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REVISION AND INTERNAL STRUCTURES OF LEUROCYCLOCERAS

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ABSTRACT. *Leurocycloceras* is revised on the basis of internal and external shell features to include Silurian species formerly included in *Cycloceras* and *Geisonoceras*. Internal structure is uniform and of the type of "*Orthoceras*" *brucense*, which species falls within the genus as redefined. The known American species are summarized and one new one is described. Mention is made of European forms. The nomenclatorial problem and isomorphism of early Paleozoic "*Cycloceras*" is summarized.

A dolomitized internal mold shows details of the cameral deposits. A new type of lobation of cameral deposits, evidence of vascular tubes in the cameral mantle and of parasitic organisms living in cavities in the cameral deposits are discussed.

INTRODUCTION.

An exceptional specimen consisting of dolomitized fillings of camerae of *Leurocycloceras* cf. *niagarense* (Hall) loaned by the United States National Museum made possible a study of the surfaces of the cameral deposits in a form group previously designated as that of "*Orthoceras*" *brucense* (Williams) because at the time when its structural features were noted, no described genus was known to be restricted to the group (Flower 1939, pp. 53-58). Foerste (1928, p. 267, Pl. 54, Fig. 3; Pl. 57, Fig. 5) had reillustrated and redescribed this species, which he referred to *Cycloceras* McCoy. That generic designation was not followed for two reasons: (1) The genotype of *Cycloceras* is so inadequately known that no other species can be placed in the genus with certainty (Miller, Dunbar and Condra 1933, p. 45), and (2) the ornamentation of the species was not typical of *Cycloceras* but instead suggested *Geisonoceras*.

Study of this and related species shows that Foerste was correct in recognizing the affinities of this species with others from the Silurian which he placed in *Cycloceras*. As his specimens were internal molds which cannot be expected to retain surface detail, he assumed that the absence of fine transverse surface markings such as are generally considered typical of *Cycloceras* was more apparent than real. However, a closely related form, described below as *Leurocycloceras bucheri* Flower n. sp., from the Laurel limestone of the Middle Silurian of Indiana, where the surface features are very clearly preserved, shows that except for the annuli the surface was actually smooth. Further study showed that there was gradation between forms of cycloceroid aspect with relatively narrow and prominent annuli, and forms of geisonoceroid aspect, with the annuli so broad and flat that the really striking surface features are the transverse grooves or striae which represent the interspaces of cycloceroid forms. Species with such external features have been placed in *Geisonoceras* in the past. The Laurel material also furnished the basis for the study of much of the internal structure by which forms of such different external aspect can be connected.

SYSTEMATIC DESCRIPTION.

LEUROCYCLOCERAS Foerste emend. Flower

Genotype: *L. raymondi* Foerste, Racine dolomite of Wisconsin.

Leurocycloceras Foerste, 1928, Denison Univ. Bull., Sci. Lab. Jour., Vol. 23, p. 272.

Conch orthoceraconic, slender, circular or slightly compressed in section. Sutures straight and transverse or slightly oblique, if oblique sloping orad on the dorsal (antisiphonal) side. Surface of shell marked by low annuli, in some shells so broad and flat that the interspaces appear as narrowly incised striae on an otherwise smooth exterior. Internal features are typical of the group of "*Orthoceras*" *brucense* (Flower 1939, pp. 53, 56-57), consisting of moderately developed episeptal deposits, strongly developed hyposeptal deposits and no siphonal deposits (Plate 2, Fig. 5). The connecting ring is unknown, and must have been either very poorly calcified or else altogether absent. The septal necks are unusually long and straight, and in advanced stages of growth may be entirely enclosed by cameral deposits which join through the septal foramen (Plate 2, Figs. 4, 5). Conchial and septal furrows have not been observed in the genus.

Discussion.—The genus as here defined is confined to species of Middle Silurian age. The slender form of the conch, the tendency for the development of a compressed section and the eccentricity of the siphuncle coupled with a corresponding asymmetrical curvature of each septum so that the septal foramen is at the point of greatest septal depth, have been found highly useful in recognizing the genus among other associated forms, particularly when preservation is such that the diagnostic surface features of the shell are not clearly shown.

The following list presents the known American species. The references given here pertain to Foerste's descriptions and illustrations which are more accurate and more detailed than the originals of the older species. The species are divided roughly into two groups on the basis of surface features as a matter of convenience. Such a division is not infallible, and *L. bucheri* suggests that the "geisonoceroid" ornament may occur in the early stages of all species.

I. Annuli narrow and prominent; appearance of conch annulated.

L. niagarense (Hall) (Foerste 1928, p. 266, Pl. 55, Fig. 2; Pl. 57, Fig. 1; Pl. 75, Fig. 10). Racine dolomite of Illinois.

L. jolietense (Foerste) (Foerste 1928, p. 268, Pl. 55, Fig. 1). Joliet limestone of Illinois.

L. austini (Foerste) (Foerste 1928, p. 269, Pl. 56, Fig. 1, Pl. 75, Fig. 6). Cedarville dolomite of Ohio.

L. semotior (Foerste) (Foerste 1928, p. 269, Pl. 56, Fig. 2; Pl. 57, Fig. 3). Joliet limestone of Illinois.

L. junciforme (Foerste) (Foerste 1928, p. 270, Pl. 56, Figs. 3-4). Cedarville dolomite of Ohio.

L., sp. (Foerste) (Foerste 1928, p. 271, Pl. 57, Figs. 2, 6, 7). Port Byron dolomite of Illinois.

L. raymondi Foerste (Foerste 1928, p. 272, Pl. 56, Fig. 5; Pl. 57, Fig. 4). Racine dolomite of Wisconsin.

L. wisconsinense Foerste (Foerste 1928, p. 273, Pl. 56, Figs. 6-7). Racine dolomite of Wisconsin.

II. Annuli broad and flat, surface apparently smooth with narrowly incised distant tranverse striae.

L. bucheri Flower, n. sp., Laurel limestone of Indiana.

L. brucense (Williams) (Foerste 1928, p. 267, Pl. 54, Fig. 3, Pl. 57, Fig. 5). Guelph dolomite, Bruce peninsula, Ontario.

L. (?) *byronense* (Foerste) (Foerste 1928, p. 246, Pl. 51, Fig. 3). Port Byron dolomite of Illinois.

L. franklinense (S. A. Miller) (Foerste 1928, p. 255, Pl. 52, Fig. 5). Laurel limestone of Indiana.

L. rochesterense (Foerste) (Foerste 1928, p. 254, Pl. 53, Fig. 1). Rochester shale of New York.

The following key will serve to present some of the more salient distinctive character of the American species.

KEY TO AMERICAN SPECIES OF LEUROCYCLOCERAS

A. Small, slender species with low transverse annuli; maximum rate of expansion 2 mm. in 100 mm.

- B. Depth of camerae greater than conchial diameter .... *semotior*
- BB. Depth of camerae not greater than conchial diameter
  - C. Depth of camerae subequal to conchial diameter; gerontic camerae occurring beyond diameter of 25 mm. .... *austini*
  - CC. 2-3 camerae in length equal to adoral conchial diameter; gerontic camerae at diameter of 20 mm. ...... *junciforme*

AA. Small, slender species with markedly oblique annuli. Rate expansion 2-3 mm. in 100 mm.

- D. Annuli prominent, close .... *raymondi*
- DD. Annuli very faint, more distant .... *wisconsinense*

AAA. Size larger; rate of expansion at least 5 mm. in 100 mm.

- E. Rate of expansion large; more than 10 mm. in 100 mm.
  - F. Size small, septum one-third conchial diameter in depth .... *byronense*
  - FF. Size large, septum not more than one-fifth conchial diameter in depth .... *jolietense*
- EE. Rate of expansion moderate
  - G. Conch attaining diameter of 50 mm.; annuli convex ephebically .... *niagarense*
  - GG. Conch smaller; annuli considerably flattened.
    - H. Sutures oblique, annuli obscurely rounded in ephebic portion .... *bucheri*
    - HH. Sutures transverse. Annuli definitely flattened
      - I. Siphuncle twice as far from dorsum as from venter, annuli occurring about 7 in 20 mm. throughout .... *brucense*
      - II. Siphuncle only slightly eccentric, annuli occurring four in length of 20 mm. ..... *franklinense*

L. rochesterense, known only from flattened individuals is not included It resembles *L. franklinense* and *L. brucense* in surface features, but is much larger than either species. If allowance is made for distortion, the species will run out near *L. brucense.*

Related European Species.—On the basis of Barrande's illustrations it is possible to recognize a species from the Silurian of Bohemia as belonging to *Leurocycloceras. L. sarcinatum* (Barrande, 1866, p. 149, Pl. 341, Figs. 19-20) is based upon a single camera and was given a specific name largely because of the peculiar structure shown on the surface of the septum. Here are shown paired radial grooves almost identical with those shown on *Leurocycloceras* cf. *niagarense* described below. The specimen obviously represents the internal mold of episeptal deposits and is not, as Barrande supposed, the surface of a septum. The similarity is so striking that there can be little doubt but that it is closely related to this American species.

The anomalous *Orthoceras truncatum* Barrande (Pls. 341-343) shows several features which suggest *Leurocycloceras.* The section is faintly compressed, the surface bears fine, distant transverse striae comparable to the ornamentation of *L. brucense* and its allies. The slightly eccentric siphuncle has very long straight necks and the connecting ring in its universal absence suggests that it was very poorly calcified or else originally absent. According to Barrande, some 400 specimens are known which retain at the most six camerae. The quantitative evidence supports his suggestion of natural truncation of the apex during life. However, the structures shown on adapical septal surfaces which have been interpreted as representing cementation of the broken apex are open to a very different interpretation, and more probably represent the surfaces of hyposeptal deposits. The camerae have evidently been broken at the point of greatest weakness, namely along the region of the pseudoseptum. Here, as in *Leurocycloceras*, the final fusion of episeptal and hyposeptal deposits is considerably delayed, and the deposits are normally narrowly separated until a very late stage of growth. This furnished a line of weakness at which the shell may be expected to yield under such stresses as would be supplied by movement of the animal and the action of waves and currents. The apical ends of specimens of *Leurocycloceras bucheri* are typically broken at this region (Pl. 3, Fig. 3), but it is not certain whether truncation is natural or accidental.

The episeptal deposits of *Orthoceras truncatum* differ only slightly from those of *Leurocycloceras* cf. *niagarense.* They have been illustrated by Barrande on Pl. 342, Fig. 6. Here are shown radial, paired grooves which differ from those of *Leurocycloceras* mainly in being joined for a short distance along a mid-dorsal line extending from the siphuncle. The ventral portion of the surface of the episeptal deposit is not shown, being covered by the deposit, and only the septal surface is shown there.

The surfaces of the hyposeptal deposits as shown on the apical ends of various specimens show considerable variability, but many of the features shown have their counterpart in *Leurocycloceras* cf. *niagarense*. A median ridge or depression extending dorsad of the siphuncle to the antisiphonal wall of the conch has its counterpart in deposits of *L.* cf. *niagarense* in an advanced stage of growth (Pl. 1, Fig. 19).

Other specimens illustrated by Barrande show the presence of a strongly inflated mass of the hyposeptal deposit about the siphuncle which has its counterpart in the more adoral camerae of *L.* cf. *niagarense.* Other features shown have no known counterparts in the American species, and their interpretation is doubtful. On Plate 341, Figs. 15 and 16, is shown a surface with concentric markings and also ridges running from the siphuncle to opposite walls of the conch. Their position is not in accord with the symmetry of the section, but this suggests only that the specimen must have been slightly affected by pressure. Fine radial lines are seen on surfaces associated with a mid-dorsal ridge (Pl. 341, Figs. 1-2). The absence of similar fine lines on *L.* cf. *niagarense* may be due to the coarsely granular nature of the dolomite which comprises the internal mold, and the difference may therefore be more apparent than real.

A longitudinal section (Barrande, Pl. 343, Fig. 15) shows striking similarities with *Leurocycloceras bucheri* (Pl. 3, Fig. 3). Here the apex represents a septal surface, orad of which are seen thin episeptal deposits. The anomalous feature of this individual is the absence of any trace of cameral deposits except in the apical camera. This suggests the possibility that the regular and gradual development of deposits which can be seen readily in a series of camerae of many typical orthoconic cephalopods, is here modified. Further, the possibility that deposits may have developed in camerae slightly previous to natural truncation is suggested.

Aside from a few anomalous features if the surfaces of the broken ends, which may not seem so peculiar when more surfaces of deposits have been studied, there is nothing in this species which cannot be explained in terms of normal cameral deposits and breaks in the shell which may or may not have been made during the life of the organism. Further, most of these features can be duplicated in American species of *Leurocycloceras*, to which genus the species is here referred with doubt.

Nomenclature of Early Paleozoic Cycloceras.—*Cycloceras*, as pointed out by Miller, Dunbar and Condra (1933, p. 45), is based upon the Mississippian *Orthoceras annulare* Flemming, selected as genotype by Bassler (1915, Vol. 1, p. 325), and is so little known that no other species can be referred to the genus with certainty. It is exceedingly improbable that the early Paleozoic species which resemble *Cycloceras* externally are in reality related to it. None of the earlier Paleozoic "*Cycloceras*" species are known to extend into the Upper Silurian. The next higher form of cycloceroid aspect is the genus *Neocycloceras* Flower and Caster (1935, p. 210), which ranges from the Conewango series of the Upper Devonian into the basal Mississippian. The genus is cyrtochoanitic and on the basis of the siphuncular outline has been placed tentatively in the Pseudorthoceratidae. (Flower, 1939, p. 180.) In the Pennsylvanian occurs the orthochoanitic genus *Brachycycloceras* Miller, Dunbar and Condra (1933, p. 105). Miller and Furnish (1938, p. 150) have referred a Mississippian species of America to *Perigrammoceras* Foerste (1924, p. 224), a genus which Miller, Dunbar and Condra (1933, p. 46) regarded as a synonym of *Cycloceras* McCoy. The reason for this change of view has not been stated.

Shimizu and Obata (1936, pp. 20-21), in their wholesale descriptions of nautiloid genera, did not neglect the opportunity to propose new names for early Paleozoic cycloceroid conchs. They proposed *Paleocycloceras* based upon *Protocycloceras hupehense* Shimizu and Obata (=*Protocycloceras deprati* Yu, *non* Reed), but the structure of the siphuncle is not definitely known, and the proposal of the genus is based upon an unsubstantiated belief by the authors that the siphuncle is orthochoanitic instead of holochoanitic as in *Protocycloceras*. Genera are hardly to be recognized upon such meagre grounds. They also proposed *Foersteoceras* based upon *Cycloceras selkirkense* (Whiteaves) of the Red River formation of Manitoba, of Middle or Upper Ordovician age. The description is hardly adequate, but the species is definitely orthochoanitic. The name need concern no one, however, as *Foersteoceras* Shimizu and

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PLATE I.

Internal molds of camerae of *Leurocycloceras* cf. *niagarense*
Figs. 4-11 enlarged x1.4; others natural size.

Fig. 1. Lateral aspect of a series of adapical camerae, dorsum on right, showing uniformity of radial markings throughout the series. The ventral process is seen as a gap in the internal molds on the left of some of the members of the series.

Fig. 2. Dorsal aspect of the molds of four adoral camerae. The mid-dorsal groove, marked by a slight notch, is in line with the siphuncle. Dorso-lateral grooves are seen on extreme left. The right side is incomplete.

Fig. 3. Lateral aspect of the same specimen, dorsum on right, showing prominence of the dorso-lateral groove and relative weakness of other lateral impressions. The apical end shows the tubular markings continuing from the camera onto the siphuncle.

Fig. 4. Episeptal surface of most adoral camera preserved. The mid-dorsal ridge is very obscure in this camera.

Fig. 5. Another adoral episeptal surface showing development of mid-dorsal line and the close association of the three lateral tubes at their origin.

Figs. 6-11. A series of selected camerae showing gradual elimination of the smooth outer area. Note rapid decrease in size, owing to increasing development of pseudoseptum. Concentric ridges shown on central area. Impression of ventral process reduced adapically.

Fig. 12. Hyposeptal surface of same camera as Fig. 4, showing regular radial markings and irregular circumferential tubes about central impressed area.

Fig. 13. Another adoral camera, similarly viewed, to show variation.

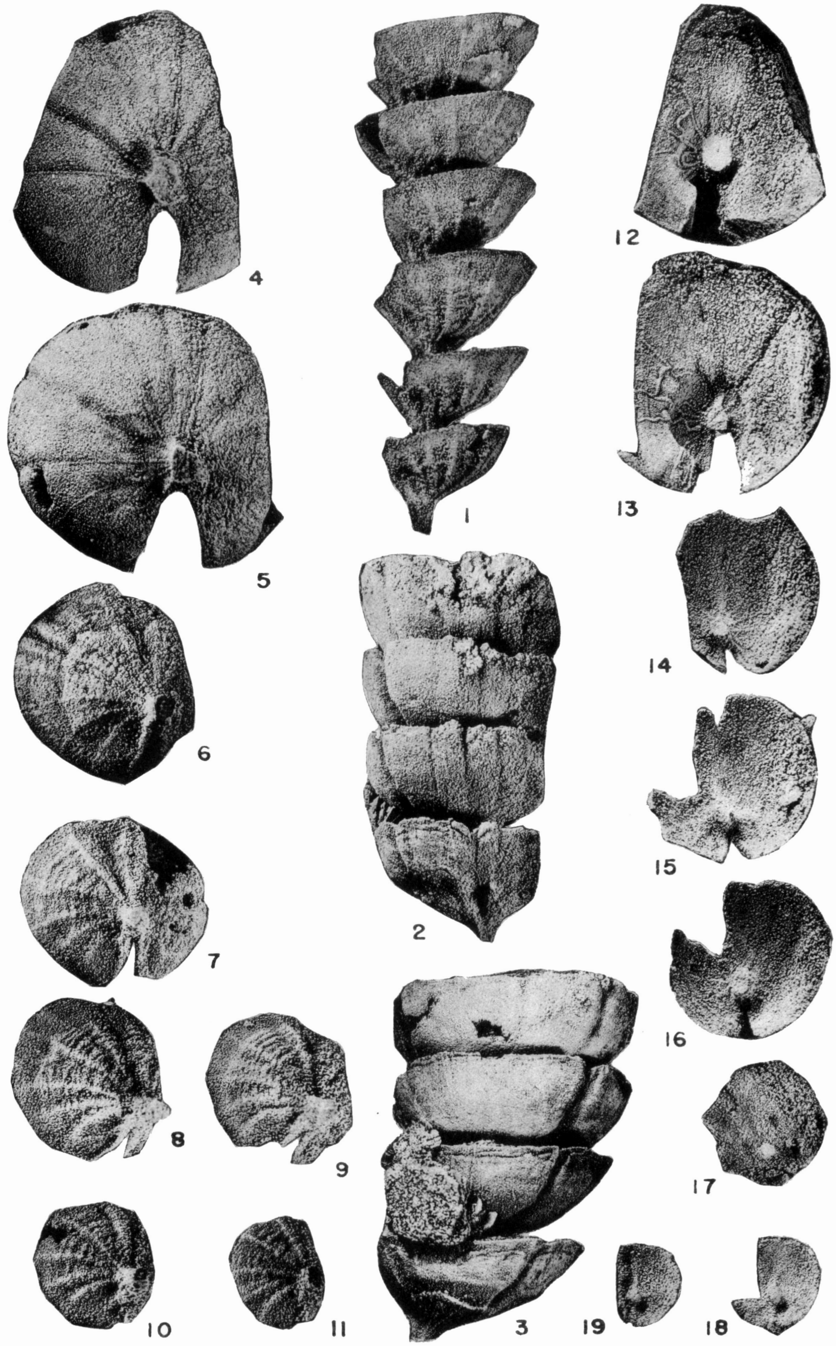
Figs. 14-19. Progressive series of selected camerae showing gradual loss of radial markings (14-16), complete absence of markings (17), and final appearance of mid-dorsal groove, a septum on the mold in Figs. 18-19.

PLATE II.

Figs. 1-3. Enlargements of hyposeptal surfaces of adoral camerae of same specimen as Pl. I, showing variations in details of circumferential tubes. In Fig. 1 the tubes are apparently not continuous with one another but lie in part within and in part outside of the central inflated area. Fig. 2 shows similar irregularities and in addition numerous radial tubes adjacent to the mid-ventral mass. Fig. 3 shows the most regular condition noted.

Fig. 4. A vertical section of *Leurocycloceras bucheri* n. sp., enlarged to show continuity of episeptal and hyposeptal deposits of adjacent segments which join through the septal foramen, clearly shown on the dorsal (left) side. A similar condition is present on the right, but by reason of the proximity of the surface of the deposit to the septal neck and the vestigial condition of the pseudoseptum the appearance of a connecting ring is simulated. The section is vertical, the strong ventral concentration of the cameral deposits being due to the section passing through the mid-ventral process of the deposit.

Fig. 5. A more typical section of the same, as shown on holotype, x2. The pseudosepta are clearly shown throughout. Adapically deposits of the camerae tend to join through the septal foramen.



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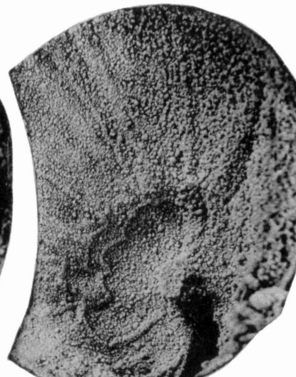

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Obata 1936 is preoccupied by *Foersteoceras* Ruedemann (1926, p. 65), which is based upon *Trochoceras turbinatum* Hall of the Cobleskill limestone, Upper Silurian, of New York.

None of these genera solves adequately the problem of the correct generic designation for early Paleozoic species formerly referred to *Cycloceras*. Holochoanitic Beekmantown forms have been commonly and correctly referred to *Protocycloceras*. Black River and Trenton species of ellipochoanitic structure present a different problem. Such of these species as the writer has examined possess more or less expanded siphuncular segments and heavy cameral deposits, and do not seem to be generically distinct from *Tofangoceras* Kobayashi, based upon a species from the Middle Ordovician of Manchuria. "*Cycloceras*" *selkirkense* (Whiteaves) is a representative of an apparently small group of orthochoanitic species of the Ordovician which may prove to constitute a valid genus, but proposal of a name for these forms should, in the opinion of the writer, await more careful morphological study.[1] *Leurocycloceras* fortunately disposes of the nomenclatorial problem of all Middle Silurian species which have been referred to *Cycloceras* in the past, in America, but most of the European species of Silurian "Cycloceras" are unrelated, and possess very different internal structure.

Leurocycloceras bucheri Flower, n. sp.

Plate 2, Figs. 4-5; Plate 3, Figs. 1-4.

Conch orthoceraconic, very slender, faintly compressed in section, expanding at a rate of between 2 mm. and 3 mm. in a length of 40 mm., except at the extreme adapical portion where the expansion is slightly more rapid. There the conch increases from 3 mm. to 6 mm. in a length of 22 mm. The height of the shell is normally 2 mm. greater than its width up to a diameter of 35 mm., which is the greatest observed.

Sutures straight, slightly inclined orad on the dorsal or antisiphonal side. Camerae deep, two occurring in a length equal to an adoral diameter of from 6 mm. to 20 mm. decreasing in depth in proportion to diameter so that two and a half occur in a similar length at 25 mm., and three at from 30 mm. to

[1] After this paper was submitted Dr. Curt Teichert (Jour. Paleont., vol. 14, p. 592, Nov., 1940) has published identical views concerning *Foersteoceras* Shimizu and Obata.

35 mm. Septa strongly curved, the depth being nearly half the conchial diameter adapically and about one-third the conchial diameter adorally. The curvature of the septum is asymmetrical, the greatest depth occurring at the septal foramen. Siphuncle only slightly eccentric adapically, later assuming a position about twice as far from the dorsum as from the venter. At a conchial height of 6 mm. the siphuncle is .8 mm. in diameter, 3 mm. from the dorsum and 2.2 mm. from the venter. At a later stage the siphuncle is 2 mm. in diameter, 3 mm. from the venter and 6 mm. from the dorsum, and at the latest stage observed the siphuncle is 3 mm. in diameter, 9 mm. from the venter and 15 mm. from the dorsum.

In section the septal necks are long, about one-fifth the depth of the camera, and are parallel to the axis of the conch. No true siphonal deposits are developed. Deposits of the camerae are typical of the genus, consisting of thin episeptal and massive hyposeptal deposits. These fuse along a pseudoseptum. (Pl. 2, Fig. 5.) In advanced stages of growth the hyposeptal and episeptal deposits meet also through the septal foramen, completely enclosing the septal necks. In one such specimen (Pl. 3, Fig. 4), the surface of the deposits closely simulates the appearance of a connecting ring on the ventral side, but close inspection shows that it lies within the septal foramen and is not in contact with the septal neck. In this specimen the deposits have completely filled the camerae ventrad of the siphuncle, and the pseudoseptum cannot be made out there clearly. On the dorsal side, however, the deposits are thin. The explanation for the very strong contrast between the dorsal and ventral development of the deposits is found in the strictly vertical section, which is cutting through the mid-ventral process of the deposits shown in the internal molds of *L.* cf. *niagarense*. Similar phenomena have been observed on other sections which are strictly vertical.

The surface of the shell is marked in the early stages by distant, narrowly incised, evenly placed, transverse striae (Pl. 3, Fig. 2). Between six and seven interspaces occur in a length of 20 mm. Adorally the interspaces become more convex, and the striae become broader and more obscure, producing the ornament typical of *Leurocycloceras*. The spacing of the surface features scarcely increases, so that in a conchial diameter of 23 mm. there are only seven or eight annuli in a length of 20 mm., and the same condition is retained up to a diameter of

35 mm. The living chamber and the gerontically shallowed camerae have not been observed in this species.

Discussion.—This species, which is quite abundant in the Laurel limestone at Westport, Indiana, differs from *L. franklinense* (Miller), also from the Laurel limestone of Indiana, in the much more closely spaced surface features, also in the slightly greater elevation of the annuli. *L. franklinense* is not well enough known to permit a more careful comparison of other features, being known only from the type which is an incomplete living chamber. Probably the closest species is *L. brucense* (Williams) of the Guelph dolomite of Ontario, which has more distantly spaced and flatter annulations, a more eccentric siphuncle and transverse sutures.

L. bucheri has played an important part in the study of the structures of *Leurocycloceras* because of its excellent preservation. The silicious Laurel limestone is a medium which yields excellent sections and shows fine preservation of internal features, while the dolomites in which so many American Silurian orthoceracones occur, are not usually favorable for the preservation of such internal structures.

Types.—Holotype and three paratypes, to be deposited in the Paleontological Research Institution, Ithaca, New York.

Occurrence.—In the Laurel limestone, about two miles east of Westport, Decatur County, Indiana.

CAMERAL DEPOSITS OF LEUROCYCLOCERAS CF. NIAGARENSE.

Specimens of *Leurocycloceras* in the Laurel limestone furnish excellent material for the study of deposits of the camerae in longitudinal section, but cross sections fail to reveal any trace of radial differentiation of the deposits such as was reported for *Pseudorthoceras* (Flower, 1939, pp. 36-38), or for *Striacoceras* (Flower, 1936, p. 31, Pl. 3). This was due partly to the frequent occurrence of calcite within the cavity of the camerae as well as in its deposits, and partly, as was subsequently found, because of the very slight relief of most of the surface features. The dolomitized filling of a series of camerae from the Racine dolomite supplied the missing information, and brought to light not only the structures, but also a considerable portion of the ontogenetic development of the deposits. Unfortunately the exterior of the specimen is not known, and due to the adapical development of the pseudoseptum the internal molds of the camerae increase more rapidly in diameter when traced orad than did the outside of the shell. Accurate specific identification, which depends largely upon proportions of the shell, was therefore not possible, and the specimen is referred to *Leurocycloceras niagarense* (Hall) with doubt, as its proportions suggest that species more closely than any other.

Episeptal and hyposeptal deposits were originally discrete. They join first in a mid-ventral tongue-shaped process extending from the ventral wall toward the siphuncle. This is developed early and as a consequence is seen on the most adoral of the camerae, while in older camerae it becomes increasingly smaller, and finally disappears completely. Whether this is because the growth of the ventral process was retarded later, so that it became engulfed in the remainder of the deposit as the pseudoseptum developed, or whether there actually was variation in the deposit of adapical and adoral camerae, it is impossible to determine with only a single specimen. Experience in other groups indicates that the ontogeny of deposits is generally uniform throughout the camerae, and that engulfing is the more logical explanation.

The Episeptal Surface.—The molds of the episeptal deposits are characterized by a series of narrow, radial grooves and ridges radiating from the siphuncle to the edge of the deposit surface. These are constant in number and are paired throughout, but their aspect changes as they are traced adapically and more advanced stages of growth of the deposit are encountered. The deposit surface first bore a series of radial elevations. In the center of each there was a shallow but very distinctly outlined tubular furrow. These occurred one pair flanking the ventral process, and three lateral pair which are closely associated at their point of origin on the siphuncle. A fifth pair of grooves on the internal mold shows no trace of the tubular impressions. A pair of dorso-lateral ridges with tubular impressions follow, which were separated by a median elevated ridge which is absent on the most adoral of the molds (Pl. 1, Fig. 4), but can be seen on all following camerae. The surface between the radial impressions is smooth in the early stages of growth. At the seventh camera from the adoral end of the specimen there is seen a beginning of a differentiation of the deposit into a thick outer region and a thinner central region. Here all radial impressions become concave on the deposit, being convex on its mold, and the central area is further marked by concentric scalloped ridges, all well rounded and sometimes poorly defined, which suggest lines of growth in their appearance. Gradually the outer smooth area is reduced and finally it completely disappears, as the episeptal and hyposeptal deposits join along a pseudoseptum, thereby reducing the cameral space from its periphery. After the loss of the outer area the deposits encroach farther centrad, but no further modifications of the surface pattern are apparent. In the most adapical of the camerae available all surface features become obscure, but this appears to be because the details are becoming increasingly fine and adapically they are too small to be preserved by the coarsely granular dolomite of which the molds are composed.

Hyposeptal Surface.—The adoral surfaces of the molds of the camerae reflect the condition of the hyposeptal deposits. At the earliest available stage the thickening of the deposit around the siphuncle is very prominent, being reflected by a central impressed area on the molds. In the outer area the deposit bore six pairs of radial ridges corresponding exactly in position to those on the episeptal surface. Those corresponding to the prominent dorso-lateral grooves, the fourth pair from the ventral mass, are the most prominent. Within each ridge there was a tubular impression similar to those already noted on the episeptal surface. The radial impressions on the central inflated area are more numerous and more irregular and roughly at the edge of the area, there occur tubular impressions roughly circumferential in their course but quite irregular and varying considerably in the details of their form in successive camerae. Three adjacent camerae are shown on Pl. 2, Figs. 1-3, enlarged to show the details of these structures. In Fig. 1 a lateral tube apparently curves back into the siphuncle. Circumferential tubes associated with the dorso-lateral grooves tend to lie slightly outside of the central inflated area. Fig. 2, the next hyposeptal surface, shows some similar features but is chiefly notable for the numerous tubes which flank the ventral process of the deposit. Fig. 3 shows the most regular development noted in the circumferential tubes, and is further of interest in that it shows traces of more numerous and finer radial markings on the outer portion, which suggest similar structures noted in *Orthoceras truncatum* by Barrande.

Tracing the hyposeptal surface into more adapical and therefore more advanced stages, there is seen a rapid loss of differentiation of the deposit into a central and a peripheral area. This is accompanied by reduction of clarity and finally the loss of all traces of the radial vascular markings (Pl. 1, Figs. 13-19). This is followed by the development of a median groove located dorsally on the mold, representing a groove in the surface of the deposit.

Preservation.—It will be noted that the right side of the camerae, as oriented in accordance with the symmetry of the organism is poorly preserved, normally incomplete, and frequently altogether lacking, especially in the adapical portion of the specimen. The dolomite represents only the sediment which penetrated the dead conch, and the distribution suggests that the shell came to rest on its left side. Sediment penetrated the conch incompletely and came to rest against that side of the shell, leaving the right side to be filled in by infiltrated material, probably calcite, which was subsequently dissolved with the shell. It is quite characteristic of such incomplete internal molds in orthoceracones that filling becomes less and less complete as the apex is approached; consequently the progressive reduction of the right side of the molds as they are traced apicad is the condition to be expected. Similar phenomena are well shown in the siphuncle of the holotype of *Adnatoceras naplense* (Flower 1939, Pl. 3, Fig. 2). The episeptal deposits are most clearly shown on the left side of the various molds, which are for the most part illustrated in a slightly oblique position to secure the best view of the surface features. The opposite side of the molds shows the best preservation of detail on the right instead of the left side, the dolomite on the left side being too coarse for the preservation of the fine structures involved.

Interpretation of Internal Structures.—It has been shown previously (Flower 1939, pp. 45-51), that cameral deposits are the result of the secretion of tissues within the camerae, for which the term *cameral mantle* was proposed. A reconstruction of the form, origin and development of the tissues was postulated. Briefly, the origin of the cameral mantle involved the splitting of the posterior mantle, leaving behind a layer of epithelial tissue attached to the septal surface when the animal migrated forward in the shell previous to the development of a new septum. Extending forward from the recently separated mantle tissue was the siphonal strand, within which the spicular connecting ring was secreted by mesoderm. Later the outer part of this strand, which has become cameral rather than siphonal tissue, extends over the convex surface of the newly formed septum.

Leurocycloceras shows several typical features, but in other respects it is unique, and some of its more peculiar features, although probably confined to the genus, have a considerable bearing upon the problem of the nature of cameral tissues.

The mid-ventral process and the radial and concentric ridges, particularly as shown on the episeptal surfaces of the more adapical camerae, indicate folding of the cameral mantle. This device reconciles growth of the cameral mantle with restriction of the cubic content of the camera as deposits develop, and removes the necessity of resorption of cameral tissue. The pattern of folding, as can be readily seen, is very different from that found in the Pseudorthoceratidae, or any cephalopods possessing mural deposits which have been studied up to the present. Nevertheless it is evident that the same physiological conditions are involved in the folding in both instances. Enough data has not yet been gathered to permit a careful comparison between the deposit surfaces of *Leurocycloceras* and other orthoceracones possessing episeptal and hyposeptal deposits. Such Actinoceroidea as possess similar deposits, which have been studied up to the present and which will be discussed in detail elsewhere, agree with *Leurocycloceras* only in the development of a mid-ventral process, but the process is complexly pitted and lobed in *Actinoceras*, *Elrodoceras* and *Armenoceras*, the three genera which have been most adequately studied.

The most significant feature of the deposits is the series of radial tubular impressions extending from the siphuncle to the periphery of the camerae. These are regular in number, symmetrically paired, with the symmetry in accord with the symmetry of the organism as a whole. Further, the grooves on the episeptal and hyposeptal surfaces are perfectly aligned, and meet at the edges of the molds, forming slight notches which are quite evident in the illustrations. Obviously such regular structures are an integral part of the organism. The tubular impressions are so sharply defined that it is at once evident that more than a folding of the mantle is involved; rather they must be the impressions of structures in the cameral mantle itself. The nature of the impressions is such that it is obvious that vascular structures are concerned, and the only convincing interpretation which presents itself is that these tubes must represent large blood vessels which have developed within the camerae of *Leurocycloceras.* The circular system of connecting tubes shown on the hyposeptal surfaces of the adoral camerae is irregular and more variable, but its connection with the radial tubes is clear, and the irregularities can be duplicated in vascular structures in other organisms. Therefore these tubes are similarly interpreted.

The development of a rather solid connecting ring in most Nautiloidea precludes the possibility that large blood tubes may have passed direct from the siphonal to the cameral tissues. Had such tubes existed, they would have needed perforations in the connecting ring large enough to be readily observed. Although many cephalopods have been examined with this particular point in mind both by Teichert and the writer, no trace of such perforations has been found. Therefore it was necessary to conclude that the exchange of metabolic materials between cameral and siphonal tissues must have taken place by means of very fine blood tubes, of the nature of capillaries, which could pass through the minutely porous connecting ring without modifying its structure, or else by osmosis. As cameral tissues

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PLATE III.

Leurocycloceras bucheri Flower n. sp.

Fig. 1. Paratype, lateral aspect, x1, showing development of low annuli.

Fig. 2. An earlier stage from another paratype, showing "geisonoceroid" ornament. x1.

Fig. 3. Apical end of specimen shown in Fig. 1, showing breakage of apical end, still in matrix, at the pseudoseptum. Episeptal and hyposeptal deposits join through siphuncle. Deposits of apical camera discolored. x2.

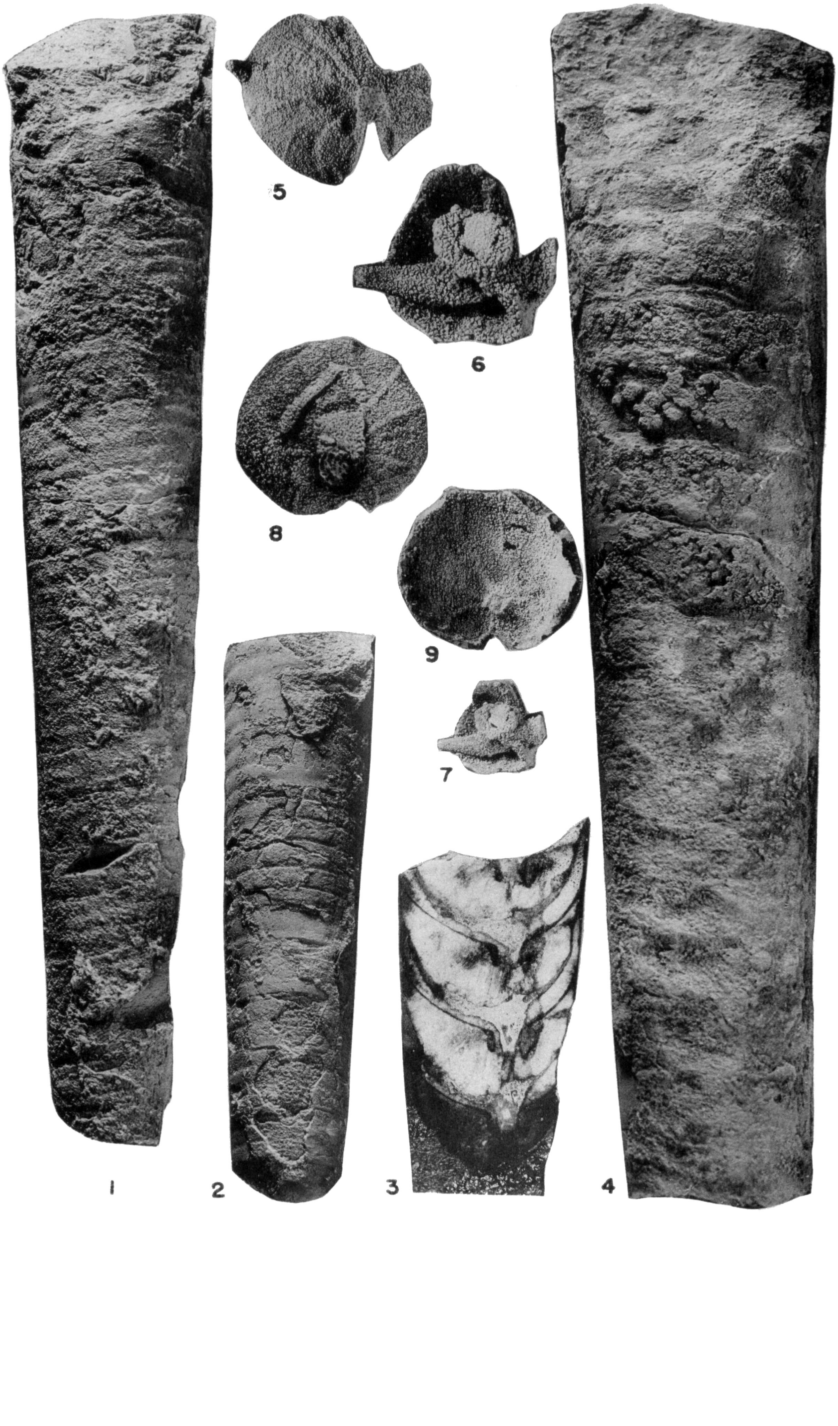
Fig. 4. Adoral portion of holotype, xl, largest individual observed, showing spacing of septa.

Leurocycloceras cf. *niagarense* (Hall)

Fig. 5. Mold of camera showing subconical cavity near margin.

Figs. 6-7. Mold of earlier camera, x2 and x1, showing camera traversed laterally by a similar cavity in hyposeptal deposit.

Figs. 8-9. Episeptal and hyposeptal surfaces of mold of camera with vermicular cavity in episeptal deposits. Note loss of episeptal surface detail in vicinity of parasite. Hyposeptal surface shows radial markings normally lost at this stage of development. Slightly greater than x1.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were evidently highly organized, and as there was other reason to suppose that it had originated in part from the siphonal strand within which the connecting ring was subsequently secreted by mesoderm, it seemed that it was more reasonable to believe that fine blood tubes were not only present, but had preceded the connecting ring in ontogenetic development.

The development of the siphonal vascular system of the Actinoceroidea is paralleled very strikingly by the cameral vascular system in *Leurocycloceras*. The generalized condition was probably not greatly dissimilar from that of *Nautilus*, with the siphonal strand containing numerous, fine blood tubes. In the Actinoceroidea these have been specialized and reduced to a series of few regular, large tubes. It is conceivable that where the connecting ring is absent a similar specialization may be possible within the camerae instead of the siphuncle. It is reassuring to find that in *Leurocycloceras*, the only genus yet to show evidence of such specialization, the connecting rings are uniformly, and from quantitative evidence, normally absent. So far as is known this development is unique. Probably the same condition will be found to hold in a genus now in process of study which differs from *Leurocycloceras* only in external features, and which is believed to represent its expression in the later Paleozoic. Such other forms as show uniform absence of the connecting ring are longiconic coiled cephalopods which do not develop cameral deposits and which consequently cannot be expected to show traces of vascular tubes within the camerae even had such tubes been developed.

The alignment of the tubes on the episeptal and hyposeptal surfaces suggests that one rather than two series of tubes may have been involved in each camera, the tubes entering the camerae adorally, running to the periphery on the hyposeptal surface and returning to the siphuncle on the episeptal surface. This suggests a striking parallelism with the vascular structures of the siphuncles of some of the Actinoceroidea, such as *Nybyoceras* in which a double series of radial canals is clearly developed. In both instances there are doubtless represented distinct afferent and efferent tubular systems, a hypothesis which finds further support in the presence of two major tubes in the central canal of such of the Actinoceroidea as *Elrodo-*

ceras. Certainly it is to be expected from the nature of the blood system of the remainder of the cephalopod, and other Mollusca as well, that venous and arterial systems should be distinct within the siphuncle and camerae. Further, the fact that the siphuncle of *Nautilus* is supplied with blood by one of the major arteries suggests very strongly that in the past the tissues of the phragmocone were more active metabolically and were more abundantly and perhaps more elaborately supplied with blood. The more recent structural studies of Nautiloidea are bringing to light much direct evidence to support this view.

Parasitic and Commensal Organisms.—Quite aside from the lobation of the cameral mantle and the regular vascular system of the camerae which has left its impression on the cameral deposits, there are cavities in the cameral deposits which are best explained as the work of parasitic and commensal organisms. These are erratically spaced within the camerae, only three examples being known in the entire specimen. Their position in the camerae is variable, and they show no orientation with regard to the symmetry of the organism. These markings are of two sorts, and were evidently formed by two different species. One represents a tubular vermiform cavity, the other a short subconical cavity.

A single example of the vermiform cavity is known. This is shown on Pl. 3, Fig. 8. It lies shallowly developed within the episeptal surface of the deposit, and directly adjacent areas of the surface of the deposit have lost the normal radial and concentric markings. The mold of this camera is considerably thicker than those of either adjacent camerae. The features of the episeptal surface are partly obliterated. The hyposeptal surface, normally without markings in this region of the phragmocone and this stage of growth, shows the radial tubular markings which are characteristic of a younger stage of growth of the deposits in more adoral regions of the shell. (Pl. 3, Fig. 9.) The evidence shows that the organism lived within the camera during the life of the cephalopod, and was responsible for retardation and modification of the growth of the cameral deposits, though affecting only the camera in which it dwelt.

Two examples of subconical cavities are known. In one camera (Pl. 3, Fig. 5), a small subconical cavity occurs near the periphery of the cameral space, into which it opens at its larger end. A second conical mold occurs in one of the most adapical camerae, which it nearly traverses laterally (Pl. 3, Figs. 6-7). Neither of these structures is associated with any retardation or modification of the cameral deposit. Taken alone, this might be interpreted as indicating that such cavities were made in the cameral deposits after death. However, the vermicular cavity was clearly made during the life of the host and makes it seem probable that these subconical cavities may have been similarly formed. Further evidence of this is found in the apparently closed end of the cavity shown in Pl. 3, Figs. 6-7, which suggests that the deposits grew around an invading organism. This organism, of unknown affinities, is evidently to be regarded as a commensal rather than a parasitic form, for although there is no evidence of benefit which the host may have derived from the presence of its guest, there is also no evidence of any harmful effect.

There is of course doubt concerning the nature of the organisms which are responsible for the cavities. The elongate nature, lack of branching and rather definite form show that they are clearly not the work of boring sponges, but must be attributed to some unknown wormlike organisms.

Foerste (1933, p. 57) describes commensal worms in the conchs of *Centrocyrtoceras*, but those organisms apparently lived within the shell wall and grew adorally so that the apertures of their tubes were always at the aperture of the conch. Neither of the two types of cavities found in *Leurocycloceras* resemble this form remotely.

The presence of parasitic organisms in the cameral deposits of cephalopods has not hitherto been noted. Remarkable as these forms are in their occurrence in a seemingly inaccessible part of the host, they are in reality not exceptional when compared with living parasitic organisms in regard to their habitat.

Previous sections through various orthoceracones have shown irregular cavities occasionally occurring in the cameral deposits for which no suitable explanation has been offered. The cavities normally fail to show any regular form, and from sectioned specimens alone it was not evident whether they were natural, the work of solution, or the result of some previously unrecognized factor. The molds now known of such cavities show that they are the work of parasitic and commensal organisms in *Leurocycloceras* cf. *niagarense*. Further, the presence of three such cavities in a single individual suggests that such things were not uncommon, and that the cavities seen in sections, where their form is not evident, may likewise represent the work of parasitic worm-like organisms.

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