MUSCLE-ATTACHMENT IMPRESSIONS IN SOME PALEOZOIC NAUTILOID CEPHALOPODS

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ABSTRACT—Muscle-attachment impressions are described for the first time from representatives of the nautiloid suborders Oncoceratina (Oncoceras sp., Beloitoceras sp., Diestoceras sp.), Ascoceratina (Billingsites deformis (Eichwald)?), Discosorina (Parryoceras euchari Sweet & Miller), and Rutoceratina (Metacoceras sp.), and notes concerning the probable configuration of such impressions in certain Paleozoic Barrandeoceratina (Charactoceras?) and Triassic Lyroceratina (Proclydonautilus ursensis Smith) are included. Muscle-attachment impressions are not known in the Endoceratina and Actinoceratina; in known Ellesmeroceratina, Michelinoceratina, and secondarily straight Tarphyceratina (Lituitidae) the retractors were attached dorsally ("dorsomyarian"), whereas in described Barrandeoceratina, coiled Tarphyceratina, Ascoceratina, Oncoceratina, and Discosorina, these muscles were attached ventrally ("ventromyarian"). Described Rutoceratina, Nautilina, Solenochilina, and Lyroceratina are similar in that the retractors were attached laterally ("pleuromyarian"). In several cases, similar attachment patterns suggest adaptive convergence, rather than relationship, and their taxonomic significance is thereby reduced.

INTRODUCTION

O_{to} our knowledge of the configuration and arrangement of the muscle-attachment impressions in fossil cephalopods, primarily, it seems, because well preserved specimens exhibiting these features are not particularly common and most investigators have apparently attached only minor systematic importance to them. In 1957, Mutvei prepared a summary of the literature concerning muscle-attachment impressions in fossil nautiloids and, in the same work, included descriptions and illutrations of several additional examples found by him in a collection of well preserved specimens from the Ordovician and Silurian of Sweden. Other forms are described by Miller (1951, p. 38, pl. 5, fig. 1) and illustrated by Kummel (1953, pl. 2, figs. 11,12; pl. 11, figs. 1,2). In addition to these reports, Foerste (1930) seems to have interpreted the "basal zone" of at least one group of Paleozoic nautiloids as part of the muscle-attachment ring or "annulus," even though he apparently did not attach any particular taxonomic significance to this feature.

Crick (1898a) described the muscle-

EXPLANATION OF PLATE 42

- FIG. 1—Billingsites deformis (Eichwald)? Ventral view, ×1, of a specimen from the Upper Ordovician Cape Phillips formation, on the eastern part of Little Cornwallis Island, Canadian Arctic Archipelago, Geol. Surv. Canada, No. 12231.
 - Archipelago. Geol. Surv. Canada, No. 12231.
 2,3—Parryoceras euchari Sweet & Miller. Ventral views, ×1, of the holotype and paratype of this species. Both specimens from the Upper Ordovician Cape Phillips formation, Marshall peninsula, Cornwallis Island, Canadian Arctic Archipelago. Geol. Surv. Canada Nos. 12243, 12244.
 - 4—Beloitoceras sp. Ventral view, ×1.5, of a specimen from the Upper Ordovician Cape Phillips formation, eastern part of Little Cornwallis Island, Canadian Arctic Archipelago. Geol. Surv. Canada, No. 12235.
 - 5—Oncoceras sp. Ventral view, ×1.5, of a specimen from the Upper Ordovician Cape Phillips formation, eastern part of Little Cornwallis Island, Canadian Arctic Archipelago. Geol. Surv. Canada, No. 12233.
 - 6,7—Diestoceras sp. Ventral and lateral views, ×1, of a large body chamber showing a well preserved annular elevation. Upper Ordovician Boda limestone, Osmundberget, Dalarna, Sweden. Univ. Uppsala, Paleontological Institute, No. D739.



attachment impressions in several ammonoid species, chosen from a large collection to exhibit these features in a variety of conch forms, and concluded his remarks by pointing out (p. 108) that ". . . indications of the muscular attachment of the Ammonoid animal, instead of being rare, seem to be fairly common." Nevertheless, Arkell et al. (1957, p. L81) remark that ammonoids ". . . very rarely retain vague muscle scars," and they seem to attach no particular importance, taxonomically or otherwise, to the forms described by Crick and others.

Because so little is known about muscleattachment impressions in fossil cephalopods, the several specimens in collections at hand that exhibit these features are of more than ordinary significance and merit detailed description. These specimens, which form the material upon which the present report is based, were assembled over a period of several years and from a number of different localities. Several well preserved specimens were found in collections made by Dr. Raymond Thorsteinsson, of the Geological Survey of Canada, from Upper Ordovician strata on Cornwallis Island in the Canadian Arctic Archipelago. Professor C. H. Summerson, of The Ohio State University, supplied a fragmentary Metacoceras from the Pennsylvanian of Kentucky, and Professor Per Thorslund, of Uppsala University, Sweden, sent to the writer on loan a large collection of Upper Ordovician nautiloids, including several that show muscle-attachment impressions, from the Boda limestone of Sweden. The latter were collected largely by the late Professor Elsa Warburg, of Uppsala. The writer is indebted to all these men for making their collections available to him for study, and to Mr. Harry Mutvei, of the Naturhistoriska Riksmuseet, Stockholm, for discussion of problems pertaining to the muscle-impressions in nautiloids. Illustrations accompanying this paper were prepared by the writer and financed by a liberal grant from the Graduate School of The Ohio State University.

MUSCLES AND MUSCLE-ATTACHMENT IMPRESSIONS IN NAUTILUS

The musculature and muscle-attachment impressions in *Nautilus*, the only living tetrabranchiate cephalopod, have been ade-

quately described in several places (Owen, 1832; Waagen, 1870; Dewitz, 1879a, 1879b 1880; Schröder, 1881; Appellöf, 1893. Griffin, 1900; Willey, 1902; Miller, Dunbar, & Condra, 1933; Mugglin, 1939; Flower, 1946; Miller, 1947; Stenzel, 1952; Mutvei, 1957), hence it seems unnecessary to review these discussions in any detail here. A summary of the observations referred to is appropriate, however, so that the structures to be described may be understood in relation to presumably comparable features in Nautilus. It should perhaps be pointed out that all of these reports are in essential agreement as to the structure and relationship of the principal musles in Nautilus and their areas of functional attachment on the shell; however, the several authors use different terminology and, to a minor degree. their interpretations are at variance with one another. For these reasons, the following discussion is based on the recent work of Stenzel (1952) and Mutvei (1957).

In *Nautilus*, a complex of three different muscle systems is attached, somewhat indirectly, to the inner side of the shell along a transverse sinuous ring-shaped elevation near the adapical end of the body chamber. This attachment area and the ring of muscles attached to it are referred to as the "annulus" by most writers; however, the designation "annular elevation" (Mutvei, 1957) for the shell-attachment zones seems preferable and is used in this report. The term "annulus" is restricted to the ringshaped muscle-complex attached to the shell along the annular elevation.

The most conspicuous of the three muscle systems attached to the annular elevation includes a pair of powerful retractor ("shell") muscles, about 5 cm. long, each of which is anchored at its adoral end to a short process on the internal cephalic cartilage. These muscles diverge adapically in the form of a V (as viewed from above) to form the sides and part of the ventral wall of the body within the pallial cavity (Stenzel, 1952). Each retractor is attached, by means of a transversely fibrous epithelial layer, to broad subtriangular antero-lateral expansions and somewhat narrower dorsolateral portions of the annular elevation (stippled area of Textfig. 1). The weakly developed longitudinal mantle muscles of Nautilus appear to be

attached, in much the same fashion as the retractor muscles, to a narrow zone along the adapertural edge of the annular elevation (solid black area of Text-fig. 1), whereas a third system of subepithelial muscle tissue is functionally attached along the thin sinuous adapical edge of the elevation, coincident with, or only slightly orad of the youngest suture of the phragmocone (crosslined area of Text-fig. 1).

Mutvei (1957) terms the transverse annular zone of epithelium that includes the termini of the mantle and retractor muscles best to avoid the use of such terms in the description of fossil forms.

MUSCLE-ATTACHMENT IMPRESSIONS IN FOSSIL NAUTILOIDS

At the present time, about 550 genera and approximately 3,000 species of nautiloid cephalopods are recognized. These are distributed rather unevenly among 82 families which, in turn, are grouped together in 13 suborders. It may be of interest, then, to note that the configuration of the annular elevation, or part of it, is known from rep-



TEXT-FIG. 1—Diagrammatic representation of the annular elevation of Nautilus, approximately $\times \frac{1}{2}$. Longitudinal mantle muscles attached along heavy black line; retractor-muscles attached to stippled areas; subepithelial muscles attached along cross-lined area. Heavy black, and stippled areas composed conchial zone I; cross-lined area represents conchial zone II. (After Mutvei, 1957.)

"epithelial zone I", and refers to that portion of the annular elevation along which this band is attached as "conchial zone I". In like manner, Mutvei terms the posterior band of whitish mantle tissue, containing the termini of the subepithelial muscles, "epithelial zone II," and applies the designation "conchial zone II" to the adapical margin of the annular elevation to which this band is attached. These terms seem free from positive objection and are perhaps more precise than the older denomination, "annulus", employed previously for both the epithelial and conchial zones. Parts of epithelial zones I and II have been regarded as forming a dorsal aponeurotic band; the adapertural edge of the annulus between the lateral expansions of epithelial zone I makes up the antero-ventral aponeurotic band of several authors; and the adapical margin of the annulus has been termed the posteroventral aponeurotic band. However, since there is apparently some question (Mutvei, 1957) as to whether or not these tissue bands are actually aponeuroses in Nautilus, it seems

resentatives of only 31 genera, belonging in 20 or 22 of the 82 currently recognized families, and distributed among 11 of the 13 suborders. This tabulation, which includes the several specimens described in the present contribution, but does not include the many phragmoceroids described by Foerste (1930), emphasizes our lack of knowledge about the structure, position, relationship, and attachment patterns of muscles in fossil nautiloids, and suggests that we must know a good deal more about the annular elevation in fossil cephalopods before this feature can be accorded any particular significance taxonomically.

Ellesmeroceratina.—This suborder includes 11 families of primitive nautiloids, to which some 280 named species are referred. Muscle-attachment impressions have been described (Dewitz, 1879a; Schröder, 1881; Mutvei, 1957) from representatives of only one species, Baltoceras burchardi (Dewitz). B. burchardi has a relatively large, marginal or submarginal siphuncle and a virtually straight conch that may be slightly curved apically toward the siphuncular (ventral?) side. Presumably, this indicates that the conch is slightly endogastric. The adapical and adoral edges of the annular elevation are close together and parallel to the adoral suture on the ventral and ventrolateral sides of the body chamber, but the adoral edge of the elevation swings broadly toward the aperture dorsolaterally, forming a low, broad salient on the dorsum. This salient apparently represents, in large part at least, the locus of attachment for the retractor muscles.

Endoceratina and Actinoceratina.—Muscle-attachment impressions have not been reported from the many known representatives of the suborders Endoceratina and Actinoceratina, both of which find their origin in late Lower Ordovician members of the Ellesmeroceratina.

Michelinoceratina.-The suborder Michelinoceratina includes a host of straight or slightly curved nautiloids characterized, in general, by a primitively tubular, but secondarily cyrtochoanitic siphuncle. Early representatives of this suborder are closely similar to contemporaneous and presumably ancestral species included in the Baltoceratidae (Ellesmeroceratina), but differ from the baltoceratids in that the connecting rings are thin and apparently homogeneous, rather than thickened. To the best of the writer's knowledge, the configuration of the annular elevation is known from representatives of only five of the several hundred named species of the Michelinoceratina, "Geisonoceras" scabridium (Angelin), "Orthoceras" angulatum Wahlenberg, Orthoceros regulare (Schlotheim), Lyecoceras gotlandense Mutvei, and Lyecoceras longistriatum Mutvei. Existing information with regard to the types of the first two species listed is inadequate to suggest their familial or even their proper generic reference. It is distinctly possible, however, that "G." scabridium is, indeed, a Geisonoceras; "O." angulatum is reminiscent of longitudinally fluted orthoceracones referred by many writers to Kionoceras. Lyecoceras gotlandense and L. longistriatum represent a generic category erected by Mutvei (1957) for slightly depressed annulated endogastric cyrtoceracones from the lower Ludlovian Hemse Group, on Gotland, Sweden. Lyecoceras ap-

parently has an eccentric orthochoanitic siphuncle located somewhat closer to the convex (dorsal) side of the conch than to the concave (ventral) side. Sutures in both known species form a broad lobe on the dorsal and dorsolateral portions of the conch, and a low rounded saddle on the venter. The apertural margin is said to bear a hyponomic sinus on the concave side of the conch and a well defined septal furrow on the convex side. It should be noted that there is considerable external similarity between the two known species of Lyecoceras and Barrande's Cyrtoceras cognatum and C. pergratum, both of which were referred by Foerste (1936) to the genus Calocyrtoceras. The presence or absence of a hyponomic sinus cannot be determined from Barrande's illustrations (1866, pl. 199, fig. 35-45) of C. cognatum, but there is a suggestion of such a feature on the concave side of the conch in one of his illustrations of C. pergratum (1866, pl. 199, fig. 7), a species closely related to C. cognatum. Foerste (1936) distinguished the genus Cyrtocycloceras from Calocyrtoceras by the fact that no longitudinal striation occurs on the shell of typical representatives of the former, whereas the types of the latter bear prominent longitudinal striae. The writer regards differences of this character as dubious grounds for generic subdivision, insofar, at least, as other features of these two genera are almost precisely similar. Lyecoceras is reminiscent externally of both Calocyrtoceras and Cyrtocycloceras, the types of which are also of about the same age. It seems distinctly possible, therefore, that Lyecoceras, Calocyrtoceras, and Cyrtocycloceras are all names for virtually the same group of species and that Calocyrtoceras and Lyecoceras should be suppressed in favor of Cyrtocycloceras, which is the oldest available name for the group. The writer hesitates to do this, however, for he has not been able to make direct comparisons between the several types involved. It does seem clear, however, that the species at present distributed among these three genera belong in the same family, for which Flower (in Flower & Kummel, 1950) proposed the name Paraphragmitidae.

In all of the michelinoceratinid species enumerated above, the elements of the annular elevation are similar in distribution to those of *Baltoceras burchardi*; that is, the expanded portion presumed to be the locus of attachment of the retractor muscles is situated on the dorsal side of the conch. In all these species, however, the expanded dorsal portion of the annular elevation is distinctly bifid, being separated into two more or less distinct portions by an adapically-directed, mid-dorsal notch in the adoral edge of the elevation.

Ascoceratina.-This suborder includes a group of bizarre early Paleozoic nautiloids with essentially straight or slightly cyrtoceraconic conchs, and siphuncles characterized by planoconvex segments that become broadly expanded in mature camerae. Furthermore, natural truncation of the earlyformed portions of the conch seems to have taken place in virtually all known representatives of the suborder and, in more advanced members, the adoral few camerae were altered in shape so that they came to lie above (rather than behind) the animal's body. Insofar as the writer is aware, no previous mention has been made of the annular elevation in any species referable to this suborder.

One of the ascoceratinids in Upper Ordovician collections available to the writer shows the annular elevation, or portions of it, and, for that reason, this specimen merits somewhat more detailed description than it it has received previously (Sweet & Miller, 1957). The specimen illustrated by figure 1, on Plate 42, is a representative of the family Ascoceratidae, and has been tentatively identified (Sweet & Miller, loc. cit.) as Billingsites deformis (Eichwald)?. It is not necessary to repeat a detailed description of this form here, but it should be pointed out that further preparation of this specimen has disclosed faint but well preserved traces of the annular elevation. On the dorsum and the sides of the specimen, the elevation consists of a narrow raised band, parallel to and immediately orad of the last-formed sigmoidal suture. On the venter, however, the raised adapical edge of the annular elevation remains parallel to the adoral suture, whereas the ridge-like adoral edge of the elevation swings prominently forward to form a distinct ventral salient, subdivided by a midventral notch into two subequal lobate portions. Presumably, these two ventral elements of the annular elevation represent the areas to which the retractor muscles were affixed. It should also be noted that the internal mold bears a distinct mid-ventral ridge, indicating the presence on the inner surface of the shell itself of a longitudinal mid-ventral groove. This is almost certainly an expression of the conchial furrow, a structure known to be located in the mid-ventral interior of the nautiloid conch.

Oncoceratina .- Earlier concepts of the suborder Oncoceratina (Flower, in Flower & Kummel, 1950) have recently been revised (Flower, in Flower & Teichert, 1957) so that this group is now conceived to include, for the most part, compressed exogastric cyrtoceracones and brevicones with ventral siphuncles, the segments of which are tubular in primitive forms, but expanded in later, more advanced species. In four of the 12 familes currently included in the Oncoceratina, the siphuncle is empty, whereas in the remaining eight, it contains specialized actinosiphonate deposits. Although the Oncoceratina includes some 120 genera, to which several hundred species have been referred, the writer is unaware of any previous description of muscle-attachment impressions, as such, from a valid representative of any of these species. Several such specimens occur, however, in collections of the Geological Survey of Canada from the Upper Ordovician of Cornwallis Island, in the Canadian Arctic Archipelago. A ventral view of one of these specimens, described by Sweet & Miller as Oncoceras sp., is shown by figure 5. Plate 42 of the present report. From this illustration, it can be seen that the adapical and adoral edges of the elevation are close together laterally (and, presumably, dorsally), being separated only by a narrow "basal zone," consisting of a transverse row of quadrangular loculi immediately adjacent to the adapical extremity of the body chamber. On the venter, however, the adoral edge of the elevation projects broadly toward the aperture to outline a small, but nevertheless distinct retractor-attachment area, divided into two elements by a broadly V-shaped, mid-ventral notch. The transversely subelliptical areas included between conchial zones I and II on the venter are "pitted," indicating that the surfaces of the slightly raised bosses of shell material were similarly pitted or nodose. Such elevational

irregularities occur also in illustrated representatives of *Discoceras angulatum* (Saemann) and "Geisonoceras" scabridium (Angelin) (Mutvei, 1957, text-fig. 12,15), and longitudinally lineated elevations are shown by Mutvei (1957, text-fig. 13,16,17) in Lyecoceras? sp., Lyecoceras gotlandense, and "Orthoceras" angulatum Wahlenberg.

A ventral view of an oncoceratid identified as *Beloitoceras* sp. by Sweet & Miller (1957, p. 46, pl. VI, fig. 5) is shown by figure 4, Plate 42. The annular elevation in this form consists of a narrow dorsal and lateral band, enclosing the "basal zone," and a bifid ventral salient similar in location and general proportions to that shown by *Oncoceras* sp., described above. As in *Oncoceras*, it appears that the retractor muscles were functionally attached to the ventral side of the shell in *Beloitoceras*.

A large, incomplete internal mold, representing the body chamber of a Diestoceras. is shown by figures 6 and 7 on Plate 42. This specimen, which was collected from the Upper Ordovician Boda limestone, at Osmundberget, Dalarna, Sweden, clearly exhibits a virtually complete annular elevation. This consisted, on the original shell, of a slightly raised transverse band, some 5 mm. wide, at the adapical extremity of the body chamber, marked adorally by a narrow incised serrate groove separated from the adoral septum by a row of subquadrangular nodes or bosses. Ventrally, the adoral edge of the annular elevation is produced into a broad adapically convex sinus, and the zone of subquadrangular nodes is replaced by a pair of surficially tuberculated, adapically convex bosses, presumably representing the loci of retractor-muscle attachment. Dorsally, the adoral edge of the annular elevation forms a slight broad salient, separated from a "basal zone" of markedly reduced width by a second incised line. This specimen of Diestoceras is similar to Oncoceras and Beloitoceras in the gross distribution of the elements of the muscle-attachment ring, but differs from them in that the presumed loci of retractor-attachment are produced toward or onto the last-formed septum, rather than adorally along the walls of the body chamber. This is perhaps a result of the greatly shortened, contracted body chamber of Diestoceras.

Discosorina.-The suborder Discosorina includes a group of some 345 species, distributed at present among about 42 general These genera are grouped (Flower, in Flower & Teichert, 1957) into 8 families. and are thought to represent a stock derived. independently of other nautiloids, from early Ordovician Plectronoceratidae (Ellesmeroceratina). To the best of the writer's knowledge, the muscle-attachment impressions of this group have not previously been described, as such, although Foerste (1930) appears to have regarded the "basal zone" in a majority of the discosorinid species he described as some part of the "annulus", or annular elevation. Two specimens of Parryoceras euchari Sweet & Miller in collections of the Geological Survey of Canada, show clearly the relationship between the "basal zone" and the retractor-muscle attachment areas, and, for that reason, they merit additional discussion here.

Parryoceras euchari is an endogastric cyrtoceracone referred by Sweet & Miller (1957) to the family Cyrtogomphoceratidae. The adapical extremity of the body chamber on both the holotype and the single known paratype of this species is marked (Pl. 42, figs. 2, 3) by a transverse row of quadrangular depressions (a "basal zone"), which represents a similarly transverse, nodose, or tuberculated band of shell material on the inner portion of the original shell. The adoral and adapical edges of the "basal zone" are marked by fine irregularly serrate raised lines that are interpreted to mark the adoral and adapical edges of the annular elevation. On the ventral side of the conch, the quadrangular depressions of the "basal zone" are replaced by two transversely subelliptical areas, representing surficially nodose ventral bosses of shell material in the original shell. These ventral impressions seem clearly to represent the areas of retractor-attachment.

It is reasonable to presume, as Foerste seems to have done, that the "basal zone", so characteristically developed in many, if not most Discosorina, represents some part of the annular elevation. Unfortunately, little attention seems to have been paid this feature in the past, and it is not possible to make direct comparisons of the material at hand with other Discosorina.

Tarphyceratina.-Included in this sub-

order are four families of cyrtoceraconic, or variously coiled nautiloids, all similar in that the connecting rings of the siphuncle are thick and complex and the siphuncle as a whole tends, at least in primitive forms (and in the early parts of advanced forms), to be located ventrad of the center of the conch. The four families of Tarphyceratina (Bassleroceratidae, Tarphyceratidae, Trocholitidae, and Lituitidae) include some 170 species, distributed among about 42 named genera. The configuration of the annular elevation is not yet known in members of the cyrtoceraconic Bassleroceratidae, but it has been reported from representatives of Estonioceras impressum (Hyatt), E. perforatum Schröder, E. imperfectum (Quenstedt), and Planctoceras falcatum (Schlotheim), which probably belong either in the Tarphyceratidae or in an as yet unnamed tarphyceratinid family; from Discoceras angulatum (Saemann), and Discoceras sp., of the Trocholitidae (Mutvei, 1957); and from Lituites procerus Remelé (Noetling, 1882) and perhaps from Rhynchorthoceras helgoevense Sweet (Sweet, 1958), representatives of the Lituitidae.

In known tarphyceratid and trocholitid species, the expanded portion of the annular elevation thought to be the site of attachment for the retractor muscles is located on the ventral side of the conch (Mutvei, 1957), but in the two known lituitids, this retractorattachment area is dorsal in position, having perhaps migrated to such a position as the mature conch uncoiled.

Barrandeoceratina.-Included in this suborder are six families of coiled nautiloids similar to, and almost certainly derived from the Tarphyceratina. Representatives of this suborder are distinguished from the Tarphyceratina, however, by the fact that the siphuncle is primitively tubular, central to ventral in position, and composed of thin, homogeneous connecting rings. Present knowledge concerning the configuration of the annular elevation in the Bassleroceratina is based upon the several upper Ordovician specimens described by Mutvei (1957) as Uranoceras? longitudinale (Angelin). Although the generic and familial reference of these specimens is open to question, there seems to be little doubt but that they belong in the Barrandeoceratina as that group is presently understood, and the writer is inclined to suspect that they represent an undescribed genus of Apsidoceratidae, rather than belonging in *Uranoceras* or the Uranoceratidae, a dominantly Silurian group. In all of Mutvei's specimens, the expanded areas of retractor attachment are ventral in position; on one of them, a well marked septal furrow is shown on the dorsal side of the conch.

The same collections from the Upper Ordovician Boda limestone of Sweden that yielded the representatives of Uranoceras? longitudinale described by Mutvei, also contain several undescribed specimens of Charactoceras (Apsidoceratidae), one of which exhibits the lateral and ventrolateral portions of the annular elevation. In this specimen, as in the ones described by Mutvei, the expanded retactor-muscle scars seem to be ventral in position. A similar configuration of the annular elevation is suggested by an incomplete structure at the adapical end of the body chamber of a large apsidoceratid collected by the writer from the Upper Ordovician Gastropod limestone (substage 5a), at Stavnestangen, Ringerike, Norway. This specimen is incomplete, and its generic affinities are questionable; however, it seems to be intermediate in form between Mutvei's Uranoceras? longitudinale and the Boda limestone Charactoceras. It bears a well marked septal furrow on the concave, slightly impressed dorsal side; the adapical and adoral margins of the annular elevation are subparallel laterally, but near the ventrolateral margins of the conch, the adoral margin appears to swing orad, indicating the presence on the venter of a broadly expanded retractor-muscle attachment area.

Rutoceratina.—The suborder Rutoceratina, which includes a rather large and superficially heterogeneous assemblage of middle and late Paleozoic and early Mesozoic (Triassic) nautiloids, had its inception in the Devonian, and appears to be connected genetically with the Oncoceratina. The Rutoceratidae, the ancestral radical of this suborder, formed broad-whorled conchs that were, for the most part, gyroceraconic in plan and rather highly ornamented by frills, wings, nodes, and spines. However, both cyrtoceracones and trochoceracones occur in the Rutoceratidae, and the conchs of some species appear to have been virtually straight. From this family, or its derivatives, there developed several more or less closecoiled groups, referred to the families Tetragonoceratidae, Koninckioceratidae, and Tainoceratidae. The Tetragonoceratidae is a Devonian family; the Koninckioceratidae is a first recognized in the Mississippian and continued until the end of the Paleozoic; the Tainoceratidae also appears to have roots in the Mississippian, but it is well represented in the Triassic.

The configuration of the annular elevation has been reported or figured previously from representatives only of the Tainoceratidae: a Triassic species of Germanonautilus (Mojsisovics, 1882), Metacoceras (Mojsvaroceras) turneri (Kummel, 1953, pl. 2, figs. 11,12) from the Upper Triassic of California, and a species of Pleuronautilus (Mojsisovics, 1873). In addition to these, a specimen at hand, identified only as Metacoceras sp., exhibits a complete annular elevation, which appears to be typical of the group to which it belongs.

The last named specimen, collected from the Middle Pennsylvanian Kendrick shale of eastern Kentucky by Professor C. H. Summerson, is an incomplete internal mold of an immature individual. As can be seen from the four views of this specimen on Plate 43 it is some 68 mm. in length, and represents parts of seven camerae of the phragmocone and the adjacent adapical portion of the body chamber. The outer whorl, of which this specimen is a fragment, is 23 mm. high and 33 mm. wide at the adapical end of the segment preserved. The venter is broadly convex; the lateral zones are flat or slightly concave and meet the venter at virtually a right angle. The dorsolateral zones are faintly convex and rather abruptly set-off from the lateral zones, which they join at an angle of about 135°. The dorsum is broadly concave and separated from the dorsolateral zones by narrow acutely rounded umbilical shoulders. Approximately six camerae occur in a ventral distance equivalent to the maximum width (39.5 mm.) of the phragmocone. Sutures are sinuous, forming broad ventral lobes, asymmetrical ventrolateral saddles, and slight lateral lobes, separated from faint dorsolateral lobes by low asymmetrical saddles. The dorsum bears deep broadly V- shaped lobes, separated from the dorsolateral lobes by prominently rounded saddles on the umbilical shoulders. A longitudinal row of low, broad nodes occurs on the ventrolateral corners of the internal mold, suggesting that a similar, but perhaps somewhat more prominent series of ornaments occupied that position on the shell. The venter is marked by a faint, longitudinal ridge, indicating the position of the conchial furrow.

On the dorsum of the specimen in question, the annular elevation consists of a narrow V-shaped band, 2 mm. wide, parallel to the adoral suture of the phragmocone. The adapical margin of this band is parallel to the suture for the full circumference of the conch, but, dorsolaterally, the adoral edge of the elevation is produced orad and, in the lateral zones, it describes broad asymmetrical salients, projecting some 10 mm. beyond the adoral suture and outlining transversely subelliptical areas presumed to be the loci of retractor-muscle attachment. On the venter. the annular elevation is represented by a slightly sinuous band, some 3 mm. in maximum width, subdivided into two narrowly elliptical areas by a slight mid-ventral notch. It should also be noted that, in the lateral zones, there is a faint transverse ridge separating the elliptical areas of retractor attachment from the posterior margin of the elevation. As in Nautilus, this line probably represents the posterior margin of the retractor-attachment area. It merges both ventrally and dorsolaterally with the anterior edge of the elevation.

Although direct connections have not yet been established, it is probable that the coiled suborders Solenochilina, Lyroceratina, and Nautilina developed from the Rutoceratina rather than from species in the dominantly coiled suborders Barrandeoceratina and Tarphyceratina. All three suborders are characterized by coiled conchs and the configuration of the annular elevation is known from at least a few representatives of each suborder. Foord & Crick (1890) published the only figures and descriptions of which the writer is aware of the annular elevation in Solenochilus, the typical (and and sole) genus of the Solenochilidae Solenochilina. The writer is unaware of any published description of the muscle-attach-

ment configuration in a representative of the Lyroceratina, but in a recent work by Kummel (1953, pl. 11, figs. 1,2) there is an illustration that appears to show at least the lateral portion of the elevation in Proclydonautilus ursensis Smith, an Upper Triassic species of the family Clydonautilidae, from the Hosselkus limestone of California. In the Nautilina, the muscle-attachment arrangement is known in Aphelaeceras, Cenoceras, Cimomia, Eutrephoceras, Grypoceras, Nautilus, Pseudaganides, Syringoceras, and Vestinautilus (Mojsisovics, 1873, 1882; Foord & Crick, 1889, 1890; Crick, 1898; Foord, 1900; Loesch, 1914; Miller, 1951; Mutvei, 1957). In known representatives of all three suborders, the expanded, subelliptical or subtriangular areas of retractor attachment occupy a lateral position on the annular elevation and the gross shape and arrangement of conchial zones I and II appear to be much the same as in Nautilus.

TAXONOMIC SIGNIFICANCE OF THE ANNULAR ELEVATION IN FOSSIL NAUTILOIDS

In a recent paper, Mutvei (1957, p. 232) states that "... in spite of the fact that the annular elevation is so far known only in a small number of fossil nautiloids, it is already possible to foresee its great importance to nautiloid taxonomy." Certainly, it is true that all features providing information about the organization of the animal should be carefully evaluated in a search for the phylogenetic relationships that zoological classification attempts to mirror. Indeed, a careful study of the arrangement of the muscles in fossil nautiloids might yield much valuable information as to the anatomy of these animals were it not for the fact that traces of muscle-attachment impressions are not commonly preserved.

Mutvei (1957) points out that known muscle-attachment impressions in fossil cephalopods can be divided into three categories: (1) a group, here termed "dorsomyarian", in which the loci of retractormuscle attachment are dorsal in position, (2) a category, here designated "pleuromyarian", in which the retractors are functionally attached to the lateral portions of the conch, and (3) a group in which the retractors were attached ventrally ("ventromyarian''). Dorsomyarian annular elevations are found in the Ellesmeroceratina, in the Michelinoceratina, in secondarily straight or endogastric Lituitidae (Tarphyceratina), and in all known ammonoids, regardless of conch form (Crick, 1898). In all the nautiloid groups just enumerated, the conch plan is essentially that of an orthoceracone, endogastric cyrtoceracone, or brevicone. Dorsomyarian Michelinoceratina are thought to have evolved from the Baltoceratidae, dorsomyarian Ellesmeroceratina characterized by conchs of similar form. However, even though it has been suggested (Schindewolf, 1942) that the Lituitidae were likewise derived from straight "Orthoceracea", the bulk of structural and stratigraphic evidence (Sweet, 1958) indicates otherwise and the family is now thought to be closely related Trocholitidae (Tarphyceratina), to the which apparently have a ventromyarian annular elevation. Hence, it seems probable that the dorsomyarian elevation of the lituitids is, like the development of heavy cameral deposits in the same group, an "acquired" character, to be associated, most probably, with the late assumption of a secondarily longiconic conch. It seems reasonable to suppose that if the dorsomyarian condition were mechanically satisfactory in groups with a fundamentally straight or slightly curved conch, the same plan would be similarly satisfactory in groups that attained this same form secondarily by uncoiling. In nautiloids, then, the association of dorsal retractor-attachment and longiconic conchs may be a reflection of similar adaptation, attained independently in groups only remotely related genetically. Therefore, any general use of this feature to characterize a phylogenetic sequence, or a major taxonomic unit, would be open to question.

Ammonoids were almost certainly derived from nautiloids, but the source of this group in the Nautiloidea is, as yet, a moot question. A considerable body of opinion favors *Bactrites*, or some similar form, as the ammonoid ancestor, and *Bactrites*, itself, a longiconic orthoceracone with a marginal siphuncle, has been referred, at one time or another, to both the Nautiloidea and the Ammonoidea. If *Bactrites* is considered to be the ammonoid ancestor, whether or not it is an ammonoid or nautiloid, it seems con-

sistent to predict that it, like known Michelinoceratina, was dorsomyarian. Furthermore, it may be that ammonoids attained stability with respect to muscle-attachment, as they seem to have done with respect to siphuncular structure, early in their history. This could explain the fact that ammonoids seem invariably to be dorsomyarian, regardless of the adaptational plasticity suggested by the conchs of late Mesozoic representatives of the order. If, on the other hand, ammonoids descended from early Paleozoic coiled nautiloids, like Barrandeoceras, as Spath (1933) suggests, the adaptive or mechanical significance of the dorsomyarian condition disappears. That is, the early Paleozoic coiled nautiloids appear to have been ventromyarian and rather closely related in other ways.

pleuromyarian nautiloids are Known coiled, generally involute forms, similar to Nautilus; furthermore, they all belong in families known, or thought to be rather closely related on the basis of other features and derived, fundamentally, from a common radical in the ventromyarian Oncoceratina. This suggests, as does the gross similarity in conch plan, that pleuromyarian nautiloids were adapted to virtually the same mode of life. Consequently, the lateral position of the retractor-muscle attachment impressions is of taxonomic significance. However, it appears to define only a very large group, within which detailed relationships must still be determined from a combination of other features.

The ventromyarian annular elevation is apparently characteristic of early Paleozoic coiled nautiloids belonging in the suborders Tarphyceratina and Barrandeoceratina, but it is also present in several families of the Oncoceratina, in one of the three families of Ascoceratina, and in at least one endogastric family of the Discosorina. The Tarphyceratina and Oncoceratina are thought (Flower, 1954, etc.) to be closely related and it is probable that they represent two of the adaptively and structurally specialized derivatives of a common ancestral group (the Ellesmeroceratidae) in the Ellesmeroceratina. The Barrandeoceratina are closely related to the Tarphyceratina and probably developed from that group. The Discosorina, on the other hand, are primitively endogas-

tric forms, thought (Flower & Teichert, 1957) to represent a stock derived independently from early Ordovician Plectronoceratidae, the group that almost certainly gave rise to the Ellesmeroceratidae, as well. One might then, regard the ventromyarian condition of Parryoceras euchari as the condition prevalent in the Discosorina and might expect to find that, in exogastric Discosorina. the retractors were also attached ventrally. as they are in the Oncoceratina. This implies that the group, or groups, of early Ordovician Ellesmeroceratina ancestral to the Barrandeoceratina, and Tarphyceratina, Oncoceratina on the one hand, and the Discosorina on the other, were probably similar in being ventromyarian and that the Baltoceratidae, from which the majority of dorsomyarian forms seems to have been derived. represent a group of Ellesmeroceratina specialized not only with respect to conch form and siphuncular structure, but also with respect to the arrangement of the elements of the muscle systems.

The Ascoceratidae, which seem also to be ventromyarian. are generally thought (Flower, 1941, 1954) to have developed from the Michelinoceratina, a group apparently characterized by dorsally situated retractor-attachment impressions. Late in their development, however, ascoceratids cast off the early longiconic portions of the conch and became inflated, somewhat exogastric brevicones; hence, it may be that this group is, at least in part, homeomorphic with other ventromyarian nautiloids with regard to the location of principal elements of the annular elevation.

Jackson (1890) pointed out long ago that, in pelecypods, the monomyarian condition of the adductors is attained independently in several only distantly related groups, apparently in connection with adaptive shifts in the relative positions of the hinge and body axes. Swinnerton (1947) describes graphically the attainment of a monomyarian condition in certain types of pelecypod adaptation, the implication being that a similar condition would be found in most pelecypods, regardless of their ancestry, adapted to the conditions he outlines. The conclusions of Jackson and Swinnerton with regard to pelecypods cannot, of course, be applied directly to cephalopods, but it seems

probable that, in at least certain cases, the attainment of dorsomyarian or ventromyarian musculature in nautiloids, like the development of monomyarian musculature in pelecypods, represents not relationship but adaptive convergence. Consequently, in nautiloids, as in pelecypods, it seems best, at least for the present, to accord muscle-attachment patterns a secondary taxonomic role. In connection with other features of the cephalopod shell, however, muscle-attachment patterns may be expected to provide information concerning the mode of life, adaptations, and specializations of fossil cephalopods-areas of cephalopod paleobiology about which we know very little.

REFERENCES

- APPELLÖF, A., 1893, Die Schalen von Sepia, Spirula, und Nautilus: K. Svenska Vetensk. Akad., Handl., bd. 25, no. 7, p. 1-106, pls. 1-12
- ARKELL, W. J., FURNISH, W. M., KUMMEL, BERNHARD, MILLER, A. K., MOORE, R. C., SCHINDENWOLF, O. H., SYLVESTER-BRADLEY, P. C., & WRIGHT, C. W., 1957, Cephalopoda, Ammonoidea: Treatise on Invertebrate Paleontology, R. C. Moore, editor, Part L, Mollusca 4, i-xxii, 490 p., Lawrence, Kansas. Univ. Kansas Press and Geol. Soc. America.
- BARRANDE, JOACHIM, 1866-1877, Systême Silurien du centre de la Bohême: Pt. 1, v. 2, Cèphalopodes. Prague, pls. 108–244 published in 1866: Texte 1 in 1867; pls. 351–460 in 1870; Texte 2 in 1870; Texte 3 in 1874; Texte 5 in 1877.
- CRICK, G. C., 1898a, On the muscular attachment of the animal to its shell in some fossil Cephalopoda (Ammonoidea): Linnean Soc. London,
- Trans., s. 2, v. 7, p. 71–113, pls. 17–20. –, 1898b, Descriptions of new or imperfectly known species of Nautilus from the Inferior Oolite, preserved in the British Museum (Nat. Hist.): Malacolog. Soc. London, Proc., v. 3, pt. 3, p. 117-139.
- DEWITZ, H., 1879a, Die Wohnkammer regulärer Orthoceratiten. Gesell. naturf. Freunde Berlin,
- Sitzungsber., 1879, no. 3, p. 27–38. , 1879b, Der Verwachsungsband der Vaginaten. Gesell. naturf. Freunde Berlin, Sitzungsber., 1879 no. 9, p. 133-147.
- , 1880, Beiträge zur Kenntnis der in den Ostpreussischen Silurgeschieben vorkommenden Cephalopoden: Phys.-ökon. Gesell. Königs-
- berg, Schr., Bd. 20, p. 162–180, pl. 4. FLOWER, R. H., 1941, Development of the Mixochoanites: Jour. Paleontology, v. 15, p.
 - 523-548, pls. 76-77. —, 1946, Ordovician cephalopods of the Cincinnati region: Bull. Am. Paleontology, v. 29, no. 116, p. 1-656, pls. 1-50.
 - , 1954, Cambrian cephalopods: New Mexico Bur. Mines, Bull. 40, p. 1-48, pls. 1-3.

- , & KUMMEL, BERNHARD, 1950, A classification of the Nautiloidea: Jour. Paleontology, v. 24, p. 604-616.
- & TEICHERT, CURT, 1957, The cephalopod order Discosorida: Univ. Kansas, Paleont. Con-
- trib., Mollusca, art. 6, p. 1–144, pls. 1–43. FOERSTE, A. F., 1930. Three studies of cepha-lopods: Denison Univ. Bull., Jour. Sci. Labs., v. 29, no. 10, p. 265-381, pls. 41-63.
- , 1936, Silurian cephalopods of the Port Daniel area on Gaspé Peninsula, in eastern Canada: Denison Univ. Bull., Jour. Sci. Labs., v. 31, p. 21–92, pls. 4–26.
- FOORD, A. H., 1900, Monograph on the Carboniferous Cephalopoda of Ireland, part 3: Pa-laeont. Soc. Mon., p. 49–126, pls. 18–32.
- , & Скіск, G. C., 1889, On the muscular impressions of Coelonautilus cariniferus, J. deC. Sowerby, sp., compared with those of the recent Nautilus: Geol. Mag., Dec. 3, v. 6, p. 494-498.
- -, & --, 1890, On the muscular impressions of some species of Carboniferous and Jurassic nautiloids compared with those of the recent Nautilus: Annals and Mag. Nat. History, s. 6, v. 5, p. 220–224.
- GRIFFIN, L. E., 1900, The anatomy of Nautilus pompilius: Nat. Acad. Sci., Mem., v. 8, mem. 5, p. 101-230, pls. 1-17.
- JACKSON, R. T., 1890, Phylogeny of the Pelecypoda. The Aviculidae and their allies: Boston Soc. Nat. Hist., Mem., v. 4, no. 8, p. 277-400, pls. 23-30.
- KUMMEL, BERNHARD, 1953, American Triassic coiled nautiloids: U. S. Geol. Survey, Prof. Paper 250, p. 1–95, pls. 1–19.
- LOESCH, K. C., 1914, Die Nautilen des weissen Jura: Erster Teil: Palaeontographica, Bd. 61,
- p. 57–146, pls. 10–15. Mojsisovics, E. M., 1873, Das Gebirge um Hallstatt. 1. Die Cephalopoden der hallstatter Kalke: K.-K. geol. Reichsanst., Abh., Bd. 6, Hft. 1, p. 1–82, pls. 1–32.
- , 1882, Die Cephalopoden der mediterranean Triasprovinz: K.-K. geol. Reichsanst., Abh.,
- Bd. 10, p. 1–322, pls. 1–94. MILLER, A. K., 1947, Tertiary nautiloids of the Americas: Geol. Soc. America, Mem. 23, p. 1-234, pls. 1-100.
- , 1951, Tertiary nautiloids of west-coastal Africa: Mus. Congo Belge, Ann., ser. 8, sci.
- geol., v. 8, p. 1–88, pls. 1–31. —, DUNBAR, C. O., & CONDRA, E. C., 1933, The nautiloid cephalopods of the Pennsylvanian system in the Mid-continent region: Nebraska Geol. Surv., s. 2, Bull. 9, p. 1-240, pls. 1 - 24.
- MUGGLIN, FRANZ, 1939, Beiträge zur Kenntnis der Anatomie von Nautilus macromphalus G. B. Sow.: Naturf. Gesell. Zürich, Vjschr., Jahrg. 84, no. 1-2, p. 25-118.
- MUTVEI, HARRY, 1957, On the relations of the principal muscles to the shell in Nautilus and some fossil nautiloids: K. Svenska Vetensk. Akad., Arkiv. för Min. och Geol., bd. 2, no. 10, p. 219–254, pls. 1–20. NOETLING, FRITZ, 1882, Ueber Lituites lituus

Montfort: Deutsche geol. Gesell., Zeitschr.,

- Bd. 34, p. 156-192, pls. 1-11. OWEN, RICHARD, 1832, Memoir on the pearly Nautilus (Nautilus pompilius Linn.) with iflustrations of its external form and internal
- structure: London, p. 1-68, pls. 1-8. SCHINDEWOLF, O. H., 1942, Evolution im Lichte der Paläontologie. Bilder aus der Stammesentwicklung der Cephalopoden: Jenaische Zeitschr. f. Medizin u. Naturwiss., Bd. 75, p.
- 324-386, pl. 1. SCHRÖDER, HENRY, 1881, Beiträge zur Kenntnis der in ost- und westpreussischen Diluvialgeschieben gefunden Silurcephalopoden: Phys.ökon. Gesell. Königsberg, Schr., Bd. 22, p. 54-96, pls. 2-4.
- SPATH, L. F., 1933, The evolution of the Cephalopoda: Biol. Rev., v. 8, p. 418-462.
- STENZEL, H. B., 1952, Living Nautilus: Treatise on Invertebrate Paleontology, R. C. Moore, editor, preprint of Part H, Cephalopoda, Nautiloidea, p. 2-19.

- SWEET, W. C., 1958, The Middle Ordovician of the Oslo region, Norway. 10. Nautiloid ceph-alopods: Norsk Geol. Tidaskr., bd. 38, hft. 1. p. 1-178, pls. 1-21.
- , & MILLER, A. K., 1957, Ordovician cephalopods from Cornwallis and Little Cornwallis islands, District of Franklin, Northwest Territories: Geol. Surv. Canada, Bull. 38, p. 1-86, pls. 1-8.
- SWINNERTON, H. H., 1947, Outlines of Palaeontology, 3d ed.: London, Edward Arnold & Co. 393 p.
- WAAGEN, WILLIAM, 1870, Über die Ansatzstelle der Haftmuskeln beim Nautilus und den Ammoniden: Palaeontographica, Bd. 17, no. 5, p. 185-210, pls. 39-40.
- WILLEY, ARTHUR, 1902, Contribution to the natural history of the pearly Nautilus: A. Willey's Zool. Res. pt. 6, p. 736-830, pls. 75-83. Cambridge Univ. Press.

EXPLANATION OF PLATE 43

FIGS. 1-4-Metacoceras sp. Left lateral, dorsal, ventral, and right lateral views, ×1.5, of a fragmentary internal mold of part of the outer volution. Kendrick shale (Middle Pennsylvanian), near junction of Brushy fork and Home branch of Buffalo Creek, Pike County, Kentucky (NW¹/₄ central rectangle, Harold, Kentucky quadrangle). Ohio State Univ. Geol. Mus. No. 19367.

