

# A new Silurian gastropod from Wisconsin and the ecology of uncoiling in Palaeozoic gastropods

JOHN S. PEEL



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*Kiviasukkaan nelsonae* gen. et sp. nov. is described from Niagaran dolomites (middle? Silurian) of Wisconsin, U.S.A., and tentatively assigned to the Trochonematacea. The slight tendency to uncoil in the final whorl promotes a discussion of other uncoiled and open coiled Palaeozoic gastropods and their modes of life. It is proposed that Palaeozoic gastropods were more diverse in their feeding habits than comparison with extant archaeogastropods would suggest.

John S. Peel, *Grønlands Geologiske Undersøgelse, Øster Voldgade 10, DK-1350 København K, Denmark. June 24th, 1975.*

The close correspondence between the form of the molluscan shell and an unvarying logarithmic spiral has been recognised for many years (Moseley, 1838; Thompson, 1942; Raup, 1966). Such a relationship is clearly exemplified within the Gastropoda where apparently uniform logarithmic expansion forms the familiar regular spires of *Turritella*, *Trochus* and *Helix*. In detail, however, even *Turritella* shows slight allometry during growth (Andrews, 1974) while many gastropods show greater departures from the single logarithmic spiral in response to the changing functional requirements of the developing individual (Gould, 1969a; Peel, 1974).

In this paper a new gastropod which becomes slightly uncoiled during the last whorl is described from the Niagaran (middle? Silurian) of Wisconsin. An attempt is made to assess the significance of this change, and the better developed uncoiling and open coiling seen in other Palaeozoic gastropods, in terms of mode of life. A recent functional study of the present day *Vermicularia spirata* by Gould (1969 b) provides a model for this discussion.

## A new Silurian gastropod from Wisconsin

*Kiviasukkaan nelsonae* gen. et sp. nov., described below, is based upon a single specimen, as is the case with many other Palaeozoic

gastropod taxa. However, the combination of good preservation and unusual morphology is deemed sufficient to justify naming it.

It is difficult to satisfactorily refer *Kiviasukkaan* to a higher classificatory group. The nature of the whorl profile with a reduced, graduate, spire passing by way of an angular periphery onto an inflated base suggests comparison with some members of the pleurotomariacean subfamily Raphistomatinae Koken, 1896. However, genera placed here by Knight et al. (1960) are usually anomphalous and are readily distinguished by the deep anal sinus which culminates in a slit generating a selenizone at the whorl periphery. *Kiviasukkaan* is phanerocephalous and lacks a slit and consequent selenizone, although slight prosocyrct curvature of the suborthocone growth lines on the lower whorl surface below the peripheral angulation suggests a weak emargination.

The subsutural shoulder and peripheral angulation typical of the pleurotomariaceans *Lophospira* Whitfield, 1886 and *Loxoplocus* Fischer, 1885 seem to find parallels in *Kiviasukkaan*. In addition, the latter is also comparable to *Kiviasukkaan* in showing a definite tendency towards uncoiling with increased growth; a result of progressive increase in the rate of whorl translation (Raup, 1966). However, as with members of the Raphistomatinae, *Lophospira* and *Loxoplocus*, together with other forms assigned to the Lophospiridae Wenz,

1938 by Knight et al. (1960) and Peel (1975a), are readily delimited from *Kiviasukkaan* by their distinct anal emarginations.

An incipient sinus located on a peripheral angulation, of the type seen in *Kiviasukkaan*, is often characteristic of euomphalacean archaeogastropods. However, no members of the superfamily, as currently understood (Knight et al., 1960), exhibit the strongly angulated, turbiniform shell of *Kiviasukkaan*. A somewhat comparable lack of whorl contact is seen in *Serpulospira* Cossmann, 1916 and *Nevadaspira* Yochelson, 1971.

*Kiviasukkaan* resembles *Globonema* Wenz, 1938 from the Upper Ordovician of Norway which was originally proposed as a subgenus of *Trochonema* Salter, 1859 but transferred by Knight et al. (1960) to the trochinid family Holopeidae Wenz, 1938. Both genera have shouldered profiles and angular peripheries associated with a prominent circumbilical angulation. Similar circumbilical structures are well developed in other holopeids, notably in *Straparollina* Billings, 1865 from the Lower Ordovician, and *Rachospira* Perner, 1903 from the Upper Silurian of Czechoslovakia. However, both of these genera, and to some extent *Globonema*, have convex, somewhat globose, whorls which lack the gradate profile and ontogenetic uncoiling characteristic of *Kiviasukkaan*.

A circumbilical angulation of the type seen in *Kiviasukkaan* commonly suggests the presence of an anterior notch on the basal lip which might be interpreted as indicating affinity with the Caenogastropoda (Cox, 1959). In caenogastropods an anterior notch reflects the development of a siphon in association with the acquisition of a single monopectinate ctenidium and a more efficient system of respiration. However, archaeogastropods with bipectinate ctenidia are by far the most dominant gastropod Order in the Lower Palaeozoic where caenogastropods are principally represented by high spired loxonemataceans and subulitaceans. Globose caenogastropods are rare prior to the Upper Palaeozoic while strongly angulated shells of the type seen in *Kiviasukkaan* are absent.

The balance of available evidence supports closest comparison of *Kiviasukkaan* with

members of the Trochonematacea Zittel, 1895, to which superfamily tentative assignment is made. However, it cannot be stated that this placement is other than a matter of temporary convenience; a more secure family assignment must await future study. Knight et al. (1960) commented that a miscellany of gastropods have previously been included within this superfamily but they reduced this number to include only genera with somewhat angular whorl profiles and shallow emarginations. Ordovician and Silurian trochonemataceans closely resemble *Lophospira* and *Loxoplocus*, discussed above, but may be distinguished by their shallow emarginations, in similar fashion to *Kiviasukkaan*. In addition, the relatively high spired trochonematacean *Eunema* Salter, 1859 is comparable to *Kiviasukkaan* in showing a similar degree of uncoiling during ontogeny.

#### *Kiviasukkaan* gen. nov.

*Type species.* — *Kiviasukkaan nelsonae* gen. et sp. nov.

*Derivation of name.* — Finnish, "stone-dweller".

*Diagnosis.* — Moderately large, narrowly phaneromphalous gastropod with about four whorls which show a slight increase in the rate of whorl translation during ontogeny such that the apertural portion of the final whorl is not in contact with the previous whorl. Whorl profile divided into a flattened, yet shouldered, upper whorl surface and a convex base by an acute peripheral angulation at about five sixths of whorl height. Aperture sub-circular at maturity with a weak anterior sinus emphasised by the circumbilical angulation.

*Discussion.* — *Kiviasukkaan* is distinguished from *Trochonema* by the shape of the whorl profile below the periphery. In the latter genus a spiral angulation of the same degree of prominence as the subsutural shoulder and peripheral angulation delimits a vertical outer whorl surface from the flattened base. In *Kiviasukkaan* the lower whorl surface is shallowly convex, without the spiral angulation,

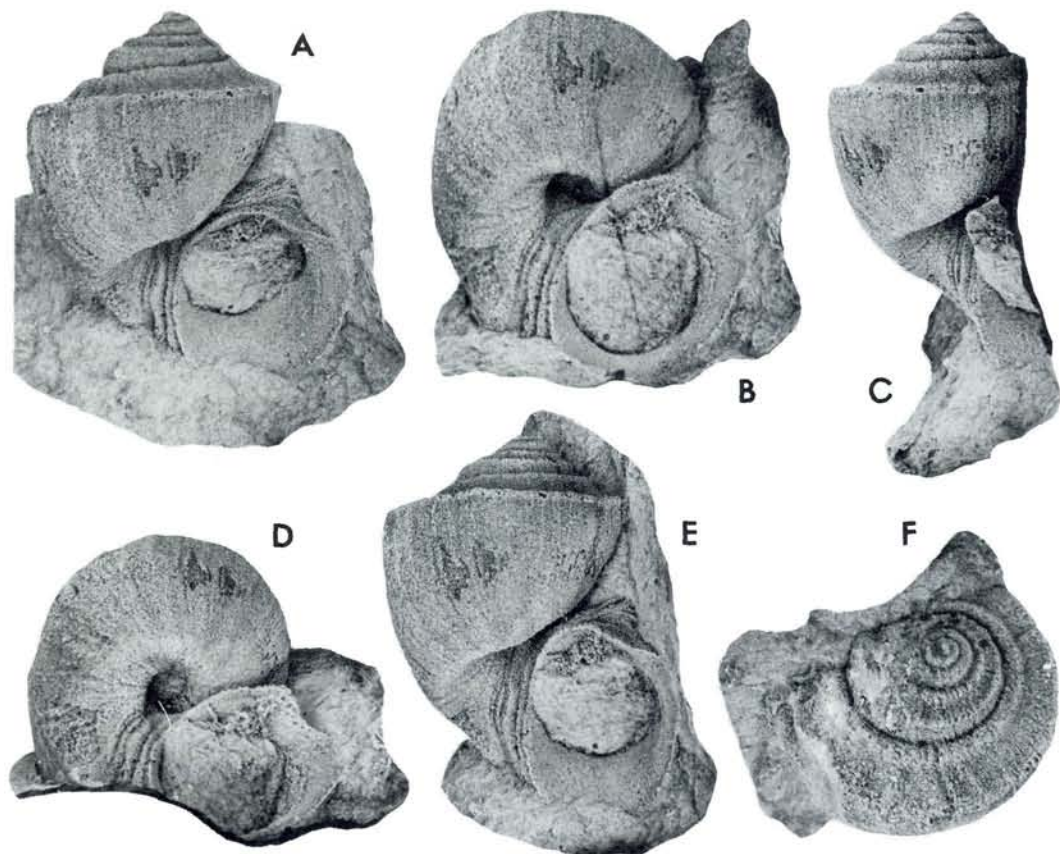


Fig. 1. *Kiviasukkaan nelsonae* gen. et sp. nov. Latex impression of external mould of holotype, GPM 10912, X 1.3 A. Lateral view showing increased sutural slope of penultimate whorl produced by increased rate of whorl translation; latex background to spire cut away. B. Oblique umbilical view showing circumbilical angu-

lation. The shallow invagination in the outer lip is spurious. C. Lateral view; right side of mould imperfect. D. Axial view of umbilicus. E. Slightly oblique lateral view showing narrow gap between final and penultimate whorls. F. Oblique view of upper whorl surface.

prior to passing over the circumbilical angulation into the umbilicus. *Trochonemopsis* Meek, 1872 has a higher rate of whorl expansion than *Trochonema*, with the subsutural shoulder reduced and the lowest of the remaining spiral angulations forming the periphery. It may be similarly delimited from *Kiviasukkaan*.

*Eunema* Salter, 1859 is also similar to *Trochonema* in terms of whorl profile but is higher spired. A slight tendency to increase the rate of whorl translation in the later whorls (Knight, 1941) reflects the same trend in *Kiviasukkaan*.

*Proturritella* Koken, 1889 and other, Upper Palaeozoic, presumed trochonematids differ from *Kiviasukkaan* in possessing prominent spiral or reticulate ornamentation.

*Kiviasukkaan nelsonae* gen. et sp. nov.  
Fig. 1 A-F.

*Derivation of name.*— In honour of Dr. Katherine G. Nelson, University of Wisconsin at Milwaukee.

*Material.* — GPM 10912, the holotype and only known specimen, in the collection of the Greene Paleontological Museum, University of Wisconsin at Milwaukee. The specimen is preserved as a mould of the shell exterior.

*Horizon and locality.* — Niagaran dolomite, probably of the Manistique Formation (late Llandovery – Wenlock) at Ashford, Wisconsin, U. S. A.

*Diagnosis.* – As for genus.

*Description.* – Type species of *Kiviasukkaan* with about four whorls. Protoconch unknown; early whorls seemingly with more rounded upper whorl surface than the last two. Profile of later whorls divided into upper and lower surfaces by a prominent angulation at about five sixths of whorl height. Upper whorl surface of final whorl convex, shouldered, immediately below suture with previous whorl; becoming concave towards periphery such that ultimately flat, perpendicular to axis of coiling. Lower whorl surface uniformly, shallowly convex between periphery and the circumbilical angulation, thereafter curving rapidly into the narrowly phaneromphalous umbilicus. In early whorls, whorl embracement is just below the peripheral angulation. In final whorl, rate of whorl translation increasing such that embracement is successively lower on the previous whorl; the whorls no longer in contact at the latest known growth stage (aperture of holotype). Sutural slope and depth of suture increasing during final whorl until whorls no longer in contact. Aperture subcircular at latest, uncoiled, growth stage; seemingly with more angular base in earlier whorls. Outer lip near othocline with some suggestion of a weak emargination at the peripheral angulation; a shallow anterior sinus located on the circumbilical angulation. Ornamentation of coarse growth lines, which may be somewhat lamellose near the aperture, crossing the spiral angulations. Shell thick, structure unknown.

*Discussion.* – *Kiviasukkaan nelsonae* most closely resembles *Globonema kokeni* Wenz, 1938 from the Upper Ordovician of Norway but may be distinguished by having the peripheral angulation located higher on the whorl. In addition, the upper whorl surface in *Globonema* is convex, with the increased inflation resulting in a less prominent shoulder to the whorl than in *Kiviasukkaan nelsonae*.

The change in the nature of coiling in *Kiviasukkaan nelsonae* is partly obscured in the holotype as a result of the state of preservation. The impression of the last half whorl, with the exception of the aperture, is not preserved in the external mould and consequently appears to be buried in the matrix in the illustrated latex impression. However, in aper-

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tual view (fig. 1A), steepening of the sutural slope indicates an increase in the rate of whorl translation, culminating in separation of the whorl at the preserved aperture (fig. 1A, E). In addition, there is a clear increase in the proportional distance between successive whorl peripheries, when measured between the aperture and penultimate whorl as against between the penultimate and antipenultimate whorls (fig. 1A).

The preserved aperture is sub-circular (fig. 1A, B, E) but it is difficult to conclusively demonstrate the shape of the aperture in earlier whorls. However, the prominent circumbilical angulation on the base of the whorl (fig. 1B) indicates some degree of anterior – posterior elongation. It is probable that with uncoiling of the whorl, and consequent loss of impression of the previous whorl, the aperture assumed a sub-circular form. Comparable modification of whorl shape after uncoiling is documented by Gould (1969b) in *Vermicularia spirata*.

*Dimensions of holotype.* – Height = 37 mm, width = 34 mm.

### Uncoiling and open coiling in Palaeozoic gastropods

The degree of uncoiling in *Kiviasukkaan* is slight when comparison is made with the many other Palaeozoic gastropods characterised by partial or complete separation of the whorls during growth. In a review of some of these genera Yochelson (1971) discriminated between the terms 'uncoiled' and 'open coiled' in the description of the nature of whorl separation. The manner in which some shells, for example *Vermicularia*, change their parameters of shell growth during ontogeny such that later whorls deviate from the pattern of earlier whorls and cease to be in contact with each other was termed 'uncoiling'.

In 'open coiled' shells, for example *Nevadaspira* Yochelson, 1971, the shell parameters remain essentially constant during growth but the cone of the gastropod shell is too narrow to allow the whorls to touch. Open coiling results from the combination of several fac-

tors, of which the rate of increase in the width of the shell cone or tube is only one. Other important parameters are the rate of whorl translation, namely the rate of helical coiling in the dimension of the coiling axis, and the position of the whorl relative to the axis of coiling, a measure in the plane to which the coiling axis is normal of the rate at which the whorl moves with increased growth away from the axis (Raup, 1966).

In such terminology the shell of *Kiviasukkaan* would be properly described as uncoiled during the final growth stage.

While discussing the mode of life of *Nevadaspira*, Yochelson (1971) observed that the open coiled shell was not at all suited to the normal, mobile, benthonic existence typical of most marine gastropods and concluded that the gastropod was sedentary. Gould (1969b) discussed coiling in a present day *Vermicularia* from Bermuda noting that uncoiling is typically developed after the regularly coiled juvenile becomes associated with, and ultimately attached to a substrate. Thus, arguments have been advanced to suggest that both types of coiling in which contact between successive whorls is lacking may be the result of assumption of a sedentary habit. These arguments are further supported by the observation of Gould (1968) that unattached specimens of *Vermicularia spirata* in an atypical, argillaceous, environment lacking substrates in a Bermudan pond show uncoiling in less than 1 per cent of the examined large empty shells.

On the basis of the studies of Gould and Yochelson it would appear quite reasonable to suggest that many uncoiled or open coiled Palaeozoic gastropods may also have been sedentary, although there is no reason to assume that all such coiling forms are indicative of a similar mode of life. Indeed, the variety of geometric form exhibited by gastropods with original or subsequent separation of the whorls in itself argues against such an interpretation.

Unfortunately, little is currently known about the feeding habits of Palaeozoic gastropods. Most are grouped within the Class Archaeogastropoda whose recent members are herbivorous. Caenogastropods are principally represented by high spired loxonemataceans and subulitaceans, with a few minor groups

of uncertain affinity in the Upper Palaeozoic.

It has generally been presumed that Palaeozoic gastropods were dominantly herbivores, as a result of comparison with recent archaeogastropods. However, the post Palaeozoic expansion of caenogastropods and the appearance of other gastropod groups may have produced some diminution in the ecologic diversity of archaeogastropods as a result of competition in habitats at the periphery of the tolerance limits imposed on the latter by their less efficient ctenidia.

It is suggested that while the majority of Palaeozoic gastropods, particularly the abundant and widely distributed taxa, were probably herbivorous, a significant proportion developed other modes of feeding.

In this context the adaptation by some platycerataceans to coprophagous feeding is widely accepted (Bowsher, 1955). In addition, Yochelson (1971) proposed that the open coiled *Nevadaspira* was a ciliary feeder and this feeding habit can also be suggested for other sedentary forms and some of the many high spired gastropods common in Ordovician and younger strata. Evidence of a carnivorous mode of life has not been recognised although Boucot (1975, p. 239) hinted that such forms may be present in the Palaeozoic. It should be noted that Carriker & Yochelson (1968) and Sohl (1969) reviewed the occurrence of shell borings in Palaeozoic invertebrates and concluded that there was little evidence to justify referring these to attacks by carnivorous gastropods. However, the elimination of this single specialised feeding pattern need not preclude the presence of other carnivorous habits. It is a comparatively small step from sedentary coprophagous feeding on echinoderm calices to more active benthic scavenging. A number of platycerataceans not commonly associated with echinoderms, for example some species of *Cyclonema* Hall, 1852, may have lived in this way. Again, no major distance need separate such a mobile scavenging existence from an active carnivorous role, perhaps feeding on colonial organisms in similar fashion to recent cowries feeding on ascidians.

While recognising the limitations placed upon ecological interpretations, it is possib-

le to assemble most Palaeozoic uncoiled or open coiled gastropods into four loose morphological categories. The first comprises low spired shells which may vary from orthostrophic to hyperstrophic in their coiling pattern. Here are found *Ecculiomphalus* Portlock, 1843 and many of the gastropods discussed by Yochelson (1971) in connection with *Nevadaspira*. A second group included high and moderately high spired gastropods which become uncoiled during ontogeny principally as a result of increase in the rate of whorl translation. Genera in this group include *Loxoplocus*, *Semitubina* Cossmann, 1918, *Helmithozyga* Knight, 1930 and possibly *Eunema*. *Platyceras* (*Platyceras*) Conrad, 1840 and *P.* (*Orthonychia*) Hall, 1843 form a small, clearly differentiated, group on account of their coprophagous mode of life on the calices of fixed echinoderms. The fourth group, to which *Kiviasukkaan* may be assigned, includes a miscellany of unrelated gastropods characterised by changes in coiling pattern during the last stages of growth.

In addition to *Ecculiomphalus* from the Ordovician and Silurian (fig. 2), the currently recognised group of low spired, open and uncoiled gastropods includes *Lytospira* Koken, 1896 from the Ordovician and Silurian, *Nevadaspira* and *Straparollus* (*Sinistrispira*) Jhaveri, 1969 from the Devonian, *Straparollus* (*Serpulospira*) Cossmann, 1916 from the Devonian and Carboniferous, and *Phanerotinus* Sowerby, 1844 from the Carboniferous. All are characterised by a narrow, tube like shell with partial or complete separation of the whorls. Yochelson (1971) discussed the mode of life of *Nevadaspira* and, as noted above, concluded that the high degree of whorl separation

precluded a mobile benthonic existence. He suggested some sort of analogy with vermetids and proposed that in a functional sense *Nevadaspira* may have been a ciliary feeding 'sedentary worm'. Hyperstrophic, open coiling was interpreted as a natural consequence of growth of the dextrally coiled, sedentary animal on a muddy substratum.

Support for this 'sedentary worm' functional morphology is in fact supplied by comparison with a late Cretaceous serpulid worm. *Ditrupa* (*Tertraditrupa*) *canteriata* (Hagenow, 1840) has a narrow, tube like shell which is coiled into a wide, open, hyperstrophic spiral in similar fashion to *Nevadaspira* and in response to its habitation of a soft substratum (N. Svendsen, personal communication, 1975).

The model proposed for *Nevadaspira* can easily be applied to most of the above mentioned genera. *S.* (*Serpulospira*) appears different because the shell is normally orthostrophic and coiled such that the early whorls are in contact. However, Linsley (1968) has demonstrated the extreme variability of uncoiling within the subgenus which itself tends to support the interpretation of a sedentary life habit. It is possible that the difference in coiling from that seen in the other genera discussed above reflects association with a substratum of different, probably harder, type. Indeed, the more normal coiling of the early whorls may suggest the presence of a mobile juvenile stage as described by Gould (1969b) in the high spired *Vermicularia spirata*. The pleurotomariacean *Calairops* Whitfield, 1886 from the Lower Ordovician, and possible *Dirhacopea* Ulrich & Bridge, 1931 from the Upper Cambrian and Lower Ordovician, may have had a similar mode of life to *S.* (*Serpulospira*).

A number of other low spired, open coiled gastropods may possibly be interpreted in a comparable way to the above mentioned genera. In this category are included *Macluritella* Kirk, 1927 from the Lower Ordovician, *Meandrella* Perner, 1903 from the Lower Devonian, *Pseudotubina* Koken, 1896 and *Colubrella* Koken, 1896 from the Triassic. These genera are distinguished from the previously discussed forms by their greater rate of whorl expansion. The implication of this difference in terms of anatomy and functional morphology

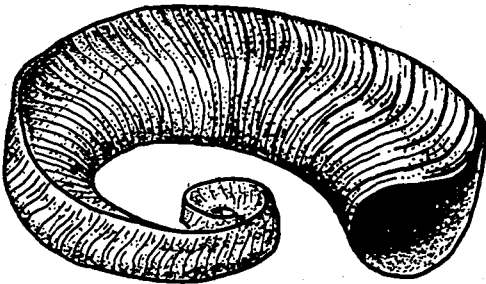


Fig. 2. *Ecculiomphalus*, oblique view showing hyperstrophic open coiling, X 1.0.

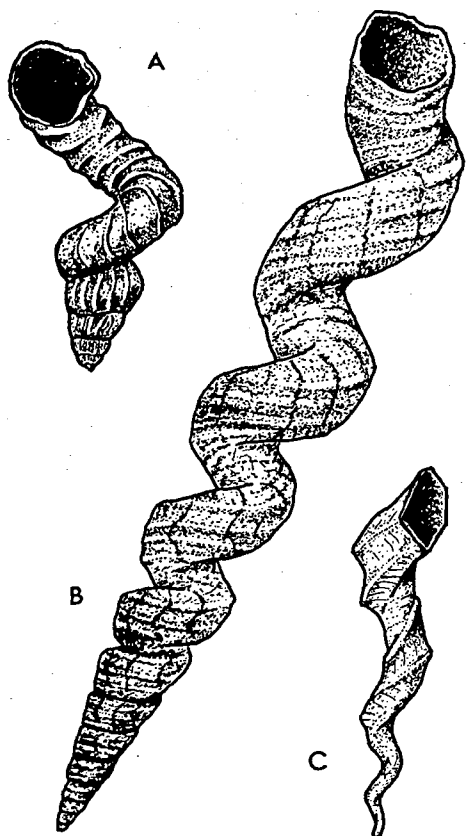


Fig. 3 A. *Helminthozyga*, a tiny uncoiled form from the Carboniferous, X 16. B. *Vermicularia spirata*, a present day uncoiled ciliary feeder, X 3. C. *Loxoplocus*, an uncoiled Ordovician-Silurian pleurotomariacean; early whorls not preserved, X 0.8.

is not known. However, Andrews (1974) recently argued that the narrow, slowly expanding, tube like shell of the many whorled *Turritella* or *Vermicularia* developed partly in response to elongation of the gill associated with the assumption of ciliary feeding. If this is accepted, some support is gained for the interpretation of members of the *Ecculionphalus* group as ciliary feeders since narrow, slowly expanding whorls are characteristically present. On the other hand, the same argument should then be invoked to suggest that the more rapidly expanding forms enumerated above were probably not ciliary feeders. The issue is beyond settlement. However, it is possible that the rapidly expanding open coiled shell of genera of the *Meandrella* group may not have been unduly inconvenient to a mo-

bile benthonic animal. If the near planispiral shells were carried by the gastropod in bellerophonacean fashion (the axis of coiling transverse to the direction of movement and parallel to the substratum; the aperture anterior) most of the weight of the body mass would be concentrated in the last fraction of the final whorl, allowing adequate control of the shell during movement. In this respect, members of the group resemble gastropods currently placed in group four, discussed below.

The second group of uncoiled gastropods comprises relatively high spired forms morphologically reminiscent of *Vermicularia spirata* (fig. 3B). Included here are *Loxoplocus* from the Ordovician and Silurian, *Semitubina* from the Lower Devonian and *Helminthozyga* from the Carboniferous (fig. 3). The various genera can be considered to be sedentary ciliary feeders by analogy with the similarly uncoiled *Vermicularia* (Gould, 1968; 1969b). The recent genus commonly has attachment scars on the whorls as a result of occasional cementation to supporting substrates, although these may be expressed only weakly on the shell. Attachment scars of this type do not appear to have been recorded in the Palaeozoic analogues but this could partly be an artifact of preservation. It is also quite possible that such supporting cementation is a consequence of the relatively long and narrow, irregularly coiled shell of *Vermicularia*. The Palaeozoic species appear to have shorter, more regularly coiled shells in which the tube occupied by the gastropod animal is of greater width. The greater regularity of the uncoiled portion of the shell may indicate that a high degree of support by cementation was not required by the more robust Palaeozoic genera. It should also be noted in this context that Gould (1968) has described unattached specimens of *Vermicularia spirata*, although individuals in this atypical mud dwelling population generally lacked indications of uncoiling.

The increased width of the gastropod tube of the Palaeozoic forms when compared to *Vermicularia* may be construed as an argument against the interpretation of ciliary feeding, as discussed above with reference to the

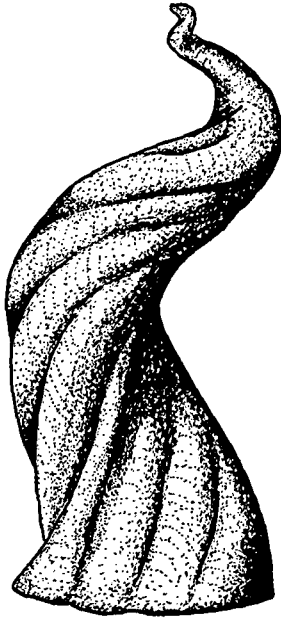


Fig. 4. *Platyceras* (*Orthonychia*), an open or uncoiled coprophagous dweller on echinoderm calices, X 1.

*Meandrella* group of low spired gastropods. However, it should be remembered that *Loxoplocus* and *Semitubina* were probably archaeogastropods with bipectinate ctenidia, as distinct to the monopectinate ctenidia of *Turritella* and *Vermicularia*. The effects of this difference in the structure or even number of ctenidia upon the form of a mantle cavity adapted to ciliary feeding are perhaps impossible to estimate. It is certainly possible that another arrangement of ctenidia and mantle cavity was required and that this was at variance with the elongate ctenidium and long narrow mantle cavity of the recent species. Knight et al. (1960) considered *Helminthozyga* to be a caenogastropod and, as such, the tiny genus probably had a single monopectinate ctenidium.

The low degree of uncoiling, relative to *Vermicularia*, observed in *Helminthozyga* and some species of *Loxoplocus* produces some degree of similarity to members of group three, discussed below. Orientation of the two groups during life is markedly different, however. In *Vermicularia* and members of the second group the apex points downwards and

growth is upwards (fig. 3). In *Platyceras* (*Orthonychia*), group three, the apex is uppermost with the aperture opening downwards (fig. 4). Inversion of *Helminthozyga* does not produce a form comparable to *P.* (*Orthonychia*) since the aperture in the former opens laterally, nearly perpendicular to the axis of coiling. In *P.* (*Orthonychia*) the aperture faces downwards, in a direction parallel to the axis of coiling, as a consequence of the limpetoid mode of life.

Gould (1969b) proposed that uncoiling in *Vermicularia* was an adaptation towards rapid growth along the axis of coiling. He quoted a personal communication from W. J. Clench suggesting that the loose coiling of certain siliquariids living in sponges enabled the gastropods to keep up with the growth of their host. The uncoiling in *Vermicularia*, and probably in the Palaeozoic genera also, served to provide early access to the rain of detrital food particles and also quick elevation above bottom sediment which may have clogged the delicate ciliary mechanism (Gould, 1969b, p. 433). The latter function may have been particularly important to the Palaeozoic aspidobranchs since this type of ctenidial structure is especially susceptible to clogging (Yonge, 1947).

Constituent genera of the family Platyceratae Hall, 1859 commonly show severe modifications in shell form as a result of their inferred coprophagous mode of life on the calices of fixed echinoderms (Bowsher, 1955). Individual shells are not attached to the calyx but a somewhat limpetoid, sedentary, mode of life may be assumed over the anal area of the echinoderm. In such a situation a strongly coiled shell with marked inequalities in the rate of growth between the inner and outer lips is apparently sometimes less efficient than a cap shaped shell with subequal growth at all points on the periphery. Consequently, the rate of whorl translation is greatly increased to produce the twisted cone of *Platyceras* (*Orthonychia*) (fig. 4). Alternatively, a high rate of whorl expansion results in the production of the lower cone of *P.* (*Platyceras*). Regularly coiled, naticiform, shells with irregular peristomial margins indicative of the coprophagous habit do occur, however,



possibly suggesting a degree of specificity between certain of the shell forms and the respective hosts.

The fourth category of shells showing a partial lack of whorl contact is undoubtedly a conglomeration of forms and functional adaptations. However, all are characterised by uncoiling only in the latest growth stages. In the bellerophotacean *Charalostrepis* Knight, 1948 the last whorl uncoils yet the laterally compressed whorl shows no pronounced change in shape during this last half whorl. The unrelated genus *Grandostoma* Horný, 1962 also uncoils during the last half whorl but in this case the aperture is strongly expanded to form a bell shaped final growth stage (fig. 5).

The Silurian or Devonian genera *Scoliostoma* Braun, 1838, *Codonocheilus* Whiteaves, 1884 and *Brilonella* Kayser, 1873 have moderately high spired shells in which the last half whorl diverges strongly from the regular pattern of the earlier whorls.

The major feature relating these diverse modifications is the time of their appearance, the coiling changes being confined to the late stages of growth. Yochelson (1971) referred to a number of features of this kind as gerontic but it is probably better to regard the deviations as features of maturity developed in response to the differing functional requirements of the adult. Subsequent reduction in the rate of shell growth might cause the shell to become rugose or thickened, features commonly associated with gerontism, but this should not be allowed to mask the possible functional significance of the uncoiling.

In *Grandostoma* (fig. 5) the shell expands strongly in the later growth stages to produce a bell shaped final growth stage with explanate margins. The adaptation is probably associated with life on a soft substratum (Peel, 1974; 1975b). The high rate of whorl expansion results in concentration of the soft parts in the final quarter whorl, in comparable fashion to members of the low spired *Meandrella* group discussed above. Uncoiling consequently has an insignificant effect on shell stability in *Grandostoma* when considered relative to the functional needs of the adult. Indeed, carried to a logical extreme, the pro-

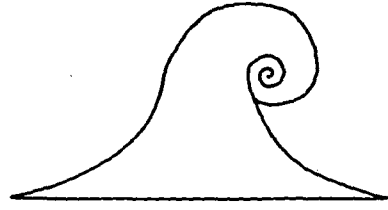


Fig. 5. *Grandostoma*, schematic lateral profile showing bell shaped form and explanate aperture of this Ordovician bellerophontacean, X 1.

cess parallels that seen in recent fissurellacean limpets where the coiled protoconch is strongly differentiated from the widely expanded, cap shaped shell of the adult (Boutan, 1885).

In *Codonocheilus* (fig. 6) the change in orientation probably enabled the moderately high spired, yet wide, shell to be carried with the axis of coiling parallel to the direction of movement. A similar function may be attributed to the uncoiling in *Kiviasukkaan*. This advantageous orientation is typical of many caenogastropods and is in part related to the development of an anterior siphon and efficient mantle cavity with a pectinibranch ctenidium. Anterior siphons are not developed in archaeogastropods, which comprise the great majority of Palaeozoic gastropods, where the ctenidia are aspidobranch. As a result of the mantle cavity structure, archaeogastropod shells are generally oriented with the axis of coiling strongly oblique to the direction of movement of the animal. In consequence of this orientation, high spired shells are not developed by recent archaeogastropods due to their instability in the relatively high energy conditions to which most archaeogastropods

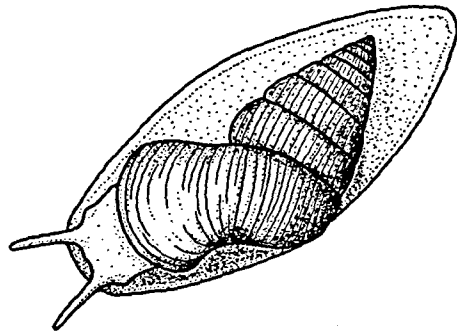


Fig. 6. *Codonocheilus* from the Silurian of Canada, restored to show shell orientation after uncoiling, X 4.

are restricted by the structure of their ctenidia (Yonge, 1947; Vermeij, 1971). The change in coiling direction during the last whorl in *Codonocheilus* conceivably overcomes this problem by reorienting the mantle cavity relative to the earlier whorls, and the early whorls relative to the direction of movement of the gastropod.

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### Dansk sammendrag

Gastropoden *Kiviasukkaan nelsonae* n. g. og n. sp. af mellem? Silur alder fra Niagara dolomitterne i Wisconsin, U.S.A., beskrives og placeres foreløbigt i Trochomenatacea. Foranlediget af at skallens sidste vinding har en svag udrullet tendens, diskuteres andre palæozoiske gastropoder, som dels er snoet i en åben spiral dels ikke er oprullede, ligesom deres palæoøkologi omtales. Det foreslås, at palæozoiske gastropoder var mere diverse i deres fødevaner end sammenligninger med recente archæogastropoder lader formode.

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