe that these differences are due to the widely separated ontogenetic stages represented by the two specimens. Figure 1 F indicates a conservative estimate of the relative position of the two known specimens in a relatively complete shell. According to this estimate, the holotype, 6.5 mm in length, is separated from the 13 mm of the paratype by an interval of 56 mm, which should contain approximately 35 camerae. The resultant shell, as restored, would have a length of 76 mm. This is necessarily an estimate. The early stage shows a greater rate of expansion than does the late stage. Evidence is lacking to show whether the shell becomes more slender gradually or suddenly, and if suddenly, at what point the decrease in rate of expansion occurs. It should be noted also that the estimate makes no prediction as to the nature of the apical end. It is reasonable to believe that not far apicad of the holotype, the shell contracted rapidly to a blunt apex, whereas the siphuncle diminished to its initial proportions only gradually. This has been found true of the Ellesmeroceratidae, the closest relatives of the present form in which the initial portion of the shell has been observed (Flower, manuscript). Likewise, there is no certain evidence that the paratype represents a mature living chamber. The usual features of maturity, crowded adoral septa and internal thickenings of the wall of the living chamber, are not evident. On the other hand, it is not certain that these features were present in mature individuals of Cambrian cephalopods.

The significant point of the shell proportions is that the wide unknown interval between the stages represented by the two types makes the differences in cross-section, sutures, and structure of the siphuncle eminently reasonable in terms of ontogenetic changes. This hypothesis finds further confirmation in the evident lengthening of necks and suppression of vestiges of the siphuncular bulbs shown even in the short portion of phragmocone preserved in the paratype.

Detailed morphology of the siphuncle. The siphuncular structures of this species are so remarkable that it is necessary to describe and illustrate them in far more than usual detail. It should be noted that the two types, as illustrated, do not represent their original condition. The siphuncles are exposed by subjecting the entire specimens to very slow and gentle etching. In this way a thickness of not over .4 mm was removed from their original surfaces. The etching produced no significant relief, as is commonly the case, but instead produced surfaces so smooth that they have a dull polish. Though rounded, the ventral surfaces show essentially transverse longitudinal sections of the siphuncle at the point of its greatest width. All structures are apparent as variations in color. The specimens were photographed under water, to eliminate as much reflection as possible, to the maximum enlargement permitted by the camera available. Further enlargement was made from the negatives. The slight color variations, all shown in tones of gray and yellow, proved difficult to photograph. Features brought out dearly on one type of negative were obscure on another, or shown in such extreme contrast as to be unintelligible. Owing to the significance of these structures, it was eminently desirable that they be illustrated by unretouched photographs. The photographs are supplemented by drawings (fig 2 A-B) based upon tracings from photographs, to which are added fine structural details which otherwise could have been shown only by costly reproduction of many of the negatives.

The holotype is illustrated X 10 (pl 1, fig 10), with siphuncle and septa retouched. One of the most satisfactory photographs (pl 2, fig 11) is shown X 20. The detailed structure is shown in Figure 2 A.

At the extreme base of the holotype (pl 2, fig 11) is seen a portion of an incomplete segment crossed obliquely by the surface at the base of the specimen. This is not illustrated at the base of Figure 2 A. Orad of this lies the first complete segment. Here the septal neck on the right points obliquely inward; its mate on the other side seems slightly re-curved, suggestive of slight distortion of the specimen. The bulb is expanded to twice the width of the segment across the septal foramen. The ring is relatively thin on the left, and close study shows an indication of two thin layers represented by material of slightly different color and texture. On the right side the ring is thicker, irregular, but again shows evidence of two layers. It is largely the outer surface of this ring which appears as a conspicuous dark band in Plate 2, figure 11.

The second segment shows septal necks which are essentially parallel with the shell axis. The ring is visible on the right; the conspicuous dark line indicates its inner but not its outer surface. The calcite of which it is composed is so similar in texture to that occupying the camera, that the outer surface of the ring is not apparent. On the right side, the connecting ring is missing; its normal position is crossed in part by a large oolite, one of several occupying the cavity of the siphuncle. In this and some other segments, where the connecting rings are destroyed, oolites and other small detrital material have not only filled the cavity of the siphuncle but have spread into the camerae for a short distance. This invasion is shown more clearly in the third segment, where the connecting ring is destroyed on both sides. The fourth camera shows again some difference in the curvature of the septal neck on the left and right sides. The connecting ring is present; it shows a definite thickness, but no differentiation of layers within the ring is apparent. The fifth segment, in which even the septa and septal necks are so similar in color to the surrounding materials that they can scarcely be detected in the unretouched photograph (pl 2, fig 11), has also lost the connecting ring. The sixth segment, though likewise shown with only slight color differentiation, exhibits typical septal necks (again somewhat different in curvature on the right and left sides), as well as relatively thick connecting rings, thicker on the right than on the left side of the exposed surface. The last segment is incomplete, but of interest in that on the left both the inner and outer surfaces of the ring are apparent, though on the right the connecting ring is represented only by a dark line.

The paratype (pl 1, fig 9; pl 3; fig 2 B) shows somewhat better color differentiation. Superficially, the segments of the siphuncle here appear to be composed of nearly holochoanitic septal necks, and to be essentially tubular. Close examination, however, shows that in the basal segments the material of the connecting ring outlines expanded parts of the segment, clearly greatly reduced siphuncular bulbs. In the first complete segment the material of the connecting ring can be seen extending outward into the camera. On the right, its outer (cameral) surface is irregular, and may be incorporated with some adventitious material in the camera. On the left, the outline is relatively clear. Differentiation of the inner surface is relatively poor. In the second segment the outline of the ring is relatively rounded on the right, but on the left it is again incorporated probably with material in the camerae. Here there is indication of layering of the materials of the connecting ring, as shown in Figure 2 B. The third segment shows connecting rings which are less expanded into the camerae, but the inner and outer surfaces are both fairly well differentiated. In the second and third segments a diaphragm, plainly visible from both the photographs and the drawing, passes obliquely from the septal neck of the third segment to that of the second. The diaphragm is, in general, apparently similar in texture to the material of the connecting ring, though denser, darker, and much more readily visible because of its greater color contrast with surrounding materials. At its point of greatest depth, close to the right side of the siphuncle in the present section, the structure is separated briefly into several discrete diaphragms.

The succeeding segments of the siphuncle differ from those previously noted in that they show a progressive increase in the length of the septal neck; and the material of the connecting ring, still relatively thick, becomes less and less produced into the camerae, until the expansion of the segment into a siphuncular bulb at this region is lost completely.

Discussion. It is evident from a close survey of these two sections that in the early part of the siphuncle the septal necks are between one-third and one-fourth the length of the segment. They are supplemented by connecting rings which outline expanded portions of the siphuncle, termed the siphuncular bulbs. The attitude of the tips of the septal necks varies, as do the thickness and composition of the connecting ring. There is, however, good evidence that the thick rings are composed of several different layers. The destruction of the connecting ring by invading matrix in several of the segments indicates that it was a weak, possibly a poorly calcified, structure. The frequency with which it is destroyed in the present specimen is significant. Given a slightly weaker structure, it is reasonable to suppose that a series of camerae might show no trace of the rings. This condition was found in sectioning specimens of *Plectronoceras cambria* (Ulrich, Foerste, Miller, and

Unklesbay, 1944). At the same time, the evidence of the fragility of these structures in *P. mutabile* causes one to give credence to the single connecting ring which Kobayashi reported in *Plectronoceras.*

The paratype is so different in the structure and general aspect of its siphuncle, that when the specimens first came into the writer's hands he was impressed by the fact that on the one hand it was incredible that these two specimens, the first valid cephalopods from the Upper Cambrian of North America, could come from the same bed, the same locality, and yet represent two different species and genera. On the other hand, the structure was so different, that if they were described as one and the same species, anyone so minded could reasonably maintain that they were so different that identifying them as belonging even to the same genus was unwarranted. Such a large interval of phragmocone remains unknown between the two specimens, that the ontogenetic change postulated in the siphuncle is eminently possible in the missing interval. Close study of the paratype revealed that, in spite of the long septal necks, the earlier segments did contain greatly reduced vestiges of the siphuncular bulbs so extremely well developed in the early stages. These features, though inconspicuous in the paratype, place the identity of the two specimens upon relatively safe ground. It should be noted in this connection that the premise maintained in recent years by several paleontologists, namely, that in a given association one may expect to find only a single species of any one genus, need not receive serious consideration. Such a contention can be easily contradicted on the basis of numerous living assemblages. That it should receive any serious attention from paleontologists can be interpreted only as an indication of sad inexperience with living faunal associations. Curiously, it also involves as a premise that the proper scope of a genus, on which there is no wide agreement, witnessed by frequent accusations of "splitting" and "lumping," has been adequately determined. Anomalously also, the differences of these two specimens upon which *Palaeoceras* is based are great enough that, in the light of general past usage, they would be placed in different genera, and perhaps different families.

The features of the genus will serve to distinguish *P. mutabile* from all previously described cephalopods.

Types. Holotype and paratype, Bureau of Economic Geology, University of Texas.

Occurrence. Both specimens are from the San Saba limestone member of the Wilberns formation, from the Threadgill Creek section, northern Gillespie County, Texas. The material was collected by Mr. Howard Ellinwood, 67 feet below the top of the 281 feet of the San Saba limestone member. Two feet below these specimens *Eurekia, Monocheilus, and Euptychaspis* were collected. *Palaeoceras mutabile* occurs in beds which may safely be assigned to the upper part of the Trempealeauan. The base of the Trempealeauan in this section occurs not at the base of the San Saba limestone, but in the upper part of the underlying Point Peak shale. The holotype of *Kygmaeoceras perplexum,* described below, occurs in the same bed with *P. mutabile.*

REVISION OF THE FAMILY PLECTRONOCERATIDAE

The dilemma presented by the Plectronoceratidae has been outlined previously. That cephalopods exhibiting siphuncular bulbs appeared to be confined to eastern Asia, and had been studied only by Kobayashi, whose illustrations were so retouched that critical evaluation of the problem was impossible, caused much perplexity. The undoubted evidence of siphuncular bulbs presented in *Palaeoceras mutabile,* described in the preceding pages, supports the reality of these structures. It does not, of course, prove the reality of the bulb in *Plectronoceras.* In the light of this new evidence, however, the organic nature of the structures becomes a highly reasonable inference.

On this basis the family Plectronoceratidae is redefined as follows: Shells small, compressed in cross-section, endogastric cyrtocones or orthocones. The siphuncle is close to the venter, composed of segments with short septal necks. The connecting rings, evidently very poorly calcified in the earliest genus *Plectronoceras,* outline expanded portions of the siphuncle between the short, straight septal necks, for which the term siphuncular bulb is appropriate. The connecting rings, when preserved, are evidently appreciably thick, and show a layered structure. In late stages of more advanced genera there is a progressive prolongation of the septal necks, which may extend finally nearly to the preceding septum. The connecting ring is retained and is still thick, but the siphuncular bulbs become reduced and finally are lost altogether.

The genera of the Plectronoceratidae will now be reviewed briefly.

Plectronoceras Ulrich and Foerste

Genotype: *Cyrtoceras cambria* Walcott

Plectronoceras Ulrich and Foerste (1983) Science, new ser, v 78, p 289.

____ Ulrich and Foerste (1936) Denison Univ., Sci. Lab., Bull., v 30, p 284.

____ Kobayashi (1935) Japanese Jour. Geology and Geography, v 12, p 19.

Flower (1941) Palaeontographica Am., v 3, n 13, p 13.

-----------Miller (1943) Biol. Rev., v 18, p 100.

____ Ulrich, Foerste, Miller, and Unklesbay (1944) Geol. Soc. America Special Paper 49, p 133.

-----------Flower (1947) Ohio Jour. Sci., v 47, p 160.

____ Flower and Kummel (1950) Jour. Paleontology, v 24, p 606.

Plectronoceras contains cephalopods which are tiny compressed endogastric cyrtocones. Cross-section compressed, with venter more narrowly rounded than dorsum (fig 3 E). Sutures display lateral lobes and slope forward somewhat on the dorsal side in late growth stages. The siphuncle is ventral, with short septal necks. Connecting rings are usually lost, but Kobayashi has figured in one segment of one specimen (fig 3 A) a connecting ring outlining a siphuncular bulb. As noted above, it now seems highly probable that Kobayashi was correct in interpreting this as an original organic structure. It is evident from other sections showing no connecting rings whatsoever, that the structure was fragile, evidently poorly calcified, and is rarely preserved. The features of the two species of this genus are shown in Figure 3.

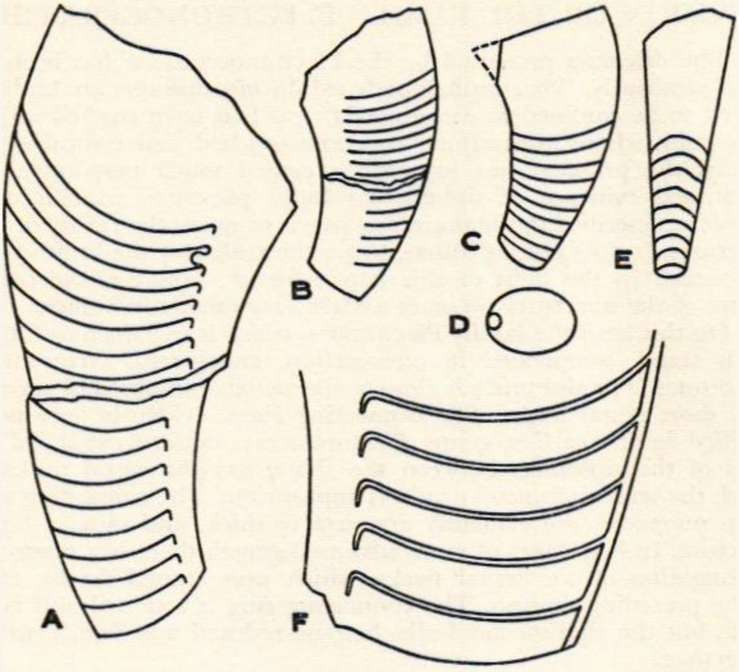


Figure 3

Plectronoceras.

A-B. *Plectronoceras liaotungense* Kobayashi: (A) vertical section showing the one reported connecting ring near the adoral end of the phragmocone. X 9. (B) exterior of the same specimen seen from the opposite side. X 5, to show differences of proportion between this species and *P. cambria.* (After Kobayashi, 1935.)

C-F. *Plectronoceras cambria* (Walcott): (C) internal molds seen from the lateral side; (D) diagrammatic cross-section, with the venter on the left as in C. (E) internal molds seen from the convex dorsal side. (F) vertical section showing siphuncle on the left, with septal necks, but no connecting rings preserved. C-E, about X 5; F, about x 20. (After Ulrich, Foerste, Miller, and Unklesbay, 1944.)

The two known species are both from the same horizon, the *Tsinania canens* zone of northern China and southern Manchuria. *P. cambria* (Walcott) is known only from one occurrence, at Pagoda Hill, about one mile west of Tsinan, Shantung province, China. Its features are shown in Figure 3 C-F. It should be noted that, though several sections have been made of this species, no connecting ring has yet been observed. *P. liaotungense* Kobayashi, from Pai-chia-shan, Wuhutsui basin, Manchuria, is rather different in rate of enlargement and suture pattern (fig

3 B), and in vertical section (fig 3 A) has yielded the one reported connecting ring which has been the cause of so much discussion and uncertainty.

The age of the *Tsinania canens* zone is a single problem, though it is called the Chaumitien limestone in north China and the Yenchou formation in southern Manchuria. Precise correlation with the zones of the Upper Cambrian of America is somewhat uncertain. It is evident that it overlies the *Chuangia* zone, which is correlated with the Ironton, the lower part of the Franconian in America (Howell, 1947; Endo and Resser, 1937, p 102). The *Tsinania canens* zone yields conflicting faunal evidence. It contains the characteristic late Franconian genus *Ptychaspis,* but it also contains some saukiid trilobite genera, in particular species assigned to *Saukiella, Tellerina,* and *Prosaukia*. The first two genera are not known in America below the Trempealeauan. Howell (1947) and Endo and Resser (1937) consider this fauna as late Franconian. C. Lochman (oral communication) would place greater weight upon the saukiids, and would regard the *Tsinania canens* zone as early Trempealeauan. Selection of either interpretation appears at present a matter of opinion. On the basis of the archaic features of *Plectronoceras,* the writer would favor the late Franconian over the Trempealeauan interpretation.

Palaeoceras Flower

The characters of *Palaeoceras* need only be summarized for contrast with the other genera, having been described in detail in the preceding pages. The shell is slender and straight. Early segments exhibit siphuncular bulbs. Later ones show progressive lengthening of the septal necks until they are almost holochoanitic, accompanied by reduction of the siphuncular bulbs. The connecting rings are appreciably thick, but were evidently fragile, being lost in some segments of the holotype. As noted, this species is known only from beds which are clearly very high in the Trempealeauan of the Llano uplift of Texas. Its features are shown in Figures 1 and 2 and in the accompanying plates.

Multicameroceras Kobayashi

Genotype: *Ellesmeroceras? multicameratum* Kobayashi

Multicameroceras **Kobayashi (1933) Tokyo Imp. Univ., Fac. Sci., Jour., sec 2, v 3, p 273.**

----Kobayashi (1935) Japanese Jour. Geology and Geography, v 12, p 20.

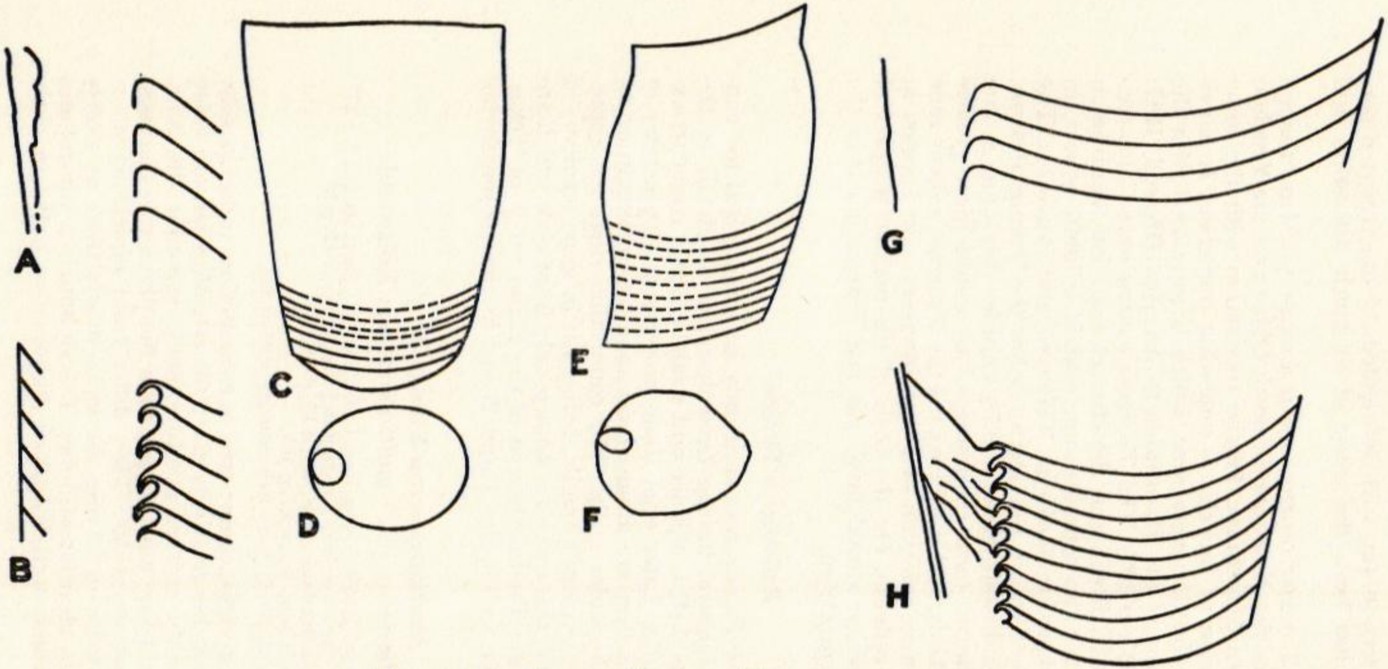
----Flower (1941) Palaeontologica Am., v 3, n 13, p 14.

----Flower (1947) Ohio Jour. Sci., v 47, p 160.

----Flower and Kummel (1950) Jour. Paleontology, v 24, p 606.

Shell essentially straight, compressed in cross-section, rather rapidly expanding. Living chamber relatively short, the rate of expansion being slightly reduced near the mature aperture. Shells resemble the Ellesmeroceratidae in size, being much larger than the previously discussed genera of the Plectronoceratidae. They differ from typical members of the Ellesmeroceratidae in having the septa nearly twice as closely spaced. Sutures display clear lateral lobes. The siphuncle is ventral and displays short necks and well-developed siphuncular bulbs in early

Figure 4



Wanwanian (Lower Canadian) Plectronoceratidae.

A-D. *Multicameroceras multicameratum* (Kobayashi): (A) vertical section through adoral part of siphuncle, showing relatively long septal necks, but no connecting rings. (B) early portion of siphuncle, in vertical section, showing on the dorsal side (right) well-developed siphuncular bulbs. (C) lateral view of adoral part of phragmocone and living chamber, with venter on the left. (D) cross-section, oriented as in C. E-H. *Sinoeremoceras wanwanense* (Kobayashi): (E) lateral view of internal mold of adoral part of phragmocone and mature living chamber, somewhat restored, with venter on left. (F) cross section, oriented as in E. (G) adoral part of phragmocone, showing siphuncle in vertical section, with long septal necks on its dorsal side, the ventral side not preserved. (H) adapical part of phragmocone, showing siphuncular bulbs on dorsal side of siphuncle, and traces of diaphragms traversing the cavity of the siphuncle. Again the ventral wall of the siphuncle is not evident. B-F, × 2; A, G, × 5; B, H, × 6.

(All drawings based upon Kobayashi's, 1933, illustrations.)

growth stages (fig 4 B). In later stages the septal necks become greatly prolonged, but the associated connecting rings have not been fully observed (fig 4 A). The gross features of the genus are shown in Figures 4 C and 4 D.

Details of the form of the siphuncular bulbs cannot be fully evaluated without a restudy of the original material. It is evident that the ontogenetic progression of the siphuncle is very similar to that shown in *Palaeoceras,* from which *Multicameroceras* differs strikingly in its form and greater size. It should be noted that the structure on the ventral side of the siphuncle is obscure. Within the siphuncle there is mottled dark and light calcareous material which does not seem to resolve itself into organic structures.

The species assigned to the genus include *Multicameroceras multicameratum* (Kobayashi, 1931), the only species which has been investigated closely as to its internal structure (Kobayashi, 1933, p 274, pl 2, fig 8; pl 3, figs 1, 3; pl 4, fig 1). In addition there is *Multicameroceras cylindricum* Kobayashi (1933, p 274, pl 2, fig 14; p14, fig 5), the interior of which has not been studied by sections. Both species are from the Wanwankou limestone and dolomite of the Niuhsintai basin of southern Manchuria.

Sinoeremoceras Kobayashi

Genotype: *Eremoceras wanwanense* Kobayashi (1931)

Sinoeremoceras Kobayashi (1933) Tokyo Imp. Univ., Fac. Sci., Jour., sec 2, v 3, p 272.

---Kobayashi (1935) Japanese Jour. Geology and Geography, v 12, pp 20, 21.
---Flower (1941) Palaeontographica Am., v 3, n 13, pp 13, 14.
---Ulrich, Foerste, and Miller (1943) Geol. Soc. America Special Paper 49, pp 63, 126.
---Flower (1947) Ohio Jour. Sci., v 47, p 160.
---Flower and Kummel (1950) Jour. Paleontology, v 24, p 606.

Shell compressed in cross-section, faintly endogastric in curvature, moderately rapidly expanding to adoral part of phragmocone and lower part of mature living chamber. There the shell becomes slightly swollen, the convexity of the dorsum increases, and the venter, formerly concave in profile, becomes convex. Farther orad the shell contracts, and continues as nearly tubular for a short distance before attaining the mature aperture. Sutures very closely spaced, with prominent lateral lobes. Cross-section compressed, relative rounding of venter and dorsum somewhat doubtful owing to poor preservation of the known material. The gross features are shown in Figure 4 E-F. The siphuncle displays siphuncular bulbs in the early stage (fig 4 H) though only the dorsal side of the siphuncle has been observed in vertical section. Farther orad, the septal necks become elongated, as in *Multicameroceras,* but the septa are much more gently bent apicad. Diaphragms cross the early part of the siphuncle (fig 4 H). Kobayashi called these structures pseudodiaphragms, but comparison with ellesmeroceroids indicates no real difference between the pseudodiaphragms and the diaphragms which cannot be accounted for by differences in preservation.

The only species assigned to the genus is the genotype, *Sinoeremoceras wanwanense* (Kobayashi). It is known only from the Wanwankou dolomite of Wan-Wan-Kou, southern Manchuria.

Since *Sinoeremoceras* and *Multicameroceras* occur together, their age is dependent upon the same considerations. The Wanwanian has been discussed by Kobayashi (1933) and by Endo and Resser (1937). There is general agreement that its age is lowermost Ordovician. Again the faunal association is anomalous. Some of the trilobites listed belong to genera, notably *Tellerina* and *Calvinella,* which are not known above the top of the Trempealeauan in North America. In the same association, however, are the Ribeiridae, which are widespread only in the Lower Ordovician, the equivalents of the Gasconade and Tribes Hill formations in North America. The same association yields true Ellesmeroceratidae, confined in America almost completely to the Gasconade and its equivalents. Some of these Ellesmeroceratidae are very closely similar to species currently being described from the Fort Ann limestone, the uppermost of several members of the lower Canadian in eastern New York. The same association contains species of *Proplina, Scaevogyra,* and *Helicotoma* among the gastropods. Also, there are trilobites of the genera *Stenopilus* and *Paraplethopeltis,* quite similar to forms which Kobayashi referred to *Plethopeltis,* prior to the differentiation of *Paraplethopeltis to Kingstonia,* a generic reference which is probably erroneous, and to *Stenopilus.* Curiously, some of these forms, in particular the *Helicotoma,* are rather good horizon markers for faunas of extremely late Gasconade age in eastern North America. It may be concluded reasonably that, with the mixture of Cambrian and late Gasconade types, the Wanwanian of eastern Asia is lowermost Ordovician and of approximate Gasconade age, but that it well may be that it represents an association of extremely early Gasconade age. Faunas of this age in America are largely undescribed. It may be noted that according to Endo and Resser (1937) the beds yielding *Shantungendoceras* in China also are Wanwanian in age. Therefore, the above remarks apply also to this inadequately known genus.

EVOLUTION WITHIN THE PLECTRONOCERATIDAE

From the preceding summary of the genera, it is evident that the morphological and stratigraphic facts are consistent with the following interpretation: The Plectronoceratidae indicate a palingenetic trend. The oldest genus, *Plectronoceras,* had evidently weak connecting rings, but there is reason to believe that it had siphuncular bulbs to the latest growth stage. This is followed by *Palaeoceras, again a* tiny shell, in which the septal necks lengthen in the ontogeny, and the siphuncular bulbs are gradually suppressed. Diaphragms are present in the siphuncle. The connecting rings are better calcified than in *Plectronoceras,* the ontogeny shows a more advanced condition, and the genus is obviously more specialized morphologically. The two Wanwanian genera, *Sinoeremoceras* and *Multicameroceras,* show as their main advance over *Palaeoceras* a great increase in size. This is not accompanied by an appropriate increase in the depth of the septa, with the result that the septa are relatively extremely closely spaced. What is known of the ontogeny of the siphuncle is not very different from that of *Palaeoceras.* One genus is essentially straight and expands to the aperture; the other is faintly endogastric, and becomes faintly gibbous adorally. Evidently form variations within the limits of slender to rapidly expanding shells, and orthocones to endogastric cyrtocones, are not very significant in the family.'

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1. *Wanwanoceras* Kobayashi (1933), a monotypic genus, based upon *Wanwanoceras peculiare* of the Wanwanian of Manchuria, was originally included by Kobayashi in the Plectronoceratidae. As interpreted in Kobayashi's description and figure, it is a small cyrtoconic shell differing from the forms here assigned to the Plectronoceratidae in having supposedly cyrtochoanitic septal necks in the *early* stage and longer orthochoanitic necks in late growth stages. If this interpretation is correct, the structure of *Wanwanoceras* is not consistent enough with either the Plectronoceratidae or Ellesmeroceratidae to be included in either family. Unfortunately, Kobayashi's figure is heavily retouched and cannot be strictly evaluated without recourse to the original material. From his illustration, the interpretation might be ventured that *Wanwanoceras* has very short necks in the early segments, to which are attached the adoral portions only of connecting rings outlining siphuncular bulbs similar to those of the Plectronoceratidae, but that in later segments, as in *Palaeoceras, Multicameroceras,* and *Sinoeremoceras,* the necks become elongated, and the connecting rings are completely destroyed in that part of his specimen. If so, *Wanwanoceras* could be placed in the Plectronoceratidae. The whole problem is so conjectural from the present evidence that tentatively it seems best to regard the genus as of uncertain position until it can be restudied.

Inadequately Known Cambrian Cephalopods

Two reported Cambrian fossils which are clearly true cephalopods, are so inadequately known that their affinities cannot be determined with certainty from the published evidence. The first, *Shantungendoceras* (Sun, 1937), in the Upper Cambrian of China, has been discussed by the writer (Flower, 1951). In summary, it may be said that its several species are slender cephalopods, slightly endogastric or straight, compressed in cross-section, with a small marginal siphuncle. The reported central siphuncle, the holochoanitic siphuncle walls, and the endocones are not supported by the material and must be rejected. *Shantungendoceras* could, on the basis of the present evidence, be assigned either to the Ellesmeroceratidae or to the Plectronoceratidae. The evidence indicates that it could not be a member of any more advanced family. Anomalously, this much discussed genus is probably not even Cambrian. Endo and Resser (1937) note that the "*Orthoceras* beds of Sun" are lower Wanwanian, basal Ordovician, and not Upper Cambrian. Endo has kindly confirmed by letter that in his opinion this statement applies to the beds which have yielded *Shantungendoceras*.

Korde (1949) described two tiny cephalopods, both known only from sectioned surfaces, from the Upper Cambrian of Angara. On the basis of this material, he described two species and two genera, which he assigned to the new family Ruthenoceratidae. The latter he placed, amazingly, in the Ascoceratida (Mixochoanites). The Chazyan Ascoceratida are extremely primitive forms, and indicate an origin of that order in the Clinoceratidae of the Michelinoceratida. As neither the Ascoceratida nor the ancestral Michelinoceratida have been known beneath the base of the Chazyan, Kordes conclusion is remarkable and worthy of closer scrutiny. Certain anomalies are involved in this interpretation, as shown in Figure 5.

Figure 5 A represents a vertical section through a typical advanced ascoceroid, *Ascoceras bohemicum* Barrande, in which the camerae are developed on the dorsal side of the inflated living chamber. Figure 5 B represents the new genus and species *Ruthenoceras elongatum*. This shell, shown in natural section, is interpreted by Korde as possessing a large living chamber on the concave ventral side and air chambers comparable to those of an ascoceroid on the dorsal side. Although Kordes figure is a halftone in which the details are obscured by strong contrast, an enlarged photograph of his published figure shows clearly that the septa on the margin of the "living chamber" are bent apicad into short septal necks, supplemented by thin, less apparent structures, plainly connecting rings. From this it is evident that *Ruthenoceras is* a curved portion of a phragmocone, and the structure which Korde interpreted as a living chamber is an unusually large ventral siphuncle. Further, Kordes section is not vertical, but oblique, which accounts for the fusiform outline of the shell and siphuncle.

A second specimen, reproduced in Figure 5 C, is the basis of the new genus and species *Angaroceras globosum*. Here again the cavity on the concave side, to the right of the figure, is a large ventral siphuncle

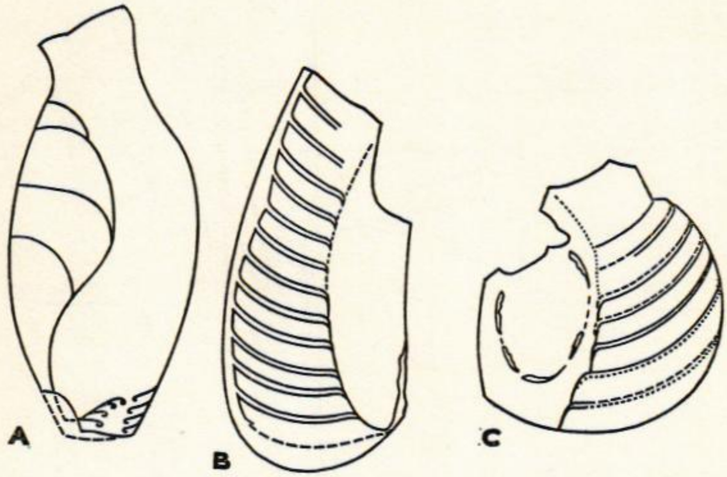

Figure 5

COMPARISON OF CAMBRIAN GENERA ASSIGNED TO THE ASCOCERATIDA WITH A TYPICAL MEMBER OF THAT GROUP.

A. Vertical section of *Ascoceras bohemicum* Barrande. × ½. B. *Ruthenoceras elongatum* Kordé. × 18. C. *Angaroceras globosum* Kordé. × 18.

(B and C are traced from Kordé's illustrations. A is after Barrande.)

and not a living chamber. Where the septa join the siphuncle, they are bent apicad to form short septal necks, apparently supplemented again by connecting rings. In this instance also the illustration shows a section which is quite obviously strongly oblique to the axis of the shell, which accounts for the apparent globose form. Within the siphuncle is an elliptical object. The interpretation of this structure is uncertain. It could be adventitious, but also, very easily, it could be an oblique section taken through a diaphragm.

The interpretation of these specimens is shown more clearly in Figure 6. Figure 6 A represents the section of *Ruthenoceras elongatum,* this time drawn with less attention to detail, and with a restoration of the missing adoral and adapical portions, indicated in broken lines. Figure 6 B shows a cross-section of this specimen. Kordé's original figure is slightly oblique to the shell axis. The position of lines 1, 2, 3 on Figure 6 B indicates the approximate position of the corresponding lines in Figure 6 A. The natural section which Korde figured is not a vertical section, but a strongly oblique one. Its position is shown in Figure 6 C, which shows a phragmocone viewed from the concave ventral side. A vertical section through the same specimen would, from all the evidence, look very much like Figure 6 D. It should be noted that there is no good basis for regarding this shell as other than a compressed, slightly curved, rather slender shell, expanding gently throughout the known portion.

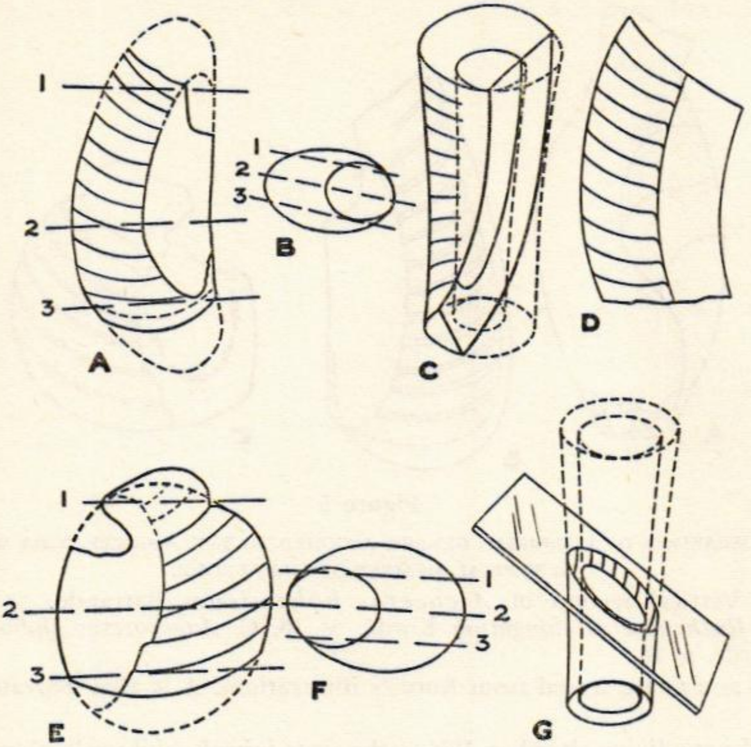

Figure 6

Restorations of *Ruthenoceras elongatum* (A-D)
and
Angaroceras globosum (E-G).

A-D. *Ruthenoceras elongatum:* (A) section of *Ruthenoceras* essentially as illustrated, with adoral and adapical ends restored. (B) cross-section. Lines 1, 2, 3 indicate the level of the section shown in A at correspondingly numbered lines. (C) position of plane of section shown in A, in relation to a complete shell, an endogastric cyrtocone viewed here from the ventral side. (D) hypothetical vertical section through the same shell.

E-G. *Angaroceras globosum:* (E) illustrated section, restored as in A. (F) cross-section. Lines 1, 2, 3 indicate the position of similar lines in E in relation to the cross-section. (G) position of the section shown in E in relation to a complete shell. A vertical section is not illustrated. It would be indistinguishable from D.

Figure 6 E-G applies a similar analysis to Kordes illustration of *Angaroceras globosum*. Figure 6 E shows Kordes figure reproduced in general outline, with the broken ends restored. Figure 6 F represents a cross-section. On it the numbered lines indicate the position of the correspondingly numbered lines in E. This time the natural section, where it cuts a cross-section of the shell, is more nearly parallel to the plane of symmetry. To employ an analogy from structural geology, the strikes of the two planes are essentially parallel, but they differ strongly in dip. This is demonstrated by the fact that the illustrated section fails to show any indication of camerae on the ventral side of the siphunde, as was true of *Ruthenoceras elongatum*. The relation of the natural section to a complete phragmocone is shown in Figure 6 G. *Angaroceras globosum* is based upon a strongly oblique natural section of a shell which, from all the evidence, was a slender endogastric cyrtocone. A vertical section of the same shell would resemble Figure 6 D so very closely that a reproduction of this figure is unnecessary. Korde's two specimens are from the same locality and horizon. From the above analysis it is evident that they do not form an adequate basis for the erection of two genera. Such differences as are indicated are the result of the widely different proportions shown in two very different planes cutting two specimens which may well be one and the same species. It is, therefore, necessary to conclude that from the published evidence there is a good basis for recognizing only one genus and one species, for which the name *Ruthenoceras elongatum* well may be employed.

Ruthenoceras is, from this analysis, an endogastric cyrtocone, probably quite slender, compressed in cross-section. It is remarkable chiefly for the large diameter of the siphuncle in relation to the rest of the shell. The cross-section was clearly compressed; the siphunde well may have been compressed also, as suggested in the accompanying figures. Only small portions of the phragmocone are known. The two specimens represent commensurate portions of two individuals; the maximum height of the shell in both is 1.5 mm. The siphuncle wall of this portion of the phragmocone is evidently composed of relatively short septal necks supplemented by connecting rings, and the segments of the siphuncle are essentially tubular.

The gross features of this shell are consistent with placing it in only two families, the Ellesmeroceratidae and the Plectronoceratidae. Reference to the Plectronoceratidae is suggested by the tiny size of the shell. The tubular segments of the siphunde and the short septal necks suggest the Ellesmeroceratidae. Nevertheless, it is possible to postulate that this could be the adoral part of a shell in which siphuncular bulbs were developed in the early stages. It should be noted that the true Ellesmeroceratidae so far known have blunt, rapidly expanding early stages, and attain in a length of 4 mm a shell height about ten times that of the present specimens. Plainly, reference of *Ruthenoceras* to either family to the exclusion of the other is not possible on the basis of the present evidence.

The specimens which Kordé described are from marine deposits 4 km from Boguchan, in Angara. The age of the beds was determined by S. V. and V. A. Obruchev as Upper Cambrian.

Clearly, *Shantungendoceras* and *Ruthenoceras* are both valid cephalopod genera. They can be placed in only two of the known families of cephalopods, the Plectronoceratidae or the Ellesmeroceratidae. To which of these families they should be attributed can be determined only when the genera are more thoroughly studied.

Cambrian Fossils Which Cannot Be Retained Within the Cephalopoda

CURVED SEPTATE SHELLS

Shelbyoceras Ulrich and Foerste

Genotype: *Shelbyoceras robustum* Ulrich and Foerste

Shelbyoceras Ulrich and Foerste, in Bridge (1930) , Missouri Bureau of Mines, 2d ser, v 24, p 207.
_____ Ulrich and Foerste (1936) Denison Univ., Sci. Lab., Bull., v 30, p 287.
_____ Ulrich, Foerste, and Miller (1943) Geol. Soc. America Special Paper 49, p 152.
______ Flower and Kummel (1950) Jour. Paleontology, v 24, p 606.

This genus is based upon a series of rather rough internal molds from slightly curved conical, rather rapidly expanding shells. The apical ends of these molds are blunt and seem to be terminated by septa. The specimens were interpreted, therefore, as living chambers of cephalopods and were compared with such curved ellesmeroceroid genera as *Conocerina.* In the ellesmeroceroids, however, the cross-section is more narrowly rounded on the concave than on the convex side. In *Shelbyoceras* the convex side of the cross-section is much narrower and more strongly rounded than the concave side.

New material from the Upper Cambrian adds materially to our knowledge of the morphology of the genus, but raises more questions as to its relationships than are answered.

This material agrees in all general aspects with the specimens previously known. However, it shows two new features. First, costae on the shell are exhibited, which slope apicad from the concave to the convex side of the shell. Second, these specimens exhibit much clearer septa than any previously seen. They show that the shell is truly septate. They fail, however, to show any definite siphuncle. Several of the septa are very well preserved on the concave and previously supposed ventral side of the shell. They are good enough to show conclusively that there is no siphuncle either close to the concave side of the shell or in the center. The septum is less clearly preserved close to the convex side of the shell. It is possible, but highly unlikely, that there is a siphuncle there.

These new facts leave two possible conclusions, but do not permit the final selection of one and the rejection of the other. The conclusions possible from this material are as follows:

1. *Shelbyoceras* may be assumed to be a cephalopod represented by such poor material that the siphuncle has not been seen. If one accepts this interpretation several others follow. The new material shows that the only possible location of the siphuncle is close to the convex side of the shell. The same side shows costae sloping apicad to outline a hyponomic sinus. It is necessary, therefore, to conclude that this side of the shell is ventral. *Shelbyoceras* differs from all cephalopods previously known below the base of the middle Canadian in being

exogastric instead of endogastric. Anomalously, it was the general resemblance of the living chambers of *Shelbyoceras* to those of the endogastric Ellesmeroceratidae of the lower Canadian which has been the basis for accepting it as a cephalopod. Turning to the oldest exogastric cephalopods, the Bassleroceratidae, there are serious differences to be found. The Bassleroceratidae are slender, strongly compressed shells, quite unlike *Shelbyoceras.* They differ from the Gasconade Ellesmeroceratidae in only two important features, the exogastric curvature and the suppression of diaphragms. In fact, the similarity of the siphuncle walls is so strong that there can be little question that the Bassleroceratidae of the middle and upper Canadian are derived from the older Ellesmeroceratidae. *Shelbyoceras, as a* cephalopod, is inconsistent with this conclusion and with the evidence upon which it is based. Acceptance of *Shelbyoceras* as a cephalopod requires the assumption that its siphuncle was tiny and inconspicuous. Yet the siphuncles in all other Cambrian, and most Lower Ordovician genera are large in relation to the cross-section of the shell. This is true of both the Plectronoceratidae and the two Cambrian genera of uncertain position, *Shantungendoceras* and *Ruthenocera.s.* It is equally true of the Ellesmeroceratidae of the lower Canadian. It is again largely true of the Bassleroceratidae of the middle and upper Canadian, the oldest true exogastric cyrtocones among the cephalopods. That *Shelbyoceras* could be a cephalopod remains a possibility, but a remote one.

2. *Shelbyoceras,* in reality, may have no siphuncle. As such, it is clearly a curved chambered shell, but is not a cephalopod. Close examination of the septa shows that while the presence of a tiny siphuncle cannot be completely eliminated, it is regarded as improbable on the basis of the material, and becomes further unlikely when it is recalled that other older cephalopods have relatively large siphuncles. I have been gratified to have this opinion supported by Dr. Josiah Bridge and Dr. Curt Teichert, both of whom have seen the present material.

Shelbyoceras, then, may join the group of early Paleozoic shells both septate and aseptate, concerning the taxonomic position of which there must remain much doubt. It well may represent a group of organisms which failed to survive the close of the Cambrian.

Material of *Shelbyoceras* is extremely rare. *S. robustum* Ulrich and Foerste is known only from the holotype, from the Eminence dolomite of Missouri. *S. bessemerense* Ulrich, Foerste, and Miller (1943) is based upon one specimen from cherts of the Copper Ridge dolomite of Alabama; two additional specimens from cherts of the Potosi formation of Missouri have been identified in terms of this species. *S. buttsi* Ulrich, Foerste, and Miller (1943) is based upon a single specimen from the cherts of the Copper Ridge formation of Alabama. *S. unguliforme* Ulrich, Foerste, and Miller (1943) is known only from two specimens from the Copper Ridge dolomite of Alabama. No two specimens seem to agree very closely in shape or proportions; as a result there are seven known specimens and four species. The three remaining specimens which have not been made the types of new species are rather poorly preserved.

The three new specimens described below from the Upper Cambrian of Texas could be interpreted as representing three more species. The variations shown by them in rate of expansion, cross-section, and general proportions are comparable to features accepted as specific distinctions in most other groups of cephalopods. It may be, of course, that these extremely rare specimens do represent distinct species of limited geographic range, but it seems much more likely that we are dealing here with fewer species within which there is an unusually wide variation in proportions. The uncomfortable fact remains that it is extremely difficult to reconcile the three specimens at hand with the previously described species, or, indeed, with each other. In such extremely rare forms, material adequate to demonstrate the presence, or absence, of variation and intergradation among the apparent species cannot be hoped for without at least another generation of collecting.

Although there is no certain solution to the problem presented by these forms at a specific level, the genus *Shelbyoceras* is known at present only from strata of Trempealeauan age. It is curious to note that when members of this genus were first discovered, they were regarded as the first cephalopods to be found in the Cambrian of North America. Some doubt was raised as to their true stratigraphic position on the basis that areas containing residual Trempealeauan cherts might possibly yield also a few pieces of chert from overlying Lower Ordovician beds which otherwise had been lost by weathering. This view is not generally held today. Nothing closely resembling *Shelbyoceras* has been found in Gasconade faunas. Today the idea that *Shelbyoceras* seems anomalous as an Upper Cambrian cephalopod has suffered a curious reversal, for subsequently Upper Cambrian cephalopods have been made known, and the present evidence indicates that *Shelbyoceras* itself is quite probably not a cephalopod at all.

It should be noted that previous descriptions have involved the assumption that *Shelbyoceras* is curved endogastrically, the venter being concave, the dorsum convex. In the following descriptions this orientation is reversed. The elusive siphuncle, if there is one, must be close to the convex side, which is also marked by the hyponomic sinus. If *Shelbyoceras* is accepted as a cephalopod, this reversed orientation must follow. If, as is believed, it is not a cephalopod, but a shell of uncertain affinities, there is no basis whatsoever for recognizing one side as ventral and the other as dorsal. The present interpretation, based upon analogy with the cephalopods, is adopted only as a matter of convenience in the absence of any better criteria.

Shelbyoceras ellinwoodi Flower, n. sp.

(pl 2, figs 1-3)

The type of this species is a rather roughly preserved internal mold of a short, slightly curved living chamber, with a cross-section which is compressed and more narrowly rounded on the convex than on the concave side. The septum at the base of the living chamber is quite strongly convex and presents a fairly regular surface. There is clearly no perforation of the septum close to the concave side of the shell nor at its center, and the only structure that could possibly be interpreted as a siphuncle is a slight irregularity of the surface close to the convex side. The suture is essentially transverse, with very faint lateral lobes. The type has a height at the base of 15 mm and a width of 12 mm. It expands to 21 and 18 mm in a length along the convex side of 22 mm. The adoral end is obviously not complete. The shell is very gently curved. The surface of the internal mold is rough, but retains slight suggestions of growth lines sloping apicad from the concave to the convex side of the shell.

Discussion. This species is typical of *Shelbyoceras* in general aspect. It differs from previously known species in the relatively gentle expansion and moderate curvature, and it is further peculiar in that the septum shown at the base of the living chamber is better preserved and clear enough to show that there is no siphuncle close to the concave side of the shell. *S. buttsi,* which is comparable to the type of *S. ellinwoodi* in size, is very different in the extremely rapid expansion of the shell, as is *S. robustum. S. unguliforme* and *S. bessemerense* are known only from living chambers of considerably smaller diameters, and presumably represent earlier growth stages in terms of actual shell dimensions. Though they are somewhat closer to *S. ellinwoodi* in proportions, they are still considerably more rapidly expanding, and it has seemed best, in view of these differences, to make the specimen herein described the type of a new species as yet unknown from other material.

Holotype. Bureau of Economic Geology, University of Texas, Austin, Texas.

Occurrence. From the Pedernales dolomite member of the Wilberns formation, in beds of Trempealeauan age, associated with *Scaevogyra* and *aff. Plethopeltis;* locality 86T-5-13A, east side of Cave Creek, Gold quadrangle, Gillespie County, Texas; collected by Virgil E. Barnes and Warren Anderson. The determination of the associated fossils is by Howard Ellinwood.

Shelbyoceras barnesi Flower, n. sp.

(p12, figs 7-10)

Shell known only from a living chamber and an external mold of a short adoral chambered portion, unusually slender, nearly straight. The assumed ventral profile is scarcely convex; the dorsum, preserved only basally, appears to be faintly concave. Cross-section at base of living chamber compressed, the side close to the supposed venter narrowly rounded, the opposite side more broadly rounded, 6.5 mm wide and 8 mm high, increasing to 11 mm and 13 mm in the basal 13 mm, beyond which the concave side is incomplete. When complete, the living chamber had a maximum length of 32 mm and a height near the aperture of 18 mm.

The surface of the internal mold bears oblique low costae, sloping apicad toward the convex side of the shell, suggesting that, as a possible cephalopod, this side may be the true venter with a hyponomic sinus. The slope of the growth lines and costae is appreciable; the living chamber would have a length of only 28 mm on the convex side, against

32 mm on the concave side, as restored. Costae are low, broad, shallow—five in the length of the living chamber. They tend to become obscure as they approach the ventral side of the shell. The septum at the base of the living chamber shows a fairly smooth surface, on which can be seen no trace of a siphuncle, although there is a faint irregularity near the narrowly rounded side which might conceivably mark the position of such a structure. The septum is moderate in depth; it shows shallow lateral lobes, and a saddle which, though well defined on the concave side, is vestigial on the ventral side. The specimen was embedded in matrix (pl 2, fig 10). Apicad of the base of the living chamber is a hollow space 7 mm long from which apparently a calcite-filled, chambered portion of the shell has been dissolved.

Holotype. Bureau of Economic Geology, University of Texas, Austin, Texas.

Occurrence. From the same horizon and locality as *Shelbyoceras ellinwoodi.*

Shelbyoceras cf. *barnesi* Flower

(p12, figs 4-6)

Tentatively assigned to the same species as the above is a second internal mold of a living chamber, also faintly costate, which differs from the holotype of *S. barnesi* in the somewhat broader cross-section, which is more narrowly rounded, almost subangular on the supposed dorsum. The ventral profile is slightly convex rather than straight, the dorsal profile faintly concave. The rate of expansion is somewhat greater than the holotype of *S. barnesi.* The septum at the base of the living chamber is very incompletely preserved; the ventral part is rough and partly missing. The shell expands from 6 mm and 8 mm to 12 mm and 14 mm in the basal 15 mm. The living chamber has a length of 22 mm on the concave (supposed dorsal) side, where the greatest length is attained, since the costae, and consequently the aperture, slope strongly apicad from the concave to the convex side. The aperture is essentially complete on one lateral surface (pl 2, fig 5), but is lost on the convex side of the shell. The low costae are slightly broader and more widely spaced than in the holotype of *S. barnesi.*

Discussion. While, as noted above, this specimen differs in several important items from the holotype of *S. barnesi,* it is tentatively assigned to that species. It is believed that both the Cambrian and lower Canadian cephalopods exhibit considerably greater latitude in proportions than most younger nautiloids. The alternate explanation of this variation would impel one to believe that there are as many species as there are extant known specimens.

Figured specimen. Bureau of Economic Geology, University of Texas, Austin, Texas.

Occurrence. From the same locality and horizon as *S. barnesi* and *S. ellinwoodi,* from the Pedernales dolomite member of the Wilberns formation, Gillespie County, Texas.

CONICAL ASEPTATE SHELLS OF THE EARLY PALEOZOIC

Conical or pyramidical shells of the early Paleozoic are unsatisfactory to classify. Such fossils generally have been placed with the pteropods, not because of any strong conviction on the part of paleontologists, but because there seemed to be no better place to put them. It is recognized, however, that these Paleozoic forms are separated from the true pteropods by a marked stratigraphic gap. The pteropods can be traced back only to the Jurassic. The Paleozoic forms begin in the Cambrian and terminate in the Mississippian.

Among these shells are some which are conical and rounded in cross-section. Nothing can be learned from such shells to indicate the nature of the animal of which they were once a part. They could belong to a bilaterally symmetrical or a radially symmetrical animal. They could be placed in almost any of the known phyla, and it is possible that they represent a phylum which is extinct. Certainly as a group they did not survive the close of the Paleozoic. Such shells are grouped together under the family name Tentaculitidae.

Other shells have a cross-section which indicates that they were part of a bilaterally symmetrical animal. This is not of much help. They could pertain to any of the phyla starting with the Platyhelminthes. Such shells are largely grouped together under the family name Hyolithidae.

A few other shells have never been assigned to either of these "families" with any degree of conviction. *Matthevia* Walcott (1912), a low conical shell of the Upper Cambrian with a peculiar internal process, is not closely similar to either the hyolithids, the tentaculitids, or to the gastropods. It was originally described as a gastropod, an assignment which is not particularly convincing, inasmuch as no other gastropods are known with similar internal processes. De Chardin (1931) described as *Biconulites* a peculiar fossil which appears to be composed of several imbricating conical elements. It is still not certain that *Biconulites* does not consist of "pteropod" shells washed together (Kobayashi, 1937).

One of the fossils submitted to the writer for study from the Upper Cambrian of the Llano uplift belongs to this general group of conical shells of uncertain position. From its triangular cross-section, it should be assigned to the Hyolithidae rather than the Tentaculitidae. Regrettably, but understandably, it makes no contribution to the knowledge of this group of conical shells, beyond the description of a new genus and species.

Kygmaeoceras Flower, n. gen.

Genotype: *Kygmaeoceras perplexum* Flower, n. sp.

Shell straight, very slowly expanding; cross-section in the form of a narrow, high isosceles triangle, with all angles slightly rounded. The lateral surfaces bear costae which slope apicad as they approach the flattened (ventral?) base of the triangle, but disappear and do not cross it. The costae are continuous, though faint, over the narrow dorsal side in the adult, though they are not visible on the dorsum in the young stage.

The shell shows no trace of septa, and there is no good reason to believe that it is a cephalopod. Instead, it is one of a vexing group of conical shells of the Cambrian, the taxonomic position of which remains doubtful.

Ulrich, Foerste, Miller, and Unklesbay (1944, p 90, pl 45, figs 1-2) have figured and described as *Walcottoceras?* sp. a fragmentary shell from the Signal Mountain formation of Oklahoma which, though the triangular cross-section is not evident, bears such a strong resemblance to the species described below, that it is clearly to be referred to *Kygmaeoceras. It* is not adequate for specific comparison, but certain differences in proportion are obvious, and it probably represents a different species.

Kygmaeoceras perplexum Flower, n. sp.

(pl I, figs 1-4, 6-8)

The essential features of this shell have been embraced in the generic description. The available material contains two specimens, evidently conspecific, but representing very different growth stages, and consequently showing some minor differences. The holotype, the larger of these two specimens (pl I, figs 2-4), consists of an internal mold 26 mm long, increasing from a height of 5 mm and a width of 4 mm to 6.5 mm and 5 mm at the adoral end. The cross-section is that of an isosceles triangle with a narrow base; the base and sides are both very slightly convex, the lower angles rounded, the apex narrowly rounded, subangular. Costae slope apicad from the narrow apex toward the base, suggesting that the base of the triangle marks the ventral side of the shell. This orientation is, of course, uncertain, as it is based upon an analogy with cephalopod shells, but is tentatively adopted in the absence of any other evidence of orientation. The costae fade out as they approach the venter, and do not cross it. They are spaced four in a length of 10 mm throughout the length of the specimen. The external mold, from which a rubber impression was taken (pl 1, fig 1), is slightly longer than the internal mold taken from it, but supplies no additional information, other than showing very faint traces of growth lines which are parallel to the oblique costae of the side. The type, which is broken at several places, shows that there are absolutely no septa or other internal structures.

The paratype is a much smaller shell which shows a cross-section less definitely triangular and more rounded. The venter is slightly flattened, but still markedly convex; the dorsal angle is more rounded. This specimen (pl 1, figs 6-8) increases from 1.6 mm and 2.0 mm to 2.0 mm and 3.00 mm in a length of 14 mm. The sides bear six pairs of costae, which are more transverse in the region of the dorsal angle and are more strongly curved as they approach the venter, than in the holotype. They are absent on both the venter and dorsum.

Types. Holotype, Bureau of Economic Geology, University of Texas, Austin, Texas. Paratype, collection of the writer (presented by Dr. J. L. Wilson).

Occurrence. Both of the types are from the San Saba limestone member of the Wilberns formation of the Llano uplift of Texas. The holotype (locality TC-1393) is from 1393 ft above the base of the Threadgill Creek section, Gillespie County, Texas. It was collected by Mr. Howard Ellinwood two feet above a layer yielding *Eurekia, Monocheilus,* and *Euptychaspis,* a fauna indicating Trempealeauan age. The paratype is from the top of the San Saba limestone member near Camp San Saba, 11 miles south of Brady, McCulloch County, Texas.

REPORTED CEPHALOPODS, DUBIOUSLY CAMBRIAN

As noted above, the genus *Shantungendoceras* is probably of Wanwanian, Lower Ordovician, age rather than Cambrian, as reported by Sun. The problem of the age of the Wanwanian beds, which contain some saukiid trilobites of Cambrian aspect, has been discussed previously in connection with the genera *Sinoeremoceras* and *Multicameroceras.*

One other reported occurrence of a cephalopod in the Cambrian should be mentioned, although it is doubtful whether the fossil is a cephalopod. Moreover, the Cambrian age of the strata from which it comes is highly questionable. Rusconi (1952, p 53, fig 12) has described a fossil which he named *Cycloceras? salagasterensis* from the Cambrian of Salagastra, Mendoza, Argentina. The associated fauna appears to be Ordovician rather than Cambrian; admittedly, however, the descriptions and illustrations of many of the associated species are too general to permit a close critical analysis. The supposed cephalopod is illustrated as a reconstruction based upon two pieces which are placed in contact. As such, it is represented as a shell with low, closely spaced annuli, faint longitudinal markings, and curved in such a way that the complete shell, as restored, would have the form of a *Hamulina* or an *Ancycloceras.* Shells of this aspect are completely unknown among the early Paleozoic nautiloids. It seems probable, therefore, that Rusconi has placed in juxtaposition two fragments which lay originally some distance apart. As a cephalopod, this shell is unlike anything previously known beneath the top of the Canadian, and it suggests only remotely the Middle Ordovician genus *Centrocyrtoceras.* No evidence of septa can be found in the illustration, and such structures are not mentioned in the description. Without septa, there is no evidence that this fossil is a cephalopod. Clearly, it has no relationship with any real cephalopods known from the Cambrian.

The Primitive Cephalopods

In the preceding pages the extant evidence on the true Cambrian cephalopods has been presented in detail. Other fossils, formerly attributed to the cephalopods, are discussed and removed from that group. It is pertinent now to approach the problem of whether our Cambrian forms are truly archaic, or whether they represent early specializations. This question can be answered only by surveying the Cambrian cephalopods in relation to younger forms.

DESCENDING THE STRATIGRAPHIC COLUMN

By tracing the cephalopods downward in the stratigraphic column, it becomes evident that there is progressive reduction in variation, both in form and in structures. This feature is shown best by beginning at the Chazyan. This point is selected because it is the beginning of many orders, families, and genera which extend for a considerable distance upward; many families, and indeed many genera, continue to the top of the Ordovician. This survey is made in reference to the recent classification of Flower and Kummel (1950). (See fig 7.)

The order Endoceratida is represented in the Chazyan by the first representatives of the family Endoceratidae, which extends upward to the Richmond. In addition, there are some bizarre genera, as yet inadequately known morphologically, and a few genera with short septal necks and specialized endosiphuncles, which are specialized derivatives of the dominantly Canadian Proterocameroceratidae, and are at present retained in that family.

The order Actinoceratida is represented in the American Chazyan by a group of specialized genera. They include *Gonioceras* of the Gonioceratidae, a possible *Ormoceras* of the Ormoceratidae,[2] and a small undescribed *Nybyoceras* of the Armenoceratidae. Teichert (1933) described *Cyrtonybyoceras* from the Chazyan of Newfoundland. Possibly the Toufangian cephalopods described by Kobayashi and Endo may be Chazyan. Teichert and Glenister (1952) report *Armenoceras* from the Chazyan Larapintine group of Australia. Clearly, the actinoceroids were well specialized by Chazyan time. The only possible older occurrence of actinoceroids in the world is that of the Maruyama beds of southern Manchuria. These beds, possibly slightly older than the American Chazyan, are the only known source of the genus *Polydesmia,* regarded as the most primitive known actinoceroid.

The age of *Bathmoceras,* regarded by the writer as the ancestor of the actinoceroids, is questionable. It is clearly either latest Canadian or earliest Chazyan. The occurrence of *B. linnarssoni* Angelin in the Glauconitkalk of Sweden suggests a pre-Chazyan age.

The Ellesmeroceratida are represented by a few poorly known

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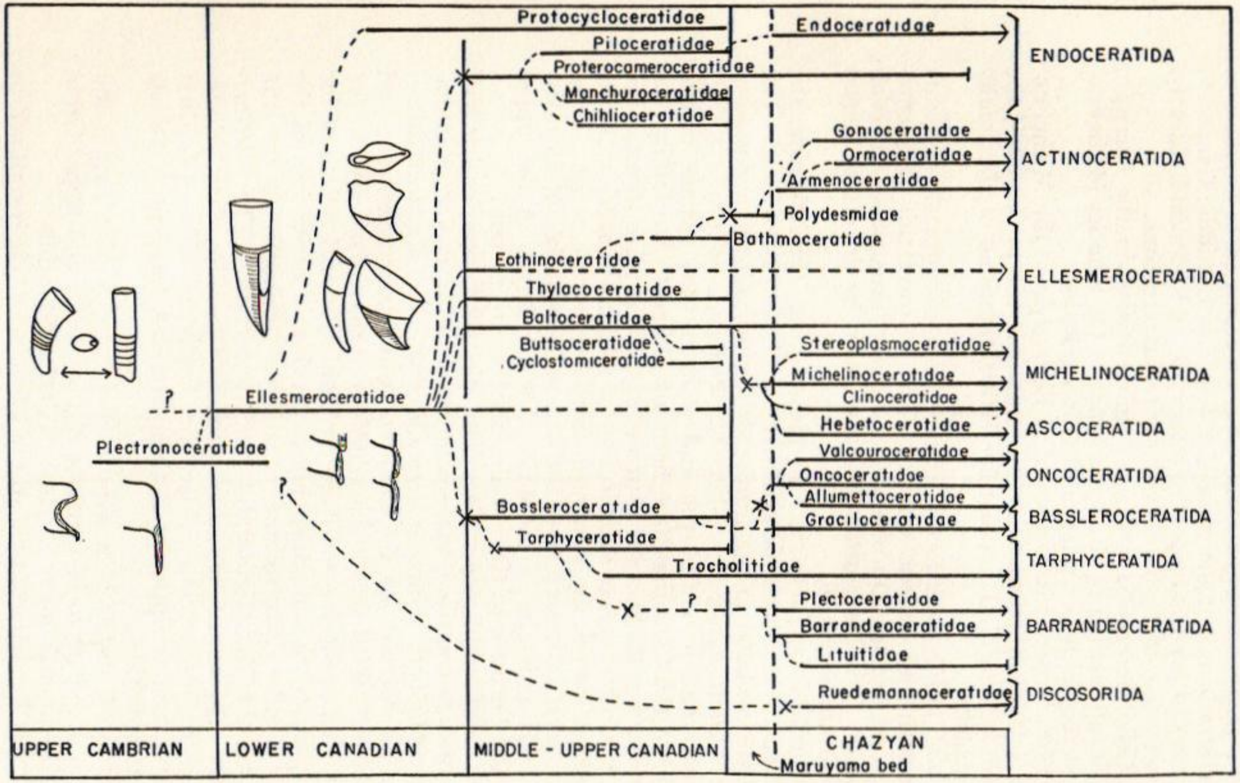
[2] The single described form is based upon a specimen in the New York State Museum labeled as Chazyan. Possibly it may have been derived instead from overlying strata of Black River age. Block faulting in the Champlain valley produces confusing field relationships, in view of which such an error is highly possible.

Figure 7



PHYLOGENY OF EARLY PALEOZOIC NAUTILOIDEA, FROM UPPER CAMBRIAN THROUGH CHAZYAN.

The range of the families is indicated by heavy lines. Transverse lines indicate their termination; arrows indicate the survival of families beyond the close of the Chazyan. The older cephalopods belong exclusively to the order Ellesmeroceratida. To define its scope, the point of inception of the other orders which are derived from it is marked by an X. The essential features of the two primitive families, the Ellesmeroceratidae and Plectronoceratidae, are indicated by sketches.

members of the family Baltoceratidae, which extends upward into the Mohawkian. Unknown as yet in the Chazyan is any form referable to the Eothinoceratidae, but the genus *Eothinoceras* is middle Canadian, and the genus *Cyrtocerina* ranges from Lowville to Richmond. Clearly, some representative of the family existed in Chazyan time.

The Michelinoceratida were well differentiated in the Chazyan. The order is represented by the appearance of the families Michelinoceratidae, Stereoplasmoceratidae, and Clinoceratidae.

The order Ascoceratida, regarded as derived from the Michelinoceratida and closely allied with the Clinoceratidae, is represented by the three known genera of the subfamily Hebetoceratinae of the family Hebetoceratidae.

The small family Graciloceratidae of the Bassleroceratida appears in the Chazyan and extends upward. The Oncoceratida are represented by genera of the Oncoceratidae, Allumettoceratidae, and Valcouroceratidae. The Discosorida are represented by the oldest known genus, *Ruedemannoceras.*[8]

Of the coiled families four are present, the Trocholitidae, the Plectoceratidae, the Barrandeoceratidae, and the Lituitidae. The Lituitidae are confined to the European section and are regarded as derived from the Barrandeoceratidae. The Plectoceratidae are typically a group characteristic of Chazyan and younger strata. Some costate coiled shells of the Canadian have been attributed to the family, but this matter requires study of the structure of the Canadian forms (ordinarily not possible, because silicification of all known specimens prohibits investigation of the structure of the siphunde wall). These families comprise the beginning of the Barrandeoceratida. Of the order Tarphyceratida only the Trocholitidae, which begin in the upper Canadian and persist into the middle Silurian, are present.

In the middle and upper Canadian, discussed together because, where sections are complete, there is no major stratigraphic or faunal break, the cephalopod fauna is very different. The Endoceratida is represented in America by the families Proterocameroceratidae and Piloceratidae, to which should be added from the Asiatic section the bizarre Manchuroceratidae and Chihlioceratidae, specializations of the piloceroid persuasion, but independent breviconic derivatives of the dominantly slender Proterocameroceratidae. Actinoceroids are unknown, as are the Michelinoceratida and Ascoceratida. The Ellesmeroceratida are represented by rather specialized families, the Cydostomiceratidae, the Protocycloceratidae, the Thylacoceratidae (Teichert and Glenister, manuscript) , the Eothinoceratidae, the Baltoceratidae, and the Buttsoceratidae.

In addition, it should be noted that two genera, *Clelandoceras* and *Cumberloceras,* appear to be survivors in the middle and upper Canadian of the dominantly lower Canadian Ellesmeroceratidae.

The family Bassleroceratidae of the Bassleroceratida is confined to

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[8] Teichert and Glenister are currently describing the first Canadian cephalopod attributed to the Discosorida. It is a small orthoconic shell not closely similar to *Ruedemannoceras* or to any of the post-Chazyan genera.

the middle and upper Canadian; its most prolific development is in beds of middle Canadian age.

The order Tarphyceratida makes its appearance in the middle Canadian and becomes prolific and varied in the higher Canadian. The Trocholitidae appears in the early upper Canadian. As noted above, some Canadian cephalopods have been referred to the Plectoceratidae of the Barrandeoceratida, a matter which must be accepted for the time being with some reservation.

The lower Canadian cephalopod faunas are much less diverse morphologically and taxonomically. With very few exceptions, the known genera are assignable to the family Ellesmeroceratidae, none of which are known in earlier strata, and only two genera of which survived the close of the Gasconade. With them are two genera, *Walcottoceras* and *Rudolfoceras,* which are the earliest of the Protocycloceratidae. The Endoceratida are unknown, as are the Bassleroceratida and Tarphyceratida. The only other lower Canadian elements are the two genera discussed above, *Multicameroceras* and *Sinoeremoceras,* currently referred to the family Plectronoceratidae, and the inadequately known *Shantungendoceras.*

The three true cephalopods of the Upper Cambrian have been discussed above in detail. The two adequately known genera are placed in the Plectronoceratidae. From the extant evidence, the one inadequately known genus could be a member either of this family or of the otherwise younger Ellesmeroceratidae.

It should be noted that the Canadian-Chazyan contact represents a significant faunal break. No genera are known to pass through this boundary. Of the nineteen families present in the Chazyan, which include the Polydesmiidae of the Actinoceratida, but exclude the Bathmoceratidae, only four have been found in earlier beds: the Proterocameroceratidae, Baltoceratidae, Trocholitidae, and, doubtfully, the Plectoceratidae. The orders Actinoceratida, Michelinoceratida, Ascoceratida, Oncoceratida, Discosorida,[4] and probably the Barrandeoceratida make their first appearance above this boundary.

An even more crucial period in the history of cephalopods is the break between the Gasconade and the Roubidoux. With the reservation that he considered the Tribes Hill lower Canadian and younger than the upper Ozarkian Gasconade, this is the Ozarkian-Canadian boundary proposed and rigorously defended by Ulrich for many years. The middle and upper Canadian contain four families of the Endoceratida, which makes its initial appearance in this interval. It marks the inception of the two families of the Tarphyceratida, and of the ancestral stock of this order, the Bassleroceratidae of the Bassleroceratida. The order Ellesmeroceratida is represented by the appearance of the families Baltoceratidae, Thylacoceratidae, Eothinoceratidae, and Bathmoceratidae. Only two genera of the dominantly high Canadian Protocycloceratidae are found below the boundary in the Gasconade. One of these is *Walcottoceras,* which could be placed in either the

[4] Teichert's new genus is an exception. It is a small orthoconic shell unlike the large cyrtocones by which the Discosorida are represented in Chazyan and younger rocks.

Protocycloceratidae or the Ellesmeroceratidae with about equal justice; it marks the transition between the families. The current decision to place the genus in the Protocycloceratidae was influenced largely by the fact that this procedure simplified definitions of the respective families. Two genera in this interval are assigned to the otherwise dominantly lower Canadian Ellesmeroceratidae.

The lower Canadian contains the first prolific development of cephalopods as abundant and conspicuous contributors to marine faunas. It is to be emphasized again that the stock in the lower Canadian is composed of the younger of the Plectronoceratidae and the bulk of the Ellesmeroceratidae, but that only two genera belonging to one of the more advanced and younger families, the Protocycloceratidae, have been found there.

The Cambrian-lower Canadian break is marked by the contrast of the three genera of tiny cephalopods of the Upper Cambrian with the two larger genera of the lower Canadian assignable to the same family, and fifteen of the seventeen genera of the Ellesmeroceratidae. As pointed out above, the two adequately known Cambrian genera belongs to the Plectronoceratidae. The one inadequately known genus could belong to that family or to the Ellesmeroceratidae, from the present inadequate evidence..

FEATURES OF PRIMITIVE CEPHALOPODS

From this stratigraphic survey, it is evident that the oldest cephalopods are those contained currently in two families of the Ellesmeroceratida, the Ellesmeroceratidae and the Plectronoceratidae. Other families and orders are plainly derived from these two; further, the origin of most of them in the Ellesmeroceratidae, which is the younger of the two and very possibly the more advanced, is quite evident.

From consideration of these two families it is evident that the archaic cephalopods possessed the following features:

1. Form was variable within the limits of orthocones and endogastric cyrtocones.
2. The cross-section of the shell was compressed.
3. The siphuncle was relatively large and close to the ventral side.
4. The siphuncle wall was made up of relatively short connecting rings supplemented by rather thick and frequently complex connecting rings. Diaphragms within the siphuncle are certainly a relatively early feature, and one not retained in later cephalopods.

It is possible to make further postulates which are reasonable in the light of the present evidence. First, the archaic cephalopods were tiny shells. All of the Cambrian shells are relatively much smaller than those of the lower Canadian. Second, it is very possible, though not definitely proved, that the Plectronoceratidae are actually more primitive than the Ellesmeroceratidae. This premise will be opposed by the natural tendency to believe that the tubular siphuncles of the Ellesmeroceratidae, being theoretically simpler, should represent the more primitive condition. However, closer examination of the facts, and some pertinent theoretical considerations, show that this idea is not necessarily true.

At the beginning of septation and the development of a siphuncle, the first shells were built which we can recognize as true cephalopods. When this happened, the animal first developed the ability to add material to the aperture of the shell so rapidly that shell growth outstripped a proportionate increase in size of the body mass. The animal therefore moved forward in the shell, secreting a septum behind the main body mass. It left behind, however, a siphonal strand, the apex of which must have been attached to the apex of the shell. Why? The answer is found in the clear evidence that cameral tissues must have been archaic features in cephalopods. The direct evidence of their existence is found only in younger cephalopods which developed cameral deposits. Such deposits are found in the Michelinoceratida, Actinoceratida, Oncoceratida, Discosorida, and Tarphyceratida. Clearly, the cameral deposits are formed only under specialized physiological and ecological conditions, but their pattern indicates conclusively that they were secreted by tissues so uniform in these diverse groups, that it is quite evident that cameral tissues must have been possessed by the common ancestor of these lines. A similar situation was encountered in the erratic distribution of actinosiphonate deposits in the siphuncles of the Oncoceratida. It could be explained there only on the assumption of a fundamental tissue pattern common to the entire group. When physiological conditions permitted an extensive growth of the connecting ring inward, its form was dictated by this tissue pattern, which was clearly common to the whole order, and evidently was developed in the earliest known representatives. The same conclusion must be reached to explain the uniformity of cameral deposits; the main difference is that it is necessary to postulate the existence of cameral tissues in the common ancestor of the several orders in which the deposits are developed. Clearly, the latest group which could possibly be the ancestors of these forms is the Ellesmeroceratidae. It becomes eminently reasonable that the tissues may have been present in the Plectronoceratidae as well. It must be remembered in this connection that the pre-Chazyan history of the Discosorida is virtually unknown. This order, characterized by thick connecting rings and broadly expanded siphuncles, could only have been derived from some point in the two older families of the Ellesmeroceratida. Morphologically, an origin in the Plectronoceratidae is more convincing than one in the Ellesmeroceratidae.

Returning to the subject of the Plectronoceratidae, it is eminently possible that when septation developed in the cephalopods, the septa so built tended to constrict the siphonal strand. The natural result would be that the siphuncle would tend to swell out into the camerae in between the regions bounded by the septal necks. The connecting ring, secreted upon the surface of the siphuncle, or better, perhaps within its surface, would tend to preserve the outlines of such swollen segments as are shown in the siphuncular bulbs of the Plectronoceratidae. This becomes even more probable if, as has been shown, there is good reason to believe that, in addition to the above considerations, expansion of the siphuncle within the camerae would be facilitated by the development of cameral tissues.

On this basis, it is at least reasonable to believe that the remarkable and unexpected siphuncular bulbs, which characterize the oldest of our true and adequately known cephalopods, well may be an archaic feature, and that the subsequent modification from expanded to tubular segments may be an early specialization. If so, the Ellesmeroceratidae may be derived from the Plectronoceratidae.

The diaphragms are an ancient feature, confined to these two families, and well may be primitive. It is not known definitely whether they mark the secretion of materials separating off early portions of the siphuncles, or whether the siphonal strand possibly was withdrawn gradually forward in the siphuncle as shell growth and septation progressed. Either is possible, in view of the probability that cameral tissues did not function in the oldest cephalopods. Quite evidently they did not secrete calcareous materials; it is highly doubtful also whether gas was secreted in the camerae of the first cephalopods.

One apparent anomaly in deriving the Ellesmeroceratidae from the Plectronoceratidae is the extremely long septal necks found in the adoral camerae of the specialized Plectronoceratidae. Septal necks are ordinarily very short in the Ellesmeroceratidae, although there are some exceptions to this rule. There are several possible explanations for this seeming discrepancy. If one compares the Plectronoceratidae of the Wanwanian with contemporaneous Ellesmeroceratidae, it is at once evident that the most easily observed difference is that the camerae are about twice as closely spaced in the members of the Plectronoceratidae. This is not apparent in their Cambrian forerunners, but comparison of Cambrian and Wanwanian Plectronoceratidae suggests that increase in size of the shell, in terms of width and height of the cross-section, has not been accompanied by a proportional increase in the distance between the septa. Such a proportional increase in the space between the septa does occur, however, if one postulates a change from the Wanwanian Plectronoceratidae to the contemporaneous Ellesmeroceratidae. It is this change, without a proportional increase in the length of the septal necks, which would, and quite probably did, result in the apparent change from very long necks in the adoral short camerae of the more advanced Plectronoceratidae, to the relatively short necks in the much deeper camerae of the typical Ellesmeroceratidae.

Cambrian Conical Septate Shells

The Lower Cambrian contains two genera of tiny conical septate shells, *Volborthella* and *Salterella*. Opinion as to whether these fossils were cephalopods has varied widely. No attempt will be made to review the extensive literature on the subject. Adequate references have been supplied by Schindewolf (1928, 1934) for *Volborthella,* and by Kobayashi (1937) for *Salterella*. Prantl (1948) subsequently has reported *Volborthella* from the Middle Cambrian of Bohemia. Recently Lochman (1952) has described new forms of *Salterella* from the Lower Cambrian of Mexico. Other subsequent references have been confined largely to expressions of opinion that these fossils are not true cephalopods (Miller, 1943).

Discussion of the problem of these two anomalous genera has been delayed until this point, because the conclusions reached depend primarily upon the evidence outlined in the preceding section. From this evidence it is clear that, as one traces the cephalopods downward in the stratigraphic column, one finds uniformity of structural features in the two oldest families, the Ellesmeroceratidae and Plectronoceratidae, and reason is indicated for regarding the Plectronoceratidae as the more archaic of these two families. The pattern for the primitive cephalopods arrived at by this method is so remote from that of *Volborthella* and *Salterella,* that their position as cephalopods now becomes a most unconvincing hypothesis.

Both *Volborthella* and *Salterella* are circular in section. They possess a central axial tube which has been called, perhaps unwisely, a siphuncle. The symmetry of the shell is so fundamentally radial that no one has ever ventured to suggest which side might be dorsal, and which was ventral. This is widely at variance with the pattern found in the oldest unquestionable cephalopods. Their cross-section, suture pattern, and the ventral position of the siphuncle indicate a profound bilateral symmetry which we may properly accept as primitive. Bilateral symmetry was fundamental not only to the cephalopods, but to the mollusca as a whole; it is a feature which was well established in the animal kingdom as far back as the phylum Platyhelminthes. There are, to be sure, departures from this pattern and a return to radial symmetry. But the secondary radial symmetry thus attained is always superficial, and is a specialized condition always connected with the return of the organism to a sedentary mode of life. Radial symmetry developed in the sedentary echinoderms, in the attached tubes of the Bryozoa, and in attached tubes of sedentary tube-dwelling worms. In every case, the organism retained some traces of its fundamental bilateral symmetry. It is retained in the plate arrangement of the echinoderms, as well as in the muscle scars and other features of the Bryozoa. Radial symmetry is not retained, it is true, in the calcareous tubes of some of the annelids, but it is retained in the soft parts. The annelid tubes are of such simplicity that no structures reflecting the bilateral symmetry of the organism are retained. It is conceivable that conical shells of the Tentaculitida were produced by bilaterally symmetrical organisms, but the simple tubes, without muscle scars, retain no evidence by which we can support this contention. The highly organized shells of the oldest of the unquestionable cephalopods retain abundant evidence of a bilaterally symmetrical organism. That there is no such evidence in either *Volborthella* or *Salterella is,* in the opinion of the writer, one of the clearest indications that these two fossil genera had nothing to do with the true cephalopods.

There are other differences. The septa of the older nautiloids are thin and uniformly curved, so that they represent sections of the surfaces of spheres; they are gently and usually quite uniformly curved with the convex side pointing apicad in the shell. The so-called septa of *Volborthella* and *Salterella* are very different. Those of *Volborthella* are cones; the walls are straight in vertical section. In *Salterella* the conical shape is modified, the "septa" are faintly sinuate, and the adoral surface is faintly concave near the center and convex near the periphery of the shell. The axial tube, which has been called a siphuncle, is straight-walled; the wall is thin and homogeneous in structure. Schindewolf's restoration of *Volborthella* (Schindewolf, 1928, p 70, fig 1), showing thin distant septa terminating in septal necks supplemented by connecting rings, finds absolutely no support in any of the published material.

In *Volborthella* the entire "phragmocone" is composed of alternating layers of arenaceous and argillaceous material. Thinsections (see Gurich, 1934, pl 12; Schindewolf, 1934, pl 19, particularly figs 6b, 7b) show the "septa" as alternating bands of light arenaceous and dark argillaceous material. They cannot be resolved readily into thin septa separating cameral spaces filled with matrix. Further, they show embedded in the "phragmocone" angular grains of sandy material. The appearance of the "phragmocone" in thinsection suggests overwhelmingly that these structures were built up as solid entities and that, as growth proceeded, grains of foreign material were entrapped by the organism. The whole pattern is very similar to that which is commonly observed in thinsections of calcareous algae, particularly *Cryptozoon proliferum* of the Hoyt limestone of New York. Interpretation of *Volborthella as* a cephalopod must involve the supposition that all of the known material owes its present condition to extensive replacement. Yet the thinsections show phenomena, as just noted, which it is impossible to interpret on such a basis. Giirich (1934) has concluded that *Volborthella is* an original arenaceous agglutinative structure. He compared it with certain agglutinative protozoa, and also with agglutinative structures found in recent ascidians, but concluded that the extant evidence was not adequate to permit assigning *Volborthella* to either of these groups. Schindewolf (1934) has reasserted his earlier contention (1928) of the cephalopod nature of *Volborthella,* but has failed to explain away the extremely convincing evidence of the original arenaceous nature of the "shells" of *Volborthella.* Indeed, some of his illustrations seem to corroborate Gurich's views rather than to refute them.

Salterella, though possessing a similar general pattern, appears to be quite a different sort of organism. Its shell was apparently calcareous. The septa, slightly sinuate in vertical section, are definitely thick. This feature, indicated by Clark (1925) in his restoration based upon silicified material, is corroborated now amply by the sections published recently by Lochman (1952). Lochman's sections show further indications of thick walls built up of successive laminae, but not separated by any appreciable cameral space. Kobayashi (1937) reviewed the problem of *Salterella,* including mention of *Biconulites* and *Volborthella*. He concluded that *Biconulites* was a pteropod, and that *Volborthella* and *Salterella* were allied, constituting a "solid group of fossils intermediate between the hyolithids and the nautiloids, but closer to the latter." His contributions to the knowledge of the morphology of *Salterella are* significant. He showed that the silicification of Clark's original material of *Salterella conulata* was secondary, and not primary. He showed that the thick septa were produced into tubes which could be compared with septal necks, and noted that, although such tubes were present in the species which he studied, they did not appear to be present in some other species. His acceptance of the view that *Volborthella* and *Salterella* represent essentially similar organisms, does not seem to be corroborated either by the present material, or by any explanations made up to the present as to how an original calcareous shell could be replaced, so as to show the sort of features which *Volborthella* exhibits in thinsection.

It must be remembered that the old concept of *Volborthella* and *Salterella* as primitive cephalopods was based primarily upon a concept which has since been abandoned, namely, that the generalized *"Orthoceras"* type was a primitive cephalopod. Such shells, now retained in the order Michelinoceratida, are in part superficially radially symmetrical. But even where the cross-section is circular, and the siphuncle central, the bilateral symmetry is proclaimed by the hyponomic sinus of the aperture, and the conchial and septal furrows of the shell. It is further demonstrated by the bilateral symmetry and marked concentration on the ventral side of the shell of cameral deposits, siphonal deposits, or both. Further, such shells are not primitive, but specialized. They are not particularly ancient; the oldest ones known are Chazyan. The truly primitive cephalopods belong to the Ellesmeroceratidae and Plectronoceratidae of the Ellesmeroceratida. Reason has been advanced above for regarding the Plectronoceratidae as the real archaic stock. Whether or not this is accepted, the pattern of the oldest true cephalopods, outlined above, is widely at variance with those of *Volborthella* and *Salterella.*

What, then, can be said concerning the relationships of these two genera? The case which Gurich has presented for the agglutinative nature of the shell of *Volborthella* appears valid. He has pointed out similarities both with the Protozoa and the ascidians, but in neither group, admittedly, are their forms closely enough similar to permit a definite assignment of this genus. Its radial symmetry may indicate that it sprang from a group low in the animal kingdom. It does not necessarily indicate that such a conclusion must be accepted. The writer favors the interpretation that *Volborthella* well may be an early specialization of the Protozoa which failed to survive the Cambrian. Certainly its position high in the animal kingdom is opposed by the failure of all workers to demonstrate anything other than an apparent radial symmetry. Were the shells only simple tubes, this would not be significant, but with the complexity of the shells, the absence of any evidence of radial symmetry safely may be considered significant. Nevertheless, the evidence is so inconclusive, that it seems far wiser to place *Volborthella* admittedly among invertebrates of uncertain position, than to attempt placing it in any known group on the basis of the present available evidence.

Salterella is equally remote from the cephalopods in the absence of any evidence of bilateral symmetry and the thick imbricate structure of the "septa." It is potentially a better candidate for a position with the hyolithids than is *Volborthella,* but the present evidence is insufficient to warrant making any such assignment except in the most tentative way. The present evidence does not warrant placing *Salterella* with certainty in the Mollusca; it does not, vexingly, permit one to assign it with certainty to any known class or phylum.

There is no inherent reason why these two genera, or for that matter the other shells discussed above, including the Hyolithidae, 1 entaculitidae, and the genus *Shelbyoceras,* which the writer refuses to assign to either group, should be members of any group known from living representatives. Evolution is a wayward process; surely it is not too much to believe that it indulged in many experiments which left records in our earlier Paleozoic but which failed to survive beyond. From the present evidence it is easier to believe this of many of these fossils which have been assigned more or less tentatively to the cephalopods, than it is to place them in any known class or even phylum of the animal kingdom.

It should be noted that there is not the wide stratigraphic gap separating shells of the aspect of *Volborthella* and *Salterella* of the lower Cambrian from the first true cephalopods of the Upper Cambrian that is indicated by the literature. Though dominantly Lower Cambrian, shells of this type have been found in Middle Cambrian strata (Prantl, 1948). Further, Dr. Virgil Barnes has submitted to the writer for study some supposed cephalopods from the Upper Cambrian of Oklahoma. Though the present material is too poor to merit description, these fossils appear to be small chambered shells of the *Salterella* persuasion, but are clearly not identical with that genus. Dr. Teichert informs the author that he has had submitted to him small septate shells from the Upper Cambrian of Australia, again represented by material too sparse and too fragmentary to merit description. Neither his material, nor that of the present writer, has shown any structures which could be interpreted as siphuncles. This matter is mentioned here largely because there is no record in the literature of tiny, septate, straight, conical shells in the Upper Cambrian.

Summary

The family Plectronoceratidae, characterized by siphuncular bulbs, contains the oldest adequately known cephalopods. Evidence is shown for regarding the family as containing the most primitive of the cephalopods. As presently constituted, it contains four genera, *Plectronoceras, Palaeoceras, Sinoeremoceras,* and *Multicameroceras*. The inadequately known Cambrian genus, *Ruthenoceras (=Angaroceras)* could from the extant evidence belong to the Plectronoceratidae or Ellesmeroceratidae. These two families together contain the oldest true cephalopods.

Shelbyoceras, Volborthella, Salterella, and the conical aseptate shells currently embraced in the Hyolithidae and Tentaculitidae are not, from the present evidence, connected with the primitive cephalopods, nor necessarily with each other. The shells supply so little evidence of the nature of the organism of which they were once a part, that they cannot be referred with certainty to any class or phylum, but must be regarded as invertebrates of uncertain affinities.

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ADDENDUM

As proof of this paper is received, the work by Teichert and Glenister mentioned in footnotes 3 and 4, and referred to on page 36 as manuscript, has been published.

Teichert, C., and Glenister, B. F. (1954) *Early Ordovician cephalopod faunas from northwestern Australia,* Bull. Am. Paleontology, v 35, n 150, 112 pp, 10 pls, 18 figs.

Explanation of Plates

PLATE 1

KYGMAEOCERAS and *PALAEOCERAS*

FIGURES PAGE

1-4, 6-8. *Kygmaeoceras perplexum* Flower, n. sp. 32
Holotype (figs 1-4), X 2. 1. Artificial rubber cast from natural external mold, showing dorso-lateral surface, with dorsum on left. 2. Internal mold viewed from the narrow dorsal (?) side. 3. Lateral view of internal mold, dorsum on left. 4. Ventral view of internal mold, showing narrow, strongly flattened surface. From the San Saba limestone, Threadgill Creek section, Gillespie County, Texas; upper Trempealeauan.
Paratype (figs 6-8), X 2. An internal mold representing a much earlier growth stage. 6. Ventral view. 7. Lateral view, venter on left. 8. Dorsal view. From the San Saba limestone, near Camp San Saba, McCulloch County, Texas; upper Trempealeauan.

5, 9, 10. *Palaeoceras mutabile* Flower, n. sp. 10
5. Rubber impression from natural external mold of holotype, lateral view, X 2. 9. Ventral view of paratype, an internal mold representing adoral part of phragmocone and part of living chamber. Surface slightly etched to expose siphuncle. X 8, unretouched. 10. Internal mold of holotype, ventral view, slightly etched to expose siphuncle and septa. Septa and siphuncle have been slightly retouched. This internal mold occupied the apical three-fourths of Figure 5. X 10. Both specimens are from the San Saba limestone, Threadgill Creek section, Gillespie County, Texas; upper Trempealeauan.

PLATE 2

SHELBYOCERAS and *PALAEOCERAS*

FIGURES PAGE

1-3. *Shelbyoceras ellinwoodi* Flower, n. sp. 28
Holotype (figs 1-3), X 1. A chert internal mold of a living chamber. 1. Convex ventral surface. 2. Lateral view, venter on left. 3. Apical view, venter on left. From the Pedernales dolomite, east side of Cave Creek, Gold quadrangle, Gillespie County, Texas.

4-6. *Shelbyoceras* cf. *barnesi* Flower 30
Specimen tentatively referred to this species, an internal mold of a living chamber. X 1. 4. View of concave dorsal surface. 5. Lateral view, dorsum on left. 6. Apical view, dorsum on left, showing septal surface. Same horizon and locality as the preceding.

7-10. *Shelbyoceras barnesi* Flower, n. sp. 29
Holotype (figs 7-10), X 1. A chert internal mold of a living chamber. 7. Lateral view, venter on left. 8. Apical view, showing septal surface, venter on left. 9. Ventral view. 10. Dorso-lateral view of internal mold in its original matrix, showing cavity at base of living chamber, where a small chambered portion of the shell was removed by solution. Dorsum on left. Same horizon as the preceding forms.

11. *Palaeoceras mutabile* Flower, n. sp. 10
Ventral view of the holotype. A fragment of a phragmocone, the surface of which has been gently etched to expose the siphuncle. X 20, unretouched. See Plate 1, fig 10.

PLATE 3

PALAEOCERAS

PAGE

Palaeoceras mutabile Flower, n. sp. 10
Enlargement of same specimen shown in Plate 1, fig 9, adapical half only, showing in greater detail the form of the segments of the siphuncle and the diaphragm. X 20, unretouched.

Plate 1: *Kygmaeoceras* and *Palaeoceras*

Plate 2: *Shelbyoceras* and *Palaeoceras*

Plate 3: *Palaeoceras*

Index

Numbers in italics indicate figures; **boldface** indicates main references.