MEMOIR 9

The Phragmocone of Ecdyceras

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Contents

(Note. 5 text figs—explanations are in the text at the appropriate places.)

Abstract

Ecdyceras proves to have a rather long phragmocone, at the base of which a rather flat, thick septum suggests loss of earlier growth stages by truncation. This shallow basal septum is followed abruptly by very deeply curved septa, their edges extended far forward. Episeptal deposits, thin centrally and thick peripherally, result in a peripheral zone in which the shell material was essentially solid and an axial zone in which cup-shaped cavities remain in the camerae; with growth, the axial zone widens adorally at the expense of the peripheral zone. The siphuncle, beyond a basal arcuate stage, is tubular and thick-walled, with diaphragms, later becoming thin-walled and showing slightly fusiform segments. Septa are thin, the necks ambiguous from the present material, but evidently vestigial.

Chazyan material studied is indecisive at the specific level, but indicates that the extended septal margins of young stages are responsible for the apparent thickening of the base of the living chamber on the basis of which *Pachecdyceras* was distinguished. A new species, E. *expansum* is described from the Viola Limestone of Oklahoma.

Ecdyceras is remote in structure from other cephalopods, requiring its separation into a family and an order by itself. Origin is obscure, but only derivation from the Ellesmeroceratida seems possible.

Introduction

This paper is devoted primarily to the description of some remarkable phragmocones which are plainly to be attributed to the genus *Ecdyceras,* and which result in a drastic revision of previous concepts of the morphology and taxonomic position of that genus. These phragmocones show a structure so completely alien to that of other known orthoconic nautiloids—indeed, to all other nautiloids—that the genus is isolated in evolution, and forms connecting it with simpler nautiloids are as yet unknown. The material here described is from the type section of the Chazyan, southwest of Chazy, New York. Some problems attend the detailed interpretation of the section, but it will suffice to note that the phragmocones were collected in sight of the locality which yielded the original material of *Ecdyceras*, and the occurrences are separated stratigraphically by somewhat less than 6o feet. The matter involves some questions of interpretation, discussed more fully below.

The phragmocones show septa which are extremely prolonged forward at their margins, and indeed, there is developed a peripheral zone in which episeptal deposits fill completely the narrow spaces between the steeply inclined septa, except in adoral camerae where the deposits are immature or wanting altogether. The result is an appearance in sections so- foreign to that of other cephalopods that without strong evidence to the contrary, one could suggest that these forms belonged to some other fossil group. A casual glance at such a specimen as is shown in the lower part of Plate 1, figure **2** will show a general resemblance of this part of the section to that of *a Beatricea (Aulacera),* though the bottom of the figure as oriented here would be interpreted as the top of the stromatoporid. The anterior part of the same figure resembles a section through a belemnite shell, showing the phragmocone surrounded by a rostrum.

Oddly, while the phragmocones of this form are quite probably the large orthocones noted by Brainerd and Seely (1888), as B4 and C6 in their first description of the type section of the Chazyan, they have until now escaped close study. However, I myself have described the living chambers not once, but twice. Two specimens, one a mature living chamber with only the septum at its base, and another slightly smaller individual with one attached camera, formed the basis of *Ecdyceras sinuiferum* Flower (1940. A third specimen, superficially similar, but with shell material thickened over the basal half of the living chamber and showing an internal surface with a bilaterally symmetrical pattern of shallow longitudinal ridges and grooves, was the basis of *Pachecdyceras murale* (Flower, 1947). It is evident from the phragmocones described here that the effect observed in this specimen is quite clearly produced by the greatly prolonged edges of septa in the axial zone of an immature *Ecdyceras,* and not, as was previously thought, a thickening of the interior of the shell wall. It is further evident that, in the light of this explanation, *Pachecdyceras* becomes a synonym of *Ecdyceras,* since the features by which it is recognized are those clearly to be found in a sufficiently young living chamber of *Ecdyceras.* However, the suggested conclusion that the species are one and the same does not necessarily follow. While it is unsafe to lay down laws as to the limits of proportion in this bizarre form based on observation of other and more normal cephalopods, it is evident that the two specimens shown in Plate 1, figures t and **z** and figures 10 and II show such widely different proportions that, without strong evidence to the contrary, they must be regarded as distinct species; their inclusion in a single species is absurdly contrary to all experience. While it can be stated reasonably that the living chamber which was the type of *Pachecdyceras murale* could have belonged to the phragmocone shown in Plate r, figures 10 and 11, it could hardly have belonged to the specimen shown in Plate 1, figures r and z; commensurate parts of the latter phragmocone would show the central, shallowly curved part of the septum to be much smaller in proportion to the shell cross section. There is such adoral reduction of the peripheral zone in both forms, however, that one cannot say with which of these remarkable forms the types of *Ecdyceras* *sinuiferum* should be matched. Thus, the present material offers evidence which is indecisive at the specific level. Earlier collections being unavailable and the possibility of collecting more material in the near future being remote, it seems that progress will be served best by the description and illustration of the remains now at hand, with such interpretation as the material indicates.

The peculiar nature of the materials, the bizarre morphology shown, and the indecisiveness of the materials at the specific level have required a somewhat unusual arrangement in the present work. First is a general description of *Ecdyceras* based upon the Chazyan materials. The new specimens are described individually. To avoid commitments which the material does not justify at the specific level, the specimens are indicated by numbers. Some satisfaction was derived from referring to them as Thing r, Thing 2, etc.; for, like the creatures thus designated in Dr. Suess' delightful children's classic, *The Cat with the Hat,* they have had, when once let out, a most upsetting effect, here upsetting concepts of cephalopod morphology and classification. There follow brief descriptions with reillustration of the two types of *Ecdyceras* and a third living chamber from the same association, and redescription of the type of *Pachecdyceras murale.* Then there is a brief discussion of the problem at the specific level. A following section discusses the occurrence of the Chazy materials. Curiously, a number of my colleagues, when first confronted with these remarkable phragmocones, were reluctant to believe that the phragmocones had any relation to the originals of *Ecdyceras* or *Pachecdyceras;* the occurrence, which has considerable bearing on the matter, therefore seems to need rather full discussion. Next is a brief mention of the other occurrences of the genus, a brief mention of the Arnheim *E. foerstei,* and a description of a new species E. *expansum,* from the basal Viola Limestone of Oklahoma. Neither form is represented by material contributing further to a knowledge of the phragmocone.

There follows a brief formal redescription of *Ecdyceras,* discussion of its morphological and evolutionary isolation, and the required erection of an order and of a family for its reception.

General Description of the Chazyan Materials

The *Ecdyceras* of the type section of the Chazyan appears commonly on weathered surfaces showing specimens far larger and longer than the specimens here described, but the present material shows phragmocones in which a shallow, thick basal septum is followed abruptly by a series of very deep septa over a length of 160 mm to the extreme base of the living chamber, with the septa curving forward marginally at least 20 and more probably 3o mm farther. The phragmacone in this length expands from a height of 12 mm and an estimated width of 14 mm to a height of 20 mm and a width of 3o mm in the basal 75 mm. At the level of the suture at the base of the mature living chamber, the phragmocone is estimated to be 5o mm in width and 4o mm in height. Our largest living chamber, the holotype, increases in width from 43 to 47 mm in the incomplete length of 100 mm, and by interpolation, proportionate length increasing with the growth stage, the complete living chamber on such a larger piece of phragmocone would be in excess of 120 mm in length and would attain an adoral width of 55 mm.

The shell wall is thick, its surface strongly rugose, with numerous irregular transverse markings. Thinsections show the shell wall to be composed of numerous lamellae sloping forward from the inner to the outer surface. The several sections made show wide variation in shell thickness. The sections fail, however, to show the expected persistent differences in inner and outer shell layers comparable to those of *Nautilus.* Obviously, the persistent preservation of lamellae such as are shown here, particularly in Plate x, figures 7-9, require either special materials or special preservation phenomena or both. In rather wide experience in the examination of cephalopod shells by thinsection, no similar walls have been encountered, with one exception. Rather, typical shell walls in the Nautiloidea show only coarse and irregular calcite crystals; evidently the walls were originally aragonite, and with the general replacement by calcite, all fine textures and structures showing different layers were lost. The suggestion is that in *Ecdyceras* the shell wall could hardly be preserved as it is unless it was originally largely or completely calcitic. A somewhat similar specialization has been reported in the Pectenidae among the Pelecypoda. The only example of even remotely similar structure in fossil cephalopod material known to the writer is found in a small portion of the dorsal part of the shell wall of an *Eremoceras,* which is to be described and figured in a work now in an advanced stage of preparation, a work dealing with the order Ellesmeroceratida. In the *Eremoceras* the lamellae are much more steeply inclined and show rhythmic variation in spacing, so that the resemblance is not at all close. The rugose markings on the surfaces of *Ecdyceras,* also projected imperfectly on the internal molds, as shown by the holotype, show the development of a broad gentle sinus on the venter and are transverse dorsally and laterally.

Curiously, while lamellae of the shell wall are preserved with general fidelity, the obscurity of the septa and cameral deposits suggests that they were originally aragonitic and have been altered to calcite. Further, the material shows considerable areas in which the calcite is in coarse crystals, obscuring the original structure further, and in places, obliterating even such prominent features as the boundaries of the cameral spaces in the axial zone, as shown at the base of figures i and 2, Plate 1.

An interesting feature of this material is that, although the phragmocones had apparently peripheral zones of solid organic calcareous material and only restricted cameral spaces in the axial zones, with the addition of the perforation of the phragmocone by a small, largely tubular, siphuncle, many of the specimens show some distortion of cross section, clearly a slight flattening which may be thought of as involved in compaction of the sediments. That such flattening should affect shells which were very nearly solid may seem astonishing, but I have encountered similar compaction in endosiphuncles of Endoceratida from the highest 20 feet of the Garden City Formation in northern Utah; so it is evident that even quite solid shell parts may yield to pressure, though the condition is not widely known and is apparently not noted in the literature.

The basal septum is nearly flat and quite thick. The two examples shown exhibit some slight differences, and it is not certain which condition is closer to their original state. In Thing i there is some indication that the septum may be a double structure, or may have consisted originally of two layers. No such condition is apparent in Thing z, but instead a small triangular area near one corner supplies another, different, suggestion of two structures which may not be joined completely.

Very deep septa, their margins greatly extended forward, follow the basal septum abruptly. Our two specimens showing this ontogenetic change have marked differences: In Thing x a series of septa show progressive increase in depth; centers of earlier septa were plainly resorbed to permit the formation of the central parts of later ones. In Thing z there is no such truncation of earlier by later septa, and the transition in form from the basal septum to the first of the deep ephebic septa is the more abrupt.

As can be seen from the figures, the two most complete specimens (pl. r, fig. i and 2, io and 11) show wide variation and irregularity in the form and spacing of the septa, but the two specimens show such disparate patterns that one cannot logically consider further intraspecific variation as responsible. The first shows a long, narrow axial zone one-third to one-fifth the height of the shell. In cross section (pl. x, fig. 5), this axial region is revealed as elliptical, with rather sharp attenuation of the ventrolateral margins. This is followed by a portion in which the axial zone expands conically and then abruptly contracts before conical expansion is resumed. No such development is found in Thing 2; rather, the axial zone is relatively broad from its beginning, and the adoral reduction of the peripheral zone is most gradual.

The solidity of the peripheral zone is due partly to the closeness of the steepened peripheral parts of the septa, but clearly there is supplementary material between the septa. This material, when traced axially, is seen to thin and to lie against the anterior faces of the septa. In apical camerae the material, clearly an episeptal deposit, fills the cameral spaces peripherally, but as one examines camerae progressively younger and closer to the living chamber, a region is found in which deposits are thin and evidently young, followed by a region in which such deposits are apparently absent. This is the normal pattern shown by cameral deposits in relation to the growth of the shell as a whole. In some septa there are possible thin hyposeptal deposits also, but they are relatively thin, and whether erratic in distribution or only erratic in preservation is not completely clear from the present material. The thick bands separating the cup-shaped cavities in the axial zone are clearly compounded largely of rather surprisingly thin septa with thick episeptal deposits on their anterior surfaces. Extension of surfaces of septa and deposits into the peripheral zone is generally indicated, but crystallization has left the details obscure, and indeed, the prevalent lineation thus produced is generally faint; rarely can any line be traced for any appreciable distance.

The siphuncle, which lies a little more than half way between the center and the venter, shows some variations in outline. In Thing 1, the base is arcuate and there are obscure traces of segmentation; beyond this region it is straight, tubular, and rather thick-walled, without obvious segmentation, but near the extreme adoral end slightly fusiform segments are outlined, though it must be noted that, from the steep inclination of the septa, expansions on the dorsal and ventral sides which seem aligned probably pertain to different segments. In Thing z the siphuncle is not visibly basal, but where it first appears it is tubular and rather undulate in its course. Beyond this region segments change rapidly, assuming a fusiform outline on the dorsal side but not on the venter, a condition which is maintained to the base of the living chamber. Several thinsections were made, and although the specimens show such alteration as to make interpretation somewhat difficult, it is evident that the siphuncle, thick-walled in the young, is thinner in the later stages; while the steep septa approach the siphuncle from the ventral side without obvious modification into necks, it is surprising that no good necks can be seen on the dorsal side. The apical part of the siphuncle in Thing shows several obvious diaphragms which seem extensions of the siphuncle wall, but adorally there are some regions simulating diaphragms in which it is more likely that the siphuncle has wobbled slightly to one side, so that the plane of the section cuts its rather thick wall tangentially.

Description of the Chazyan Specimens

I. DESCRIPTION OF THE NEW MATERIALS

THING I

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

This specimen is a portion of a phragmocone embedded in matrix, the adoral end, which was near the edge of a slab, weathered, the surface projecting orad from dorsum to venter. The phragmocone expands from a height of 13 mm and an estimated width of 16 mm to 22 and 32 mm in the basal 8o mm and attains a width of 4o mm in the next 70 mm where the corresponding height is estimated at 27 mm. In all, the specimen is 18o mm long, but the adoral end is too incomplete for estimation of height or width. The specimen was sectioned vertically in three parts, and the two opposing surfaces thus attained are shown in Plate 1, figures and 2.

The sectioned surfaces show septa which are clearly apparent only in a narrow axial zone over the lower two thirds of the specimen; beyond this the axial zone widens conically, though irregularly, there being an abrupt contraction at the base of the adoral fifth, beyond which conical expansion is resumed. The peripheral zone which surrounds the axial zone is filled in with calcite which is evidently considerably recrystallized. It shows local faint traces of septa which slope strongly forward from the axial zone to the periphery, but such traces are discontinuous and erratic. Curiously, without the siphuncle, the apical portion of this remarkable form has the superficial appearance of a sectioned *Aulacera (Beatricea)*, while the adoral portion with the conically expanding axial zone bears a superficial resemblance to a section through a belemnite phragmocone encased in a rostrum. At the extreme adoral end of the specimen a small region of matrix lying orad of the last septum in the center of the specimen apparently represents the extreme base of a living chamber filled with matrix.

It is evident that the mature part of the phragmocone is composed of extremely deeply curved septa, supplemented by episeptal deposits on their anterior surfaces; the episeptal deposits are thick peripherally, apparently filling the narrow spaces between the steeply inclined septa completely, but narrow in the axial portion, leaving deep cup-shaped cavities, the apical faces of which are strongly convex, the adoral faces strongly concave.

The most astonishing feature of the specimen is the presence at its base of a thick, extremely flat septum, pierced by the siphuncle which continues a little way apicad of the septum. The presence of such a septum suggests most strongly ( ) that the early part of the shell was very different from the known portion, (2) that this early part was almost certainly lost during life as a normal process, and (3) that in this respect there is a remarkable parallel between *Ecdyceras* and the Ascoceratidae, in which similar loss of an immature stage, very unlike the adult in aspect, was shown by Lindstrom (189o).

The siphuncle, which is visible on one or the other of the surfaces shown throughout most of the section, lies about half way between the center and the venter apically but is slightly more eccentric adorally; apically it lies well within the peripheral zone, but as the axial zone expands adorally it comes to join with and eventually to include the siphuncle. In gross aspect the siphuncle is peculiar. It penetrates the shallow basal septum, is arcuate, curves convexly toward the venter for a short distance, then straightens, the walls here being thick; the diaphragms, apparently continuous with the walls and similar to them in texture, are seen crossing the siphuncle. Adorally, however, the siphuncle segments are more lax, irregular in outline, and show some trace of slightly fusiform outline of the segments.

The opposing surfaces of the apical part of the specimen are shown enlarged in Plate 1, figures 3 and 4, and a further enlargement of the lower part of figure 3, showing the siphuncle, is seen in Plate 4, figure 6; an enlargement of the anterior part of Plate I, figure 4, again showing the siphuncle, is illustrated in Plate 4, figure 7. Some difficulty attends interpretation of the apical part of the specimen because the cup-shaped cavities of the axial zone are wanting in the extreme apex, but the visible anterior margin of only one such body indicates that recrystallization of calcite is involved in this absence. Three features here are of particular interest: the nature of the basal septum, the details of the structure of the siphuncle, and the pattern formed by the earliest septa. Text Figure 1 shows an interpretation of the structure of the siphuncle, and the ventral part of the basal septum. The septum appears extremely thick and shallow. It is composed of light calcite and evident recrystallization makes impossible the certain distinction of original structures from replacement phenomena. The ventral side shows a suggestion of two layers, the apical one being extended as a rather thick septal neck.

Dorsad of the siphuncle (pl. 1, fig. 3) the basal septum is thick, and as it approaches the dorsum it is bent forward into a short mural part of the septum which thins rapidly adorally, being wedge-shaped in the section. The dorsal wall of the siphuncle as it passes through the basal septum is dark and homogeneous; no indication of extension of a septal neck is shown there, but on the ventral side the septum is extended apicad as a short neck, thinning rapidly as its tip is approached. Here the inner surface of the neck can be traced, curving ventrad in the middle of the thick septum, and a dark band, discontinuous with this line but aligned with it, passes to the shell wall. The anterior limit of the thick septum is seen close to the siphuncle but disappears ventrally in light calcite, and though there is a strong suggestion that the septal material is extended forward here, along the inside of the shell wall, its course and limits cannot be determined with certainty.

As can be seen, the apical end of the siphuncle expands slightly apicad of the basal septum. On the ventral side, light calcite of the siphuncle merges with similar light calcite of the anterior part of the basal septum. Orad, the siphuncle swings toward the venter, but curvature of the ventral outline is smooth and without clear traces of such segmentation as one would ordinarily expect. The dorsal outline, however, is more eventful, and beyond a strongly convex region there is a narrow concavity toward which is pointing an oblique

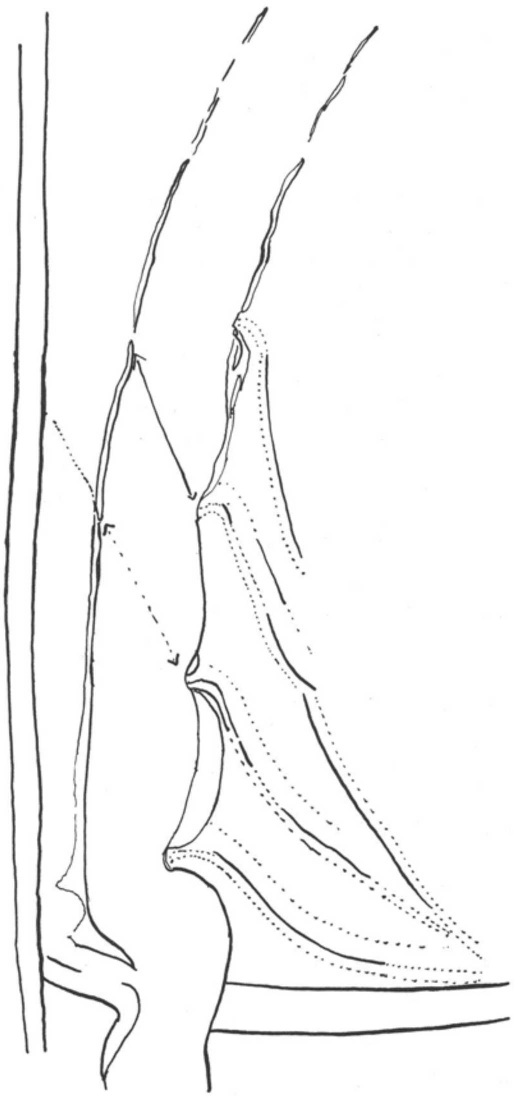

Figure I

OUTLINE DRAWING OF THE BASAL PART OF THING I, SEEN IN SAGITTAL SECTION, SHOWING THE VENTRAL PORTION ONLY, WITH SHELL WALL, BASAL SEPTUM, AND SIPHUNCLE, WITH AN ATTEMPT TO RESTORE EARLY EPHEBIC SEPTA

dark band, logically a septum, which must, if continued, join the basal septum in the center of the phragmocone and which may well curve to form a vestigial septal neck at this slight excavation in the siphuncle outline. A second segment of the siphuncle shows a wall slightly convex, markedly thickened, and represented by dark material. Aligned with its adoral end are traces of a second septum which slopes apicad strongly as it is traced dorsally, and it too must eventually join the dorsal septum. On the dorsal side of the siphuncle there can be seen indications of two other excavations which appear to represent segmentation of the siphuncle, and more or less aligned with each of these are traces of additional septa, steepening progressively as they are traced toward the dorsum. (See text fig. I and pl. 4, fig. 6.)

Farther orad (pl. 4, fig. 7) the siphuncle has curved to a position some distance from the venter and has become perfectly straight and tubular. The walls are thick and fail to show any divisions which can be interpreted as septal necks and connecting rings; rather, the whole of the wall, at least potentially a connecting ring, is thick and though rather irregular shows light material comprising most of its width, with the inner and outer surfaces thin dark bands. At two points near the apical end of the figure and at one near the adoral end, the material of the siphuncle wall extends across the cavity of the siphuncle as diaphragms. Here interpretation of the diaphragms as regions in which the plane of the section cuts the lateral part of the siphuncle wall tangentially is not convincing, and although such an explanation could be invoked, I think it is untrue, for similar structures are shown farther orad in Plate 4, figure 8.

The really curious features of the apical portion of the phragmocone involve an early arcuate portion of the siphuncle with obscure segmentation indicated, and an adoral straight portion in which segmentation is not apparent but in which diaphragms have developed. Traces of the septa show definitely that several early septa are developed, showing increasing depth and curvature, and that the older septa were apparently resorbed where they intercept the course of the newer septa.

In addition to the real septa, episeptal deposits are secreted on the anterior septal faces; such deposits are relatively thin in the axial region, though showing some apparent variation, but thicken peripherally, and, from all indications, occupy the entire spaces between septa in the peripheral zone. The presence of the episeptal deposits, and even perhaps of layers in these deposits, accounts for some of the faint, strongly inclined dark lines retained erratically in that zone, which are too numerous to be explained as simply vestiges of surfaces of the septa. Interpretation and restoration involve some uncertainties, but the possibilities of variation in the interpretation have very definite limits which are shown by the two interpretations given in Text Figures 2 and 3.

A portion near the middle of Plate I, figure I is shown enlarged in Plate 4, figure 8. Here there are various indications of continuity of the thick, curved bands separating the cup-shaped cavities of the axial zone from the peripheral zone; also shown in greater detail is the wide variation in the length and width of the cavities. The siphuncle is straight and thick-walled; in several places the wall continues across the siphuncle cavity. The two anterior examples shown near the middle of the figure may possibly represent regions at which the plane of the section is tangent to the siphuncle wall; but in the lower part, half way between the center and the base of the figure, a dark band showing both surfaces strongly curved, with the convexity directed apicad, is apparently a true diaphragm. The section shows the peripheral zone with steeply inclined lamellae, obviously representing the septa with the episeptal deposits but with details obscured by re-crystallization; the margins show sections through the shell wall.

Over the basal 90 mm of the specimen the axial zone is narrow, rather irregular, but largely parallel-sided; the cup-shaped cavities vary in width from 5 to 7 mm, being at the most less than one-third the height of the shell and at the least one-fourth of that height. The cross section (pl. 1, fig. 5) shows them to be depressed, with the dorsum arched, the venter flat, quite similar to the cross section of the shell. However, beyond the basal 90 mm the axial zone widens conically so that in 3o mm it increases from 5 mm, one-fourth the shell height, to 18 mm, three-fourths of the shell height. Beyond this point the sides of the axial zone are parallel for a short distance, aver which there is an abrupt contraction followed by fairly rapid conical widening as before, which continues to the adoral end of the specimen. This portion of the specimen is shown enlarged in Plate 1, figure 6. Septa are irregular in spacing and thickness, close observation indicates that in some cases episeptal deposits are recrystallized with the calcite of the cavities of the camerae, but in others the cameral deposit is differentiated from the inorganic calcite. In the conically widening axial region the episeptal deposit is very thin in the central portion and can be seen widening when traced to the dorsum or to the venter. As is common in other cephalopods, a series of camerae is seen in which the deposits are progressively more immature when traced orad; and while recrystallization of the peripheral zone adorally makes determination of the matter uncertain, it is probable that in the extreme adoral camerae the deposits are vestigial or absent altogether. The adoral septa of the ventral side show definite curvature, the adoral surface being slightly convex on the venter, a feature not developed

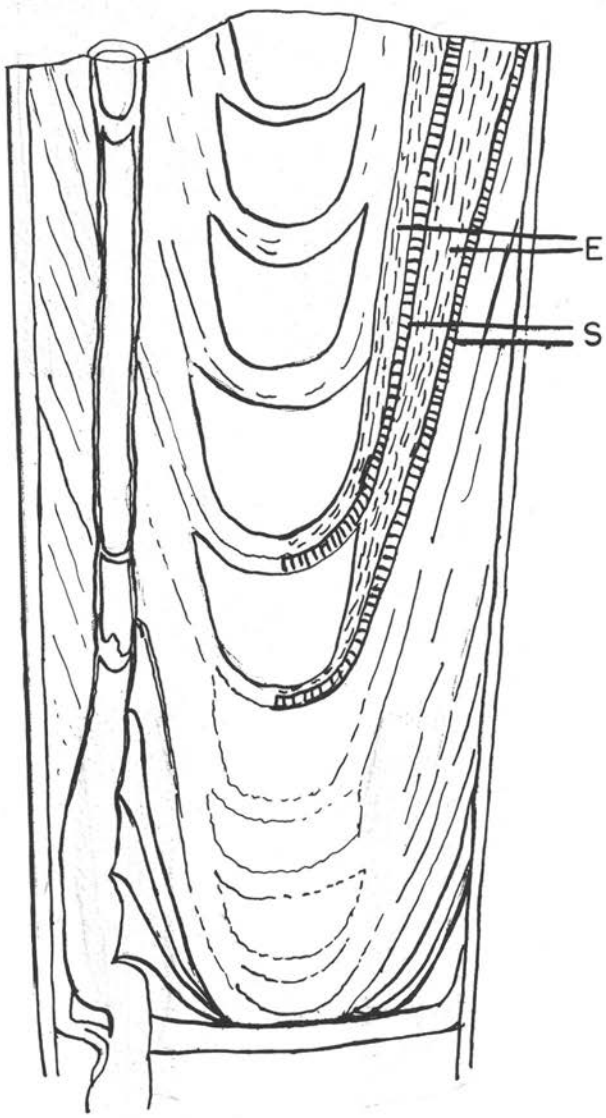

Figure 2

AN INTERPRETATION OF THE STRUCTURES OF THE SURFACE SHOWN IN PLATE 1, FIGURE 3, WITH THE ANTERIOR PART OF THE SIPHUNCLE AND SOME FEATURES SHOWN IN PLATE 1, FIGURE 4, THE OPPOSING SURFACE INTERPOLATED

On the right, restoration of the Septa (S) and the episeptal deposit (E) is attempted for two septa. Basal septa are restored, but no attempt was made to differentiate their episeptal deposits in the restoration. The number and form of the apical cup-shaped cavities of the axial zone is necessarily inferential.

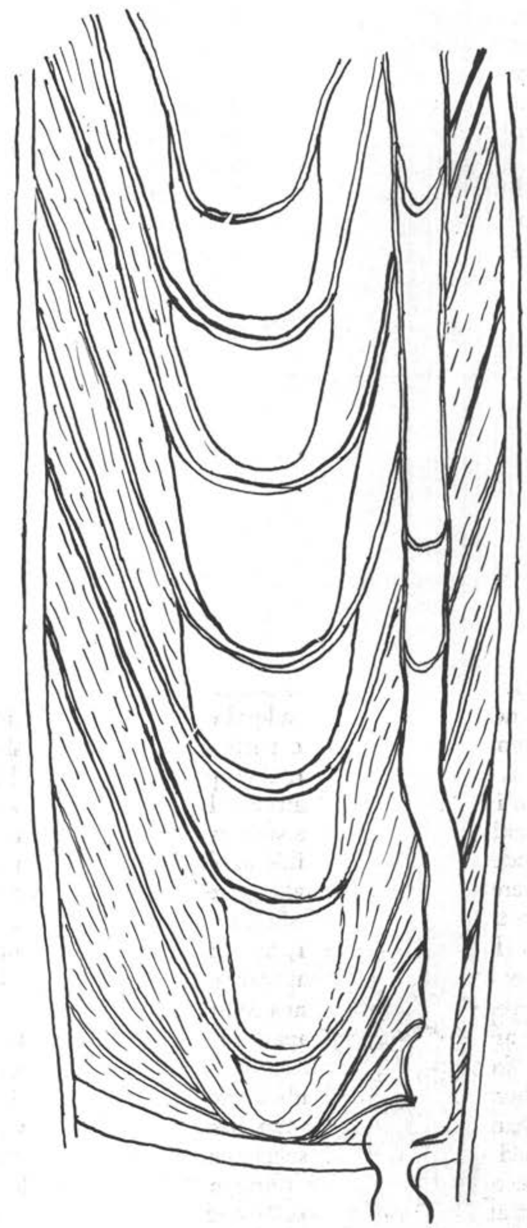

Figure 3

A SECOND INTERPRETATION OF THE SAME PORTION, SHOWING A DIFFERENT SPATIAL ARRANGEMENT OF THE CUP-SHAPED CAVITIES OF THE AXIAL ZONE IN THE BASAL PORTION; SEPTA AND EPISEPTAL DEPOSITS ARE MORE FULLY DIFFERENTIATED in the earlier part of the phragmocone. The siphuncle is intersected by the surface shown in Plate 1, figure 6, in the basal portion, and again in the extreme adoral end. In the lower part, the siphuncle appears tubular but the walls are not obviously thickened, as was the case in the earlier portion, and there are no diaphragms. At the adoral end two fusiform siphuncle segments are seen, the widening concentrated at the adoral end of each segment, and the widening of dorsum and venter is apparently nearly aligned. The septa are still steep and still slope forward where they intersect the siphuncle, probably for the length of one camera or of one siphuncle segment; if this is so, the obvious horizontal alignment suggested by the section is false. Opaque sections fail to show the septal necks here. Matrix in the center of the phragmocone indicates the extreme base of a living chamber.

Discussion. This specimen is remarkable in showing beyond the flat basal septum a series of deep septa in which the earlier ones were resorbed during or prior to the development of younger and still deeper septa which otherwise would have intercepted them. It is remarkable also in showing the long, narrow, tubular axial zone followed by conical expansion of that zone, abrupt contraction, and a second region of conical expansion.

THING 2

Pl. 1, fig. 10, II; pl. 2, fig. I, 2

This specimen consists of a portion of a phragmocone 120 mm long increasing from a height of 14 mm and an estimated width of 2o mm to a height of 24 mm and a width of 4o mm. The adoral end had attached to it an irregular fragment extending 25 mm farther orad, representing a portion of the living chamber around which the strongly extended edges of the septa are found (not illustrated). An adoral portion with a maximum length of 8o mm was sectioned 'vertically, the two halves shown in the upper parts of Plate 1, figures 10 and I I. A cross section was taken at the base of this portion but is not figured. It is the adoral end of a small portion missing from between the two parts of the specimen shown in Plate 1, figures 10 and II, the apical surface of which was broken irregularly. An additional basal portion was sectioned but neither side shows the siphuncle for much of its length, and indeed, it was impossible to obtain a perfect vertical section here because the adoral exposed surface failed to indicate clearly the position of the shell in the matrix. This specimen shows (lower part of pl. i, fig. 10) clear evidence of a very shallow basal septum, comparable to that shown in Thing I. However, the nature of succeeding septa is quite different. Septa are much farther apart in spacing, the axial zone is broad from the inception of the mature deep camarae, the peripheral zone is uniformly narrow. Indeed, were it not for the clear preservation of the basal septum, one would be tempted to consider this specimen as representing the homologue of a portion of a phragmocone comparable to that shown at the extreme anterior end of Thing 1. The illustrations show the irregularity of curvature and spacing of the septa, and detailed measurements are not necessary. Further enlargements of the extreme adoral part of the side of the specimen shown in Plate 1, figure 10, are presented in Plate 2, figure I, and the apical part of the same fragment, showing early septa and part of the siphuncle, is shown in Figure 2 of the latter plate.

The extreme base is anomalous, shown in the lower part of Plate 1, figure 10, on a surface consisting of two intersecting planes, and also shown restored in Text Figure 4. The siphuncle is not exposed. The basal septum is very shallow and thick and its sides extend forward as thick flanges, merging orad with the gray calcite of the first septum. It is odd that the shell wall does not penetrate to the apex but terminates in rather sharp, oblique surfaces on either side of the section. There is plainly nothing like the early crowded septa of Thing 1, which truncate each other, but rather here, the first septa are widely spaced. The first observed mature septal surface is rather broadly and gently curved; it forms the apical end of a broad area of gray calcite which could be interpreted

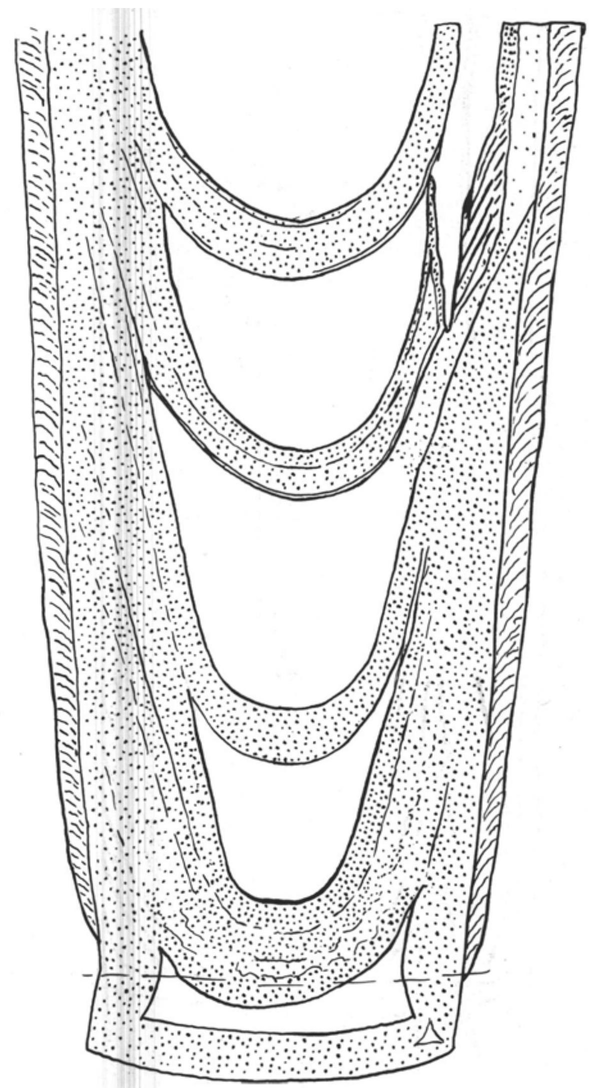

Figure 4

DRAWING OF ENLARGEMENT OF BASE OF THING 2, AS SHOWN IN PLATE I, FIGURE I I

The dotted transverse line at the lower part indicates the intersection of two planes. The siphuncle, in the upper right, is seen only in the adoral part of the section. The broad, forward projecting edges of the basal septum merge with dark calcite. It is not plain whether the first ephebic septum is thickened or whether two septa with their deposits are here in juxtaposition, but, plainly, there is no development of early ephebic septa, the earlier ones resorbed and truncated by the later ones, such as that developed in the preceding form.

either as a greatly thickened episeptal deposit or as replacing completely the material between this and the next septum. The latter interpretation seems the more probable of the two. In either case, the anterior surface of this gray region is sharply defined, is narrowly curved centrally with the sides extending steeply forward, and appears to be a septum with a thin episeptal deposit. The area of light calcite which follows is the nearest approach seen in this specimen to the small cup-shaped cavities which are so numerous and conspicuous in the small apical axial zone of Thing i. The next septum has similar straight, steeply sloping sides, but its axial part is a little less deeply curved. The broad band of gray calcite seen here is readily interpreted as a septum thickened with an episeptal deposit. The forward sloping sides surround an area of white calcite which broadens adorally and is bounded by another broad gray band of a septum, this one more broadly and shallowly curved. Two others follow, outlining broad axial elements, but variable and irregular in shape. The anterior part of the section shows some of the siphuncle but cannot be resolved clearly into septal necks and connecting rings.

The adoral portion of the section shows wide variation in expression of the septa and the deposits as well as of the siphuncle. The apical septum shown in Plate 2, figure z is a broad gray band of calcite; this band must incorporate the episeptal deposit, but the next septum is thin and shows two clear surfaces. Either the episeptal deposit was never developed here or by some quirk of replacement it is incorporated in the light calcite above. This calcite shows a band of more opaque white material bounding the central cavity, a band such as is common in the outer part of calcite filling an enclosed space inorganically. The next septum is represented by a broad band of gray calcite again; the next is thinner and lighter in color; several later septa, more broadly curved and shallower, show no apparent deposits centrally. Near the periphery, bands can be seen, plainly representing the anterior faces of the episeptal deposits. Camerae farther orad show shallower septa but are increasingly irregular, an effect which is partly explained by crushing to which the specimen has been subjected.

The siphuncle, clear over the entire anterior sectioned part, shows variable outlines. In the basal portion the siphuncle is slender and sinuous; orad of that region, the dorsal wall of the siphuncle is nearly straight where it is essentially in contact with the strongly forward sloping septum, but it tends to expand abruptly beyond the apparent anterior limit of the septum. The siphuncle wall along the septum seems to be composed of several layers, but the interpretation of the structure here is doubtful. One would be tempted to suggest a recumbent long septal neck, but thinsections of other specimens have failed to show any support for such an interpretation. It is necessary to admit that the present material shows such recrystallization that it is not possible to interpret the original nature of the siphuncle wall with certainty, and that more and better material will be required before such a study is possible. In more anterior segments the expanded part of the dorsal wall of the siphuncle becomes shorter and at the same time rather erratic, apparently from increased displacement due to crushing, and the segments still farther orad are ambiguous both as to original outline and structure. Near the adoral end of the section, however, it is possible to make out very steeply inclined lamellae between the siphuncle and the ventral wall, evidently septa and deposits, and the various lamellae, apparently uniform in present texture at least, are plainly in contact and build a solid structure there.

THING 3

Pl. 2, fig. 5; pl. 3, fig. 2

This is a portion of a shell, weathered from the dorsum as shown in Plate 2, figure 5, showing matrix in the base of the living chamber and calcite-filled camerae. The specimen is 75 to 8o mm long and shows a maximum width of 35 mm at midlength, the left side of the living chamber being lost anteriorly. It has closely spaced mature septa, their forward-prolonged edges seemingly jointed; calcite replacement leaves differentiation of possible cameral deposits and inorganic calcite in the camerae complex, but probably these adoral camerae lack organic deposits. The peripheral zone, developed in other specimens, is here vestigial and is not sharply set off from a wide axial zone. One could say that the peripheral zone is wanting here.

A vertical section was made through the siphuncle of the phragmocone, shown in Plate 3, figure 2. The extreme left shows the shell wall, here replaced and with the lamellar structure lost. Between it and the siphuncle are numerous steeply inclined lamellae in which septa and any possible cameral deposits are indistinguishable. It is important to note, however, that the lamellae apparently fill this region of the shell solidly. There is next an irregular band of light calcite with scattered round spots and irregular bands of gray vesicular calcite; this is plainly a replacement phenomenon.

The siphuncle is filled with matrix and is somewhat distorted, probably by compaction. Vexingly, while possible rather thick connecting rings can be made out on the dorsal side in the anterior segments, their real nature seems questionable, for there has been extensive alteration here. On the right (dorsal) side of the siphuncle the thin septa, not clearly differentiated from surrounding material and visible only as thin dark bands, terminate outside the calcite of the anterior segments. These are shown most clearly in the second siphuncle segment from the adoral end, but one cannot distinguish septal necks and connecting rings here with any certainty. It is possible that some of the calcite lying on the dorsal side of the siphuncle might be calcite material filling spaces on the upper side of the siphuncle cavity, supplementing an incomplete filling of the matrix. On the dorsal side of the siphuncle, the gray bands slightly anterior to the septa represent vesicular gray inorganic calcite developed on the surfaces of the episeptal deposits, here quite thin. Such material, indeed, forms a thick lining of the original cameral space. Whatever structure may have been present originally in the episeptal deposits is lost. The interior is now altered to light calcite with locally thinner gray linings of vesicular calcite.

THING 4

Pl. 2, fig. 4; pl. 3, fig. 1, 11

This is a portion of a phragmocone 8o mm long, expanding in width from 22 to 33 mm in the adoral 6o mm. It is weathered from the dorsal side, and the natural horizontal section shows eleven rather irregular septa, all with rather wide axial zones and with the peripheral zone extremely narrow. Septa are widened by thick but rather variable episeptal deposits, the two structures together forming gray bands of calcite.

A vertical thinsection was made from the apical part, shown in Plate 3, figure 1, and a horizontal section through the siphuncle was made from the adoral part, shown in Plate 3, figure 11. The vertical section shows on the left the shell wall, with some imbricating but relatively thin lamellae. Between the shell wall and the siphuncle there is only the faintest trace of the steeply inclined lamellae of the septa; replacement has occurred, leaving small dark nodules of gray calcite in a field of clear calcite. The siphuncle is made up of elongate segments showing slight and rather variable expansion concentrated on the dorsal side and developed largely in the anterior half of each segment. Septa can be seen on the dorsal side of the siphuncle; they join the siphuncle without any apparent development of the septal neck. The lines marking the anterior faces of the episeptal deposits swing strongly forward as they approach the siphuncle; each deposit itself is largely replaced and is filled with clear and vesicular calcite, as are the cameral spaces. There is a lining of vesicular calcite in the siphuncle, which is, from all indications, probably inorganic. The evident advanced condition of replacement leaves the nature of the siphuncle wall rather ambiguous. As noted before, the septal necks are not obvious but the wall shows indications of thick granular material, which appears, however, to lie outside the siphuncle proper and to be an adoral extension of the episeptal deposits. The true siphuncle wall appears to be extremely thin. It may be noted that the dorsal side of the siphuncle shows an expansion of the anterior part of the segment in the first and third segments illustrated, but not in the second. The septa which join the siphuncle on the dorsal side are anomalous, indeed unique, among cephalopods in their extreme thinness. It is not impossible that such very thin septa may be recurved in septal necks which, being equally thin, are not certainly recognizable; it is further possible that such necks might outline the anterior expanded part of the segments noted, but an interpretation in terms of septa without real development of necks is equally possible and more consistent with other observations.

The cross section made from the adoral part of this specimen shows some irregularities suggesting that the whole phragmocones had been crushed slightly, but vestigial necks can be seen sloping apicad with connecting rings represented by slightly darker material.

THING 5

Pl. 1, fig. 7-9; pl. 2, fig. 3; pl. 4, fig. 4-5

This specimen consists of a portion of a living chamber embedded in matrix with a maximum length of I 10 mm, 20 mm high and 35 mm wide at the base where fragments of the anterior marginal parts of the phragmocone are retained (see pl. 2, fig. 3). Several cuts were made through or tangential to the shell wall, revealing a thick wall composed of numerous conspicuous lamellae sloping obliquely forward and outward and indicating a shell of considerable thickness with originally a strongly rugose surface, a condition indicated but shown less conclusively by other material. Several thinsections were made through the shell wall. They show consistently fine lamellae, the presence of which so consistently preserved suggested most strongly a shell wall of original calcitic rather than aragonitic elements. Plate 4, figure 5 is a tangential section taken from the strongly curved lateral wall of the shell; the portion cut away was ground into a thinsection shown in Plate I, figures 7-9. Some, but not nearly all, of the variation in thickness shown is attributable to the angle between the shell and the plane of the section, but the difference between figures 7 and 8 and figures 9, Plate r, is certainly real. No clear inner layer of the shell is evident.

The nature of the shell wall in *Ecdyceras* as seen in thinsection is almost but not quite unique among Paleozoic nautiloids. The usual appearance of shell walls in nautiloids is quite different; most commonly they are occupied with irregular calcite crystals and fail to show growth lines or any real layering of structure. Such a condition is plainly derived and not original and is to be attributed to replacement of the original aragonite by calcite. There are cases known in other molluscs, however, in which this general composition is modified; the Pectens in particular show shells containing appreciable amounts of calcite. It is not unreasonable to believe that *Ecdyceras* represents a similar specialization among the Cephalopoda. The only other cephalopod in which I have observed structure at all similar is not yet figured. It is a species of *Eremoceras,* and even there the lamellae are steeper, the surface is not similarly rough and rugose, and the lamellae are preserved only in a small part of one thinsection.

II. THE TYPE MATERIAL OF ECDYCERAS *SINUIFERUM* Pl. 2, fig. 6-9; pl. 3, fig. 9, 10, 12; pl. 4, fig. 1-3

The holotype of *Ecdyceras* sinuiferum, here figured on Plate 3, figures 6-9, is an internal mold of a living chamber showing shadows of faint transverse rugose markings which describe a shallow, broad sinus across the strongly flattened venter but are elsewhere transverse. At the base is a septum 20 mm deep. Its suture describes a broad, rather deep lobe across the ventral face and a pair of lateral rounded saddles, separated by a broad shallow dorsal lobe. The septum is 20 mm deep, and its margins are so inclined forward that special lighting was necessary to bring out the suture in the present illustrations. The living chamber expands from 26 and 36 mm at the anterior limit of the suture to 32 and 42 mm in a length of 90 mm, beyond which the adoral end extends irregularly to an obliquely weathered surface, originally the surface of a ledge. The siphuncle on the septal surface is most indistinct but clearly rather close to the venter, and well ventrad of the nearly central point of greatest septal depth. In lateral view, the septum slopes more strongly forward from the point of greatest depth on the dorsum than on the venter.

The paratype is shown in Plate 4, figures 1-3. From its smaller diameter and more rapid expansion, it represents a younger growth stage than does the holotype and has attached to the base of the living chamber one additional camera, not two, as was mistakenly stated in the original description. The specimen, 118 mm in length, expands from its basal suture, where it is 17 mm high and 25 mm wide, to a width of 36 mm and an estimated height of 25 mm, near the adoral end which is incomplete and irregular. The dorsum is largely destroyed. The venter is flattened, as in the holotype, and the suture shows the same deep ventral lobe and shallow dorsal lobe separated by lateral saddles. The camera attached to the base of the living chamber has a length of 14 mm, but of this length, a distance of only 6 mm separates the two septa. A vertical section shows the camera filled with matrix, with no trace of cameral deposits. There is a rather large siphuncle, its outline rather obscure, which suggests considerable replacement of original materials. It appears that the septal necks are virtually nonexistent. The segment is essentially straight dorsally, though slightly convex near the anterior end, and considerably more strongly expanded ventrally, its adapical end being nearly in contact with the ventral wall of the camera.

A third living chamber associated with and collected with the two types, but not previously figured and not properly a paratype, is figured in Plate 3, figures 9, 10, and 12. It shows a portion of a shell 125 mm long expanding in width from 37 to 44 mm in 105 mm. Both ends are broken obliquely. The dorsal surface (fig. 9) is quite well preserved and shows, better than the associated types, the rugose character of the shell wall. The specimen is crushed, the ventral side distorted and preserved only in part, while the dorsum remains well and evenly arched in cross section. The basal 25 mm is calcite-filled and obviously consists of a series of crushed camerae, but structural details are destroyed by distortion.

III. THE TYPE MATERIAL OF PACHECDYCERAS *MURALE*

Pl. 3, fig. 4, 5

Pachecdyceras murale Flower (1947) was based upon a single living chamber. It shows a shell similar in general to *Ecdyceras* but smaller and more rapidly expanding, with what appears to be a shallower septum at the base. A peculiar thickening of the shell wall on the basal part of the living chamber shows a pattern of longitudinal ridges and depressions which is bilaterally symmetrical. Such a thickening has never been observed before in nautiloid cephalopods; it is unique in extending well forward from the basal septum for half the apparent length of the living chamber. However, the phragmocones here described supply another and a completely unexpected explanation for the features shown by this specimen. It is evident that the holotype of this species with the paratype and holotype of *Ecdyceras sinuiferum* form a series showing living chambers of progressively larger size, particularly in relation to the cross sections of the shells; there is also a progressive adoral reduction in rate of expansion. Further, the three forms can be interpreted as showing an adoral reduction in the extent to which the margins of the septa are extended forward. As seen from the sectioned phragmocones, this is a change which clearly took place in the ontogeny of the genus. Furthermore, the sections of phragmocones show that the edges of septa, with or without episeptal deposits, supply the obvious explanation of the apparent thickening of the shell at the base of the living chamber of *Pachecdyceras murale.* True, longitudinal ridges and grooves forming a similar bilaterally symmetrical pattern are not apparent, but this lack is not conclusive in the light of the limited material available for the present study. There was not enough material to permit study of the phragmocones by cross sections and so to determine whether the septa, with or without the episeptal deposits, produced such a bilaterally symmetrical pattern as is shown by *P. murale.* Probably sections through much of the material would have been inconclusive, inasmuch as recrystallization commonly destroys the individuality of septa and episeptal deposits in the marginal zones. The holotype of *P. murale* is roughly, but only roughly, commensurate with the two specimens at the regions close to the basal simple septum. Orad of this septum there is initiated a series of deep septa, the first of which either are apparently incomplete centrally or have their central portions thin and fused with the initial septum. The conclusion that the two genera and species are one is strongly indicated. However, there is opposing evidence to this view; the phragmocones in the association which yielded the types of E. *sinuiferum* show profound differences, as seen in the contrast between figures I and 2 and figures 10 and I1, in Plate 1. The present material is not adequate to show whether these forms represent two distinct species, but the question is certainly raised. Comparable differences in other and more usual cephalopods would certainly indicate different species. As it is, the present material is so bizarre and so widely different from any other cephalopods described before that generalizations on variation in other species may not necessarily apply here.

IV. SUMMARY OF THE CHAZYAN MATERIALS

As already noted, it is quite evident that the wide differences shown by Things 1 and 2 cannot be resolved as a single species without setting aside all previous experience and attributing to this species a wide, almost a wild, degree of variation within the species. The living chamber on which *Pachecdyceras murale* was based could not be an immature specimen of Thing 1, for the base shows a gentle curvature of the septum in the axial zone which is far broader than in commensurate parts of that form; nevertheless, its proportions are quite closely in accord with those of Thing 2. Of the smaller fragments, Thing 3 is clearly similar to Thing 2 to the exclusion of Thing I, but Thing 4 could be attributed to either one with about equal probability of correctness. Assignment of the holotype of *Ecdyceras sinuiferum* to either of these phragmocone types to the exclusion of the other is not possible with certainty, nor is the paratype of any real assistance in the solving of this problem. These two specimens could pertain to either of these phragmocones, and solution at the specific level must await the study of other and more comprehensive material.

Occurrence of the Chazyan Ecdyceras

The Chazyan material of *Ecdyceras* was collected by the writer from the type section of the Chazyan, except for one specimen. The exception, the holotype of *Pachecdyceras morale*, was found in the Jewett collection of Cornell University. Its label indicates that it came from the Chazyan at Chazy, New York, but is without more precise information. Inasmuch as the writer has not obtained material of this genus from any other section, in spite of rather extensive collecting with particular emphasis on the cephalopods in the Chazyan of the Champlain Valley, it seems probable that the Jewett specimen also came from the type section and from essentially the same stratigraphic interval within it. There is some doubt concerning the stratigraphic interval in which interpretation of previous stratigraphic interpretations of the section is involved.

The general region from which the specimens collected in *situ* were derived is shown in Text Figure 5.

A road leading southwest from Chazy forks just beyond the edge of the village; one fork continues south, ultimately to Plattsburg, but the other road, forking to the right (southwest), leads ultimately to West Chazy. Between 0.6 and 0.8 mile along the West Chazy road beyond the

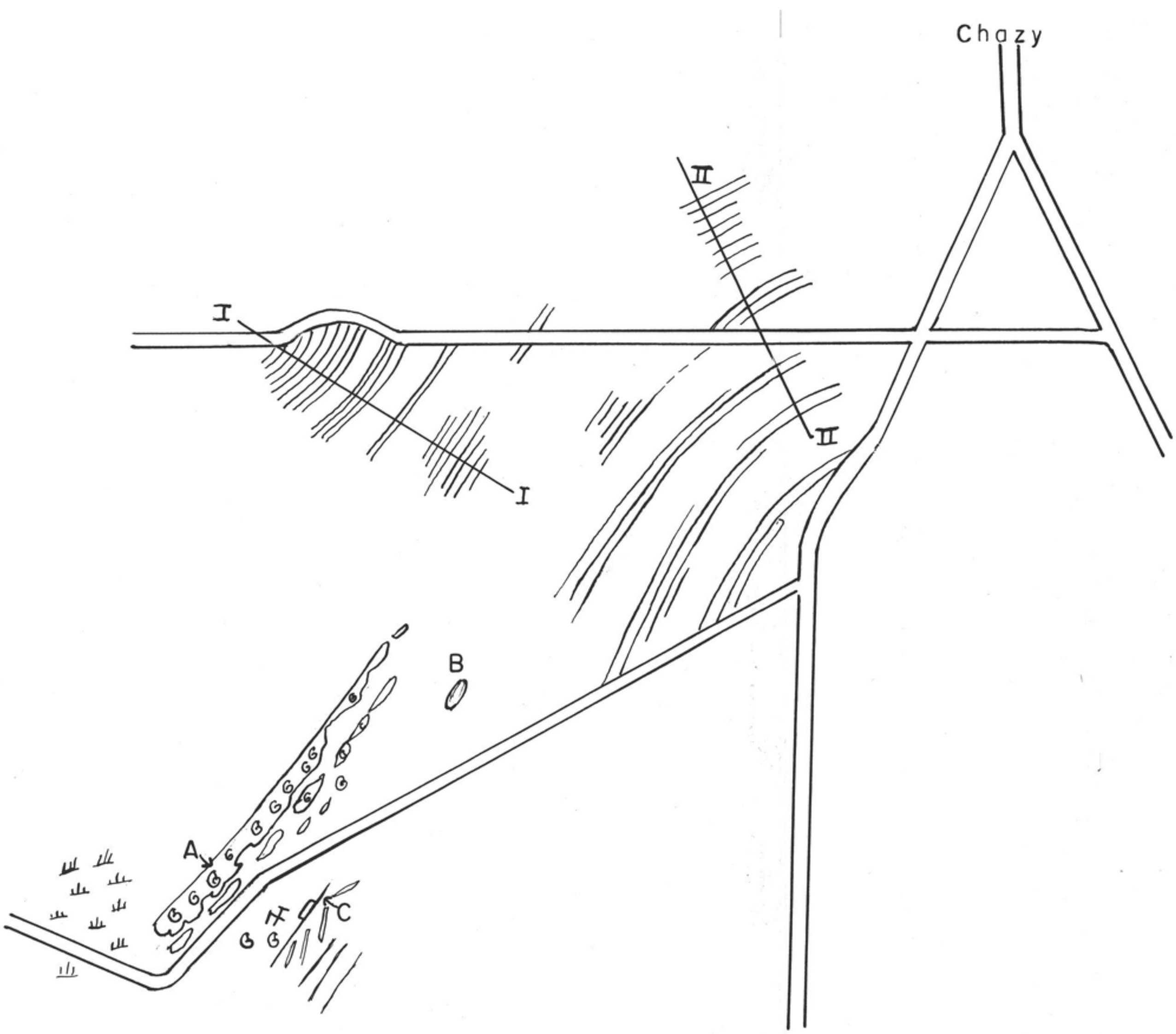

Figure 5

SKETCH OF THE CHAZYAN SOUTHWEST OF CHAZY VILLAGE, SHOWING SOURCE OF THE *Ecdyceras* MATERIALS

A indicates the prominent ledges with abundant *Maclurites*, B3 of Brainerd and Seely (1888). *B* indicates the small, stack-like outcrop logically interpreted as B4 of Brainerd and Seely, the source of the types of *Ecdyceras sinuiferum*. *C* indicates the beds, interpreted as the base of the Valcour Limestone, from which the phragmocones here described were derived. Proportions are not accurate, but the situation suggests close equivalence of *B* and *C*, contrary to previous interpretations. Above, sketched from Brainerd and Seely (1888), is the general strike and extent of exposure which those authors indicated, with I and II indicating the course of two of their measured sections.

fork, just before the road bends to the right (north) and passes through a small swale, there are extensive exposures of ledges on the northwest side of the road. Here there is a particularly prominent ledge (A in text fig. 5) with abundant *Maclurites*. Both the writer and Ruedemann (1906) interpret this ledge as B3 of Brainerd and Seely (1888). The ledge is almost but not quite the exclusive source of *Gonioceras chaziense* Ruedemann (1906); it is the source of the types and of considerable supplementary material (Flower, 1957). It is also the source of *Gonioceras brainerdi* (Flower). *Stereospyroceras clintoni* (Miller) is fairly common, and it is this same bed which has yielded much of the known material of *Ruedemannoceras boyci* (Whitfield). It contains also several endoceroid siphuncles, among them an undescribed *Cyrtovaginoceras*. Smaller fossils are scarce or inconspicuous or both. Raymond (1906, p. 542) has listed the fauna of this bed, aside from the cephalopods. It was in our initial exploration of the Chazyan of the Champlain Valley in 1935 that my father and I visited these beds and collected. We followed the strike of the most prominent of the ledges to the northwest toward Chazy, and at a point at which the ledgers become lower, and ground cover leaves only intermittent exposures, we turned back toward the road, encountering a small, stack-like outcrop of Chazyan with wavy bedding which was due to a reef-like concentration of *"Stromatocerium."** It is this small outcrop, indicated as *B* in Text Figure 5, which yielded the two types of *Ecdyceras sinuiferum* (Flower, 1941) and the third crushed living chamber, here figured in Plate 3, figures 9, 1 o, and 12. Return visits on later occasions failed to yield any more material from this spot. These beds are logically interpreted as B4 of Brainerd and Seely (1888), which they note as similar to B3 but "containing in addition to *Maclurea* various species of *Orthoceras* and large masses of *Stromatocerium."*

If, instead of proceeding to the prominent *Maclurites* ledges, at A in Text Figure 5, one passes instead to the opposite side of the road, thus ascending directly in the section, one will find a small abandoned quarry, really little more than a minor excavation. In the wall, not more than 4 feet high, there is exposed a 1- to 2-foot layer of white, sugary limestone with an abundance of rather undersized *Maclurites*, with some greenish dolomitic silt. This is followed by 1 to 2 feet of yellowish dolomite, above which are rather massive beds, weathering into slabs 4 to 1 o inches thick, on the surfaces of which are abundant large orthocones, occasional masses of *"Stromatocerium,"* and occasional slightly undersized *Maclurites*. It is these layers which have yielded the phragmocones which are the main occasion of the present work. I first encountered and collected some of these cephalopods while examining the section with Mr. Philip Oxley, who has since described the section (Oxley, 1951, p. 102) but has not mentioned the large orthocones which occur in beds that he then regarded as basal Valcour Limestone. Further, the orthocones appear to continue in fair abundance some considerable distance higher into the Valcour Limestone, over much of the so-called *Glaphurus pustulatus* zone. I say "so-called" because while the stratigraphic position of the fauna is valid, *Glaphurus* is wanting in the type Chazyan section as far as either my own experience or records indicate. Brainerd and Seely (,888) note *"Orthoceras"* not in the basal part of C but in C6, which is a z-foot bed 20 feet above the base of division C and 8o feet above the 90-foot interval of division B4 in which *"Orthoceras"* and *"Stromatocerium"* were noted. It seems rather anomalous that *Ecdyceras*, which seems to be peculiar to this one section, should have a vertical range of such great extent and that it should range in both divisions *B* and C, which were not only distinguished later as formations (Cushing, 1905) but have since been treated as stages (Oxley and Kay, 1959), a procedure which would imply some distinctness of strata and faunas. Text Figure 5 is admittedly a sketch in which proportions, reproduced from memory, are inaccurate. However, as one proceeds from A to *B* in Text Figure 5 one encounters partially concealed layers, all with a good scattering of *Maclurites* and none with abundant *"Stromatocerium."* One can see also that in Text Figure 5 there is a strong suggestion that localities B and C are essentially in the same strike, which suggests that they may be actually the same horizons.

Three collections of these cephalopods have been made from the lower beds of C at the type section. The first was made while going over the section with Philip Oxley in, I believe, 1958. A second and larger collection was made with the able help of Mr. Stanley Smith of the botany section of the New York State Museum. Both collections are at the New York State Museum and were not available for the present study. That institution lacked suitable facilities for the requisite sections, and though preliminary sections indicated the need for close study, the work had to be laid aside for other if less important duties. Having been informed (W. Goldring, *fide litt.*, 1953) that if I wanted to study my considerable collections I would have to do so at that institution, I made a third collection which supplies the main basis of the present work. This was obtained in the summer of 1958 on an occasion when I was accompanied, happily, by my wife and children, and, unhappily, by a persistent drizzle, without which the collection would have been more comprehensive.

If the above conclusions are true, previous treatments of the Chazyan type section still incorporate errors not yet resolved, involving rapid lateral facies change and also possible lenticular occurrence of some striking lithic and faunal associations. If they are not right, we are faced with an almost greater anomaly, the confinement of the remarkable genus *Ecdyceras* to this one section where, however, it is extended over a considerable stratigraphic interval involving the upper Crown Point and the lower half of the Valcour divisions. By the section of Brainerd and Seely, *Ecdyceras* should occupy at least 22 feet and probably more of division C and extend down 150 feet into the upper part of division B. It is the more curious in view of the treatment of the three divisions of the Chazyan as stages (Oxley and Kay, 1959), which would imply some real distinction capable of being recognized widely geographically. In this matter, it must be noted that the three divisions of Brainerd and Seely (,888) were given geographic names by Cushing (1905), and though Raymond (1906) noted some slight emendations in the boundaries of the significant faunal units with which he dealt, subsequent work has accepted these three divisions largely without critical inquiry as to how fundamental are the changes which mark their separation. This is the more surprising in the light of

* Galloway and St. Jean (5965) in their restudy of the Ordovician Stromatoporoidea have included several Chazyan species formerly assigned to *Stromatocerium;* these they refer with question to *Pseudostylodictyon*. No true *Stromatocerium* is known in the Chazyan, but I retain the older name here for reference in comparing with older descriptions of sections.

past and present perplexities as to the broad identification of the units. Division A was named by the Day Point Limestone and certainly the section which Cushing had in mind was that described by Ruedemann (1906, p. 398) at the Valcour shore immediately north of the fault to the south of which the Ft. Cassin beds are exposed. Raymond (1906) concluded from the fauna that these beds belonged to the Crown Point division, a conclusion later accepted by Ruedemann (1912). Though this perplexity is resolved, others remain which are not, for example, the proper position of the strata at the bay just north of Cystid Point on Valcour Island. Cooper (1956) has found the brachiopod faunas of the Crown Point and Valcour Limestones to be closely allied and that correlation of these two units together is possible over a rather wide area. In contrast, the brachiopod fauna of the Day Point member is small but so distinctive that no other strata in North America are placed as its equivalents in his chart. The writer has found the small cephalopod association of the Day Point Limestone also distinctive. One genus, *Baltoceras,* is certainly dominantly Whiterock in age, and the same may be true of *Mesnaquaceras,* while the associated endoceroids are of little stratigraphic value in the present state of our knowledge. *Murrayoceras* makes its earliest known appearance in the column here, but it is a genus which, while recurring in beds ranging from Lowville to Rockland, is completely unknown in the middle and upper Chazy faunas of the Champlain Valley.

The previous literature has involved errors in identification of strata which are probably even yet not completely eliminated and corrected. It is the belief of the writer that such misidentification is involved in the forms which, from the literature, appear common to the Day Point and Crown Point Limestones. If so, the present indications that the Crown Point and Valcour Limestones have much in common faunally, while the Day Point below retains its own individuality, would suggest that it might be profitable to review a long-overlooked question; namely, whether the Day Point is not sufficiently different from the beds above that it would be advantageous to return to the original definition of the Chazyan of Emmons (1842) which excluded these lower beds (Oxley and Kay, 1959, p. 817).

Other Occurrences of Ecdyceras

Only two occurrences of *Ecdyceras* are known outside that of the Chazyan of the Champlain Valley, discussed above; indeed, one can say outside of the type section of the Chazyan. *Ecdyceras foerstei* Flower (1946) was described from a single specimen from the Arnheim beds at the edge of Lebanon, Kentucky. The specimen consists of a living chamber and four attached camerae. The septum at the base is deep but its suture is relatively clearly defined. The specimen came from very silty limestones dominated by an association of pelecypods. It shows slight distortion. Experience with this type of preservation indicates that an attempt to study the interior by sections would be most unrewarding. It is of interest to note that the septa are thin and that there are quite clearly no episeptal deposits developed in the four observed camerae.

A second occurrence is that of *Ecdyceras expansum,* based upon the basal part of a living chamber from the basal Viola Limestone of Oklahoma, described below.

Neither of these known occurrences has yielded any of the earlier parts of the phragmocone, though associated material was examined. It seems possible that portions of phragmocones may have been found but not recognized, for the relatively solid calcite-filled portions may, under recrystallization of the calcite, lose their structure entirely. Such specimens, possibly rod-like bodies filled with coarse calcite crystals, can be developed also from calcite-filled phragmocones of Michelinoceratida, and again a similar effect could result from recrystallization of endoceroid endosiphuncles. No such forms have been recognized, nor have I found them at the type locality of *Ecdyceras foerstei,* which I had an opportunity to visit with the late Dr. W. H. Shideler. Possibly if such specimens have been found they have been discarded as unidentifiable. Specimens retaining the small cup-shaped cavities of the axial zone could be mistaken for something of the *Beatricea-Aulacera-Cryptophragmus* persuasion. Inquiry of Dr. J. J. Galloway, then close to completing a study of Ordovician Stromatoporoidea, as to whether he had encountered any such specimens yielded a negative answer. Examination of the stromatoporid collection of the U.S. National Museum, as well as several likely regional and stratigraphic collections, proved equally fruitless.

Clearly, the three occurrences of the genus known at present are most anomalous, and no convincing explanation in terms of faunal migrations can be offered. One can only hope that the present work will, in calling attention to this remarkable form, lead to future observations and discovery of additional occurrences of the genus.

Ecdyceras expansum, n. sp.

Pl. 3, fig. 6-8

All that we have of this form is the basal part of a straight living chamber, the affinities of which are indicated by the faintly sinuate suture at its base and the extremely deep rounded subconical septum, steeper ventrally than dorsally; but this is enough to indicate that the shell is an *Ecdyceras.* The fragment of living chamber expands from 2o and 29 mm at the basal septum to 26 and 40 mm in a length of 5o mm. The internal mold of the living chamber is rough, weathered, and nondescript. The suture at the base shows a very faint, broad, dorsal lobe, a deeper ventral lobe. The septum has a depth of I I mm, about half the height of the shell at this point. The septal surface is rough and the septal foramen is not apparent. The broad cross section and marked flattening of the venter are peculiar to *Ecdyceras.*

Discussion. Notable for this species is the rather rapid lateral expansion of the living chamber; in other species the living chambers are nearly tubular. The septum is typical of mature *Ecdyceras;* an immature specimen would be expected to show a much deeper septum so that in spite of the rapid lateral expansion of the shell, a feature which, indeed, has not been observed in the young of the typical Chazyan forms, there is no reason to regard this specimen as representing an immature individual.

Holotype. U.S. National Museum.

Occurrence. From the base of the Viola Limestone, from one mile southwest of the McLish ranchhouse, Oklahoma.

Revisions of Ecdyceras

Ecdyceras Flower, 1941, Jour. Paleont., v. 15, p. 246-247. ---- Flower, 1946, Bull. Am. Paleont., v. 29, n. 116, p. 19o.
Pachecdyceras Flower, 1947, Jour. Paleont., v. 21, n. 5, p. 429.

As revised, *Ecdyceras* comprises straight shells of depressed cross section, the venter prominently flattened. Attached to rather long, straight living chambers with thick rugose shell walls are phragmocones, equal to or greater than the living chamber in length, in which there is an apical, very shallow, thick septum, reasonably regarded as a septum of truncation. This is followed abruptly by a series of very deep septa, the edges extended strongly forward. Episeptal deposits are thick peripherally, filling the camerae completely, and thin axially, leaving deep, cup-shaped cavities in the camerae, thus forming a phragmocone with strikingly distinct peripheral and axial zones. With growth, the axial zone widens at the expense of the peripheral zone, which may be completely lost at the base of the mature living chamber. Deposits within the camerae thin in a short adoral interval and are apparently completely wanting in a further short adoral interval of phragmocone.

The contrast between the basal septum and those immediately following it is fully as great as the contrast between the septum of truncation and the sigmoid septa in *Ascoceras*, and it is reasonable to hope that, as was found for *Ascoceras*, ancestors of *Ecdyceras* may be found showing less abrupt ontogenetic changes. It is also reasonable to believe that the as yet unknown earlier stages of *Ecdyceras*, which from the thick, flat, basal septum may be reasonably regarded as molted during the life of the animal, were relatively simple and unlike the adult condition, again showing a parallel with *Ascoceras*, the early stages of which were described by Lindstrom (189o). Here, however, the parallel ends, for though there is evident molting in the two genera, with the removal of young stages very different from the adult shell, the adult parts are not remotely comparable. *Ascoceras* has for an adult shell one that is fusiform, thin, evidently light, with septa immensely extended forward dorsally, and with small, broadly expanded siphuncle segments. It is a form well adapted for swimming. *Ecdyceras*, on the other hand, retains a considerable length of phragmocone in which the broad cross section, the thick rugose wall, and the almost complete filling of the apical part indicate an extremely heavy shell which is, indeed, the heaviest and the most obviously benthonic of any known in the Nautiloidea.

Order Ecdyceratida

It is evident from the material described above that no other nautiloid—indeed, no other cephalopod—is known which is at all closely similar to *Ecdyceras*, and the only possible taxonomic treatment of the genus requires its separation in a family and an order by itself. The order Ecdyceratida may be defined as containing straight shells, the early part presumably molted, but leaving attached to the living chamber a long interval of phragmocone which has, beyond a single, shallow, thick basal septum, a series of septa with the edges greatly extended forward. Episeptal deposits thin centrally, leaving deep cup-shaped cavities, and are so thick peripherally that except in a short anterior region where, as usual, such deposits are immature and finally wanting, the peripheral zone is solid. The siphuncle, between the center and the venter, is thick-walled apically, traversed by a few diaphragms, and thinner adorally; but astonishingly thin septa show no clear necks and the segmentation of the connecting ring is obscure. The family Ecdyceratidae, having the features of the order, is proposed here.

Only two orders can be considered as containing its possible ancestors, the Michelinoceratida and the Ellesmeroceratida.

Origin in the Michelinoceratida is suggested by the fact that the higher Ascoceratida show in their specialized Ascoceratidae roughly parallel features: molting of early shell parts and a septum of truncation beyond which there follow highly specialized septa and siphuncles, quite unlike those of earlier shell parts. However, such specialization, with omission of transitional ontogenetic stages, is approached only by the first Ascoceratidae in the Upper Ordovician and is not perfected before the Middle Silurian. Chazyan Ascoceratida, the Hebetoceratinae of the Hebetoceratidae, are relatively simple, lacking the ascoceroid sigmoid septa and showing only slight specialization of the adoral septa and siphuncle segments.

Such a specialized condition as that shown by *Ecdyceras* suggests a comparably long history of evolution, and origin in the Michelinoceratida seems unlikely inasmuch as that order is not widely represented in beds prior to the Chazyan. Current information indicates that there were quite numerous members of the order, though apparently involving only three families, in the Whiterock, with which the Upper Red Orthoceras Limestone is probably to be correlated. Investigations as yet unpublished indicate the presence of two families, the Michelinoceratidae and the Troedssonellidae in the very latest Canadian—the Odenville and its equivalents—and rare fragments indicate the presence of Michelinoceratidae somewhat lower in the Cassinian. Though the development of cameral deposits suggests possible origin in the early Michelinoceratidae, present stratigraphic evidence suggests that *Ecdyceras* is so specialized that its origin is more likely to be found in some stock known to go back considerable further in geological time.

Such an older stock is found in the archaic Ellesmeroceratida. To be sure, *Ecdyceras* is quite remote in structure from known members of the order, but two features, the thick wall of the connecting ring and the diaphragms crossing it, are found in the more primitive members of that group, the Plectronoceratidae and the Ellesmeroceratidae. The tubular siphuncle and the well-calcified condition of the wall suggest the Ellesmeroceratidae as a possible source. Likewise, it is only in an *Eremoceras*, a member of the Ellesmeroceratidae, that anything approaching the imbricating lamellae of the shell wall of *Ecdyceras* has been found. By itself, this fact is hardly significant in view of the general loss of textures in nautiloid shell walls, but it may possibly prove significant in the light of other indications suggesting derivation of the Ecdyceratida from the Ellesmeroceratida. It is not possible to go beyond these generalizations at present, save to emphasize again that the morphological evidence of ancestry is scant and that present observations indicate such interpretations as seem possible, but which cannot be demonstrated until older forms are found bridging the morphological gap between *Ecdyceras* and its ancestors.

Acknowledgments

I am indebted to the Paleontological Research Institution and to its director, Dr. Katherine V. Palmer, for the loan of the types of *Ecdyceras* sinuiferum. For discussion of the remarkable morphological problems presented by *Ecdyceras* and for aid in the search for possible additional material, I am indebted to Dr. K. E. Caster, the late Dr. W. H. Shideler, Dr. G. A. Cooper, Miss Helen Duncan, Dr. Jean Berdan, Dr. Robert Neumann, and Dr. J. J. Galloway. There was reason to hope that phragmocones of *Ecdyceras* might have been mistakenly identified with stromatoporids of the *Beatricea-Aulacera-Cryptophragmus* persuasion, but none was found either in the collections of the U.S. National Museum, examined through the kindness of Dr. G. A. Cooper, or in the material gathered by Dr. Galloway for his recent study of the Ordovician Stromatoporoidea (Galloway and St. Jean, 1961).

I must also express my deep indebtedness to the authorities of this institution, Dr. E. J. Workman, president, and Mr. A. J. Thompson, director of the State Bureau of Mines and Mineral Resources, for adequate laboratory facilities, particularly the rather exceptional cutting equipment necessary for the study of this form, and for their willingness to publish the results of this investigation, which is more of systematic than of regional significance.

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PLATES 1-4

WITH EXPLANATIONS

PLATE 1

CHAZYAN ECDYCERAS

Figure

1-2. Opposing surfaces of a vertical section through Thing 1, × 1; venter and siphuncle are at the left of fig. 1 and at the right of fig. 2.

3-4. Enlargements, × 2.5, of the basal portion of the same specimen showing the nearly flat basal septum and traces of steeply inclined septa in the peripheral zone; the lower left of fig. 3 shows the siphuncle, penetrating the basal septum below, and arcuate immediately above; the upper right of fig. 4 shows the anterior part of the siphuncle, straight and traversed by diaphragms. See also Pl. 4, fig. 6-7.

5. Cross section, × 1, at position of the anterior transverse cut in fig. 1-2, venter below, showing position of siphuncle and shape and position of deep chambers of the axial zone. Recrystallization has destroyed differentiation of septa and deposits in the peripheral zone.

6. Enlargement, × 2.4, of the anterior part of fig. 1, showing anterior widening of the axial zone, variations in preservation of septa and episeptal deposits; showing the siphuncle at the lower left, where it is tubular, and again at the upper left where segments are fusiform in outline.

7-9. Thinsections, all × 5, through the shell wall. Fig. 7 shows a relatively thin wall with oblique lamellae, the outer surface to the left. In fig. 8 the outer surface is to the right and thickness is more variable. In fig. 9, taken from the adoral portion of Pl. 2, fig. 3, at a late growth stage, the great thickening of the wall is largely real, though exaggerated slightly because the plane of the section is not quite vertical. All from Thing 5.

10-11. Opposing surfaces of an essentially vertical section through Thing 2, × 1; note the very different proportions in comparison to fig. 1 and 2 of this plate. See also Pl. 2, fig. 1 and 2.

All material is from the type section of the Chazyan, near Chazy, New York, and is in the collection of the writer.


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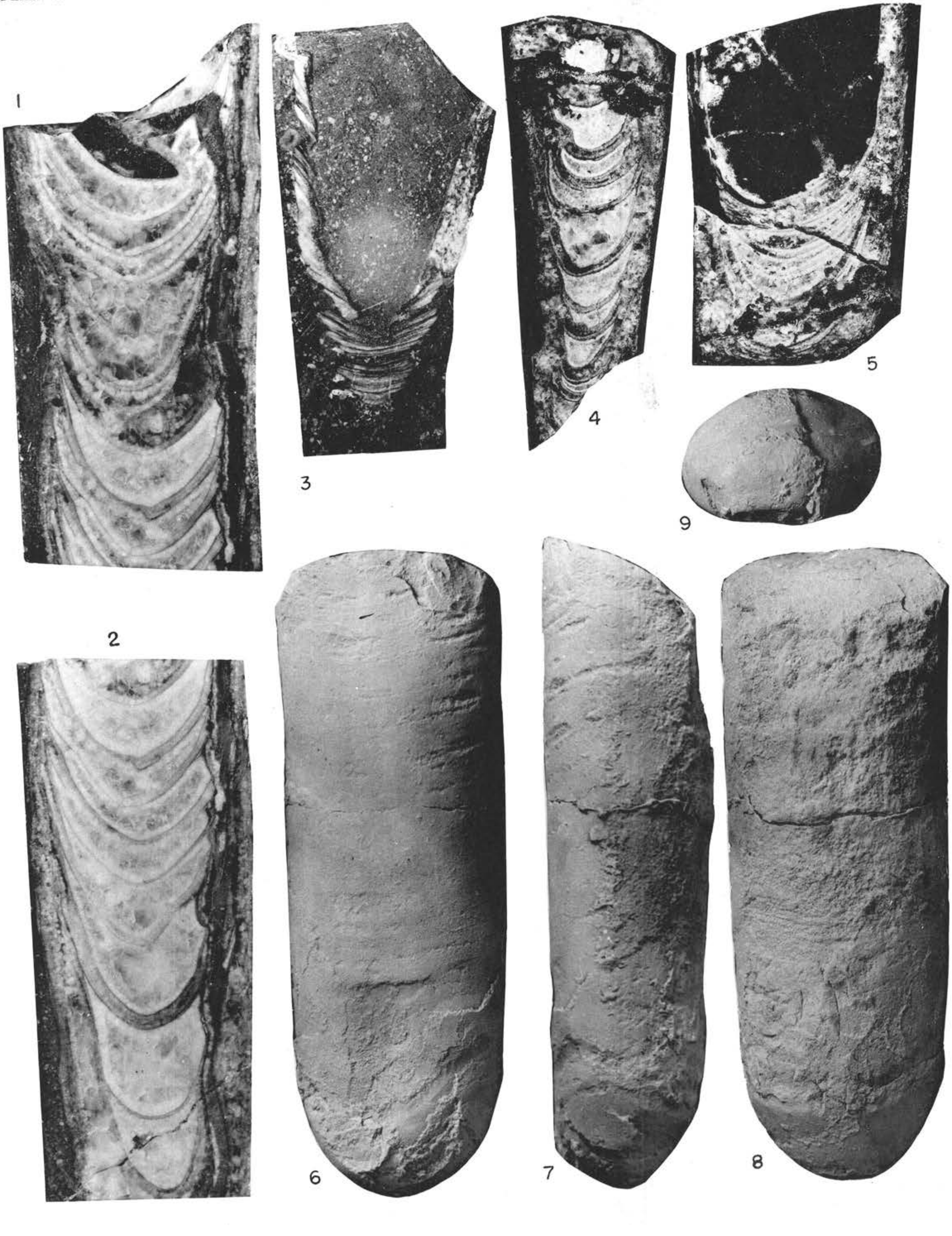
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PLATE 2

CHAZYAN ECDYCERAS

1. Enlargement, × 2.5, of the anterior end of Pl. 1, fig. 10, showing variation in septa and deposits, some displacement due to crushing, and the siphuncle at the right. Thing 2.

2. Enlargement, ×2.5, from the middle portion of Pl. 1, fig. 10, showing details of septa and deposits and, at the left, the siphuncle, which is tubular and sinuate basally but which shows irregular expansion of the anterior end of segments dorsally in the adoral portion.

3. Portion of a living chamber, × 1, sectioned and showing the thick rugose nature of the shell wall. Thing 5.

4. Portion of a phragmocone weathered from the dorsal side, × 1, showing deep irregular septa in a rather wide axial zone, their edges indistinguishable in the peripheral zone. The thinsections shown in Pl. 4, fig. 1 and 11 are from this specimen. Thing 4.

5. Portion of a specimen weathered from the dorsal side, × 1, showing the basal part of a living chamber and anterior camerae, nearly mature, but evidently representing a slightly earlier growth stage than the holotype of *E. sinuiferum*. The upper part is incomplete on the left; on the right, the extreme adoral prolongation of the septa is shown. Thing 3.

6-9. The holotype of *Ecdyceras sinuiferum*, × 1; fig. 6, ventral view; 7, lateral view, venter on left; 8, dorsal view; 9, apical view, venter below. Paleontological Research Institution No. 5939.

All material is from the Chazyan, near Chazy, New York.

PLATE 3

ECDYCERAS, from the Chazyan of the Champlain Valley, and from the Viola of Oklahoma.

1. Vertical section through the phragmocone and siphuncle from the anterior part of Pl. 2, fig. 4, × 5. Matrix at the extreme left is followed by a rather thin shell wall; between this and the siphuncle, replacement leaves a band of clear calcite with round vesicular bodies. The siphuncle itself shows some displacement from crushing; to the right, the slightly curved, dark bands are septa; more steeply inclined bands mark the anterior limits of episeptal deposits; material in the deposit is replaced, and both deposits and cameral spaces show linings of vesicular calcite with clearer calcite occupying the centers. Thing 3.

2. A vertical section, × 5, from the basal part of Pl. 2, fig. 5. The steeply inclined septa with episeptal deposits indistinguishable, are seen between the siphuncle, here filled with matrix, and the shell wall at the extreme left. As in fig. 1, lamellar calcite marks the septa and surface of episeptal deposits. Thing 4.

3. A portion of a thinsection, × 5, taken tangential to the shell wall, from surface opposing that in Pl. 4, fig. 5.

4-5. The holotype of *Pachecdyceras murale* seen from the ventral side in fig. 4, from the dorsal side in fig. 5. From the Jewett collection of Cornell University.

6-8. *Ecdyceras expansum* Flower, n. sp., three views of the holotype, all × 1, which preserved only the basal part of a living chamber; fig. 6, ventral view; 7, lateral view, venter on left; 8, dorsal view. U.S. Geological Survey collection, U.S. National Museum, from the basal Viola Limestone, one mile south of the McLish ranchhouse, Oklahoma.

9-10, 12. Three views of a crushed specimen, all × 1, a living chamber with a small portion of phragmocone at its base, associated with the types of *Ecdyceras sinuiferum*. Fig. 9, dorsal side, well elevated, uncrushed, and showing the rugose shell markings; 10, lateral view, venter on right; 12, apical view, venter below.

11. Horizontal longitudinal section through the siphuncle, × 5, taken from the basal portion of Pl. 2, fig. 4. Evident displacement is indicative of slight crushing. The shell wall is seen at the left, but not attained at the right. The siphuncle in the right third of the figure shows faint indications of vestigial septal necks, but alteration complicates the interpretation of the connecting rings. Thing 3.

All except fig. 6-8 are from the type section of the Chazyan, at the southwestern edge of Chazy, New York.


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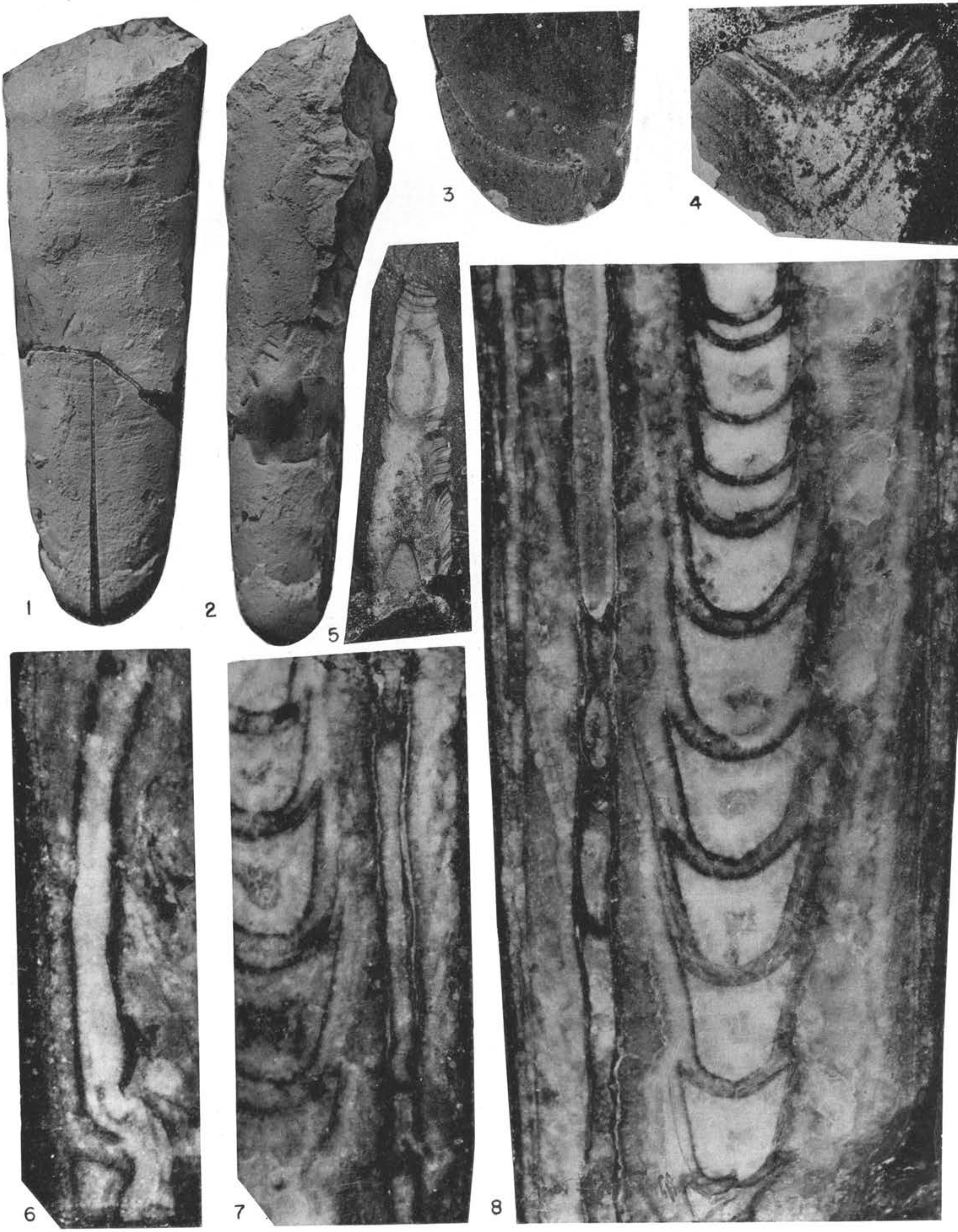
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PLATE 4

CHAZYAN ECDYCERAS

1-3. The paratype of *Ecdyceras sinuiferum* Flower, a specimen incomplete adorally but evidently representing a slightly earlier growth stage than the holotype and retaining one adoral camera. Fig. 1, ventral view, × 1; 2, lateral view, venter on left, × 1; 3, vertical section from the basal part, × 2.5, showing a vertical section through the one retained camera and the outline of the siphuncle. Note the clear absence of episeptal deposits. Paleontological Research Institution, No. 5940.

4-5. Tangential sections through the shell wall. Thing 5. Fig. 4 is a thinsection, × 5; 5 shows a chance section largely tangential to the strongly curved lateral part of the living chamber. Fig. 5 is a longitudinal tangential section, ×2, from the lateral portion of the shell wall.

6. Enlargement, about × 5, of the lower left of Pl. 1, fig. 1 and 3, showing the appearance of the siphuncle at and just beyond its passage through the basal septum.

7. Enlargement, about × 5, of the lower part of Pl. 1, fig. 2 (the anterior end of pl. 1, fig. 4), showing the succeeding tubular thick-walled part of the siphuncle, with margins of the cavities of the axial zone and indication of steeply inclined septa in the peripheral zone.

8. Enlargement, about × 5, of the middle portion of Pl. 1, fig. 1, showing details of septa and siphuncle.

All material is from the type section of the Chazyan.

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Numbers in boldface indicate main references.