SIPHUNCULAR STRUCTURES IN THE DEVONIAN NAUTILOID *ARCHIACOCERAS* FROM THE EIFEL OF WEST GERMANY

by REX E. CRICK *and* CURT TEICHERT

ABSTRACT. *Archiacoceras* is shown to have the most complex connecting ring among chambered Cephalopoda. The siphuncle of *A. subventricosum* consists of four-layered connecting rings, radiating longitudinal lamellae, and central plates. The siphuncle of an undescribed species consists of a connecting ring composed of six layers and of actinosiphonate lamellae without central plates. All ontogenetic stages of the lamellae, from budding to maturity, are observed. Based on similarities with extant chambered cephalopods, lamellae and connecting ring layers are interpreted as having functioned as structures to allow cameral fluids to be removed and, thus, to have formed part of the buoyancy regulating mechanism. The genus is re-established as endogastric. Observations of new features support the retention of *Archiacoceras* in the Oncocerida.

THE material used in this study was generously supplied by Dr. Charles Grégoire (Brussels). Unfortunately, the exact source of the material could not be determined with certainty, but, having purchased the specimens from a quarry worker, Dr. Grégoire feels confident that they came from one of the limestone quarries of the Westdeutsche Kalkwerke, south of Sötenich in the Eifel of West Germany (latitude 50° 32′ N., longitude 6° 34′ E.). The geology of this area has been described by Schmidt (1936), and its general location is indicated on a map by Jux (1960, p. 325). From Schmidt's detailed map (1936, p. 25) it is clear that the cephalopods come from strata of Middle Devonian age. Many limestone quarries are shown to be located in at least six fossiliferous units of the Middle Devonian, but unfortunately no cephalopods are included in any of Schmidt's several faunal lists. Schmidt distinguished six successive fossiliferous limestone units. The lower two (Kalk α and β) are of early Middle Devonian (Eifelian) age, the upper four (Kalk 1 through Kalk 4) are Givetian. Jux (1960, pp. 213, 216) described Kalk 3 and 4, as well as the marly beds between them, as richly fossiliferous, but did not mention cephalopods. There is, however, a distinct possibility that the material described below was taken from beds in the upper part of the Givetian section.

PREVIOUS WORK

Foerste's original description of the genus *Archiacoceras* (Foerste 1926, p. 346) was based on the descriptions and illustrations of *Phragmoceratites subventricosus* by d'Archiac and de Verneuil (1842). The original material came from Middle Devonian strata near Refrath (now Bensberg-Refrath) in the Rhenish Schiefergebirge, West Germany, about 65 km north-east of Sötenich. For the general location see Jux (1960, p. 261). Foerste later (1930, pp. 295–298) gave a greatly expanded description and discussion of *Archiacoceras* following study of several specimens from Sötenich in the collections of the Preussische Geologische Landesanstalt in

Berlin. In an emendation of his 1926 description, Foerste reported that the siphuncle of *Archiacoceras* is actinosiphonate in having internal 'vertical' lamellae. Because of the actinosiphonate nature of the siphuncle, Foerste referred *Archiacoceras* to the Actinosiphonata, a taxon proposed by Hyatt (1900) for nautiloid cephalopods in which the interior of the siphuncle is lined with vertical lamellae.

In 1939, Teichert erected the family Archiacoceratidae for endogastric cyrtocera-cones. The family, consisting of the nominal genus and six other genera, was placed in the order Cyrtoceroidea Teichert, 1933. Two of these genera were later shown to be discosorids (Flower and Teichert 1957) and the remaining four were assigned to families of the Oncocerida by Sweet (*in* Teichert *et al.* 1964). The family Archia-coceratidae currently consists of *Archiacoceras*, *Cyrtoceratites* Goldfuss (1830) (this genus may be a senior subjective synonym of *Archiacoceras*), and *Devonocheilus* Shimanskiy (*in* Zhuravleva 1962).

Flower (1943, pp. 57–62) was the first to describe details of the siphuncular features of *Archiacoceras* from two specimens of the type species. He questioned Foerste's description of *Archiacoceras* as endogastric (siphuncle on the concave side of the phragmocone) because he reportedly observed a 'well defined septal furrow' (p. 57) on the siphonal side of the phragmocone. In chambered cephalopods, a septal fur-row is accepted as a feature of the dorsal side of the conch. The shell form of *Archiacoceras* was thereafter described as exogastric, and this condition was accepted by Sweet (*in* Teichert *et al.* 1964, p. *K*312). The subject of the shell form will be taken up later. In his description of the siphuncular features, Flower (1943) suggested that bullettes (a discosorid feature) occur in the area of the septal foramen and gave an expanded description of the actinosiphonate lamellae. He concluded that the connecting ring of *Archiacoceras* consisted of two layers, that the actinosiphonate lamellae were outgrowths of the connecting ring, and that many lamellae contain a 'central rod'. Flower's specimens came from Gerolstein in the Rhenish Schieferge-birge, about 40 km south of Sötenich.

In the first attempt at modernizing the classification of Devonian nautiloids, Flower (1945) rejected Teichert's Cyrtoceroidea on the basis that it was not a natural group and placed *Archiacoceras* in a category of 'genera of uncertain position', without making reference to the family Archiacoceratidae.

Flower (*in* Flower and Kummel 1950) erected the order Oncoceratida for primitively compressed, essentially exogastric cyrtocones with suborthochoanitic to cyrtochoanitic ventral siphuncles. Actinosiphonate deposits were considered to be common in various members of the group and Flower acknowledged that some forms displayed a depressed section and endogastric curvature. The Archia-coceratidae, with *Archiacoceras* Foerste and *Wadeoceras* Teichert (1939) as members, were placed in this order. In the same publication, Flower also erected the order Discosorida for endogastric brevicones and cyrtocones with broadly expanded cyrtochoanitic siphuncles that commonly have thick connecting rings, annulo-siphonate deposits, and, occasionally, endocones. Some exogastric forms were included in this order.

Nalivkin (1941, 1947) assigned *Phragmoceras inversum* Venyukov [Wenjukow], 1886 to *Archiacoceras*. He described the species from the Main Devonian Field of the Russian Platform (Nalivkin 1941) and from the Urals (Nalivkin 1947). Since he refers

to these forms as having thick connecting rings and radial lamellae, the generic assignment of Venyukov's species to *Archiacoceras* is probably correct.

Zhuravleva (1962) placed the following genera in the Archiacoceratidae: *Archiacoceras* d'Archiac and de Verneuil, *Devonocheilus* Shimanskiy, *Hipparionoceras* Flower, and *Turoceras* Zhuravleva.

Kuzmin (1966) described *A. rarum* from rocks of Givetian age on the south island of Novaya Zemlya, but Zhuravleva (1974, p. 94) questioned the affinities of this species with *Archiacoceras*. In particular, the lack of actinosiphonate lamellae makes this species suspect.

DISCUSSION OF *ARCHIACOCERAS* FROM SÖTENICH

Class CEPHALOPODA Cuvier, 1798
Subclass NAUTILOIDEA Agassiz, 1847
Order ONCOCERIDA Flower *in* Flower and Kummel, 1950
Family ARCHIACOCERATIDAE Teichert, 1939

Diagnosis. Compressed, endogastric cyrtocones, with large ventral, actinosiphonate siphuncle. Devonian.

Genus ARCHIACOCERAS Foerste, 1926

1926   *Archiacoceras* Foerste, p. 346, pl. 43, figs. 3A, B.
1930   *Archiacoceras* Foerste, pp. 295–299, pl. 43, fig. 3.
1939   *Archiacoceras* Teichert, p. 108.
1941   *Archiacoceras* Nalivkin, p. 259.
1943   *Archiacoceras* Flower, pp. 57–62, pl. 5, fig. 1; pl. 6, figs. 1–9.
1947   *Archiacoceras* Nalivkin, p. 158, pl. 40, fig. 4.
1962   *Archiacoceras* Zhuravleva *in* Orlov (ed.), p. 108, pl. 27, figs. 11a, b.
1964   *Archiacoceras* Sweet *in* Teichert et al., p. K312, fig. 223, 1.
1974   *Archiacoceras* Zhuravleva, pp. 94, 95, pl. 11, figs. 1, 2.

Type species (original designation). *Phragmoceratites subventricosus* d'Archiac and de Verneuil, 1842, p. 351, pl. 30, figs. 1, 1A.

Diagnosis. The following generic description of *Archiacoceras* is modified from Foerste (1930, p. 295):

Conch with endogastric siphuncle, almost in contact with slightly concave venter. The dorsal outline is more strongly curved, in a convex direction. The maximum diameters of the conch, both dorso-ventrally and laterally, are about nine camerae adapical of the base of the body chamber. From this point, the conch contracts adorally not only along the adoral portion of the phragmocone but also along all of the body chamber, where known. A length of body chamber equal to about six camerae is preserved, but there is no trace within the length of transverse markings by means of which the locations of the hyponomic sinus could be determined, nor is there any evidence at the adapertural portions of the body chamber of any abrupt contraction, as in the typical phragmoceroids. The cyrtochoanitic concavosiphonate siphuncle is relatively large and contains longitudinal lamellae that project inward from the connecting ring, but leave a large endosiphuncular canal at its centre. The sutures curve slightly adapical laterally, but curve increasingly adoral from the

ventral toward the dorsal side of the conch as they approach the adoral portion of the phragmocone.

Distribution of type species. Archiacoceras subventricosum is known from unspecified stratigraphical levels in rocks of Givetian age in the Rhenish Schiefergebirge. The recorded localities are, from south to north, Gerolstein (Flower 1943), Sötenich (Foerste 1930; this paper), and Bensberg-Refrath (d'Archiac and de Verneuil 1842; Foerste 1926).

Shell morphology

Eight of the best-preserved and most representative specimens of *Archiacoceras* were chosen from the material supplied by Dr. Grégoire. Five of these can be placed with confidence in *A. subventricosum*. Three specimens are referred to as *Archiacoceras* sp. for purposes of discussion, the distinction from *A. subventricosum* being based on differences in the form and features of the ectosiphuncle and endosiphuncle. While we are reasonably certain that such differences are not the result of intraspecific variability, we are not in a position to establish a new species without studying a larger collection of equally well-preserved specimens.

Because *A. subventricosum* and *Archiacoceras* sp. do not differ in gross morphological features, the discussion of such features pertains to both forms. The following descriptions and discussions refer to the illustrated specimens considered to be representative of *A. subventricosum* and *Archiacoceras* sp. The study, however, was based on all specimens which agree in all respects with the illustrated forms.

The largest and most complete specimen available to us (Pl. 98, fig. 1) is a steinkern measuring 275 mm along the dorsal (convex) side, 120 mm along the ventral (concave) side, and 220 mm in a straight line between the most prominent adapical and adoral points. These measurements include a basal section of body chamber, equal to the length of five camerae, and a phragmocone of twenty camerae. In cross section the outline is oval with a maximum lateral diameter of 87 mm and a maximum dorsoventral diameter of 95 mm. The phragmocone begins contracting adorally seven camerae behind the body chamber. The surface of the right ventrolateral side of the steinkern is ornamented with very weak longitudinal striations, positioned approximately 2 mm apart (Pl. 98, fig. 1). The left ventrolateral side shows no striations, presumably because of poor preservation.

None of the eight specimens show any indication of a dorsal septal furrow, although presence of such a feature was briefly mentioned by Flower (1943, p. 57). Flower has informed Teichert (in litt. 1974) that a citation of '(Flower 1939)' in which

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EXPLANATION OF PLATE 98

Fig. 1. *Archiacoceras subventricosum.* Right lateral view showing striations, ×0·6. USNM 250628.
Figs. 2–6. *Archiacoceras* sp. 2, right lateral view showing surface irregularities along the dorsal margin, ×0·6. USNM 250629. 3, sagittal section of specimen in fig. 2. Irregular spacing of camerae correlate with dorsal surface irregularities. Apparent absence of lamellae is due to the section passing through the endosiphuncular canal. Lamellae in cross section can be seen near some septal necks, ×0·6. 4, enlarged apical section of the siphuncle in fig. 3. Pseudo-bullettes (sectioned lamellae) can be seen near many septal necks, ×1. 5, an off centre serial section of the siphuncle in figs. 3 and 4, ×1·8. The apparent discontinuous lamellae in the four apical segments is due to the concavity of the siphuncle. The most adoral segments show lamellae passing from one segment to the next most adoral segment.

PLATE 98
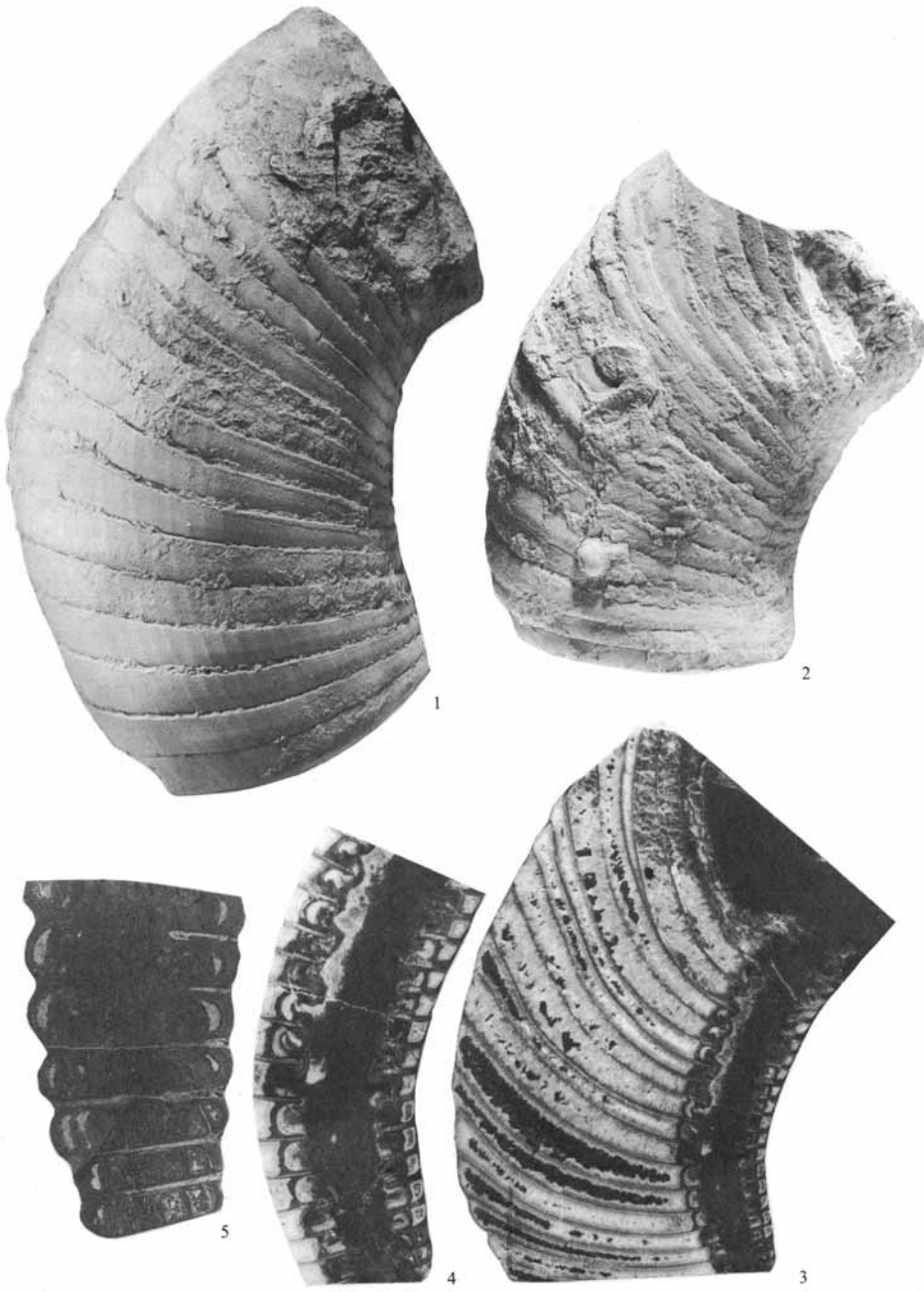
CRICK and TEICHERT, *Archiacoceras*

the observation of the septal furrow was reported was not a bibliographical reference, but an indication of the year in which the observation was made. In view of the fact that Foerste's (1930) extensive study of *Archiacoceras* and our own examination of extremely well-preserved material has revealed no evidence of a dorsal septal furrow, we must consider Flower's observation to be erroneous. We suggest, therefore, that *Archiacoceras* and the Archiacoceratidae be considered as having an endogastric shell form instead of the exogastric condition proposed by Flower (1943, and *in* Flower and Kummel 1950) and accepted by Sweet (*in* Teichert *et al.* 1964).

The outlines of the eight steinkerns show slight swellings visible noticeably along the dorsal surface (Pl. 98, figs. 2, 3), each swelling corresponding to a particular camera. This growth pattern is presumably a function of endogastric allometry, but may be unique to *Archiacoceras*. The product of this allometry is particularly well illustrated in Pl. 98, fig. 3. The irregularities of this specimen are most pronounced dorsally, diminish ventrolaterally, and disappear at the ventrolateral margin, at a distance of approximately 75 mm from the dorsal axis. Septal thicknesses are variable with the thickest parts being in the ventral and dorsal areas. The specimen shown on Plate 98, fig. 3, has septal thicknesses varying from 0·2 mm to 1·1 mm. Camera length (septal spacing) varies from 0·1 mm to 10·0 mm. The more than normal variation in camera length is primarily a function of these growth irregularities. This variability was secondarily modified by distortion of many camerae due to internal crystal growth. The length of individual camerae varies from about 3·0 mm at the ventral wall to a maximum of 10·0 at the dorsal wall. A few camerae do not exceed 5·0 mm near the dorsal wall. The fourth from the last camera (Pl. 98, fig. 3) is unusual in being extremely short. It is 2·9 mm long on the dorsal side and 3·0 mm on the ventral side, but in the area of their greatest convexity the two successive septa are in contact with each other along an area which is about 15 mm wide as measured in the dorsoventral section. Such a condition is extremely rare in chambered cephalopods and may be regarded as pathological.

Morphology of siphuncle

The siphuncle is submarginal to the ventral wall and its segments are expanded between the septa (Pl. 98, fig. 4). The dorsoventral diameter of the siphuncular segments increases from 12·0 mm adapically to 21·5 mm at the sixth segment from the base of the body chamber, after which they decrease to a diameter of 18·0 mm at the last preserved segment. In accordance with general allometry, the length of the siphuncular segments increases from 3·0 mm to 6·0 mm adorally (Pl. 98, fig. 4). The septal necks are very short cyrtochoanitic to recumbent, and are of a type commonly referred to as armenoceratid (text-fig. 1; Pl. 99, figs. 1, 2).

Connecting rings of *Archiacoceras* are thick and complex. At their adapical and adoral ends they are attached to the septa by vincula of the type found in the discosorid Ruedemannoceratidae, Cyrtogomphoceratidae, and Westonoceratidae (Flower and Teichert 1957). These structures have not been observed previously in oncocerids, but, while discosorids have only one vinculum at the adoral end of the connecting ring, *Archiacoceras* has two vincula on each connecting ring (text-fig. 1; Pl. 99, figs. 1–3). One serves to attach the connecting ring to the anterior surface of the preceding septum, and the other performs the same function on the posterior

surface of the succeeding septum. The latter occurs in several discosorids (Flower and Teichert 1957, p. 10, figs. 2A, B, C) and, although not described by the authors, a double vinculum seems to be visible in *Ruedemannoceras boycii* (Flower and Teichert 1957, pl. 1).

Description and discussion of the structures of the ectosiphuncle (excluding septal necks) and endosiphuncle present a special problem, because there is no clear separation of ectosiphuncular and endosiphuncular features. A few features are exclusively ectosiphuncular, some are exclusively endosiphuncular, and several are shared. Therefore, we have chosen to describe and discuss the siphuncle as a whole.

The siphuncle of *A. subventricosum* (text-fig. 2) is distinguished by having an ectosiphuncular surface ornamented with longitudinal ridges of various lengths and degrees of relief, a connecting ring consisting of four distinct layers, and numerous actinosiphonate lamellae consisting of distinct layers and central cores containing central plates. These features are discussed below and illustrated in text-figs. 3 and 4, and Plate 100.

The outer layer of the connecting ring, Layer *a*, is sharply set off from the calcite spar now filling the camerae (Pl. 100, fig. 1). Its thickness varies from 0·3 mm to 0·5 mm, it is white in colour and consists of fine, fibrous calcite which is structurally uniform throughout (Pl. 100, fig. 2). The next layer, Layer *b*, averages 0·4 mm in thickness, is of dark brown colour and has a finely crystalline structure (Pl. 100, fig. 2). The boundary between Layers *a* and *b* is somewhat gradational, but otherwise Layer *b* is of uniform appearance throughout. Layer *c* averages 0·3 mm in thickness,
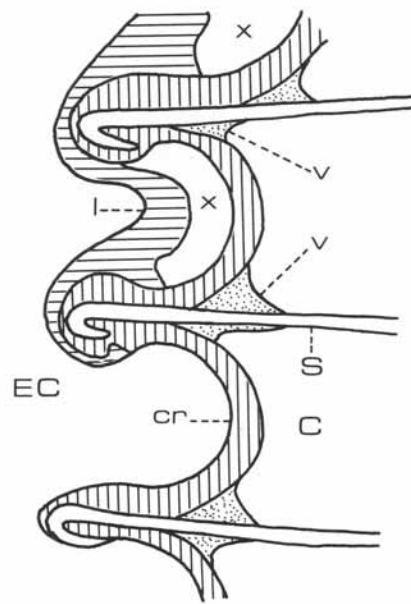

TEXT-FIG. 1. Diagram relating features of camerae, septal necks, and connecting rings. Drawn from a thin section of an *Archiacoceras subventricosum* siphuncle, ×7. C, camera; S, recumbent cyrtochoanitic septal necks; EC, endosiphuncular canal; cr, connecting ring; l, lamellae extending through three segments; v, vinculum; x, endosiphuncular space in communication with EC.

consists of more coarsely grained calcite of somewhat lighter colour, and its boundary with Layer *b* is sharp. The innermost layer, Layer *d*, is 0·2 mm thick, and consists of opaque amorphous material which may be conchiolin.

The longitudinal lamellae of *A. subventricosum* are outgrowths of the connecting ring (text-figs. 2, 3). They do not form continuous structures throughout ontogeny and rarely does the same lamella extend through more than two siphuncular segments. At any ontogenetic stage the lamellae can be separated into three growth forms: *mature*, *immature*, and *budding*. Text-fig. 4 shows a reconstruction of a portion of the ontogenetic development of lamellae, based on serial cross sections.

Mature lamellae are the major endosiphuncular structures and are considered to be at their growth maxima for two reasons: (1) They do not grow beyond an average length of 5·0 mm. All specimens are of comparable size and are considered adults due to contraction of the phragmocone near the body chamber, a feature not found in earlier ontogenetic stages. (2) The extant chambered cephalopod, *Nautilus*, deposits connecting rings at the time of septal secretion with no subsequent modification (Denton 1974; Mutvei 1975; Westermann 1975). Near the centre of each mature
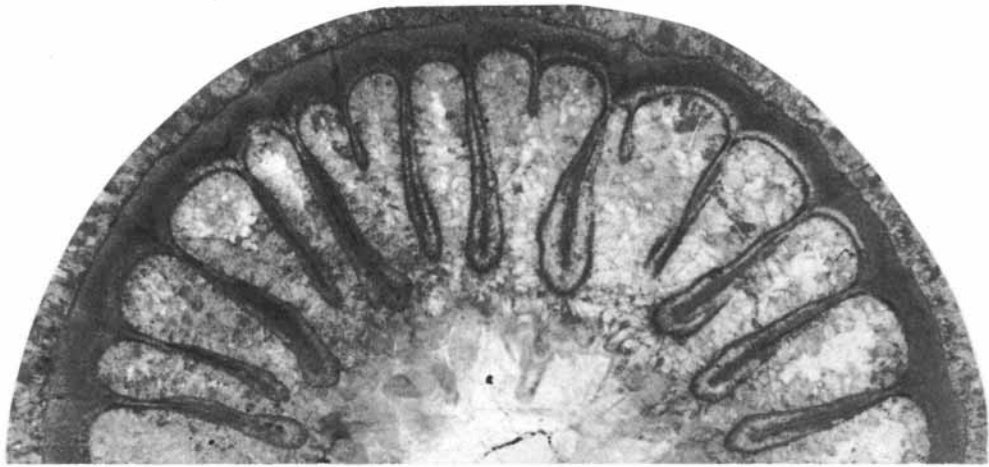
TEXT-FIG. 2. Portion of a transverse section of the siphuncle of *Archiacoceras subventricosum*, ×6. USNM 250630. The light border surrounding the ectosiphuncular wall is calcite spar of the camera. The four layers and central plates are represented.

Figs. 1–3. *Archiacoceras subventricosum*. 1, sagittal serial section through the central portion of a siphuncle, ×3·5. USNM 250630. Recumbent septal necks, thin connecting rings, and pseudo-bullettes are represented. 2, a portion of the serial section in fig. 1, ×7. In addition to the recumbent septal necks and pseudo-bullettes, the vincula can be seen on the anterior and posterior surface of each septum. 3, serial section 2 mm off centre from that of fig. 1, ×3·5. Central plates can be seen in many lamellae. Several lamellae can be seen to extend through the septal foramen. The apparent discontinuity of lamellae is an artifact of the concave segments.

PLATE 99

CRICK and TEICHERT, *Archiacoceras*
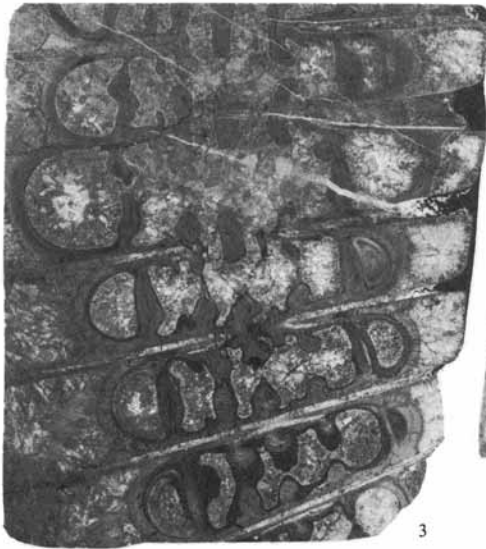
lamella is a *central core* (text-fig. 3; Pl. 100, fig. 3) of the same structure as Layer *b*. The structure of the central core is identical to that of Layer *b*, although there is no evidence of an actual connection between these two structures. Within the central core is commonly a central plate (text-fig. 3; Pl. 100, figs. 3, 4). It is not possible to determine if the absence of central plates in some lamellae is due to selective preservation or to biological causes. The latter is assumed to be the case because of the exceptional preservation of other features. Layers *c* and *d* form the outer layers of the lamellae (text-fig. 3; Pl. 100, figs. 5, 6).
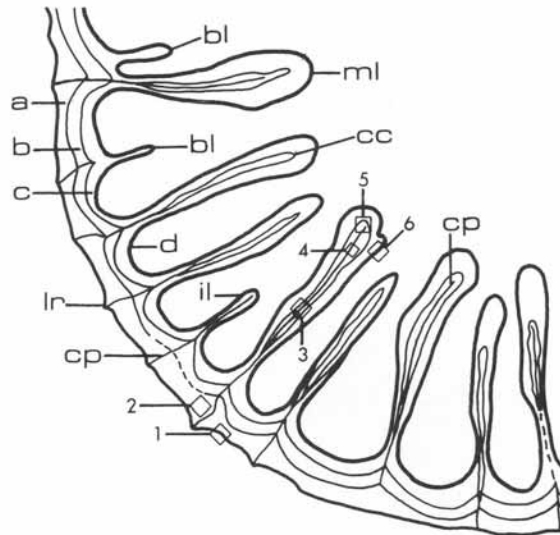
TEXT-FIG. 3. Detailed diagram of the features of part of the siphuncle shown in text-fig. 2, approximately ×7. a, Layer *a*; b, Layer *b*; c, Layer *c*; d, Layer *d*; lr, longitudinal ridges on the ectosiphuncular wall; cp, central plate; cc, central core; bl, budding lamella; il, immature lamella; ml, mature lamella. Numbers 1 through 6 indicate the location of the scanning electron micrographs of Plate 100.

EXPLANATION OF PLATE 100

Figs. 1–6.   Selected group of scanning electron micrographs of layers and a lamellae of a typical *Archia-coceras subventricosum*.   See text-fig. 3 for location of micrographs.   1, boundary of Layer *a* of the ectosiphuncle and the calcite spar of the camera, ×450.   2, structure of Layer *a*, ×825.   3, portion of the central core showing the structure of the central plate, Layer *b*, and Layer *c*, ×90.   4, contact between Layer *c* and the central plate, ×900.   5, tip of a mature lamella showing two distinct Layers *d* and *c* and the central plate, ×60.   6, contact of Layer *d* and calcite spar of endosiphuncular canal, ×250.

PLATE 100
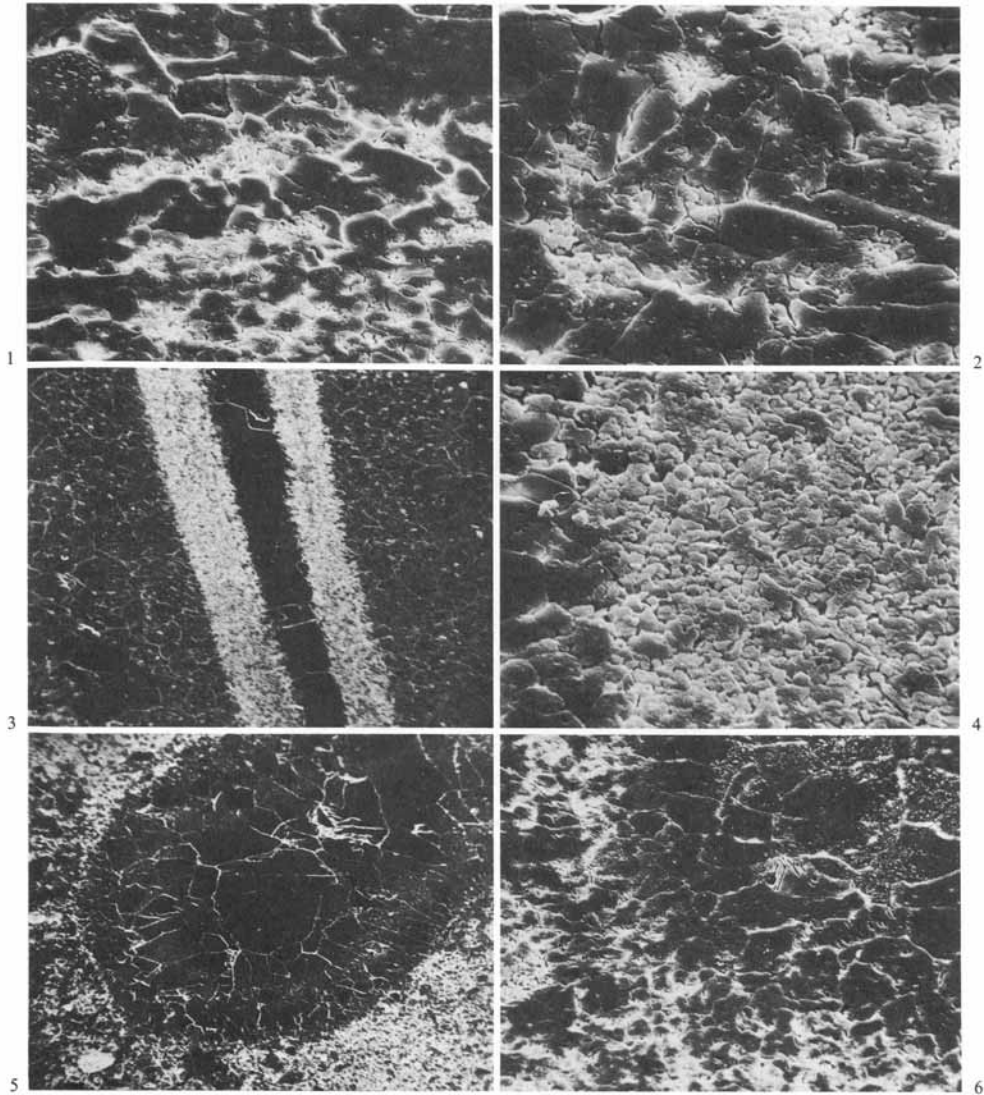
CRICK and TEICHERT, *Archiacoceras*

Immature lamellae are lamellae in an intermediate growth stage. They consist of layers *d*, *c*, and occasionally *b* without a central core but often have a central plate.

Budding lamellae are outgrowths from either the flanks of mature lamellae or the connecting ring wall between lamellae. They consist only of Layers *d* and *c*. This is the first reported occurrence of bipectinate lamellae (those that bifurcate) in *Archiacoceras*. *Actinomorpha* Flower (1943), an Ordovician form, has a siphuncle crowded with bipectinate lamellae but they lack central cores or plates. *Danaoceras subtrigonum* (McCoy) and *D. bindiense* Teichert, both from the Middle Devonian of Victoria, Australia, were reported to have bipectinate lamellae (Teichert 1940).
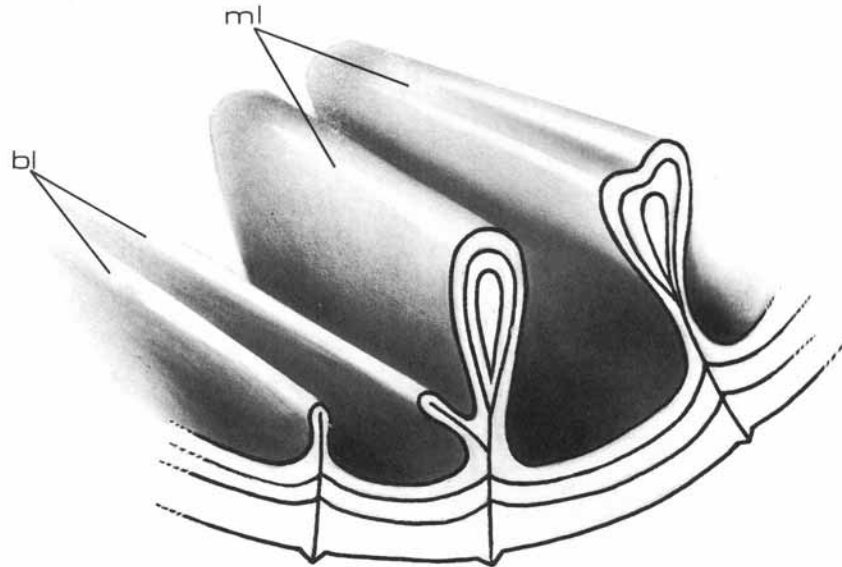

TEXT-FIG. 4. Diagrammatic representation of two stages in the ontogenetic development of the lamellae. bl, budding lamellae; ml, mature lamellae.

The ultrastructure of the connecting ring is remarkably like that of *Nautilus* as illustrated by Denton and Gilpin-Brown (1966, text-fig. 6) and Denton (1974, fig. 12). *Nautilus* has three easily distinguishable layers: an outer chalky tube, a horny tube, and an inner epithelium. The outer two layers of the siphuncle of *Nautilus* correspond rather well in form and structure to the outer two layers of the connecting ring in *Archiacoceras subventricosum*. The structure of the epithelium superficially resembles that of the lamellae of *A. subventricosum*. The two structures differ greatly in size, but this may be attributed to the fact that the siphuncle of *A. subventricosum* is considerably larger.

The siphuncle of *Archiacoceras* sp. (text-fig. 5; Pl. 101, figs. 1–3) is distinguished by an undulating ectosiphuncular surface, a connecting ring consisting of six distinct

layers, and actinosiphonate lamellae composed of distinct layers and central cores. These features are discussed below and illustrated in text-fig. 5 and Plate 101.

The undulating nature of the ectosiphuncular surface is a result of indentations at the base of mature lamellae. These are in contrast to the longitudinal ridges on the ectosiphuncular surface of *A. subventricosum* caused by the protrusion of central plates through the connecting ring. The excellent preservation reveals that the connecting rings of *Archiacoceras* sp. consist of six distinct layers (text-fig. 5). Electron scanning photographs were not available for these siphuncles; however, thin sections under high magnification with conventional microscopy were sufficient to show that the structure of the layers differs in crystal size and colour of the calcite (?conchiolin) (Pl. 101, fig. 1).
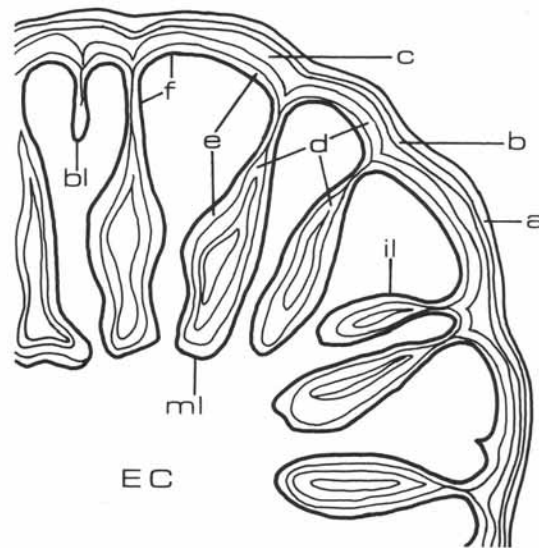
TEXT-FIG. 5. Detailed diagram of the features of an *Archiacoceras* sp. siphuncle, approximately × 7. a, Layer *a*; b, Layer *b*; c, Layer *c*; d, Layer *d*; e, Layer *e*; f, Layer *f*; bl, budding lamellae; il, immature lamellae; ml, mature lamellae; EC, endosiphuncular canal.

Layer *a* forms the outer surface of the ectosiphuncle and connecting ring and has a sharp boundary with the calcite spar of the camerae. The layer now consists of fine fibrous calcite and is uniform in thickness and structure. The sharp boundary of *a* and *b* results from the change to fine-grained calcite. Layer *b* is uniformly thinner than *a* and has a gradational contact with *c*. Layer *c*, which is the thickest layer of all, is more coarsely grained and darker in colour than *b*. Layer *c* is the first in which incipient lamellae are developed. The boundary of *c* and *d* is also gradational. Layer *d*

is of variable thickness and consists of calcite, which is more coarse grained and lighter coloured than *c*. Layers *d* and *e* have a sharp boundary due to a change from coarse-grained to a fine-grained calcite. The boundary with Layer *f* is sharp. Layer *f* consists of a dark amorphous material analogous to Layer *d* of *A. subventricosum*. Layer *f* has a uniform thickness throughout and the contact with the calcite spar of the endosiphuncle is sharp.

The lamellae of *Archiacoceras* sp. are unquestionably outgrowths of the connecting ring. They have the same general morphology as those of the type species. The mature lamellae differ by being composed of three to five layers. Only two or three of these layers are continuous with the inner layers of the connecting ring (text-fig. 5). The central core consists of two or three distinct layers, none of which show a clear connection with layers of the connecting ring. However, the crystalline structure of all but the innermost layer is similar to corresponding connecting ring layers. Immature and budding lamellae are also present, and the bipectinate nature of mature lamellae is more pronounced in this form than in *A. subventricosum* (Pl. 101, figs. 1–3). Ontogenetic stages from budding maturity can be observed in serial sections covering approximately 3·0 mm of one siphuncular segment (Pl. 101, figs. 1–3). Arrows *a* and *b* mark two stages of bifurcation. Arrow *a* (Pl. 101, fig. 1) marks development of a bud from a mature lamella. In Plate 101, figs. 2 and 3, the bud is seen to develop into an immature lamella and migrate laterally from the parent. Arrow *b* (Pl. 101, fig. 1) marks two mature lamellae near their final growth stage and sharing the same base (bifurcation and growth without migration). Plate 101, figs. 2 and 3 show continuing growth, further zonation of central cores, and eventual lateral migration. The radial distribution of lamellae is even and shows no preference in dorsal or ventral areas. This is also true for the type species. Lamellae of *Archiacoceras* sp. extend through at least two siphuncular segments. The saggittal sections of *Archiacoceras* sp. (Pl. 98, fig. 3) is a near perfect central section through the endosiphuncular canal and shows no lamellae. Plate 98, fig. 5, shows an off-centre section of the same siphuncule and shows evidence of actinosiphonate lamellae. In the uppermost segments, lamellae can be observed to extend from one segment to the next. What appear to be discrete or discontinuous lamellae within segments are, for the most part, continuous lamellae of which only the distal areas are seen in the section.

EXPLANATION OF PLATE 101

Figs. 1–3. Structure and ontogenetic development of the siphuncular features of *Archiacoceras* sp. USNM 250629. Series of three serial sections covering approximately 3 mm of one siphuncular segment. 1, details of six layers, budding lamellae, immature lamellae, and mature lamellae, × 7. Central plates are absent and bifurcation of lamellae is common. Arrow *a* marks the growth of a budding lamella from a mature host. Arrow *b* points to two mature lamellae which, at some earlier ontogenetic stage, experienced bifurcation without lateral migration. 2, 3, successive serial sections showing the continued ontogenetic development of lamellae, × 3·5. Arrows a_1, a_2, b_1, and b_2 mark lamellae following bifurcation and lateral migration. The indentations of the ectosiphuncular surface coincide with the bases of mature lamellae. Serial sections in figs. 2 and 3 are slightly oblique.

PLATE 101
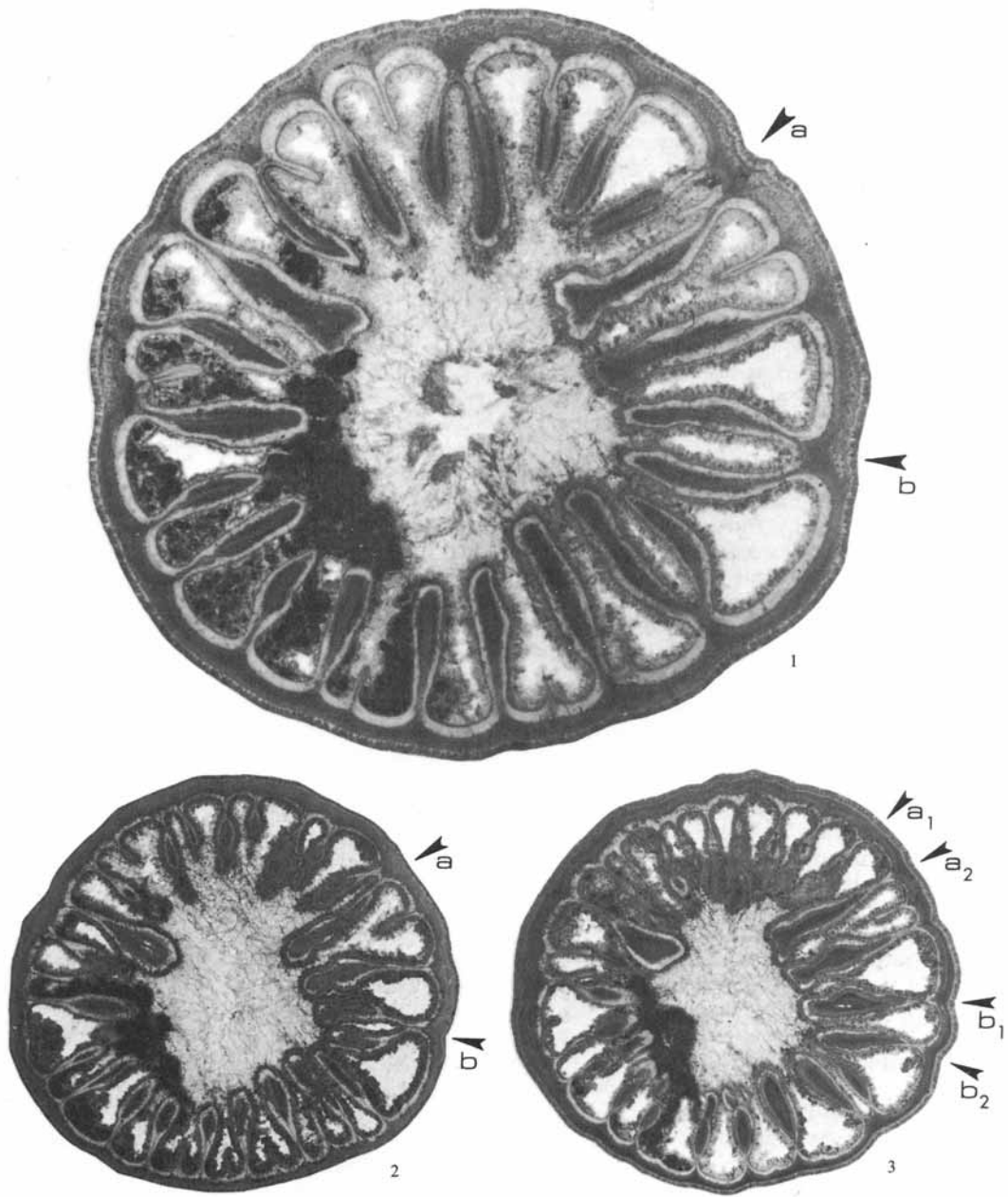
CRICK and TEICHERT, *Archiacoceras*

Formation and function of the siphuncle

Although nothing conclusive can be stated concerning the formation and function of connecting ring layers, central plates, and the lamellae, we believe that the following observations permit analogies with extant chambered cephalopods.

Formation. The secretionary sequence of the connecting ring, lamellae, and accompanying features of *Archiacoceras* occurred by one of two methods: sequential or simultaneous. Mutvei (1964*a*) proposed a sequential model whereby each layer of the connecting ring was secreted in 'phases' from epithelial cells of the siphuncular cord. Lamellae were termed 'secondary deposits' and considered to be deposited after a pause in the secretionary activity. To accomplish this last phase, the epithelium along the entire length of the siphuncular cord differentiated into numerous secretionary strips and all lamellae were secreted in one growth period throughout the whole of the endosiphuncle. The lamellae were to have grown from dorsoventral ridges on the central radial epithelium of the connecting ring (Mutvei 1964*a*, pp. 415–418). Mutvei proposed this model for oncocerids that possess radial 'endoperibolic deposits' (actinosiphonate lamellae).

Regarding this model and its relation to *Archiacoceras*, two problems are noteworthy. Firstly, the type of secondary development of lamellae by cells secreting material of a different chemical composition would produce annulosiphonate and not actinosiphonate deposits. Secondly, since we have shown that these lamellae are outgrowths of the connecting ring tissue, a simultaneous deposition of all lamellae would require that the connecting ring also be deposited simultaneously. The ontogenetic growth patterns of lamellae, particularly with regard to origination and disappearance within two to three segments, argues against 'instantaneous formation'. It is our contention that actinosiphonate structures that are demonstrated to be outgrowths of connecting ring tissue result from simultaneous deposition by secretionary cells on the dorsal face of the body proper and on the adoral portions of the siphuncular cord. This interpretation corresponds with Mutvei's detailed analyses of the secretionary patterns of *Nautilus* and *Spirula* (Mutvei 1964*b*, 1972), and with many other case studies relating the physiology of extant cephalopods to extinct forms (Denton 1974; Denton and Gilpin-Brown 1973; Packard 1972). The functional interpretation agrees with this model.

Function. Three major hypotheses have been proposed to explain the function of actinosiphonate lamellae: (1) they increase the surface area of the endosiphuncle to allow for more efficient gas removal from the chambers (Strand 1934, p. 6); (2) they serve as a counterweight to reduce buoyancy (Strand 1934, p. 7); and (3) they are gerontic calcifications of the vascular tissues of the siphuncular cord (Flower 1938, p. 172). These two authors were by no means the only workers to employ these hypotheses, but they were the first to put them in print.

Denton (1974), Denton and Gilpin-Brown (1966, 1971, 1973), Denton *et al.* (1961), Gilpin-Brown (1972), and Mutvei (1972) have shown that a combination of liquid and gas is the buoyancy medium in extant chambered cephalopods, and that the connecting rings act as an osmotic pump to remove the cameral fluid. A certain volume of gas is presumed to diffuse into the chambers. This process has been observed during removal of cameral liquid (Denton and Gilpin-Brown 1971). *Spirula*

has been shown to refill a number of the most apical chambers with liquid (Denton and Gilpin-Brown 1971). The microstructure of connecting rings in several groups of extinct cephalopods has been compared with that of extant forms and has been shown to be remarkably similar (Mutvei 1964*a*, 1972; Denton 1974; Denton and Gilpin-Brown 1973). The connecting ring of *Archiacoceras* is more complex in terms of number of layers and actinosiphonate lamellae than those discussed and illustrated by Mutvei (1964*a*, 1972) and Denton and Gilpin-Brown (1973). The siphuncles are, however, similar with regard to the position of layers and their general crystalline structure. Although the complexity of the connecting ring of *Archiacoceras* is greater, we suggest that the function of the actinosiphonate lamellae and connecting rings was one of removal of liquid from newly formed chambers. It is suggested that the cameral fluid moved through the connecting ring by osmosis and that the lamellae would have served to increase the surface area of the endosiphuncular tissue, allowing a more rapid absorption of the fluid by tissue of the endosiphuncular canal (haemocoele).

This assumption may be supported, in part, by the correlation between the size of the chamber, circumference of the connecting ring, and the number of lamellae occupying the internal surface of the connecting ring. That is, the larger the chamber, the more expanded is the connecting ring, and additional lamellae are formed in proportion to its increased size. The distance between lamellae at their base is 1·9 mm in *A. subventricosum* and 1·5 mm in *Archiacoceras* sp. The difference in spacing of lamellae may be a result of the presence of central plates in the lamellae and connecting rings of *A. subventricosum*. Such plates may have assisted in moving fluid through the connecting ring in place of the additional layers of *Archiacoceras* sp.

We are, therefore, in agreement with Strand's first alternative (Strand 1934, p. 6). We do not believe, however, that the weight added by the lamellae was a significant factor in counteracting buoyancy, because the lamellae are not completely calcified structures, but consist of the same materials as the connecting rings. This fact also rules out Flower's (1938) interpretation of the lamellae as gerontic features.

TAXONOMIC POSITION

In 1939, Teichert placed the Archiacoceratidae in the order Cyrtoceroidea, established by him in 1933, in which he proposed to unite all nautiloid forms with endo-siphuncular radial lamellae. Flower (*in* Flower and Kummel 1950) included this family in the order Oncoceratida, established in the same publication. According to Flower's interpretation, actinosiphonate structures are present only in some members of this order. Sweet (*in* Teichert *et al.* 1964) followed Flower, at the same time shortening the name of the order to Oncocerida. None of these authors took account of the structure of the connecting ring.

Zhuravleva (1974, p. 35) cited presence of 'single-layered connecting rings' as one of the diagnostic features of the order Oncoceratida, and apparently regarded this as one of the important distinctions from Discosorida for which she had previously (Zhuravleva 1972, p. 70) described the connecting rings as 'thick, not single-layered'. According to Zhuravleva, both discosorids and oncocerids may possess radial lamellae in the siphuncle, the sole distinction being that in oncocerids they originate

from the inner surface of the connecting rings and are continuous throughout the siphuncle, whereas in discosorids the lamellae originate at the bullettes and are discontinuous. While we are in no position to evaluate the general validity of these criteria, we would point out that extremely few high-magnification thin section studies have been done on oncocerids and that the siphuncular structures of almost all members of this order are poorly understood or not known at all.

Archiacoceras can be described as a large endogastric brevicone, with cyrto-choanitic septal necks, and a large ventral siphuncle with a thick, complex connecting ring and vincula. Discosorids are commonly large, endogastric brevicones. Onco-cerids are commonly breviconic, but rarely as large as *Archiacoceras* and are not commonly endogastric. Cyrtochoanitic septal necks of the recumbent type are common in both orders. Large siphuncles are more typical of discosorids, but large ventral siphuncles are not uncommon in oncocerids. Actinosiphonate structures are found only in oncocerids while discosorids are commonly annulosiphonate. A thin connecting ring is a common oncocerid feature, whereas discosorids may have thin connecting rings, but more commonly possess thick complex rings. Vincula have previously been reported only in discosorids, which most probably reflects the lack of siphuncular studies of oncocerids. The connecting ring of *Archiacoceras* is complex. Complex connecting rings have not previously been reported from oncocerids, probably for the same reason as given for vincula. A common and reportedly distinctive feature of discosorids, the two-layered bullette, is not present in *Archiacoceras*, although Flower (1943) suggested its existence as a possibility. It is common to observe structures resembling bullettes in the vicinity of the septal foramen of *Archiacoceras*, but these were found to be sectioned lamellae. In some cases such 'pseudobullettes' may appear to be discontinuous from one connecting ring to the next. In such cases, we found that the thin section had passed through the bulbous portion of a lamella and not through the base and stem. Thus, the impression of an annulosiphonate structure is created, though it is definitely not such a deposit.

It is apparent from the preceding descriptions and discussions that *Archiacoceras* combines features which, according to Zhuravleva (1972, 1974), are diagnostic of the discosorids as well as the oncocerids, because the genus possesses complex, multi-layered connectings and continuous radial lamellae. We are inclined to assign greater taxonomic weight to the presence of continuous lamellae and, therefore, prefer to retain *Archiacoceras* in the order Oncocerida.

CONCLUSIONS

Examination of exceptionally well-preserved specimens of the genus *Archiacoceras* from Middle Devonian rocks of the Eifel in West Germany has led to new insights into ecto- and endosiphuncular structures of this genus. The connecting ring is unusually complex, being composed of as many as six layers distinguished by different optical properties. The two or three innermost layers are folded inward, the folds developing into radially oriented lamellae that enclose a thin central plate and are continuous throughout several segments, perhaps throughout the length of the siphuncle. The shell is believed to be endogastrically curved, as originally suggested by Foerste (1926).

The ultrastructure of connecting rings and lamellae in *Archiacoceras* is similar to that of the connecting ring of *Nautilus*. It is, therefore, reasonable to assume that the ecto- and endosiphuncular tissues were osmotic membranes that facilitated the removal of cameral liquid and formed part of the buoyancy regulating mechanism.

The genus occupies an intermediate position between the orders Oncocerida and Discosorida. With the former it shares the continuous radial lamellae, with the latter the complex structure and thickness of the connecting ring. In addition, presence of vincula is regarded as a discosorid feature, even though in discosorids a vinculum is present only in the anterior portion of the connecting rings. We give weight to the configuration of the radial lamellae within the siphuncle and, for the time being, believe that *Archiacoceras* should be retained in the Oncocerida. We realize, however, that the problem of the relationships between Oncocerida and Discosorida is in need of restudy and that clarification can only be achieved through high-magnification thin section studies of most or all of the genera in both groups.

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REX E. CRICK

Department of Geology
University of Texas at Arlington
Arlington, Texas 76019
U.S.A.

CURT TEICHERT

Department of Geological Sciences
University of Rochester
Rochester, New York 14627
U.S.A.