https://doi.org/10.24199/j.mmv.1978.39.03 7 July 1978

THE OMPHALOCIRRIDAE: A NEW FAMILY OF PALAEOZOIC GASTROPODA WHICH EXHIBITS SEXUAL DIMORPHISM

By Robert M. Linsley

Department of Geology, Colgate University, Hamilton, New York, USA

Abstract

A careful study of the gastropod *Hypomphalocirrus rugosus* (gen. et sp. nov.) from the Middle Devonian of Northeastern Michigan demonstrated that in this population two distinct morphotypes are present. Both morphotypes persisted throughout the entire sixty feet of the limestone and over fifty miles of lateral distribution. This suggests that they might possibly be male and female dimorphs. In order to check this as a possible explanation, related species were studied from Germany, Manitoba and Australia. In all cases two morphotypes were present in an approximate one-to-one ratio, but only in Australia was a large enough sample present to be of significance (one hundred specimens from Australia, compared to a dozen specimens from Germany and Manitoba).

This study has resulted in the erection of a new family (the Omphalocirridae), one new genus (*Hypomphalocirrus*), one resurrected genus (*Liomphalus*, Chapman) and one new species (*Hypomphalocirrus rugosus*). The genus *Arctomphalus Toemachov*, 1926, is suppressed as a synonym of *Omphalocirrus*. The discovery of multispiral opercula in place in three of the genera demonstrate conclusively that these snails are dextral rather than sinistral as has frequently been suggested.

The functional significance of the dimorphism is considered a mode of life established for the organisms and the probable evolutionary sequence suggested.

Sexual Dimorphism in Gastropoda

Sexual dimorphism of shell shape, size and radular form are all well-known phenomena among living archaeogastropods and caenogastropods (Baker, 1926; Lamy, 1937; Robertson, 1971; Sohl, 1969). Most commonly the difference takes the form of a larger average (or maximum) size for the female. Differences in form generally are expressed in a greater rate of expansion of the generating curve in the female which usually results in a relatively lower spired trochoid shell (a 'fatter' shell). Both of these differences are generally thought to be adaptive to accommodate the bulky eggs produced by the female. Radular differences may reflect food differences as in the case of the archaeogastropod *Tricolia (Hiloa) variabilis* (Pease) where the female feeds preferentially on brown alga *(Padina)* while the male lives on top of the female's shell preceding and during the mating season, and presumably the radular differences in the male allow it to feed on the epiphytes on the female's shell (Robertson, 1971, p. 77).

Obviously radular differences will be of no help in sexing fossil gastropods. Similarly size difference by itself will be unrecognizable in fossil populations. However if there are morphologic differences which allow one to sort the population into two samples, then presumably a size distinction could be made.

In the case of the Omphalocirridae a variety of criteria were discovered which allowed the mature members of the population to be divided into two subsets. The most ubiquitous distinction is the type of coiling present. All members of this family are characterized by discoidal shells, but mature members can normally be designated either as orthostrophic or hypestrophic. Other features that may be used to differentiate the two subsets are the degree of development of collabral ornamentation, the degree of development of a keel or spines, the roundness of the whorl profile, and the inclination of the outer whorl face. Sorting of the population on the basis of the above features, either singly or in combination, makes it possible to show that these subsets also exhibit a distinction of the size of the individuals in these subsets. It is assumed in this paper that the subsets of the population containing the largest individuals represent the females.

Systematic Paleontology

Class	GASTROPODA Cuvier, 1797
Subclass	PROSOBRANCHIA Milne Edwards, 1848
Order	ARCHAEOGASTROPODA Thiele, 1925
Suborder	MACLURITINA Cox and Knight, 1960
Superfamily	EUOMPHALACEA de Koninck, 1881
Family	Omphalocirridae new family

Type genus *Omphalocirrus*, Ryckholt, 1860

Description: Large, dextral, discoidal gastropods varying from gently orthostrophic to gently hyperstrophic; whorl profile varying from subcircular to subtriangular, frequently with a marked circumbilical keel or spines on base; base broadly phaneromphalous; aperture subcircular. Early whorls filled with septa at maturity. Operculum disc-shaped, multispiral. All known members exhibiting varying degrees of sexual dimorphism.

Discussion: The Omphalocirridae are readily distinguished from the Helicotomidae and Omphalotrochidae in being discoidal, while most members of the latter two families possess elevated spires. The Omphalocirridae also differ from these two families in having an abundance of septa filling the early whorls. The Omphalocirridae resemble the Euomphalidae in these two characters of septation and discoidal form, but are distinguished from the Euomphalidae and all other Euomphalacea in having a calcareous, multispiral operculum and exhibiting sexual dimorphism.

As is true of all Euomphalacea the Omphalocirridae possess an aperture whose plane passes through the axis of coiling ('radial aperture'), and some of the genera possess an angulation near the upper whorl face that is interpreted as exhalent. They resemble the Omphalotrochidae in that some members of both groups possess a second angulation near the base that resembles a siphonal canal or an inhalent angulation. The uniqueness of the form of these angulations suggests that they were developed independently in each of the two groups. In each of these groups this combination of features suggest that only a single gill exists (Knight, Batten and Yochelson, 1960, p. 1196) and supports the contention that this is the case for the entire superfamily.

The Omphalocirridae also resemble the gastropods presently placed in superfamily Oriostomatacea (Suborder Thochina, Knight, Batten and Yochelson, 1960, p. 1245) in that both groups have radial apertures and multispiral, calcareous opercula. It is probable that the Oriostomatacea should be transferred to the Euomphalacea and, if it could be demonstrated that they exhibit sexual dimorphism, to the Omphalocirridae.

Genus *HYPOMPHALOCIRRUS* gen nov.

Type species: H. rugosus sp. nov.

Description: Large, dextral gastropods with spire very low to hyperstrophically depressed; whorl profile subtriangular with flattened upper, outer and lower faces joining at marked angulations; base broadly phaneromphalous; the juncture between the outer whorl face and the base typically developing canal-like projections which may also occur at juncture between upper and outer whorl faces. Earlier whorls filled with septa at maturity. Operculum disc-shaped, multispiral. Sexual dimorphism strongly developed.

Discussion: The most abundant and obvious fossil in the Rogers City Limestone is the large euomphalid gastropod previously known as *Omphalocirrus manitobensis* Whiteaves (Ehlers and Radabaugh, 1938; Ehlers and Kesling, 1970). Close study of about 200 specimens from the collections of the University of Michigan Museum of Paleontology, the U.S. National Museum and Colgate University show that this euomphalid not only is not conspecific with Whiteaves species but that both the Rogers City material and the material from Manitoba are sufficiently distinct from *Omphalocirrus goldfussi* to warrant the establishment of a new genus (also see Yochelson, 1966, p. 41).

This genus is most readily characterized by the subtriangular whorl profile and the angular meeting of the outer whorl face with the base and upper whorl face. It is obviously closely related to *Omphalocirrus* but this latter genus has a rounded whorl profile. Both of these genera possess the unusual feature of canal-like projections at the juncture of the base and outer whorl face. In addition it bears close similarity to the Australian genus *Liomphalus*, even though the latter lacks the canal-like protuberances.

Two species are assigned to this genus. One *(H. rugosus)* is herein described for the first time, while the second is Whiteaves species *H. manitobensis* (Whiteaves) from the Winnipegosis Limestone of Manitoba, Canada. In addition the specimen described from the Anderdon Limestone of the Michigan Basin (Linsley, 1968) probably also belongs to this genus, but it is too poorly known to describe formally.

Hyomphalocirrus rugosus sp. nov.
(Plates 2-6)

Herein designated type species.

Omphalocirrus manitobensis Ehlers and Radabaugh 1938

Omphalocirrus manitobensis Anonymous

Omphalocirrus manitobensis Ehlers and Kesling 1970

Description: Large, discoidal, dextral gastropods with sub-triangular whorl profile, with angular base bearing canal-like projections or a keel. Nuclear whorls smooth, simple, dextral. Whorl profile sub-triangular in shape with outer whorl face varying from vertical (parallel to axis of coiling) to inclined outward at a 45° angle. Upper whorl face varying from flat and horizontal to roundly dipping into spire; outer whorl face flattened to broadly arched, basal whorl face gently rounding into umbilicus. Junction of upper and outer whorl faces joining at an acute angle forming a smooth keel or distinctly undulating keel. Junction of outer and lower whorl faces typically sharp, occasionally rounded and bearing a series of canal-like projections or flanges which are sometimes replaced by a single or double keel in the adult. Upper suture varying from indistinct to very sharp and deep with considerable overhang of ultimate whorl; umbilical suture sharp and deeply incised, occurring just outside of the umbilical ridge of the preceding whorl. Upper shell surface flattened in youthful stages, but varying in the adult from flattened to a considerably depressed spire. Shell widely phaneromphalous with umbilical angle varying from 120° to 180°, depending on the degree of hyperstrophism. Growth lines on upper whorl face generally opisthocline, beginning perpendicular to suture and culminating at a 45° angle at the periphery; growth lines prosocyrt on outer whorl face, continuing onto base with backward obliquity and backward concavity; normal course of growth line deflected both by undulations on shoulder and canal-like projections on the base. Ornament consisting of strong collabral ornamentation in youth, giving way to simple growth lines at maturity; in mature forms, interruptions in growth frequently resulting in rugose appearance; outer whorl face sometimes developing roughened appearance in adult, even developing low canal-like projections. Shell very thick at junctures of the three whorl faces, thin at centres of each whorl face, resulting in a subcircular inner whorl profile and a subtriangular outer whorl profile. Septa abundant and evenly spaced in the early whorls of mature individuals. Operculum circular, disc-shaped multispiral, expanding counterclockwise, all volutions visible on outer surface; upper surface of each opercular volution inclined inward with slight rounding towards preceding whorl; outer face of opercular whorl parallel to axis of coil, resulting in deep, sharp suture separating each volution; early opercular volutions (first ten or eleven) increasing in size logarithmically; later volutions (last five or ten) more irregular, approximately maintaining constant size and thus increasing in an archimedian rather than logarithmic spiral; inner surface of operculum poorly known.

Holotype measuring 102·6 mm in width and 36·4 mm in height. Largest Paratype measuring 149 mm in width.

Holotype—UMMP 22377; Figured Paratypes—UMMP 22375, 22378, 22379, 22380, 22383, 22384, 57888, 57889. USNM 102939, 213754, 213755, 213756, 213757, 213758, 213759, 213760, 213761, 213762, 213763, 213764, 213765, 213766, 213767, 213768, 213769, 213770, 213772, 213773, 213774, 213775, 213776, 213777, 213778, 213779, 213780, 213781, 213782, 213783. Unfigured Paratypes—UMMP 22381, 22382, 22385. USNM 213771.

Discussion: Hypomphalocirrus rugosis is a very large gastropod (150 mm) that rivals the size of the largest Maeluritida. Among Paleozoic Gastropoda only *Straparollus grandis* (Koninck (130 mm) *Pithodea amplissa*, Koninck (140 mm) from the carboniferous of Belgium, *Arctomphalus grandis* Tolmachoff (now *Omphalocirrus goldfussi)* (170 mm) and a Carboniferous euomphalid (210 mm) reported by Yochelson (1966) as being in the British Geological Survey and Museum can compare in size with this new species.

The diagnostic features of this species are the sub-triangular whorl profile, the tendency to develop flanges at the upper angulation of the female, and canal-like projections on the base. However there is considerable variation of each of these features within the population of about two hundred individuals that were studied.

Females of *H. rugosus* can be distinguished from females of *H. manitobensis* (Whiteaves) by the presence of a second row of canal-like projections which the latter bears on the upper angulation. The whorl profile of *H. manitobensis* has the triangular profile tilted so that the outer whorl face is subparallel to the axis of coiling and the periphery of the shell is at the midpoint of the rounded whorl face rather than at the upper angulation as it is in *H. rugosus. H. manitobensis* has assumed an almost isotrophic coiling and thus appears to converge on a bellerophont-like form.

The single, poorly preserved specimen of *Hypomphalocirrus* described from the Anderdon Limestone (Linsley, 1968) is not well enough known to warrant a formal description. The chief distinction is the bundling of growth lines found in this species. Five or six growth lines are subparallel to each other and all participate in making up a single basal projection. The next set of prominent growth lines then diverge sharply from the preceding set to form the next basal projection.

Within the population of females of *H. rugosus* the degree of hyperstrophism is still highly variable ranging from USNM 213781 (pl. 6, fig. 5) where the upper surface of the penultimate whorl strikes the ultimate whorl about one-third the way down the ultimate whorl, to UMMP 213758 (pl. 4, fig. 7) where the upper surface of the ultimate whorl strikes the ultimate whorl two-thirds the way down the ultimate whorl. The geometry of the whorl profile is such that variation in the amount of hyperstrophism also is associated with other changes in the whorl profile. As the degree of hyperstrophism increases the entire triangular whorl profile of the shell rotates so that the outer whorl face varies from being inclined almost 45° to the axis of coiling in the male (see USNM 213775, pl. 2, fig. 4) to almost parallel to the axis of coiling in the female (see UMMP 22377, pl. 4, fig. 2). The roundness of the upper whorl face also seems to increase with increased hyperstrophism (UMMP 22377 and USNM 213758, pl. 4, figs. 6, 7) and of course umbilical depth decreases as hyperstrophism increases. UMMP 22377 (pl. 4, figs. 5, 6) has an umbilical angle of 180° while USNM 213759 (pl. 6, fig. 3) has an umbilical angle of about 150° and USNM 213758 (pl. 4, fig. 7) is so depressed that one could talk about an 'umbilical spire'.

Other features, equally variable, do not seem to be related to the degree of hyperstrophism. The proportionate size of the outer whorl face may be rather small (UMMP 22379, pl. 6, fig. 8) or very great USNM 213759 (pl. 6, fig. 3). Some features are obviously related to age. Immature forms of males are very difficult and sometimes impossible to distinguish from those of females. Immature forms tend to have well-developed collabral ornamentation (UMMP 22375, pl. 5, fig. 7, early whorls of USNM 213760, pl. 5, fig. 3). Immature specimens (UMMP 22375, pl. 5, fig. 7) also tend to have a smooth juncture between the upper and outer whorl faces. Rarely this feature will be carried into maturity in the females (UMMP 57888, pl. 5, fig. 4 and USNM 213781, pl. 6, fig. 5). More frequently this upper juncture develops into a scalloped flange at maturity, either with a gentle fluting (UMMP 22379, pl. 5, fig. 6 and pl. 6, fig. 1) or in a few cases very pronounced, almost grotesque fluting (USNM 213772, pl. 6, fig. 4 and USNM 213754, pl. 6, figs. 10, 11). In the holotype (UMMP 22377, pl. 4, fig. 6) the ultimate whorl is well fluted until the last

¼ volution, when the fluting ceases. There seems to be some tendency for the degree of fluting to be related to the amount of sculpture present on the outer whorl face. In general the greater the fluting, the more sculpture. The sculpture varies tremendously from raised growth lines (USNM 213754, pl. 6, fig. 11) to small ridges perpendicular to the growth lines (USNM 213759, pl. 6, fig. 3) large bumps (USNM 213765, pl. 6, fig. 7) or even canal-like foldings of the growth lines (USNM 213772, pl. 6, fig. 4).

The canal-like projections on the basal angulation are a most persistent feature of the females. Their position on the base is dependent upon the amount of hyperstrophism and the subsequent rotation of subtriangular whorl profile. Where hyperstrophism is not great and outward rotation of the outer whorl face minimal, the projections will appear to be in the middle of the whorl as seen from the base (UMMP 22378, pl. 6; fig. 2 and USNM 213760, pl. 5, fig. 3). When hyperstrophism is strongly developed and outward rotation of the outer whorl face is substantial (UMMP 22377, pl. 4, fig. 5) the projections will appear to be at the periphery of the whorl as seen from the base. The shape of these projections varies from the typical rather slender ones (UMMP 22377, pl. 4, figs. 5, 8 and USNM 213764, pl. 5, fig. 2) to very broad, spade-like projections (USNM 213767, pl. 5, fig. 5).

One specimen, UMMP 22380 (pl. 6, fig. 9) is the most aberrant of the collection. It has a very swollen, rounded whorl profile and thus seems to closely resemble *Omphalocirrus goldfussi*. In all other respects, such as the sculptured, outwardly rotated outer whorl face, etc. it resembles *H. rugosus* and I have thus treated merely as one aberrant member of a very diverse population.

The males of *Hypomphalocirrus rugosus* may be readily distinguished from the females by their flat upper whorl face and by the fact that the spire is flush, with the upper whorl faces continuous with each other rather than the depressed spire so typical in the females.

The males exhibit less variation than the females. The spire profile is very constant, maintaining an essentially flat upper surface. The outer whorl face occasionally shows a faint, revolving ornamental groove just below the periphery (USNM 213779, pl. 3, fig. 4, USNM 213773, pl. 3, fig. 6 and USNM 213778, pl. 3, fig. 9). The outer whorl face is generally flattened, but a few individuals, especially USNM 213761 (pl. 3, fig. 12) and USNM 213756 (pl. 3, fig. 13) exhibit a very rounded whorl profile. The most marked variation in the males occurs on the base relative to the circumbilical ridge. The ridge develops very early at the end of the second volution. During this early stage canal-like projections develop very much like those of the females. However in the males the projections rarely persist beyond the third whorl. An exception is USNM 213773 (pl. 3, fig. 6) which maintains very large, fully developed spines through maturity. In most mature individuals (USNM 213775, pl. 3, fig. 8 and USNM 213766, pl. 3, fig. 5) the mature whorls have only a relatively sharp ridge, perhaps with only faint suggestions of protrusions (USNM 102939, pl. 3, figs. 1, 11). In at least one example (USNM 213757, pl. 3, fig. 3) a double ridge results. In one other case (USNM 213756, pl. 3, fig. 13) there is no sign of a keel at all, but rather the base is very rounded and the growth lines are unusually rugose at maturity.

Dr G. Arthur Cooper of the U.S. National Museum kindly brought to my attention a collection of gastropods from the Miami Bend Formation of Indiana (Cooper and Phelan, 1966). Most of the collection consists of steinkerns which are generically and specifically indeterminate, but a few molds were collected which can be identified. One of these (USNM 213769, pl. 2, fig. 6) is a partially complete impression of the spire of a male *Hypomphalocirrus rugosus*. This adds one more small piece of evidence to their mass of data supporting their claim for a correlation of the Miami Bend Formation with the Rogers City Limestone.

The wide latitude of variation present in this species is in part explained by the morphological differences between the males and females. The existence of these two subsets of this population can best be seen in the graph in Fig. 1, which plots size against a measure of the degree of hyperstrophism (umbilical width divided by umbilical depth). This plot demonstrates that though the youthful individuals are inseparable, the adults separate into two distinct populations. This is, of course, perfectly consistent with an interpretation of sexual dimorphism.

Using the degree of hyperstrophism as a criterion for establishing two populations, many other distinctions were discovered which correlate with this character. The following paragraphs are formalized descriptions of the females and males.

Description of females: Large, shallowly hyperstrophic gastropods with well-developed canal-like projections at the junction of the outer whorl face with the base. Nucleus smooth, simple and dextral. Whorl profile subtriangular in shape, outer whorl face tilted in slightly from perpendicular. Upper whorl face flattened near periphery, gradually curving downward near preceding whorls and curving downward abruptly at suture, so that inner edge of upper whorl face overhangs upper whorl face of preceding whorl; upper whorl face adjoining outer whorl face at periphery with a marked keel; keel smooth in youthful stages, but at maturity keel tending to develop pronounced periodic undulations; outer whorl face gently rounded, sloping inward and downward from peripherally located junction with upper whorl face; outer whorl face adjoining base forming a keel which develops canal-like projections at a very early stage; canal-like projections generally becoming larger and better developed with maturity; basal whorl face flattened, proceeding upward towards umbilical suture from its junction with outer whorl face. Upper suture fairly deep, sharply incised with ultimate whorl slightly overhanging penultimate whorl; umbilical suture sharp and very deep, occurring outside of the canal-like projections of preceding whorl. Early whorls depressed below mature whorls resulting in hyperstrophic whorl profile. Degree of hyperstrophism quite variable, but generally increasing with maturity. Shell widely phaneromphalous, with umbilical angle varying from 150°to 180° depending on degree of hyperstrophism. Growth lines opisthocline on upper whorl face, beginning perpendicular to suture and proceeding with a forward obliquity and marked backward concavity; at periphery growth lines variable depending on the position relative to flange; presence of flange causing growth line to bend backward from its opisthocline course, making it subparallel to suture once again; growth lines continuing on outer whorl face in prosocyrt fashion; at junction of outer whorl face and base, growth lines interfered with by canal-like projections; growth lines bending back rather strongly in a U-shape to participate in formation of spine, bending forward in an 'n' shape in front of completed spine, continuing uninterruptedly where no spine is present. Ornament consisting of collabral ornament in youth, giving way to growth lines in adult; growth lines becoming crowded during spine formation causing adult to have rugose appearance; flanges or undulations developing along periphery in adult; canal-like projections around base tending to become very strong in adult; outer whorl face tending to become roughened in adult, developing low, rugose, and in extreme cases, even canal-like projections. Shell thickness exceedingly variable, being thin at centre of each whorl face and becoming very thick at junctures of whorl faces, resulting in a subtriangular outer whorl profile and subcircular to elliptical inner whorl profile. Septa abundant in earlier whorls in mature shells, unevenly spaced at about eight to twelve per whorl.

Holotype measuring 102·6 mm in width and 36·4 mm in height. Largest paratype measuring 149 mm in width.

Holotype—UMMP 22377; Figured Paratypes—UMMP 22375, 22378, 22379, 22380, 22383. USNM 213760, 213764, 213758, 213754, 213765, 213772, 213776, 213755, 213768, 213767. Unfigured Paratypes—UMMP 22381, 22382, 22385.

Description of males: Large, flat-topped orthostrophic gastropods with a subtriangular whorl profile and sharp angular base bearing either a keel or canal-like projections. Nuclear whorls smooth, simple, dextral. Whorl profile resembling an equilateral triangle with upper whorl face horizontal or perpendicular to axis of coiling. Upper whorl face flat, bending downward very slightly at the surface. Outer whorl face joining upper whorl face at a sharp angle at shell periphery, forming a sharp smooth keel. Outer whorl profile flattened to gently rounded; typically with slight concavities just below peripheral keel and just above basal keel, occasionally gently rounded from keel to keel. Basal whorl face joining outer whorl at sharp angulation and progressing flatly or with gently rounding to umbilical suture. Upper suture varying from indistinct to sharp with slight overhang of inner whorl edge over preceding whorl; umbilical suture sharp, frequently deep, normally just outside circumbilical ridge. Upper shell surface flattened, not depressed. Base widely and deeply phaneromphalous; umbilical angle varying between 120° to 145°. Growth lines on upper whorl face beginning perpendicular to the suture and proceeding opisthoclinally towards the periphery, intersecting periphery at 45° angle; growth lines prosocyrt on outer whorl face, continuing with strong collabral ornamentation, normally reducing to faint growth lines in adult; strong angular keel at periphery at junction of upper and outer whorl faces; faint revolving groove sometimes developed on outer whorl face, just below periphery. Circumbilical ridge developing early with well-developed canal-like projections; in maturity, circumbilical ridge normally reverting to single or double ridge, rarely retaining canal-like projections to maturity. Shell thick, particularly at keels, resulting in subtriangular outer whorl profile and subcircular to elliptical inner whorl profile. Septa present through much of early portion of mature shell. Shell width of largest paratype 110 mm.

Androtype—USNM 102939; Paratypes—UMMP 22382, 22384. USNM 213775, 213770, 213762, 213763, 213777, 213757, 213778, 213779, 213773, 213766, 213774, 213769, 213761, 213756, 213780. Unfigured Paratype—213771.

Discussion continued: Briefly, the main features of each sex can be summed as follows. The females tend to be larger than the males, a feature similar to so many modern gastropods and presumably related to the greater bulk of eggs of the female. The canal-like projections on the base of the males usually degenerate into a keel while in the female these projections become larger in the adults, presumably remaining functional throughout its life. Assuming that these do indeed facilitate incurrent water, this would again be consistent with the increased oxygen needs of the female in producing the bulky egg masses. In addition the increased hyperstrophicity of the female would appear to be due to, or at least accompanied by, the rotation of the whorl profile. This rotation brings the outer whorl face into a sub-vertical position (parallel to the axis of coiling) thus bringing both incurrent and excurrent openings into a peripheral position which would again facilitate water movement through the mantle. The male, with less critical circulatory demands tends to keep the incurrent opening at a slightly less favourable position in order to better position the anus at the extreme periphery. The male also tends to loose the incurrent canals, which were apparently useful during the rapid growth of youth, but no longer so crucial to success in the adult.

It is possible that the collabral ornamentation of the immature shells served to strengthen those shells. As the shell increased in size it also increases in thickness, apparently to the point where the collabral ornamentation lost its functional significance and so disappears on the adults.

Hypomphalocirrus manitobensis (Whiteaves)
Euomphalus manitobensis Whiteaves 1890, p. 100, pl. 6, figs. 2-26.

Omphalocirrus manitobensis Whiteaves 1892, p. 327, pl. 43, figs. 5-7.

(Plate 7, figures 1-8)

Description: Large, slightly hyperstrophic gastropods with one or two rows of canal-like extensions at boundaries of outer whorl face. Nucleus poorly known, apparently smooth and dextral. Whorl profile varying from subtriangular in the females, to suboval in shape in the males. In females the upper whorl face meeting outer whorl face to form a keel which may bear long canal-like projections, then proceeds roundly down to suture; outer whorl face of females broadly rounded and meeting lower whorl face at a keel which also may bear canal-like protuberances similar to those on top; basal whorl face continuing roundly up to the umbilical suture to complete the rounded equilateral triangle. Whorl profile of males more rounded with less distinct keels, bearing canal-like projections only on base. Upper suture deep, sharply incised. Umbilical suture distinct, deeper in females than in males. Aperture, as determined from observations of growth lines, gently opisthocline on upper whorl face, bending back at periphery to form upper rows of canal-like projections, continuing on outer whorl face in prosocyrt fashion and on to the base with a gently backward concavity, again involved with canal formation at the juncture of the base with the outer whorl face. Males with greater hyperstrophism than females; base of males being relatively flat while females deviating only slightly from discoidal. Ornament consisting of strong collabral ornament in males with one row of canal-like projections on the base; ornament in females consisting only of fine growth lines with two rows of canal-like projections both above and below the outer whorl face. Outer whorl face sometimes roughened in adult females. Shell moderately thick, particularly at junctions of whorl faces. Septa fairly abundant in mature individuals. Operculum thin, and disc-shaped, circular in outline, multispiral, expanding counterclockwise with all volutions visible on outer surface.

Lectotype—GSC 4173; Plesiotypes—GSC 4163a, 4174, 4175, 4176, 4177; Hypotypes—USNM 213782, 213783.

Discussion: Yochelson (1966, p. 41) has already treated the problems attendant on this species. Whiteaves (1890, p. 100) original specimens of *H. manitobensis* are steinkerns from the Dawson Bay Limestone. These are generically indeterminate. Subsequently, Whiteaves (1892, p. 327, pl. 43, figs. 5-7) redescribed this species and reassigned it to the genus *Omphalocirrus*, but this was done primarily on the basis of material obtained from the Winnipegosan Limestone which underlies the Dawson Bay Limestone. There is no certain way of knowing whether or not the specimens from these two units are conspecific. The above description is based on material from the Winnepegosan Limestone as our knowledge of *Hypomphalocirrus manitobensis* at this time is based entirely on those specimens.

The collection available for study of this species consists of fifteen specimens collected by Linsley and Cottrell in 1968 from locality 18 of the *Field Guide to Devonian Outcrops of Southwestern Manitoba* (McCabe, 1967). This locality is about one mile west of the Narrows, on Lake Winnepegosis. In addition, Whiteaves types (GSC 4174, 4176, 4177) from the Geological Survey of Canada at Ottawa were kindly made available for study. While seventeen specimens do not constitute a large enough collection on which one might base a definitive study, they do suggest that two distinct morphotypes are present and may best be regarded as males and females.

The females (pl. 7, figs. 3, 5, 6, 8) are characterized by a triangular whorl profile and have well-developed canal-like protrusions at both boundaries of the outer whorl face. As this form is regarded as having evolved from *H. rugosus*, it would seem a natural development for the undulating shoulder of the Rogers City females to have developed into the true canals of the Manitoba form, thus perfecting the current flow in and out of the mantle cavity. The females of *H. manitobensis* also resemble the females of *H. rugosus* in having a subvertical outer whorl face, a fair degree of hyperstrophicity, and rugosities on the outer whorl face.

The males of the Winnepegosis Formation differ markedly from the Rogers City forms. The males of *H. manitobensis* are *more* hyperstrophic than the females which suggests that the degree of hyperstrophism is important *only* as it affects the position of the incurrent or excurrent water streams. The basal canal-like extensions on the males of *H. manitobensis* are positioned only slightly more peripherally than their *H. rugosus* counterparts. The rest of the whorl profile of the *H. manitobensis* males is much more rounded than either the females or the Rogers City forms. However they resemble the males of the Rogers City forms by having much stronger collabral ornament than that possessed by the females.

Omphalocirrus goldfussi (Archiac and Verneuil)—(Plate 8)

Knight (1941, pp. 45, 213) and Yochelson (1966, p. 42) have both offered excellent descriptions and synonymies of *Omphalocirrus goldfussi*; (Archiac and Verneuil, 1842) and Arctomphalus grandis Tolmachoff, 1926. I am familiar with this genus only through their works and through a careful study of the plastotype material made available to me from the US National Museum. This study has led me to the conclusion that '*Arctomphalus grandis*' is the sexual dimorph (probably male) of *Omphalocirrus goldfussi*. Plate 8, fig. 7 is an illustration of the lectotype of *Arctomphalus grandis* (Specimen A-19229, Paleontologisk Museum of Oslo). Unfortunately the outer volution, represented by the broken line in the figure, is a steinkern and only an impression of the basal suture of the inner whorls remains. However comparison of this remnant with some German material of *Omphalocirrus goldfussi* (see pl. 8, figs. 4, 5, 9) illustrates that all of these specimens are similar in that they are hyperstrophic, have strong collabral ornament and have a circumbilical ridge which develops periodic nodes which are only occasionally developed into canal-like projections. Collectively, these features suggest male characters of *Hypomphalocirrus rugosus* and *H. manitobensis*. The other types of *Omphalocirrus goldfussi* (Pl. 8, figs. 1-3, 6, 8) are quite distinct from those described above. They are all orthostrophic, have much weaker collabral ornamentation and have well-developed, apparently functional canal-like extensions which appear in early youth and persist through maturity. In addition this morphotype has a very pronounced swollen form due to a greater rate of expansion of the generating curve. All of these features are consistent with the interpretation of this form as the female.

To date no opercula have been found associated with *O. goldfussi*, but I fully expect multispiralled opercula to occur in the same beds and with great fortune to be found in a life situation, well back from the aperture. It would also be beneficial if a study could be made on a large population of this species to ascertain whether or not the dimorphism apparent in the half-dozen specimens at my disposal holds true for the entire population.

Genus *Liomphalus* Chapman, 1916, p. 90

Type species: Liomphalus australis by original dcsignation

Description: Large, discoidal, septate gastropods with low to hyperstrophically depressed spire. Outer whorl profile varying from subcircular to subtriangular with circular inner whorl profile. Strong circumbilical ridge with no canal-like projections. Operculum disc-shaped, multispiral. Sexual dimorphism weakly developed.

Discussion: Like the other members of the family Omphalocirridae, this genus exhibits sexual dimorphism. However compared to the other genera, the sexual dimorphism of *Liomphalus* seems poorly developed, as though it were an incipient feature. This feature is consistent with its lower stratigraphic position and presumed ancestry to the other members of the family. *Liomphalus* also resembles the other members of this family by being septate, discoidal gastropods which bear a disc-shaped, multispiral calcareous operculum (see also Yochelson and Linsley, 1972). It can readily be differentiated from other members of this family by the presence of a circumbilical ridge without any suggestion of nodes or canal-like extensions on it.

Liomphalus northi (Etheridge) 1890
Plate 9, 10

1890 *Oriostoma northi* Etheridge, p. 64, pl. 9, figs. 6-7
1894 *Oriostoma northi* Etheridge, p. 151, pl. 9, figs. 1-4
1894 *Euomphalus (Oriostoma) northi* Etheridge; Cresswell, p. 157
1913 *Euomphalus northi* (Etheridge); Chapman, p. 227
1916 *Euomphalus northi* (Etheridge); Chapman, p. 90
1916 *Liomphalus australis* Chapman, p. 90, pl. 4, figs. 32-33
1959 *Straparollus (Euomphalus) northi* (Etheridge); Philip and Talent p. 50, pl. 7, figs. 1-21, pl. 8, figs. 1-2
1972 *Oriostoma northi* Etheridge; Yochelson and Linsley, p. 8, pl. 1, fig. 6, pl. 2, figs. 1-5
1976 *Straparollus (Euomphalus) northi* Etheridge; Tassell, p. 9, pl. 1, figs. 7, 8, pl. 2, fig. 11, pl. 3, figs. 1, 2, 7, 8

Description: Shells large, discoidal, varying from flatly orthostrophic to slightly hyperstrophic with distinct circumbilical ridge. Nuclear whorls unknown, presumably simple, smooth and dextral. Whorl profile subrectangular in youthful stages, changing to subelliptical or subtriangular in adults. Upper whorl face variable, ranging from broadly arched and confluent with upper whorl face, to gently arched and meeting outer whorl face of a distinct keel; marked keel separating upper and outer whorl faces typically present in immature forms, but disappearing in many members of the adult population; outer whorl face strongly rounded, joined lower whorl face at pronounced circumbilical ridge; lower whorl face with slight concavity inside circumbilical ridge, continuing flatly to umbilical suture. Both upper and umbilical sutures shallow but distinct; depth of sutures varying with degree of spire depression with deeper suture generally present on flattest surface. Shells varying from slightly orthostrophic to slightly hyperstrophic, sometimes bordering on isostrophic, particularly in immature shells. Growth lines orthocline on upper whorl face, opisthocyrt on outer whorl face and slightly prosocline on lower whorl face, opisthocyrt on outer whorl face and slightly prosocline on lower whorl face with gently prosocyrt bendings over keels when present. Ornament of youthful forms consisting of strong collabral lines and two keels above and below the outer whorl face; in adult forms the basal collabral ornamentation and keel invariably persist, but the upper collabral ornamentation gives way to fine, closely spaced growth lines in one-half the population; the keel separating the upper and outer whorl face frequently disappearing in one-half the adult population. Shell thinnest near parietal lip, sometimes present only as a parietal inductura; shell becoming thicker near outer lip and reaching maximum thickness (6 or 7 mm) at circumbilical ridge. Septa abundant in early portion of whorls of adult shells, becoming more widely and unevenly spaced in more mature whorls; may occasionally be placed within one-half whorls distance from the aperture. Opiculum thick, circular, disc-shaped, multispiral, expanding counterclockwise. Shell width of largest hypotype measuring 98 mm.

Figured Hypotypes—NMV P1107, P28373, P28498, P28499, P28707, P28708, P28709, P28710, P28711, P28712, P28713, P28714, P28715, P28716, P28717, P28718 and P28719.

Description of males: Shell large, discoidal, slightly hyperstrophic. Nucleus unknown, presumably normal dextral. Whorl profile varying from subelliptical to distinctly subtriangular, typically with marked bilateral symmetry converging to isostrophism. Upper whorl face typically gently arched to the keel-like shoulder separating upper and outer whorl faces; keel-like shoulder occasionally absent with upper and outer whorl faces roundly confluent with one another. Outer whorl face rather strongly convex between upper keel-like shoulder and circumbilical ridge; lower whorl face flattened to umbilical shoulder. Upper suture distinct but not sharply incised; umbilical suture slightly deeper, also sharply incised. Shell basically hyperstrophic but variable in degree. Growth lines orthocline on upper whorl face, opisthocyrt on outer whorl face and slightly prosocline on lower whorl face with gently prosocyrt areas over each keel. Ornament normally consisting of strong collabral ornament and two keels. Normally with strong collabral ornament on upper and lower whorl faces with weaker collabral ornament occasionally absent on upper and outer whorl faces. Normally with keel-like shoulder separating upper from outer whorl faces and with circumbilical ridge separating outer and basal whorl faces; upper ridge occasionally absent. Septa common in early whorls, more rare in mature whorls, but present to within one-half volution of aperture. Operculum as in orthostrophic individuals. Shell width of largest hypotype measuring 70 mm.

Hypotypes—NMV P1107, P28707, P28710, P28713, P28714, P28715, P28717, P28718, P28719, P28708.

Description of females: Shell large, discoidal with depressed spire. Nucleus unknown. Whorl profile subelliptical with long axis of ellipse perpendicular to axis of coiling, upper whorl face broadly rounded, usually continuing without interruption to outer whorl face; outer whorl face more sharply rounded. Joining lower whorl face at marked circumbilical keel; lower whorl face with slight concavity inside circumbilical ridge, then flattened before rounding into umbilical suture. Upper suture shallow but distinct; umbilical suture more shallow but also distinct. Shells basically orthostrophic tending towards planispiral, apical angle varying from 200° to 230°. Umbilical angle varying from about 130° to 160°. Growth lines closely spaced and very fine on upper whorl face, generally orthocline becoming very slightly opisthocline on outer whorl face and very slightly prosocline on base resulting in a slight prosocyrt phase over circumbilical ridge. Growth lines becoming strong collabral ornamentation as they cross circumbilical ridge onto base. Ornamentation consisting of growth lines on upper and outer whorl faces, collabral ornamentation on base, with circumbilical ridge invariably present and shoulder separating upper and outer whorl faces only rarely present. Shell thinnest near parietal lip, sometimes present only as parietal inductura, occasionally with some degree of thickness to it. Shell becoming thicker (up to four or five mm) near outer lip and reaching maximum thickness at circumbilical ridge. Septa numerous through early portion of shell, becoming more widely spaced in mature region, but occasionally present to within one-half whorl of the aperture. Operculum thick, circular, disc-shaped, multispiral, expanding counterclockwise (for more complete description, see Yochelson and Linsley, 1972). Shell width of largest hypotype measuring 98 mm.

Hypotypes—NMV P28498, P28499, P28373, P28709, P28711, P28712 and P28716.

Discussion: Chapman based the genus *Liomphalus* on some very poorly preserved specimens from the Lilydale Limestone which are undoubtedly abraded specimens of Etheridge's species *'Oriostoma northi'*. As a result his original species name of *Liomphalus australis* Chapman is invalid and should be *Liomphalus northi* (Etheridge). However, the generic name *'Liomphalus'* is still a valid and available name, and since the new evidence presented in this paper supports the removal of this species from either *Oriostoma* or *Straparollus* I have utilized the genus *Liomphalus*.

This species can be easily differentiated from other members of the Omphalocirridae by the fact that its base lacks any nodal swellings or canal-like extensions. In addition, the sexual dimorphism while present, is not as well developed as in the descendant, more advanced members of the family. The adult males of *L. northi* tend to preserve juvenile features such as collabral ornamentation on the upper whorl face in addition to a strong keel separating the upper and outer whorl faces. In addition the males develop only a modest degree of hyperstrophism. The upper surface of the females however lose both the keel and the collabral ornament so that their upper whorl face flows continuously into the outer whorl face and has only closely-spaced, fine growth lines on it. The females also tend to be slightly orthostrophic. However none of these sets of characters are inviolate. In the collection of 104 specimens available of the National Museum of Victoria, Melbourne, there were occasional hyperstrophic forms with a rounded upper whorl face (Pl. 10, fig. 12, NMV P28713) or a faint keel which faded out (Pl. 10, figs. 9, 10), but the great majority of the members of this large population could be separated with ease.

However, this incipient sexual dimorphism, the lack of canal-like projections and the low stratigraphic position of *L. northi* are all consistent with the interpretation that this form is ancestral to *Omphalocirrus* and *Hypomphalocirrus*.

Stratigraphic Distribution

The oldest member of the family Omphalocirridae is *Liomphalus northi* of the Lilydale Limestone, Lower Devonian Yeringian of Australia. It is considered to be late Siegenian by Strusz (1972).

Although the next known occurrence of a member of this family is delayed until the Anderdon Limestone of the Michigan Basin, it is probable that further examination of gastropods presently assigned to the family Euomphalidae will uncover other genera and species that should be transferred to this group. The

Anderdon form (Linsley, 1968) of *Hypomphalocirrus* is unfortunately known only from a single fragment of an immature specimen. The Anderdon find represents the first known occurrence of this family in North America. The Anderdon represents a limited facies on the southeastern flank of the Michigan basin and is thought to be Eifelian (see Fagerstrom, 1961, and Linsley, 1968). It is considered to be late Sieyenian by Strusz (1972).

The next occurrence of a member of this family is *Hypomphalocirrus rugosus* from the Rogers City Limestone of the North East corner of the Michigan Basin. This unit has been placed in the lowermost Givetian (Cooper and Phelan, 1966, Ehlers and Kesling, 1970, Linsley 1973). Although this unit does not contain the brachiopod *Stringocephalus*, it does contain other members of the *Stringocephalus* fauna such as *Atrypa arctica*, *Subrensselandia* n. sp., *Liromytilus attenuatus, Buechelia tyrellii, Carinatina dysmorphostrota* (Ehlers and Kesling, 1970, p. 29) and *Straparollus (Straparollus) cottrelli* and *S. (Euomphalus) hoffmani* (Linsley and Yochelson, 1973).

The other occurrence of *Hypomphalocirrus rugosus* in the Miami Bend Formation of Indiana adds to the already substantial array of evidence put forth by Cooper and Phelan (1966) that this unit is directly correlative with the Rogers City Limestone.

The Winnipegosis Formation of Manitoba is also generally considered to be of Lower Givetian age (Ehlers and Kesling, 1970, p. 29, Cooper and Phelan, 1966, p. 28, Baillie, 1951, p. 59) and is generally correlated by these authors as the equivalent of the Rogers City Limestone. However a study of the species of *Hypomphalocirrus* present in these two formations suggests that the Rogers City form is ancestral to the Winnipegosis form and thus must slightly antedate the latter. This view is also supported by the study of the middle Devonian carrier shell, *Straparollus* (Linsley and Yochelson, 1973) which suggests that the Rogers City species are ancestral to the Winnipegosis species. Most certainly the two formations are close in age to each other, but the evidence on hand suggests that the Rogers City-Miami Bend Formations are very slightly older than the Winnipegosis Formation.

The last known occurrences of members of this family are those of *Omphalocirrus goldfussi* from the Givetian *Stringocephalus* beds of Europe and the lone occurrence of the same species (ex-*Arctomphalus grandis*) from Goose Fiord, Ellesmere Land, from the Blue Fiord Formation of Eifelian age (McLaren, 1963, pp. 324-328).

General Considerations

The genus *Omphalocirrus*, to which *Hypomphalocirrus* is closely related, has had a checkered career in the literature, with no one being quite certain whether to place the canal-like protrusions on the 'top' or on the 'bottom'. Even within the past thirty years the beast has been flipped three times. Knight (1941, p. 213) considered the canal-like projections to be the base of the organism, but without much conviction for he was not at all certain 'that the orientation employed . . . should not be reversed' (Knight, 1941, p. 213). In 1952 (p. 37) he reversed it, indicating that he considered *Omphalocirrus* to be a sinistrally coiled Macluritacean, and that the canal-like projections served an exhalent function. This view was retained in the Treatise (Knight, Batten and Yochelson, 1960, p. I189). In 1966, E. L. Yochelson (1966, p. 43, 45) broke from the Treatise triumvirate and flipped *Omphalocirrus* once again, placing the projections on the base, assuming them to be purely ornamental with no function, and transferring the genus from the Macluritacea to the Euomphalacea.

In Whiteaves original description of *H. manitobensis* (Whiteaves, 1890, p. 100) he described a steinkern assigned to that species that had an operculum associated with it. Considerable doubt has always surrounded this association. The operculum in this fossil is positioned well back into the shell, away from the aperture and tilted at an angle that would be unusual for an intact operculum (pl. 7, fig. 2). It was impossible to demonstrate that this was not just an operculum that had floated into an empty shell. Added to this is the fact that Whiteaves original description of *H. mani-*

tobensis (Whiteaves, 1890) was based on steinkerns from the Dawson Bay Formation that are generically indeterminate and our present understanding of the species is based on material collected from the underlying Winnepegosis Formation and assigned by Whiteaves to *H. manitobensis*. To further complicate matters no opercula of a multispiral form were known either from the Euomphalacea or the Macluritacea, and the operculum ascribed by Whiteaves to *H. manitobensis* did not fit our understanding of either of these groups.

I have been fortunate enough to find opercula in place both in *H. manitobensis* (pl. 7, fig. 1) from the Winnipegosis Formation of Manitoba and in *H. rugosus* from the Rogers City Limestone of Michigan. In both instances the operculum is multispiral, set well back away from the aperture and slightly tilted to the axis of the cone of revolution of the whorl, although not as tilted as in Whiteaves specimen. Thus there can now be no doubt that *Hypomphalocirrus* does indeed possess a multispiral operculum. The discovery also lends credence to Whiteaves claim that his steinkerns (one with a multispiral operculum) from the Dawson Bay Formation are at least related to the material from the Winnipegosis Formation, if not actually conspecific.

In both opercula as seen in place within the aperture, the volutions grow outward in a counter-clockwise fashion thus demonstrating conclusively that *Hypomphalocirrus*, and by inference *Omphalocirrus*, are dextral shells, and that the canal-like projections are really on the base of the shell. Thus the orientation of this enigmatic genus is no longer in doubt and it can finally come to rest, 'spines' down.

However, the solution of the problem of the orientation of the shell of the Omphalocirridae, is only the solution of the orientation for our descriptive purposes. Saying that the beast has finally come to rest 'spines down' only relates to the orientation of figures on a plate for the purposes of comparative morphology and has nothing necessarily to do with the orientation of the shell to the substrate while the organism was living. It allows us to invoke the concepts 'dextral', 'sinistral', 'orthostrophic' and 'hyperstrophic' and to ascertain homologous portions of the shell (inhalent, exhalent, etc.). But the orientation of the shell during life remains as much of an enigma as ever.

In the majority of modern gastropods, i.e. those with either high spires or elongated apertures (cones, mitres, volutes, terebras, etc.) the 'base' of the shell is actually the leading edge or anterior-most portion of the shell relative to the living animal. In low-spired modern gastropods (turbonids, naticids, trochids, etc.) or discoidal shells (planorbids, etc.) the 'outer lip' forms the leading edge of the shell. Thus in this second group the 'base' of the shell is the left side and the spire projects back and to the right side of the animal. In all of these gastropods the shell is held dorsally over the body by the columellar muscle and the plane of the aperture is parallel to the substrate.

If the Omphalocirridae are 'typical' gastropods then the shell would be held in a dorsal position with the coiled portion resting on the operculum of the upper surface of the posterior portion of the foot (the metapodium). However the Omphalocirridae are unlike all of the above-mentioned gastropods in one important aspect. In all of the aforementioned snails the plane of the aperture is tangent to the preceding whorls (a tangential aperture) while in the Omphalocirridae the plane of the aperture transects the axis of coiling of the shell (a radial aperture) with the result that a great portion of the earlier volutions projects beyond the plane of the aperture. This would seem disadvantageous for a gastropod whose aperture is parallel to the plane of the substrate. Perhaps the Omphalocirridae have a very different relationship to the substrate. In fact it has been suggested (Linsley and Yochelson, 1973) on the basis of completely different criteria that some euomphalids [*Euomphalus (Euomphalus), E. (Straparollus)* and *E. (Serpulospira)*] lived base down with the plane of the aperture perpendicular to the substrate. In this position there would no longer be a need for the aperture to be tangent to the preceding whorls and indeed it seems to be a general character of most euomphalids to have the plane of the aperture intersect at or near the axis of coiling of the shell.

This would be an adaptation suitable for a sedentary gastropod, perhaps a deposit feeder or even a filter feeder. The organism might possibly be capable of hoisting his shell into the normal position for short journeys to new feeding grounds. More probably the shell would just be dragged along during locomotion. It would be expected that the majority of the time would be spent with the shell lying flat on the substrate and the animal largely withdrawn inside the shell, protruding only to obtain food. For such a habit an operculum would be a distinct advantage.

Whether the Omphalocirridae were filter feeders and assumed a living position of the shell lying flat on the substrate, or whether they were active grazers and thus carried the shell erect over their back is not known. Possibly the nature of their spines might afford some clue.

During his investigation of the genera *Omphalocirrus* and *Arctomphalus*, Yochelson (1966, p. 53) remarked that 'the fact that the spines develop gradually from nodes would seem to imply that they served no vital function'. Close examination of these canal-like protuberances in *Hypomphalocirrus* belie that statement. As many as ten to twelve growth lines are involved in making one of the projections, the last of which curve backward in a U-shaped fashion, and upward to form the rim of the canal-like projection (see pl. 4, figs. 5, 8). The next growth line does not bend upward but proceeds across the shell along the normal shell contour, bending forward at the position of the protuberance, thus leaving an opening ('tremata') which I suggest remains functional until the appearance of the next projection, whereupon it is filled in with secondary calcite deposits, very much as are the tremata of *Haliotis*.

However, these canal-like projections cannot be called 'tremata', because tremata (as found in *Tremanotis, Polytremaria* and the *Haliotidae*) are associated with the exhalent function and normally mark the position (or the eventual position) of the anus. In *Hypomphalocirrus* the basal position of these projections necessitates that we regard them as inhalent in function, thus resembling the inhalent (siphonal) canals of many of the modern Caenogastropoda and I propose that they be called 'inhalent tremata'. *Hypomphalocirrus* is not unique among Devonian gastropods in the development of a portion of the aperture for a specialized incurrent function. In the Raphistomatinae alone, both *Tylozone* and *Buechelia* show well developed siphonal canals and the lower lip of *Arizonella* most probably marks the position of the inhalent currents as does the plethospirid *Diplozone*. Even in the Euomphalidae, *Pleuronotus* and *Diploconula* have a basal angulation which would most probably result from a mantle fold which would make an incurrent stream more effective by being localized.

It is probable that the advent of more advanced and efficient groups during the Devonian, such as the Neritacea, the Palaeotrochacea and the Paleozygopleuridae, which would probably be more efficient, increased the pressure on the older, more conservative groups such as the Macluritacea, Euomphalacea and Pleurotomariacea. One temporary solution could be in improvement of the efficiency of water currents as evidenced by *Omphalocirrus, Hypomphalocirrus, Tylozone et al.* It was a solution that apparently was not tried again until the Pennsylvanian when we find *Knightites, Cyclioscapha*, and *Straparollus (Amphiscapha)* developing similar canals or angulations.

The primary water current in *Hypomphalocirrus* thus entered the mantle cavity by way of the incurrent canals on the base, passed the osphradium and left gill and then passed out of the mantle cavity, past the anus which was undoubtedly located at the angulation formed by the junction of the upper and outer whorl faces. In females of *H. manitobensis* this upper angulation is also equipped with a row of canal-like projections which mirror the form of those on the lower angulation, but which served an excurrent rather than an incurrent function. It is possible that the peripheral undulations in the female *H. rugosus* are antecedent to this upper row of projections.

If the interpretation of the current arrangement in *Hypomphalocirrus* given above is correct, this adds support to the concept (Knight, Batten, Yochelson, 1960) that the Macluritidae and the Euomphalidae suffered a reduction or elimination of the right gill, for there is no morphological evidence in the shell that a comparably effective water current would flow over the right gill which, in *Hypomphalocirrus* would have to be positioned under the upper whorl face.

Therefore, if the spines are indeed functional as incurrent modifications, then the shell of the Omphalocirridae must have either been carried in an upright position or if lying flat on the substrate with the left side bearing the spines (the 'base') uppermost. This latter position would thus be 'upside down' compared with our normal way of depicting these shells.

A Summary of Sexual Dimorphism and the Evolution of the Omphalocirridae

Our present knowledge of this family would suggest that *Liomphalus* first developed the diagnostic features of this family and then gave rise to two stocks, one European culminating in *Omphalocirrus* and one North American, furnishing the *Hypomphalocirrus* lineage.

The development of the operculum of this group has already been fully treated (Yochelson and Linsley, 1972). Evolutionarily the thick operculum of *Liomphalus northi* is set at the apertural margin, while in *Hypomphalocirrus rugosus* and *H. manitobensis* the operculum is much thinner and drawn well into the aperture, as far back as one-fourth volution. It also tends to be slightly rotated in this genus, which is a nice adaptation to allow a circular operculum to fit snugly inside a slightly elliptical whorl profile. The operculum of *Omphalocirrus goldfussi* is unknown but most probably exists and has not been associated with that form.

The varying reasons for the presence of septa in gastropods has also been discussed recently (Yochelson, 1971). In the case of the Omphalocirridae it seems unlikely that the septa are for strengthening the shell or for protection against breakage of the early whorls. Rather the septa would appear only to serve the purpose of body shortening. We do not know if this body shortening would result in any mass decrease. If the early chambers were filled with water, as is most probable, then presumably the mass of water would closely approximate the mass of flesh. Without a siphuncle and the complex gas-exchange cells of the cephalopods it seems most unlikely that there would be any increase in buoyancy gained by the secretion of septa in gastropods.

The features which are involved in the sexual dimorphism of this family, i.e. size differential, collabral ornamentation, differential development of keel or canals, and hyperstrophism, are all present in *Liomphalus northi* although they are not as fully differentiated in this species as they are in subsequent species. In *Liomphalus northi* the males tend to be hyperstrophic, smaller, with collabral ornamentation on the upper whorl face and a keel separating the upper and outer whorl faces. The females are more orthostrophic, larger, and have no collabral ornamentation or keel on the upper whorl face. In all cases where I have had a sufficiently large population to study, I have assumed that the largest individuals are the females. The one exception to this rule is *Omphalocirrus goldfussi*. In the six examples I have seen from Germany, those that I have called females are indeed the largest individuals. However, this makes Tolmachoff's specimen from Ellesmere Land a male yet this specimen is the largest individual in the entire family. However, as outlined below, I have other reasons for believing that this is a correct interpretation, so until someone has had an opportunity to study a large population of this species I will continue to consider Tolmachoff's specimen as a male.

In the Middle Devonian members of the family, the best indicator of sex is the relative development of the canal-like extensions, the inhalent tremata. In the Rogers City form, the female has very well developed, obviously functional, canal-like inhalent tremata on the base. In addition the junction between the upper and outer whorl face has developed a series of undulations that are presumed to act as a canal, or at least a means of localizing the excurrent flow. The male generally lacks both of these traits. The females from the Winnipegosis Limestone have developed canal-like extensions both on the top and bottom of the outer whorl face, while the males have inhalent tremata developed only on the base. This would seem an obvious improvement over the Rogers City Form and is the main reason that I consider *Hypomphalocirrus rugosus* ancestral to *H. manitobensis*. As mentioned earlier I believe the basal canals to be incurrent, while the upper canals or shoulder mark the position of the anus and is thus essentially excurrent. It is presumed that the female needs better mantle circulation to enable it to produce the more bulky egg masses. The males in both of these cases have less well developed aids to water circulation. In *H. rugosus* the adult males typically have only a keel where the incurrent canals of the female are located and have an even upper shoulder in place of the undulating shoulder of the female. The males of *H. manitobensis* have only a single set of canals at the incurrent position instead of the double set of both incurrent and excurrent found in the females. Thus the entire evolution of the North American lineage was accompanied by an improvement of water circulation in the mantle, with the females consistently better than the males.

A similar situation exists with the European stock of *Omphalocirrus goldfussi*. In this species the female has very well developed inhalent canals whereas in the males, the canals are not always well developed and are frequently only suggested by nodal swellings on the basal keel.

The Australian representative deviates from the patterns set by its descendents in that the male of *Liomphalus northi* possesses keels above and below while the female has only the lower keel. However these keels have no expression on the inner surface of the aperture and therefore may not be functional relative to water currents as are the well-developed keels of its descendents. I would suggest that this is merely a case of pre-adaptation, where the keels of the ancestral form were selected for one function (possibly strengthening the shell) and secondarily proved useful for a completely different function (isolating water currents). As a result it would not have the same selective pressures relative to the sexes in *Liomphalus* as it subsequently had in the more highly specialized offspring.

The matter of hyperstrophism is also a perplexing problem in the Omphalocirridae. In *Liomphalus northi, Omphalocirrus goldfussi* and *Hypomphalocirrus manitobensis* the males are more hyperstrophic than the females. This leads me to the conclusion that it is not the mode of coiling that is significant in itself, but the effect the coiling has on the positioning of the outer whorl face. In the genus *Hypomphalocirrus* which has a triangular whorl face, the outer whorl face of female is oriented so that it is sub-parallel to the axis of the shell. This places both inhalent and exhalent portions of the aperture on the very periphery of the shell, both placed as far from the axis of coiling as possible. If the shell is positioned in a recumbent position, inhalent tremata up, then they are in the perfect position to obtain clean water while the anus of *Hypomphalocirrus rugosus* would be placed adjacent to the substrate, while excurrent canal of *H. manitobensis* would be thrust down into the substrate. Possibly they buried their faces as does the modern detritus feeder *Xenophora* (Shank, 1969, p. 6).

In the case of *Omphalocirrus goldfussi* and *Liomphalus northi* the whorl profile of the female tends to be more inflated than that of the male, presumably to accommodate the bulkier egg masses. The male, on the other hand, has a less inflated slightly more angular external whorl profile (the internal whorl cross section being subcircular). It is possible that these differences may dictate the hyperstrophic coiling of the males and the ortho-isostrophic coiling of the female.

The final feature is one that is possessed by all members of this family and that is collabral ornamentation in the adult males. In all members the immature forms have strong collabral ornamentation, but only in the males is this juvenile feature carried into the adults. It is probable that this feature serves to strengthen the shell on juveniles and males. It is possible that this becomes unnecessary in females because they possess thicker shells, but I have no direct confirmation of this from actual observations on shells (a particularly difficult task when ninety per cent of the fauna studied consists of latex impressions).

Summary and Conclusions

All four species of the Omphalocirridae, *Omphalocirrus goldfussi*, *Liomphalus northi*, *Hypomphalocirrus rugosa* and *H. manitobensis* exhibit considerable dimorphism in their adult shells. The expressed dimorphism is completely consistent with an interpretation of sexual dimorphism in that both dimorphs are always present in all localities where extensive collections have been made and in a more or less one-to-one ratio. All species except *Liomphalus northi* are characterized by having functional inhalent tremata developed as canal-like extensions of the base. These inhalent tremata are consistently better developed in the morphotypes that have been considered as females and it is suggested that this is related to the improved circulation necessary to aerate the bulky egg mass of the females.

Acknowledgements

This study has been made possible by a series of grants extended to the author by the Sloan Foundation and the Colgate Research Council. These grants were awarded for the summers of 1967, 1968, 1969, 1970 and for a sabbatical semester of 1971 which enabled me to go to Australia to study the fauna of the Lilydale Limestone as represented in the collections at the National Museum of Victoria, Melbourne. I am particularly indebted to Mr Edmund Gill and Mr Thomas Darragh of the National Museum of Victoria for opening their facilities and collections to me and for extending the hospitality of the entire museum. I would also like to thank Dr Gary Batt of the Department of Zoology, University of Auckland for assisting with the photography of the Australian material.

For German material of *Omphalocirrus goldfussi* I am indebted to Dr Urlich Jux of the University of Cologne for taking the author to a number of collecting sites in the Paffrath area and making available comparative material for study.

Dr Hugh R. McCabe of the Department of Mines and Natural Resources of the Province of Manitoba was most kind in discussing Manitoba Geology with the author and in accompanying the author to outcrops of the Winnipegosis Formation.

The author was first introduced to the Rogers City Formation of Michigan by Dr G. M. Ehlers and Dr R. V. Kestling of the University of Michigan Museum of Paleontology. Both of these men have contributed enormously to the author's understanding of the geology of this area and to his understanding of the Rogers City Limestone in particular. I am deeply indebted for the many hours spent with them discussing both geological and biological aspects of this problem. Access to the Calcite Quarry, Michigan Limestone Operations, U.S. Steel Corporation at Rogers City, Michigan and to the Preque Isle Corporation Quarry, formerly Lake of the Woods Quarry, north of Alpena, Michigan, managed by Mr Roy Hutchinson for a consortium of steel companies, has always been graciously granted.

I would also like to express my deep appreciation to four former students who have been of great assistance in this problem. Mr John Cottrell and Mr John Hoffman spent one summer with me under the auspices of a Colgate Research Council Undergraduate Research Participation grant. They were indefatigable field workers and spent many hours preparing specimens and discussing various aspects of the problems. Cottrell was also able to accompany me to the Manitoba field area near Lake Winnipegosis. Dr Harold B. Rollins and Mr William Arendt also accompanied me to the Rogers City area for field work and in addition Rollins was of inestimable value for the photographic work he did on the Rogers City material.

Dr R. V. Kesling of the University of Michigan Museum of Paleontology, Dr G. Arthur Cooper of the U.S. National Museum and Dr Digby McLaren of the Canadian Geological Survey at Ottawa were very kind in giving the author access to the collections of their respective institutions.

Lastly I greatly appreciate the many hours of stimulating discussion of this problem provided by Dr John Morton, Department of Zoology, University of Auckland, Dr C. M. Yonge, Department of Zoology, University of Edinburgh and Dr E. L. Yochelson, U.S. Geological Survey.

Abbreviations used in this paper are as follows: USNM—United States National Museum, Washington, D.C.; UMMP—University of Michigan Museum of Paleontology, Ann Arbor, Michigan; GSC—Geological Survey of Canada, Ottawa, Ontario, Canada; NMV—National Museum of Victoria, Melbourne, Victoria, Australia.

References

Anonymous, 1960. *Fossils found in Limestone of the Calcite Quarry of Michigan Limestone operations of United States Steel Corp. at Rogers City, Michigan.* U.S. Steel Corp.

Archiac, E. J. A. d', and E. P. de Verneuil, 1842. On the fossils of the older deposits in the Rhenish Provinces, preceded by a general survey of the fauna of the Palaeozoic rocks, and followed by a tabular list of the organic remains of the Devonian system in Europe. *Trans. Geol. Soc. Lond.*, 6: 303-410, pls. 25-37.

Baillie, Andrew D., 1951. Devonian geology of Lake Manitoba-Lake Winnipegosis area: Province of Manitoba, Dept. Mines & Nat. Resources, Mines Branch, publ. 49-2.

Baker, H. B., 1926. Anatomical Notes on American Helicinidae, *Proc. Acad. Nat. Sci. Phila.*, 78: 35-56.

Cooper, G. A. and Thomas Phelan, 1966. *Stringocephalus* in the Devonian of Indiana, *Smithson Misc. Collns.*, 151(1): 1-20, pls. 1-5.

Cox, L. R. and J. B. Knight, 1960. Suborders of Archaeogastropoda: *Proc. Malac. Soc. Lond.*, 33 (6): 262-264.

Cuvier, Georges, 1797. *Tableau elementaire de l'histoire naturelle des animaux*: xvi + 710 p., 14 pl. (Paris).

Ehlers, George M. and Robert V. Kesling, 1970. Devonian Strata of Alpena and Presque Isle Counties, Michigan. *Michigan Basin Geological Society Guide Book for Field Trips.* Michigan Basin Geological Society, pp. 1-130, pls. 1-38.

Ehlers, George M. and Robert E. Radabaugh, 1938. The Rogers City Limestone, A New Middle Devonian Formation in Michigan, *Pap. Michigan Acad. Sci., Arts, Letters,* XXIII, pp. 441-446, pls. I-II.

Etheridge, R. Jr., 1890. Descriptions of Upper Silurian fossils from the Lilydale Limestone, Upper Yarra District, Victoria. *Rec. Aust. Mus.*, 1, no. 3, pp. 60-67.

Fagerstrom, J. A., 1961. The Fauna of the Middle Devonian Formosa Reef Limestone of Southwest Ontario, *J. Paleont.*, 35, no. 1, pp. 1-48, pl. 1-14.

Knight, J. Brooks, 1941. Paleozoic Gastropod Genotypes, *Spec. Pap. Geol. Soc. America*, 32, pp. 1-510, pls. 1-96.

————, 1952. Primitive Fossil Gastropods and their Bearing on Gastropod Evolution, *Smithson. Misc. Collns.* 117, (13): 1-56, pl. 1-2.

————, Batten, R. L., and Yochelson, E. L., 1960. Treatise on Invertebrate Paleontology (Moore, R. C., editor) Part I, Mollusca 1. Geological Society of America, Inc., Boulder, Colorado and University of Kansas, Lawrence, Kansas, xxiii and 351 pp.

Koninck, L. G. de, 1881, Faune du calcaire carbonifere de la Belgique, 3[e] partie, Gasteropodes: *Mus. roy. Histoire nat. Belgique, Ann. ser. paleont.*, 6, pp. 1-170, pl. 1-24 (Bruxelles).

Lamy, E., 1937. Sur le Dimorphisme Sexuel des Coquilles, *Journ. Conchyliol.*, 81, pp. 283-301.

Linsley, Robert M., 1968. Gastropods of the Middle Devonian Anderdon Limestone, *Bull. Amer. Paleont.*, 54, no. 244, pp. 333-465, pl. 25-39.

————, 1973. Paleoecological Interpretation of the Rogers City Limestone (Middle Devonian, Northeast Michigan), *Contrib. Mus. Paleont. Univ. Michigan*, 24, no. 11, pp. 119-123.

———— and E. L. Yochelson, 1973. Devonian Carrier Shells (Euomphalidae) from North America and Germany *U.S. Geol. Surv. Prof. Paper* 824, pp. 1-26, pl. 1-6.

McCabe, H., 1967. *Field Guide to Devonian Outcrops of Southwestern Manitoba.*

McLaren, D. J., 1963. Southwestern Ellesmere Island-Goose Fiord to Bjorne Peninsula, p. 310-338 *in* Fortier, Y. A. and others: Geology of the North-Central part of the Arctic Archipelago, Northwest Territories (operation Franklin), *Mem. Geol. Surv. Canada,* 320.

Milne Edwards, Henri, 1848. Note sur la classification naturelle des mollusques gasteropodes, *Ann. Sci. Nat., Zool.*, ser. 3, 9, pp. 102-112 (Paris).

Philip, G. M. and J. A. Talent, 1959. The gastropod genera *Liomphalus* Chapman and *Scalaetrochus* Etheridge, *J. Paleont.* 33, pp. 50-54.

Robertson, Robert, 1971. Sexually Dimorphic Archaeogastropods and Radulae, *Annual Reports for 1970 of the American Malacological Union*, pp. 75-78.

Ryckholt, P. de, 1860. Revue des generes qui composent la famille des Haliotidae, D'Orbigny, *Jour. Conchyliol.*, 2e ser. 4, pp. 183-188.

Shank, Paul, 1969. The Timorous Carrier Shell, Close Observation of the *Xenophora conchyliophora* Born. *New York Shell Club Notes* 151, pp. 5-7.

SOHL, NORMAN F., 1969. Gastropod Dimorphism, in Westermann, G.E.G. editor, *Sexual Dimorphism on Fossil Metazoa and Taxonomic Implications, Intern. Union of Geol. Sciences*, Ser. A, 1, pp. 94-100.

STRUSZ, D. L., 1972. Correlation of the Lower Devonian Rocks of Australasia. *J. Geol. Soc. Aust.* 18(4): 427-455.

TASSELL, C. B., 1976. A Revision of the Gastropod Fauna of the Lilydale Limestone (Early Devonian) of Victoria, *Mem. Natn. Mus. Vic.* 37: 1-21.

THIELE, JOHANNES, 1925. *Mollusca—Weichtiere: Handbuch der Zoologie*, gegründet W. Kukenthal, 5, pp. 15-256 (Berlin, Leipzig).

TOLMACHOFF, I. P., 1926. On the fossil faunas from Per Schie's Series D from Ellesmere Land with exception of brachiopods, corals, and cephalopods: *Report of the second Norwegian Arctic expedition in the 'Fram' 1898-1902*, 38, pp. 1-106, 8 pls.

WHITEAVES, J. F., 1890. Descriptions of some new or previously unrecorded species of fossils from the Devonian rocks of Manitoba, *Trans. R. Soc. Canada*, VIII, sec. 4, no. 3, pp. 93-110.

————, 1892. The fossils of the Devonian Rocks of the islands, shores, or immediate vicinity of Lakes Manitoba and Winnipegosis, *Geol. Surv. Canada, Contrib. to Cana. Paleont.*, 1, pt. 4, no. 6, pp. 255-359, pls. 33-47, Ottawa.

YOCHELSON, E. L., 1966. A Reinvestigation of the Middle Devonian gastropods *Arctomphalus* and *Omphalocirrus*, Årbok norsk Paralinst. 1965, pp. 37-48.

————, 1971. A new Upper Devonian gastropod and its bearing on the problems of open coiling and septation, *Smithsonian Contr. Paleobiology*, 3, pp. 231-241, pls. 1, 2.

———— and R. M. LINSLEY, 1972. Opercula of two gastropods from the Lilydale Limestone (Early Devonian) of Victoria, Australia, *Mem. Natn. Mus. Vict.* 33, pp. 1-14, pls. I-II.

Explanation of Plates

PLATE 2

Hypomphalocirrus rugosus n. sp. All figures are of males. All specimens except Figure 6 from the Rogers City Limestone.

Figures 1-3—Basal, apical and apertural views (x1·8) of paratype UMMP 22384, from the beach at Rockport. Note flat upper surface, strong collabral ornamentation and 45° inclination of outer whorl face.

Figure 4—Apertural view of paratype USNM 213775 (x0·75) showing subtriangular whorl profile with flat upper whorl face and inclined outer whorl face.

Figure 5—Apical view of paratype, UMMP 22383 (x1) exhibiting strengthening of collabral ornamentation near the suture.

Figure 6—Apical view (x1·1) of paratype USNM 213769 from the Miami Bend Formation in Ohio.

Figure 7—Apical view (x1·75) of paratype USNM 213770. In this specimen the collabral ornamentation is very strong in the youthful stage and becomes diminished with increasing age.

Figure 8—Apical view (x0·75) of paratype USNM 213762. Again the collabral ornament becomes weaker with increased age.

Figure 9—Cross-section (x1·4) of paratype USNM 213763 showing numerous irregularly spaced septa.

PLATE 3

Hypomphalocirrus rugosus n. sp. All figures are of males from the Rogers City Limestone.

Figures 1, 11—Oblique basal (x1·5) and basal (x0·8) views of Paratype, USNM 102939 showing flange-like projections of early whorls giving way to a continuous keel on the ultimate whorl.

Figure 2—Apertural view of Paratype USNM 213777 (x0·75).

Figure 3—Basal view (x0·65) of Paratype USNM 213757. Note continuous keel on ultimate whorl.

Figure 4—Adapertural view (0·6) of Paratype USNM 213779 showing slight suggestion of a spiral groove just below the shoulder.

Figure 5—Oblique basal view (x0·6) of Paratype USNM 213766 very large male with unusually well developed flange-like projections on the base.

Figure 6—Oblique basal view (x0·6) of Paratype USNM 213773 showing well developed spiral groove just below shoulder.

Figure 7—Basal view (x0·9) of Paratype USNM 213774.

Figure 8—Apical view of Paratype USNM 213775 (x0·6) showing well developed collabral ornamentation.

Figure 9—Oblique basal view (x0·9) of Paratype USNM 213778. Note sharp single keel on base and smooth outer whorl face.

Figure 10—Basal view (x0·9) of Paratype UMMP 57889, a mature specimen with well-developed keel and deep umbilicus.

Figure 12, 14—Basal (x0·9) and oblique basal (x0·8) views of Paratype, USNM 213761. This specimen is unusual because of the roundness of the base. Note also the well-developed flanges and the strong collabral ornamentation.

Figure 13—Basal view (x0·6) of mature specimen, Paratype USNM 213756 with a rounded base with no flanges or keel.

Figure 15—Basal view (x0·6) of Paratype USNM 213780.

PLATE 4

Hypomphalocirrus rugosus n. gen. and sp. All figures are of females from the Rogers City Limestone.

Figures 1, 2, 5, 6, 8—Oblique apical (x0·6), apertural (x0·8), basal (x0·8), apical (x0·8) and oblique basal (x0·8) of holotype UMMP 22377. A very large mature female showing well-developed basal flanges, undulating shoulder, high degree of hyperstrophism and rugose, near vertical outer whorl face, all typical features of the adult female.

Figure 3—Apical view (x0·6) of paratype UMMP 22378 showing smoothness of early whorls and the undulating shoulder.

Figure 4—Outer surface (x1·25) of operculum, paratype USNM 213768 showing the multispiral form typical of the opercula of this family.

Figure 7—Oblique apical view (x0·75) of Paratype USNM 213758, the most extremely hyperstrophic individual in the entire collection.

PLATE 5

Hypomphalocirrus rugosus n. gen. and sp. All figures are of females from the Rogers City Limestone.

Figure 1—Apical view (x0·75) of Paratype, USNM 213755. Note the degree of hyperstrophism and undulating shoulder on this large specimen.

Figure 2—Oblique basal view (x0·7) of Paratype, USNM 213764 showing well-developed projecting flanges.

Figure 3—Basal view (x0·85) of Paratype USNM 213760. This mature specimen illustrates the well-developed basal flange-like protrusions of the female, but the collabral ornamentation is better developed than is typical.

Figure 4—Apical view (x0·6) of Paratype UMMP 57888. This very large female has only moderate hyperstrophism and no development of the undulating shoulder.

Figure 5—Basal view (x1·0) of Paratype USNM 213767 showing strongly developed, spade-like basal flanges.

Figure 6—Apical view (x1·1) of Paratype UMMP 22379, showing undulating shoulder.

Figure 7—Apical view (x3·0) of Paratype UMMP 22375. Very immature specimens such as this are very difficult to sex. This individual has the degree of hyperstrophism which suggests a female, but the well-developed collabral ornamentation suggests a male.

PLATE 6

Hypomphalocirrus rugosus n. gen. and sp. All figures of females from the Rogers City Limestone.

Figures 1, 8—Oblique basal (x0·7) and apertural (x1·25) views of Paratype UMMP 22379. A thin individual with undulating shoulder, flanges and roughened outer whorl face.

Figure 2—Apertural view (x0·6) of Paratype UMMP 22378 showing strong hyperstrophism.

Figure 3—Oblique basal view (x0·5) of Paratype USNM 213759 with an unusually high outer whorl face.

Figure 4—Oblique basal view (x0·8) of Paratype USNM 213772 showing well-developed undulations on shoulder and the rugose outer whorl face.

Figure 5—Apical view (x0·9) of Paratype USNM 213781. This specimen is a female on the basis of its hyperstrophism, but exhibits the male characters of strong collabral ornamentation and smooth shoulder.

Figure 6—Oblique basal view (x0·7) of Paratype USNM 213776 showing strong flanges on base and undulating shoulder.

Figure 7—Oblique apical view (x0·75) of Paratype, USNM 213765 showing exceedingly rugose outer whorl face.

Figure 9—Basal view (x0·6) of Paratype UMMP 22380. This specimen has an unusually round whorl profile and thus greatly resembles *Omphalocirrus goldfussi*.

Figures 10, 11—Oblique apical (x0·7) and oblique basal views (x0·9) of Paratype, USNM 213754 showing rugose outer whorl face and very strong undulating shoulder.

PLATE 7

Hypomphalocirrus manitobensis (Whiteaves)

Figure 1—Oblique apical view (x1·8) of Hypotype, USNM 213783 showing operculum set of an oblique angle inside the ultimate whorl. Coiling of multispiral operculum indicates this is orthostrophic coiling.

Figures 2, 4—Whiteaves cotype, GSC 4174. The break in this steinkern marks the position of the operculum. This operculum is placed at a greater angle to the axis of the whorl than that found in Fig. 1, indicating that there was some rotation after death.

Figure 3—Oblique basal view of Whiteaves Plesiotype GSC 4176, a female showing full development of both rows of spines. Also note rugose outer whorl face.

Figures 5, 6, 8—Apertural, basal and apical views of Whiteaves Plesiotype GSC 4177a. Note the two rows of spines and the pseudoisostrophic coiling typical of the female.

Figure 7—Basal view of hypotype USNM 213782, an immature male showing well-developed basal inhalent tremata, collabral ornamentation and hyperstrophic coiling.

PLATE 8

All figures of *Omphalocirrus goldfussi* (Archiac and Verneuil)

Figures 1, 2, 9—Oblique basal (x0·8), basal (x0·75) and apical (x0·7) of latex cast (from USNM) of topotype figured by Knight (1941) of a specimen from the Puzo Collection, Ecole de Mine. This specimen is presumably a female characterized by being orthostrophic and having well-developed inhalent tremata present throughout its growth.

Figures 3, 6—Basal (x1·0) and oblique basal (x0·8) views of latex cast (from USNM) of Holotype which is housed in the De Verneuil Collection at the Ecole national superieure des Mines, Paris, France. This is presumably a female showing the weak collabral ornamentation of the base.

Figures 4, 5—Oblique basal and basal views (x1·8) of a plaster cast (from USNM) of a specimen from Sotenich, Germany, Stringocephalus Limestone (Givetian). The original of this specimen is from Humboldt Universitat, Berlin, Germany. This is presumably a male and is thus hyperstrophic, with non-functional inhalent tremata and strong collabral ornamentation of the base.

Figure 7—Basal view (x1·0) of plaster cast (from USNM) of holotype of '*Arctomphalus grandis*' Tolmachoff, 1926, specimen No. A 19229 in the Paleontologisk Museum of Oslo, Norway. The total size of this specimen is indicated by the dashed line, but the adult whorls are only represented by a steinkern. The inner whorls indicate the features typical of the male *Omphalocirrus.*

Figure 8—Basal view (x1·1) of plaster cast (from USNM) of a specimen from Vilmar, Germany. Upper Stringocephalus zone. The original of this specimen is in the Humboldt Universitat, Berlin, Germany. This specimen is hyperstrophic and shows the other male characters of incipient nonfunctional inhalent tremata and strong collabral ornamentation.

PLATE 9

Liomphalus northi (Etheridge). All figures of females from the Lilydale Limestone, Cave Hill Quarry, Lilydale, Victoria, Australia.

Figures 1-3—Apical, basal and apertural views (x2) of an immature female Hypotype NMV P28716. At this young age the females exhibit many of the male characters such as collabral ornament and a faint keel on top as well as bottom. Note however that it is orthostrophic rather than hyperstrophic as is the case with the males (cf. Pl. 10, Fig. 5).

Figure 4—Apical view (x0·7) of Hypotype NMV P28709, showing rounded upper whorl face with no keel and no collabral ornament.

Figures 5, 7, 8—Oblique apical, apical and basal views (x0·7) of Hypotype, NMV P28711, a large female showing strong keel and collabral ornamentation on the base and no keel and no collabral ornamentation on the top.

Figures 6, 9, 10—Oblique apical (x0·7), basal and apical (x0·5) views of Hypotype, NMV P28712.

Figure 11—Cross section (x0·7) of Hypotype, NMV P28499 showing septal filling of early whorls.

Figures 12, 13—Basal (x0·8) and apical (x1) views of Hypotype NMV P28708.

Figures 14, 17—Basal and apical views (x0·7) of Hypotype, NMV 28498. Note flat spire and depressed umbilicus.

Figures 15, 16—Basal and apical views (x0·5) of Hypotype, NMV P28373, the largest specimen in the collection.

PLATE 10

Liomphalus northi (Etheridge). All figures of males from the Lilydale Limestone, Cave Hill Quarry, Lilydale, Victoria, Australia.

Figures 1-3—Apical, basal and oblique apical views (x1) of Hypotype, NMV P28714, a typical male showing collabral ornamentation and keel on both top and bottom. Also note the degree of hyperstrophism.

Figures 4-6—Apical, apertural and basal views (x2) of Hypotype NMV P28719. This is a small male showing the degree of hyperstrophism typical of the males.

Figure 7—Basal view (x1) of Hypotype NMV P28707 showing very strong basal keel.

Figures 8, 11—Apical and oblique views (x0·7) of Hypotype, NMV P28717. On this strongly hyperstrophic male the upper keel becomes lost on the ultimate whorl, but the collabral ornament continues all of the way.

Figures 12, 17—Apical (x0·9) and basal views (x1) of Hypotype, NMV P28713. This male is unusual for though it is markedly hyperstrophic it has lost the keel and collabral ornament on the top.

Figures 13, 16—Apical (x1) and oblique apical (x0·7) views of Hypotype, NMV P1107. This large male exhibits all of the typical features: keel and collabral ornamentation top and bottom, and hyperstrophism. Note massive, multispiral operculum in place in the aperture.

Figure 14—Apical view (x0·7) of Hypotype, NMV P28710.This specimen still has the keel on top, but has lost the collabral ornamentation.

Figure 15—Apical view (x0·7) of Hypotype, NMV 28718. This crushed male shows strong collabral ornamentation and well-developed keel.

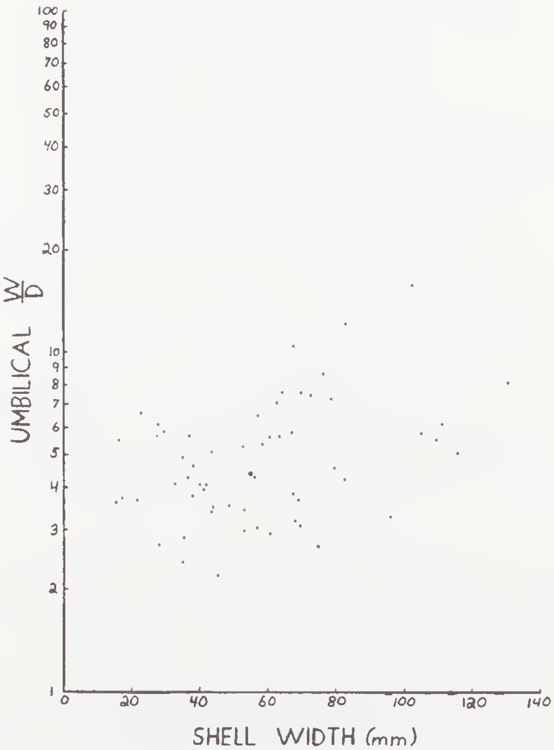
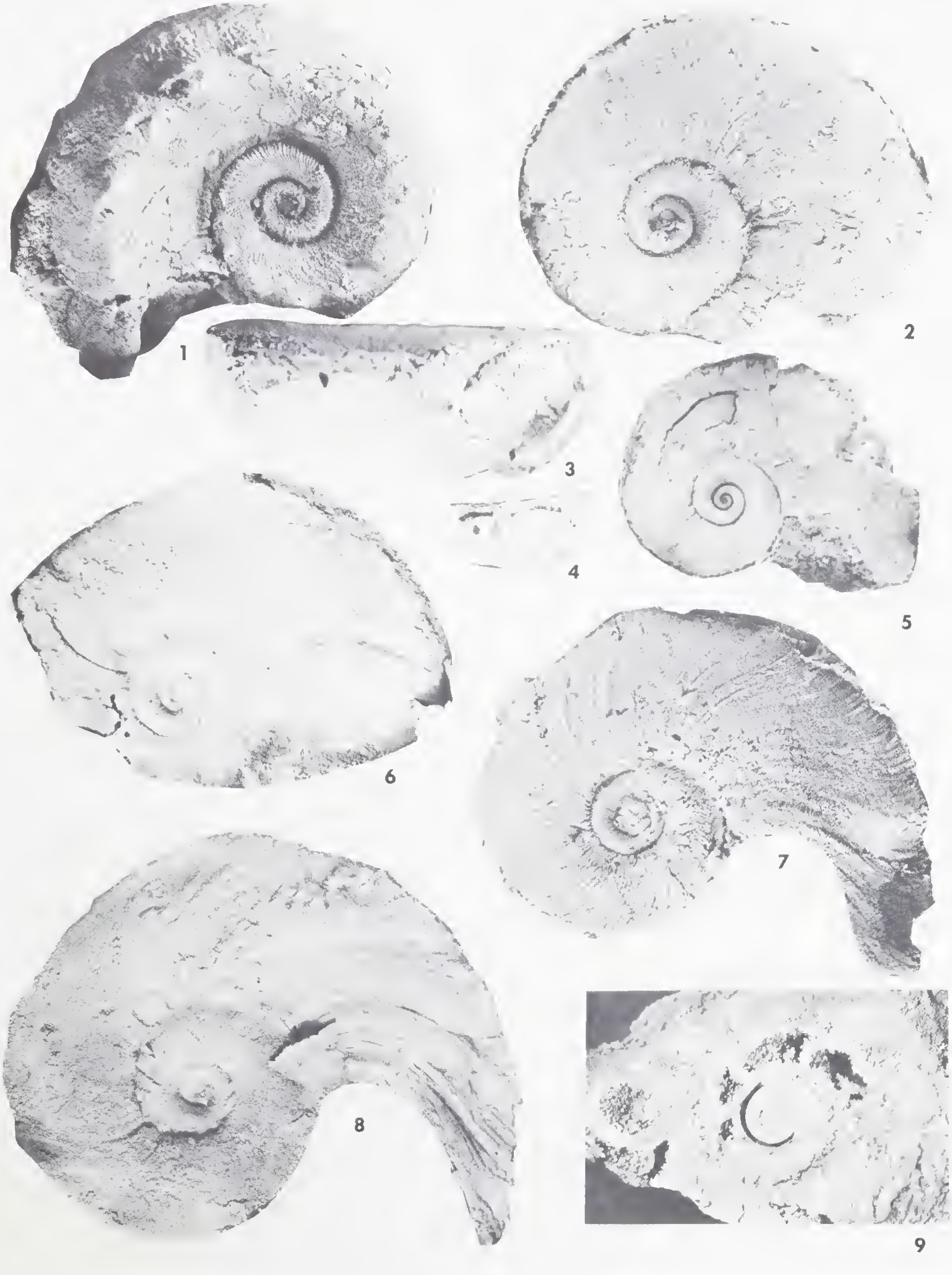
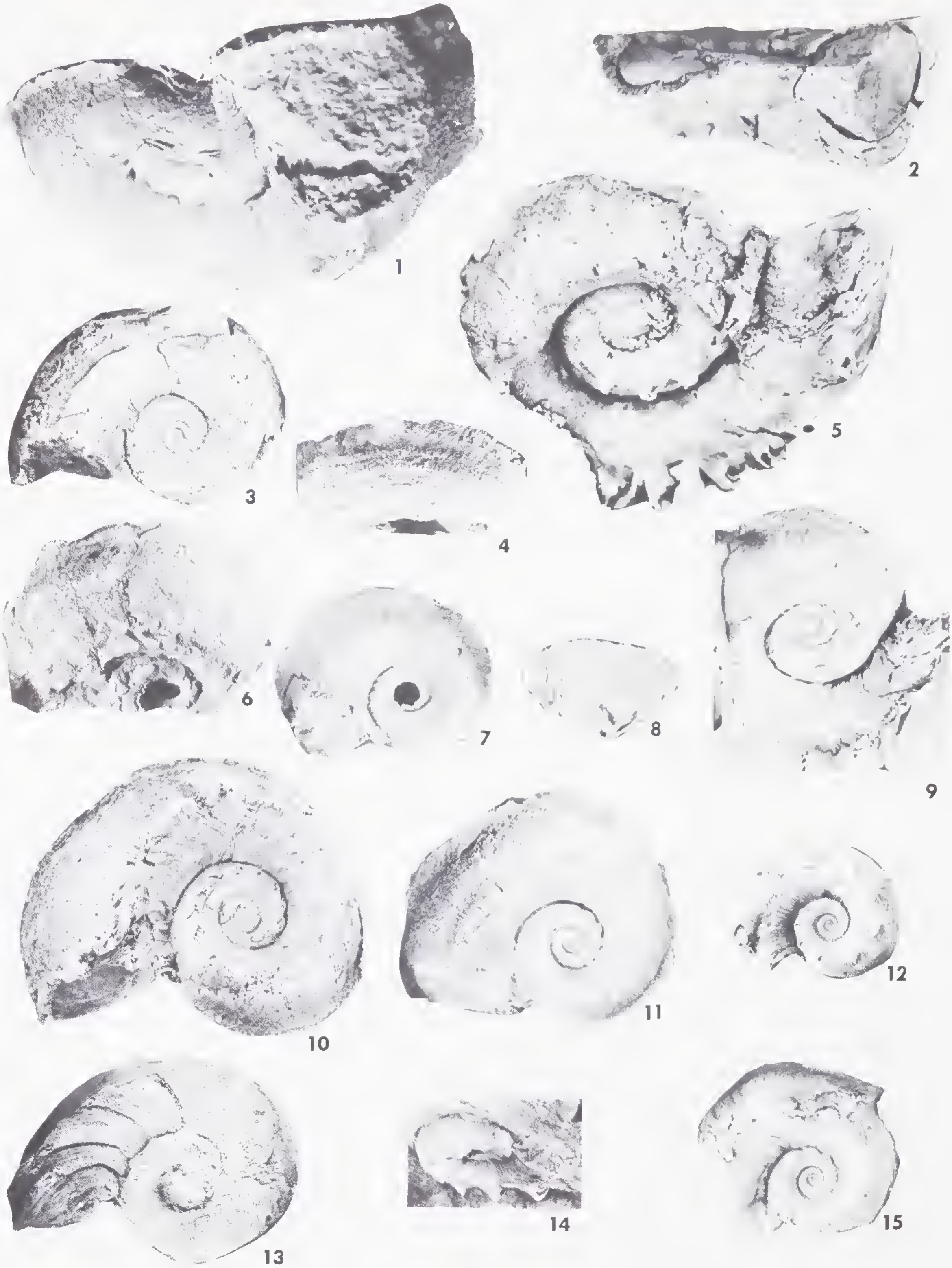
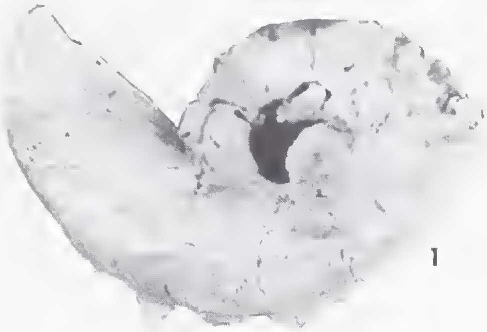


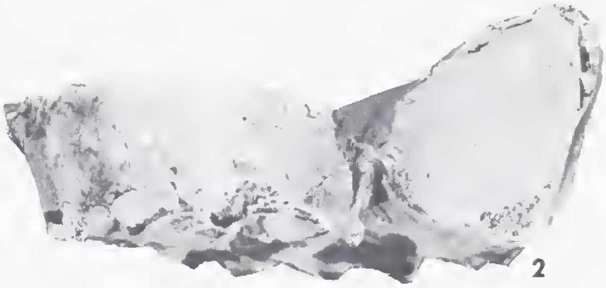
Figure 1—A plot of shell width on the abscissa versus the width of the umbilicus divided by the depth of the umbilicus, a sensitive measure of the degree of hyperstrophicity. Note that in the larger individuals the cloud of points divides into two groups of about equal numbers. This is considered as strong evidence in favour of sexual dimorphism.


1
2
3
4
5
6
7
8
9

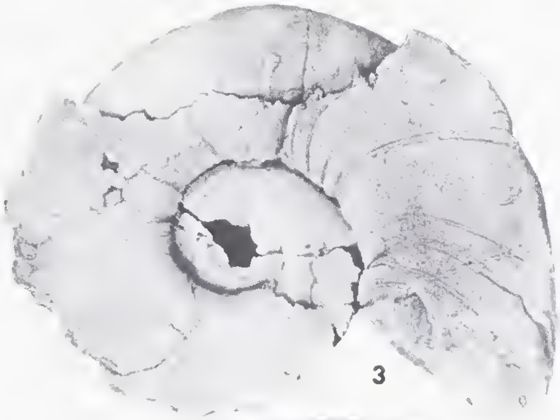

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15



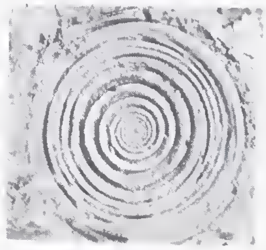
1



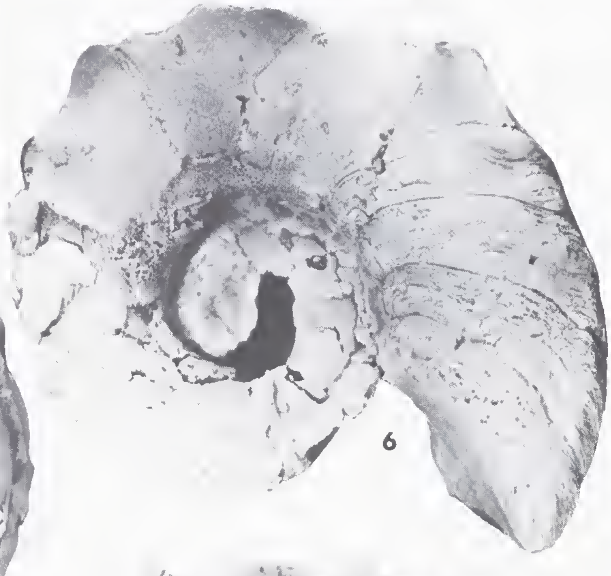
2



3

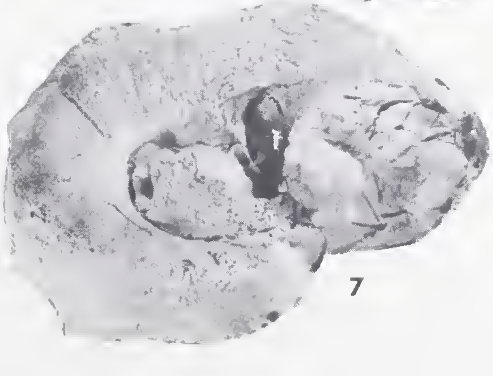


4



6

5



7

8


1
2
3
4
5
6
7


1
2
3
4
5
6
7
8
9
10
11


1
2
3
4
5
6
7
8


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17