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Survey of Paleozoic gastropods possibly belonging to the subclass Opisthobranchia

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(Mit 1 Tafel)

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Abstract

Characteristics of larval and mature shell can be used to distinguish opisthobranchs from prosobranchs, but separation is not always clear cut. Nevertheless, for more than a century a few late Paleozoic species have been assigned to opisthobranchs.

Currently *Donaldina*, *Platyconcha*, *Streptacis* and *Acteonina*, all genera with Paleozoic type-species are placed in the subclass. The first three are high-spired forms having a larval shell deviating from the mature axis of coiling. They may be allied to pyramidellaceans, but data on early whorls is so limited and the genera so poorly understood that neither opisthobranch superfamily nor even possible opisthobranch relationships are confidently determined.

Acteonia, first described from the Lower Carboniferous of Belgium, is accepted as an opisthobranch, and several Triassic species are included in the genus. Spiral grooves on the shell are morphologic feature indicative of this placement. *Girtyspira minuta* (STEVENS) from the Middle Pennsylvanian of St. Louis, Missouri, has been investigated with Scanning Electron Microscope. It shows a deviated larval shell and a narrow but distinct sutural ramp. *Girtyspira* is transferred from the subulitaceans to the opisthobranchs. *Girtyspira fusiformis* (DE KONINCK) from lower Lower Carboniferous beds of Belgian, is the oldest recognized opisthobranch. No other Paleozoic subulitacean gastropods are considered to be opisthobranchs.

Zusammenfassung

Seit über hundert Jahren werden einige jungpaläozoische Gastropodenarten als Opisthobranchier aufgefaßt, obwohl die Zuordnung aufgrund der Kennzeichen von Larvalgehäuse und adultem Gehäuse nicht immer sicher ist.

Die Gattungen *Donaldina*, *Platyconcha*, *Streptacis* und *Acteonina* haben paläozoische Typusarten. Die drei ersteren sind hochgetürmt und besitzen ein Larvalgehäuse, dessen Achse anders orientiert ist als die des adulten Gehäuses. Die Gattungen sind möglicherweise zu den Pyramidellaceen zu stellen. Ihr Umfang und ihre Morphologie sind aber noch ungenügend bekannt. *Acteonina*, erstmals aus dem Unterkarbon von Belgien beschrieben, gehört mit Sicherheit zu den Opisthobranchiern. Alle Vertreter dieser Gattung,

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in die auch einige triassische Arten aufgenommen wurden, besitzen eine Grübchenskulptur.

Gyrtispira minuta (STEVENS) aus dem mittleren Pennsylvanien von St. Louis, Missouri, wurde mit dem SEM untersucht. Die Arten zeigen ein etwas schiefes Larvalgehäuse und eine enge, aber deutliche Suturrampe. Die Gattung *Gyrtispira* wird daher nicht wie bisher als Vertreter der Subulitaceen aufgefaßt, sondern als Opisthobranchier. *Gyrtispira fusiformis* (DE KONINCK) aus dem Unterkarbon von Belgien ist die älteste bekannte opisthobranche Schnecke.

Introduction

The class Gastropoda is defined by reference to soft parts, not the shell (COX, 1960, p. 186). The opisthobranchs constitute a varied gastropod group of about 400 genera commonly placed at or below the subclass level (TAYLOR & SOHL, 1962). Definitive structures separating opisthobranchs and pulmonates from prosobranch gastropods include more or less complete euthyneury or untwisting of the nervous system, hermaphroditism, and an anus that opens to the right at the inner end of the mantle cavity, as well as other morphologic features of the soft parts.

Clearly this definition is unsatisfactory for paleontologists. Further, many of the living opisthobranchs inferred to be advanced forms have reduced shells imbedded within the mantle. Characteristically, these shells are thinner than those of non-opisthobranch gastropods, and their fossil record is both sporadic and poor. Still other living opisthobranchs, as "the nudibranchs", have no hard parts and have no known fossil record.

Among the opisthobranchs some living Cephalaspidea and Pyramidellacea are heavy-shelled. From an anatomical standpoint these are nearly transitional between prosobranches and reduced-shell to shell-less opisthobranchs. Granting that there is no conclusive way to identify a fossil opisthobranch, various morphologic features of the hard parts allow one to assign material to the subclass with varying degrees of confidence. It is appropriate to inquire when in a geologic sense, fossil opisthobranchs can first be recognized in the fossil record.

Our aim is not to trace the evolutionary history of the subclass, but simply to record a few general observations and new data derived from one Paleozoic species and to speculate on some early members of the subclass. It is our hope that this speculation will direct attention to problems of classification associated with inferred Paleozoic opisthobranch gastropods.

The gastropod larval shell

A great deal of emphasis has been placed on the nature of embryonic whorls in the major classification of gastropods. These whorls may coil either in the same general directional sense as the more mature whorl (orthostrophic) or in a different directional sense (heterostrophic). The larval shell of opisthobranchs characteristically is coiled sinistrally and the mature shell dextrally.

Also the protoconch may be "deviated" at a slight to distinct angle from the axis of the mature shell (see Cox, 1960, fig. 69, for examples of protoconchs). In some living opisthobranchs, the heterostrophic larval shell is commonly sunken below the level of the later whorls rather than protruding.

Paleontologists have placed considerable reliance on presence of a heterostrophic larval shell as an indication of opisthobranch relationships; in living opisthobranchs, the larval shell commonly is deviated in an obvious manner (Thorson, 1946). However, Thorson (1946) has shown that there are exceptions to this criterion, for the pelagic larval stage of opisthobranchs can be eliminated under certain environmental conditions. In such cases, a large globular larval shell is developed.

Exceptions are also found within the prosobranchs where an orthostrophic larval shell is to be expected. Some prosobranchs, such as the Mathildidae and especially the Architectonicidae, have a mature shell like that of many other prosobranchs but have a specialized sunken heterostrophic nucleus; Robertson (1963, p. 11; 1970, p. 69) studied the nucleus of the Architectonicidae and termed it "hyperstrophic". Robertson (1973) concluded from detailed studies of shell and soft-part anatomy of the Architectonicidae that this family could be accommodated equally well within either prosobranchs or opisthobranchs.

The nature of the early whorls is important in determining whether a fossil gastropod is an opisthobranch, but it must used along with other shell features. Batten (1966, p. 38) described the larval shell of the Late Paleozoic *Hesperiella* as deeply buried, but concluded the shell was coiled dextral hyperstrophic.

Earlier assignment of Paleozoic gastropods to Opisthobranchia

We are limiting our remarks to the taxonomic history of taxa discussed in this paper. Even so, this history spans nearly four decades. Wenz (1938, p. 48) indicated the first occurrence of representatives of the opisthobranch Superfamily Acteonacea, family Acteonidae, subfamily Cylindrobullininae, in the upper part of the Carboniferous and tentatively in the Lower Carboniferous. However, he did not complete his classification of Gastropoda, and there is no way to determine for certain what genera he included in the opisthobranchs. Zilch (1959, p. 14) placed *Acteonina* in the Cylindrobullininae, unchanged in range from that suggested by Wenz.

Termier & Termier (1952, p. 436) placed *Acteonina* within the Orthostomacea; they gave a Mesozoic range for the genus. Pčelincev (1960, p. 242) proposed the Actaeoninidae, (Superfamily Actaeonacea), within the tectibranch opisthobranchs based on *Acteonina*; it is the only genus with a Paleozoic type-species classified among the Opisthobranchia in that work. The name *Actaeonina* is an invalid emendation.

That same year, KNIGHT, BATTEN & YOCHELSON (1960, p. 1322—1333) assigned four Paleozoic genera to the Opisthobranchia. Three small high-spired gastropods, *Donaldina*, *Platyconcha*, and *Streptacis*, were included under the Streptacidae, assigned to the Pyramidellacea. *Acteonina* was placed in the Acteonidae under the Acteonacea. We know of no subsequent papers classifying Paleozoic gastropods as opisthobranchs.

Superfamily Pyramidellacea, Family Streptacididae

FRETTER & GRAHAM (1949) suggested that the living Pyramidellacea are opisthobranchs, a novel idea now generally accepted by neontologists. That paper indirectly provided stimulus for referring *Platyconcha*, *Streptacis*, and *Donaldina* to the Pyramidellacea, extending the range of the Superfamily downward into the Paleozoic. This reference is still open to alternative interpretations.

All specimens in the three above-mentioned Paleozoic genera are small, high-spired, and have a broad, shallow, apertural sinus. They have in common a larval shell which is not orthostrophic, that is, it does not coil in the same directional sense and inclination as the post-larval shell; they also are alike in being poorly known. Differences among them in number of whorls, proportions, whorl profile, and ornament might justify placing them in three separate subfamilies, if not families.

Platyconcha LONGSTAFF (1933, p. 113) was described as having three included species. One, *P. hindi*, from the Upper Carboniferous lacks the early part of the spire, and may not even be a member of the genus. *P. dunlopiana*, the type-species, and *P. tenuilineata*, both from the upper Lower Carboniferous of Scotland, are illustrated as showing a flattened larval shell. This may be interpreted either as slightly sunken below the level of the first post-larval whorl or essentially parallel with its upper surface. The type-species was redescribed and refigured by KNIGHT (1941, p. 251) who stated, "nucleus smooth for the first whorl which is markedly flattened from above, ...". We are unaware of any subsequent work on this genus. Admittedly, the early whorls are typical of other small late Paleozoic high-spired gastropods, but this is not convincingly either a heterostrophic or a sunken larval shell. Until this species is better known morphologically, we feel other known shell characters suggest that this shell belongs within the Pseudozygopleuridae, or less likely, the Palaeozygopleuridae.

Streptacis MEEK is an extremely elongate shell known from the Middle Pennsylvanian and less certainly from the Permian of the United States. All information concerning the larval shell of this genus rests on the work of KNIGHT (1931, fig. 1) who presented camera lucida sketches of the upper part of specimens of the type-species *Streptacis whitfieldi* MEEK and of *S. crenimaginus* KNIGHT and *S. scalpta* KNIGHT; these have not been redescribed or reillustrated. The larval shell of *S. whitfieldi* is raised at essentially a right angle to the main axis of the shell. Those of the other two species are obliquely inclined and also nct sunken. Subsequently KNIGHT, (1941, p. 338—339) noted that the type specimen has lost this early part of the shell. The few references to this genus since KNIGHT (1931) do not add to our knowledge of the early whorls. We have examined unfigured paratypes of both of KNIGHT's species, but these specimens did not preserve the early whorls.

Donaldina KNIGHT, known in much of the older literature as *Aclisina*, is intermediate between *Platyconcha* and *Streptacis* in the average number of whorls. The whorls are ornamented with several prominent spiral cords. Knowledge ot the larval shell rests on the works of DONALD (1898) and LONGSTAFF (née DONALD) (1918) on the upper Lower Carboniferous of Scotland and of KNIGHT (1931) on the Middle Pennsylvanian ot the United States; subsequent studies of *Donaldina*, in the United States at least, have not increased knowledge of the early growth stages. English Early Carboniferous specimens described and illustrated by BATTEN (1966) lack the early whorls. Assuming that the specimens studied, widely separated in space and geologic time, belong to the same genus, they show that the larval shell of *Donaldina* is variable among species. In some, it is less than one whorl, inclined to the axis of coiling of the post-larval shell, though never sunken. In others, it is nearly at right angles to the mature shell and completes more than one whorl.

A sinuate aperture is not a characteristic feature of the modern pyramidellacean shell, though some examples do occur. We accept the fact of an atypical nucleus in three Paleozoic genera. Many more data are needed on the range of variation of the larval shell within and among species, as well as new descriptions, to clarify stratigraphic ranges.

In some accounts on phylogeny, as deduced from anatomical studies, the Pyramidellacea are allied to the prosobranch Rissoacea (FRETTER & GRAHAM, 1962, p. 552). This suggests the likelyhood of a common stock that could have given rise to a number of high-spired gastropods. In the known Triassic and late Paleozoic faunas, high-spired gastropods are more common than in the older Paleozoic. These high-spired forms show a variety of major morphologic differences suggestive of a continuing adaptive radiation. In contrast, the older cephalaspid opisthobranchs of the early Mesozoic show no such variety and may have been confined to a single broad habitat or lineage. Until the lineages of high-spired gastropods have been traced through the Mesozoic and have been shown to include true pyramidellaceans, we think it unwise to assign any Paleozoic high-spired gastropods to that superfamily.

Superfamily Subulitacea

The subulitacean gastropods are unornamented fusiform to globose shells having a nonsinuate outer lip. They range in age from late Early Ordovician to middle Permian, but the superfamily has not been recognized in the Mesozoic. MEEK (1863) was among the first, if not the first, to suggest that some Devonian and Carboniferous members of the group might be opisthobranchs. We speculate that he based this suggestion on the presence of one or more columellar plications in these forms, and probably on the rapid expansion of the whorls common to some genera, which, combined with a smooth shell, superficially resemble the living opisthobranch *Ringicula*.

We have examined exceptionally well preserved specimens of *Ianthinopsis* from the Pennsylvanian of Texas. These among all the subulitaceans most resemble the ringiculids in general shape, though there are differences, especially in the apertural area and in the absence of spiral sculpture. A simple orthostrophic larval shell is present in *Ianthinopsis*, whereas a submerged heterostrophic larval shell characterizes the ringiculids.

Yochelson (1956, p. 45) described the Permian genus *Labridens*, a subulitacean which has an interior revolving plication on the outer part of the aperture as well as columellar plications. He stated that "The available evidence does not necessarily indicate relationship of the Nerineacea with the Subulitacea, but it is suggestive". The Nerineacea constitute a Jurassic-Cretaceous group of cephalaspid opisthobranchs, characterized in part by elaborate ridges within the shell. We have reexamined the type-specimens of *Labridens*. On the basis of the restudy, it seems unlikey that this genus or any subulitacean could have been ancestral to any nerineacean.

The Nerineacea are characterized by a deep sutural notch, best interpreted as the locus of an exhalent siphon, and an anterior canal at the base of the aperture. Variations in interior plications are used to distinguish genera and species. Because of the general elongate shell and the interior plications, some paleontologists, including d'Orbigny (1842), Stoliczka (1868), and Cossmann (1896) have emphasized a close relationship between the Nerineacea and Pyramidellacea. Taylor & Sohl (1962) followed Cossmann in combining the superfamilies in the order Entomotaeniata.

The sutural notch of the living cephalaspid opisthobranchs is duplicated in the nerineaceans, and we concur on the placement of this extinct superfamily. The strong interior plications are not restricted to the columella but occur on the inner surfaces of the outer wall, as in *Labridens*, and on the parietal wall. However, the parietal and palatal plications of the nerineaceans are far larger and far more complex than in that genus.

If any mechanical interpretation of these convolutions is needed, we suggest that wrinkling of the mantle would greatly increase the respiratory surface and supplement or even replace the gills; because the nerineaceans are much larger than pyramidellaceans, the need for oxygen is very much greater. Delpey (1941) and Termier & Termier (1952) suggested that there is an evolutionary trend for nerineaceans to acquire more plications. This is a greatly oversimplified notion, for it does not take into account changes in plications resulting from radiation of the Nerineacea into different environments (Kollmann, unpub. data).

The shell of the subulitaceans is far simpler than that of the nerineaceans. A smooth shell, an elongate aperture, and a plicated columella, are not in themselves opisthobranch features. A survey of living gastropods shows that similar shell morphology also characterizes some taxa of the meso- and neogastropods. These features are associated with infaunal or semiinfaunal life habits. The strong columellar plications of these groups function to support retractor musculature for the head and for the foot, which is usually expanded widely. Similarities in shells between subulitaceans and opisthobranchs may simply represent convergence because of life in similar habitats.

Order Cephalaspidea

The Cephalaspidea have the head enlarged and shieldlike and an external shell which is often overlapped considerably by the mantle. Shells of most Holocene cephalaspidean families show the following general features: 1. subcylindrical shape with low, immersed or involute spire; 2. elongate whorls with a large amount of overlap; 3. narrow aperture; 4. concave columella, commonly spirally plicate or folded; 5. except in ringiculids, base of aperture only shallowly excavated, if at all; 6. exhalant siphon at the suture, associated with a slit and ramp; 7. surface smoth or shallowly grooved; 8. reduced thickness of shell in some groups; 9. heterostrophic larval whorls; 10. operculum reduced or lost.

The living cephalaspidean families that have the longest fossil record, without exception have an infaunal burrowing life habit (Acteonidae, Ringiculidae, Retusidae). This life habit should be considered characteristic of the "primitive" stock of cephalaspideans. Even in the specialized saccoglossans, the bivalved gastropods, radiation is from a burrowing stock (Kay, 1968).

In the burrowing cephalaspideans, shape of the cephalic shield, the foot, and the external shell are influenced by physical forces resulting from contact with the substrate (Dacque, 1921; Gould, 1970). Although we know nothing of the soft parts in extinct cephalaspideans, the shell is large enough to allow retraction of head and foot. The columellar plications which support retractor muscles and occur in living and fossil opisthobranchs are also characteristic of Holocene burrowing neogastropod groups. The elongate narrow aperture of the opisthobranch shell is an important advantage for infaunal life. Studies on Holocene cephalaspideans by Fretter & Graham (1954) and Lemche (1956) have indicated that the mantle cavity is twisted to the right and drawn out posteriorly with a narrow opening. The anus is in the posterior part of the mantle cavity. Lemche (1956) showed that a constant stream of water was maintained within the mantle cavity, entering laterally and leaving posteriorly. This equipment effectively solves all the sanitation problems of life in a burrow or tube where only a unidirectional water flow is possible. The same general form was achieved geologically much later by Neogastropoda evolving to a burrowing life habit (Ponder, 1973).

This organization of the mantle cavity is the reason why we consider sutural structures of prime importance for the identification of fossil opisthobranchs. Most cephalaspideans have a notch at the suture. KOLLMANN (1967) showed that in the Jurassic-Cretaceous Acteonellidae, this notch is filled by shell material which forms the ramp. It is deposited not by the mantle edge but by the mantle surface. We may therefore conclude that there was an incision in the mantle below the suture. As in the acteonellids, the exhalant siphon of most other Cephalaspidea is accompanied by an accentuated ramp.

Another morphologic feature which has not received the attention it deserves is the presence of spiral striae on many living and fossil cephalaspidean shells. The function of this unusual ornament has not been studied, but it could have some importance for distribution of mucus and for shell stability in sediment burrows built by the animal. Such striations are a highly persistent sculptural element on fossil shells that are identified as being opisthobranchs by other features. Striations are not exclusively confined to opisthobranchs, however, and occur, for example, in the prosobranch epitoneaceans and other non-burrowing families.

Superfamily Acteonacea, Family Acteoninidae

As many of the shell features listed above have been generally accepted to be cephalaspidean characters for well over a century, there has been agreement that *Acteonina* D'ORBIGNY, 1850, from the Lower Carboniferous of Belgium should be placed among the opisthobranchs. For example, WOODWARD (1856, p. 180) in his popular handbook of mollusks classified this genus within the tectibranchs and gave its range "Carb.-Portlandian"; tectibranchs form an important order of opisthobranchs and were recognized as a natural grouping before the subclass Opisthobranchia was introduced into the literature.

Much confusion surrounds *Acteonina* in older works, for there have been several different designations of a type-species, commonly one of Mesozoic age. However, MEEK (1863, p. 91) was the first to designate a type and he selected *Chemnitzia carbonaria* DE KONINICK, 1843. Further, D'ORBIGNY (1850, p. 118) listed only this one species within the genus, so it may be the type by monotypy as well. D'ORBIGNY (1850) indicated the name *Acteonina* with a date of 1847, but we have not been able to determine what earlier publication he was referring to; almost all subsequent nomenclators list the genus with an 1850 date.

KNIGHT (1932, p. 190—193) discussed the matter of the type species in some detail. He judged that *Acteonina* was not a tectibranch opisthobranch and redefined the genus. However, in a later work (KNIGHT, 1936, p. 524) written after he had examined the type-specimen KNIGHT concluded that the genus belonged in the opisthobranchs. He removed all species assigned to it except the type-species, including several North American Pennsylvanian species which he had assigned in 1932.

DE KONINCK (1881, p. 68) reported his species, redescribed as *Scalites* *carbonarius*, as coming from Assise VI of the Viséan of Belgium. This is in the lower part of the upper part of Lower Carboniferous time, or approximately of Meramecian age in terms of the North American section. DE KONINCK also reported this species as occurring in Derbyshire; this may have been an unconfirmed oral report from M. J. MORRIS, as no such species is listed by BIGSBY (1878).

KNIGHT (1941, p. 31—32) redescribed and figured the holotype and a metatype. Apparently he was the last person to write on the types of *A. carbonaria*; YOCHELSON briefly examined the holotype in 1962. *Acteonina* is a small shell, and superficially it resembles a living *Conus*. The body whorl is elongate, there is a distinct ramp below the suture, and the aperture is narrow. This shape is quite different from that of other Paleozoic gastropods and would be easy to spot. The genus has not yet been found in North America in spite of careful search among large collections of Pennsylvanian and Permian gastropods.

KNIGHT (1941, p. 31) suggested that the scar left by breaking away of the larval shell from the holotype was at least suggestive that it was heterostrophic to the main axis of coiling. One other feature noted by KNIGHT has received no attention but may be quite important. He indicated the presence of spiral striae on both specimens; these striations are shown strikingly by BATTEN (1966, p. 95, pl. 10, fig. 10) on an English specimen.

When KNIGHT (1936, p. 524) corrected his interpretation of *Acteonina*, he also proposed *Girtyspira* to include: one American Mississippian and two American Pennsylvanian species that he had previously assigned to *Acteonina*; *Bulimorpha pygmaea* WELLER from the Mississippian St. Louis Limestone of Illinois; and all the remaining species assigned by DE KONINCK (1881, p. 66—69) to *Scalites*. In reexamining DE KONINCK's illustrations, we do not feel that *S. humilis* KONINCK, *S. angulatus* KONINCK or *S. tabulatus* (PHILLIPS) can be accommodated within *Girtyspira* as they are all much larger and broader shells. Until it is determined whether these three species have an orthostrophic or heterostrophic larval shell, they are better retained within *Scalites*. Only *S. fusiformis* KONINCK shows similarity to American species of *Girtyspira*. This is a rare species and according to KNIGHT (1941, p. 31) was based on two specimens. They are from the Belgian Tournaisian Assise I, just above the Devonian-Carboniferous boundary. BATTEN (1966, p. 94) identified 10 specimens from one locality in the Lower Carboniferous of England.

In his 1936 work, KNIGHT redescribed the type-species of *Girtyspira*, *Bulimella canaliculatus* HALL, from the Mississippian Salem Limestone of Indiana (KNIGHT, 1941, p. 62—63); the type-specimen lacks the early part of the whorl. We have not found any Mississippian specimens that preserve the larval shell. Species of *Girtyspira* have been reported from the Permian of the United States, but the published material does not show the early growth stages well.

Since the time of its description, *Girtyspira* has been considered an advanced gastropod, though never an opisthobranch. Because of the elongate shell, columellar plications and suggestion of a basal notch it has been placed among the subulitaceans. Reexamination of the gross morphology, especially in the sutural area, and new information on the larval shell indicate an alternative placement to that of the Meekospiridae given by KNIGHT, BATTEN & YOCHELSON (1960, p. 1321). We do not think that other members of this family or those elsewhere within in the Subulitacea show features suggestive of opisthobranch relationships, though we have done little more than survey the superfamily through various type-species.

We have reexamined some of KNIGHT's specimens of *Girtyspira minuta* (STEVENS). A few of the better specimens were studied under a Scanning Electron Microscope. This material was collected by KNIGHT from „Zone R" in the upper part of the Labette Shale (KNIGHT, 1931, p. 5) of Middle Pennsylvanian, Des Moinesian age, his locality 43 (KNIGHT, 1931, p. 76) near Stramann, Missouri. The Labette Shale is about 10 feet thick and lies above a thin coal. The overlying limestone is irregular and in some areas has an aphanitic texture suggestive of algal mat deposition; the gastropods lived in an enviroment of quite shallow water. Nearly 50 of KNIGHT's pseudozygopleurid species came from this locality.

Dr. Kenneth BRILL, St. Louis University (oral communication, June, 1974) states that KNIGHT's locality 43 is still available for study and that some fossils may be collected below the overlying Altamont Limestone. He notes that the fauna which characterizes this locality is laterally restricted in the St. Louis area, and has hypothesized that there may have been extremely quiet lagoonal deposition with limited water circulation so that only a few areas could support marine life. In the few places where gastropods do occur, most are abundant, and of small size; they show no evidence of abrasion.

The specimens of *G. minuta* in this fauna show several interesting features which indicate that this species is an opisthobranch. These features include the general shell shape (Plate 1, fig. 1); the narrow, elongate, aperture is high on the whorl: a larval shell which is clearly deviated from the more mature part of the shell (Pl. 1 figs. 2—6), and although it is at an angle, is not fully heterostrophic, but is partially hidden; and a ramp immediately beyond the suture (Pl. 1, figs. 3—6). This flattened area shows clearly on early whorls under high magnification.

Our material is not of the type-species, and we have been unable to obtain specimens of *G. canaliculata* (HALL) that preserve the early whorls; however, these two species are so similar in general form that we are convinced that the new information on larval shell and ramp is applicable to the type. Illustrations of a Chesterian age specimen of *G. canaliculata* show the ramp and upper angulation quite well (THEIN & NITECKI, 1974, p. 218, fig. 98) *Girtyspira pygmaea* (WELLER), *G. angulifera* (WHITE) and *G.* ? *alvaensis* (BEEDE) are similar in general shape to *G. minuta,* though the early whorls of these species have not been studied.

Range of Acteoninidae

One of the reasons for the long range attributed to *Acteonina* is that *Cylindrobullina* von AMMON is variously cited as either a distinct genus (HAAS, 1953) and subgenus (DIENER, 1926; and others) or as a subjective synonym (ZILCH, 1959, p. 14). We have not investigated the species assigned to *Cylindrobullina* either directly or by this synonymy. Until such investigations are made, it seems a more conservative course to ignore this synonymy of *Cylindrobullina* and the family-group name based upon it. We think it wiser to distinguish the early stock of *Acteonina* from geologically younger acteonellid opisthobranchs by placing the genus in the Acteoninidae. The excellent illustrations of *A. scalaris* (MÜNSTER) from the Triassic St. Cassian beds provided by KITTL (1894, p. 261—262, p. 9, figs. 24—31) show a variable species, if they all constitute the same taxon. Some of the specimens illustrated are extremely close to the shape of *A. carbonaria*, and we would include *A. scalaris* in our concept of the genus. HAAS (1953) illustrated several Triassic species of *Cylindrobullina* from Peru, and some may eventually be reassigned to *Acteonina*.

Girtyspira has a less distinctive shell form than *Acteonina*. It is relatively higher spired and has a shorter and wider aperture; the sutural ramp is relatively narrower and is not set off quite so sharply from the outer whorl face. It lacks spiral striae and possibly may have had a slightly different life habitat than *Acteonina*. We are placing it with question in the Acteoninidae; it may be that we are more impressed with the Paleozoic age of the type-species of both genera than with their morphologic similarity.

If *Scalites fusiformis* DE KONINCK is correctly assigned to *Girtyspira*, it is the oldest species of both the genus and of the family. The Acteoninidae are definitely Carboniferous. In American stratigraphic terminology they range from early Late Mississippian through late Middle Pennsylvanian. If the additional species of *Girtyspira* noted above are correctly included, the family ranges from earliest Carboniferous through Late Triassic.

Conclusions

Over the years, various speculations have been advanced as to the relationship of opisthobranchs to prosobranchs. Such speculation by neontologists has been based almost exclusively upon study of the anatomy of living animals and has not included whatever light the fossil record might shed on this problem. In a sense, we are trying to determine what is the oldest fossilized opisthobranch. Criteria to be used in discriminating an opisthobranch shell from a prosobranch shell are not fully understood, or rigorous in application.

Granting that, we believe it is premature to place any Paleozoic high-spired gastropods in the Pyramidellacea or anywhere else within the Opisthobranchia. If the Mesozoic history of the group is a key to the older forms, it seems unlikely that these high-spired gastropods are related to the opisthobranchs. Information concerning the larval shell of a number of species must be accumulated if any progress in their classification is to be made.

In contrast, *Acteonina carbonaria* has been generally accepted as an opisthobranch. The presence of spiral striae reinforces the other opisthobranch morphologic features and suggests that much of the shell was covered by the mantle.

Girtyspira minuta, and by inference other members of the genus, have a deviated larval shell. That alone is not evidence of opisthobranch relationships, but the presence of a distinct, though narrow, sutural ramp independently supports this interpretation. Assuming that *Girtyspira* is correctly placed, that genus provides both a slightly older and a slightly more generalized ancestral form than *Acteonina*. Devonian and older faunas need to be examined for still earlier types, but as of now the oldest gastropod likely to be considered an opisthobranch occurs in the early Early Carboniferous.

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Explanation of Plate 1

All figures are × 130, except 1 which is × 35

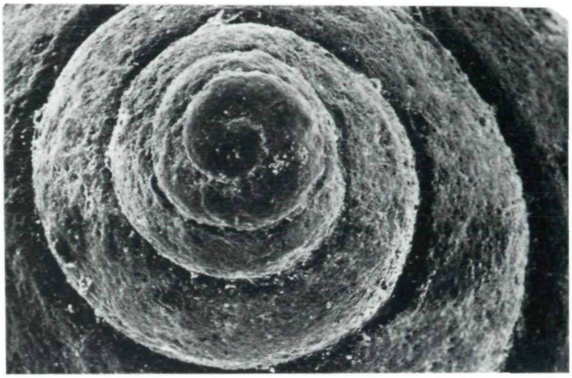
Figs. 1—6. *Girtyspira minuta* (STEVENS)

Fig. 1. Apertural view; right side of specimen is partially obscured by backscatter from mounting medium; apparent fold at base of columellar lip is a small piece of matrix. USNM 210897.

Figs. 2, 3, 4, 6. Top, oblique, and two side views of a specimen to show inclined and partially sunken larval shell; sutural ramp is distinct by the time the third whorl develops. USNM 210898.

Fig. 5. Oblique side view of another specimen, showing angulation at outer edge of ramp. USNM 210899.

1



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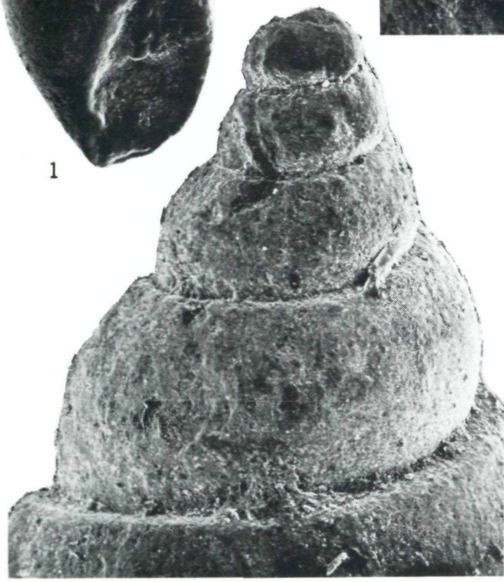

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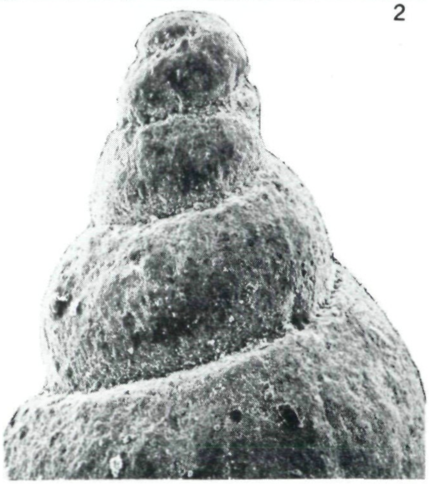

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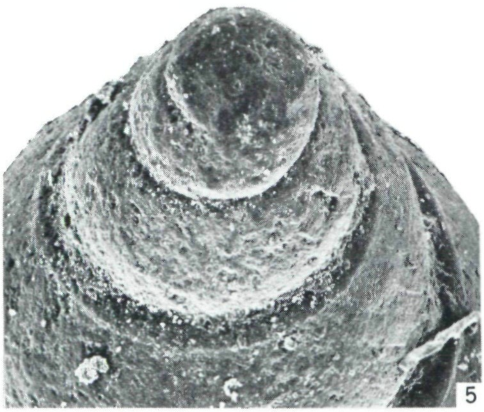

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