Larval development, musculature, and relationships of *Sinuitopsis* and related Baltic bellerophonts

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Sinuitopsis neglecta Perner (2 = *Pharetrolites elegans* (Kroken)), a bellerophont occurring in the Ordovician of the Baltic region and Bohemia, has bilaterally symmetrical 'metameric' muscle scars similar to those of *Cyrtolites*. Spirally coiled monoplacophorans with *Cyrtolites*-like muscle scars are shown to be closely related to the bellerophontid 'gastropods' with unknown muscle scars. This is indicated by the time gradients in both the characteristics of conch morphology and mode of larval development. Volkhovian *Sinuitopsis(?)* sp. has weakly separated small embryonic shell; Volkhovian to Uhakuan *Modestospira* sp. shows a distinct boundary between smooth small embryonic and strongly ornamented remaining (larval ?) shell; involute Lasnamägian *Kokenospira estona* (Koken) has relatively large, smooth embryonic shell with a sharp boundary between embryonic and adult ornamentation. The synonymizing of Cyrtonellida Horný, 1963 with Bellerophontida Ulrich & Scofield, 1897 and their inclusion into Monoplacophora is proposed.

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During the last thirty years the question of evolutionary relationships of Bellerophontida has several times been said to be closed, and then reopened. Its history has been reviewed last by Peel (1976, in Berg-Madsen & Peel 1978, 1980). In short, the discussion concerns the question whether the typical bellerophonts are spirally coiled pretorsional Monoplacophora or torsioned, bilaterally symmetrical Gastropoda. The presence of bilaterally symmetrical muscle scars on the anal side of the conch has been treated as evidence for the lack of torsion, while the presence of symmetrical longitudinal scars on the umbonal sides of the conch has been treated as evidence for post-torsional anatomy of the soft body. Division of the transverse muscle belt into several paired muscle scars was the reason for assignment to the class Monoplacophora. The value of all of this evidence is rather disputable because some Recent limpet-shaped torsioned gastropods have symmetrical muscle bands partially divided into numerous muscle attachments (see Mac Clintock 1963, Hoagland 1977).

The aim of this paper is to present some new data on the muscle scars and on the morphology of the larval shells of Ordovician bellerophonts from the Baltic palaeozoogeographic province. Relationships among these Baltic species and other Early Palaeozoic coiled Monoplacophora are discussed. Methods of phylogenetic reconstructions used here are concordant with the 'stratophenetic approach' of Gingerich (1979).

Muscle scars of *Sinuitopsis neglecta*

Some species of bellerophonts characterized by discoidal conchs with a shallow anal sinus commonly occur in the Lower Caradocian of the Baltic region (Fig. 1B). Their generic and specific assignment is still obscure and detailed taxonomic revision of them is needed. Yochelson (1963) redescribed the holotype of *Temnodiscus elegans* Koken, 1925 from the unit 4 of Norway, which belongs to this group of species, and assigned it tentatively to the genus *Pharetrolites* Wenz, 1943. Neben & Krueger (1973) illustrated specimens of the same or, at least, closely similar species from an erratic boulder of Backsteinkalk type under the name *Pharetrolites* sp. I have found several specimens of this form in an erratic boulder of identical lithology. One of them has well-preserved visible muscle scars (Fig. 1A). Existence of this finding has been
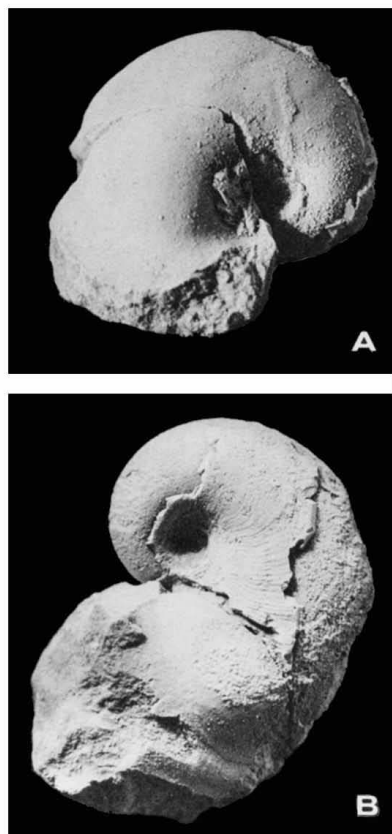
Fig. 1. Sinuitopsis neglecta Perner, 1903, Lower Caradocian, erratic boulder of Baltic origin ('Backsteinkalk'), Zgierz, Poland; lateral views of adult specimens, ×3. A Internal mould with well preserved muscle scars; ZPAL Ga 1/30. B. Specimen with partially preserved conch wall, ZPAL Ga 1/31

noted (Dzik 1978, p. 297) by use of the name *Pharetrolites elegans* (Koken). A more detailed study shows species identity of these specimens with *Sinuitopsis neglecta* Perner, 1903, known from the Early Caradocian and also probably from the Lower Llanvirnian of Bohemia (Horný 1963a). Bohemian topotype materials of *S. neg-*

lecta and those from Baltic erratic boulders are much better preserved than the holotype of *P. elegans*, therefore synonymy of these two names cannot be stated with certainty. It is possible that in the Baltic Caradocian two related species, differing in the width of the conchs, occur. Identity of my Baltic materials with the Bohemian ones is, however, evident. Even if it is also identical with *P. elegans, S. neglecta* should be its proper name in accordance with the law of priority.

The shape of the muscle band of *S. neglecta* is almost identical with that of Devonian *S. acutilira* (Hall, 1861) (see Rollins & Batten 1968), although generic identity of these species is rather doubtful if the range of genera used by Horný (1963a) is accepted. The only significant difference in the pattern of muscle scars between these species lies in the shorter distance between the band of muscle attachments and aperture in *S. acutilira*. This feature seems to be correlated with the shape of conchs of these species (cf. Fig. 3). In the whole set of muscle scars two distinct parts can be distinguished: (1) a pair of round subanal scars and (2) a laterally-dorsal thin belt tending to separate distinct lateral parts. Subanal scars are poorly visible in the discussed specimen of *S. neglecta*. Their exact position cannot be stated with certitude, though some indistinct elevations on the surface of the mould in the proper place for these scars in other known 'cyrtonellids' are seen here. Probably weak development of these scars is caused by a relatively thin wall in this part of the conch of *S. neglecta* (this may also apply where other bellerophonts have only preserved umbonal scars, cf. Peel 1980). Dorsolateral scars are much more distinct. They consist of obliquely disposed pairs of lateral scars and probably an unpaired dorsal (Fig. 1A). The shape of the lateral scars suggests functional and developmental connection with the dorsal one.

Additional, small muscle scars associated with the band described by Horný (1965) in *Cyrtolites ornatus* Conrad, 1838, are not seen in *S. neglecta*. They probably exist here but, because of the already mentioned relatively small thickness of the shell, they are indistinct. However this kind of additional muscle scar can be easily mistaken for 'shadows' of scars originating during irregular growth of the shell. Temporal retardation of growth may produce several complete sets of muscle scars along the conch (see, for example, Bialyi 1973, Erben 1960, Dzik in press).
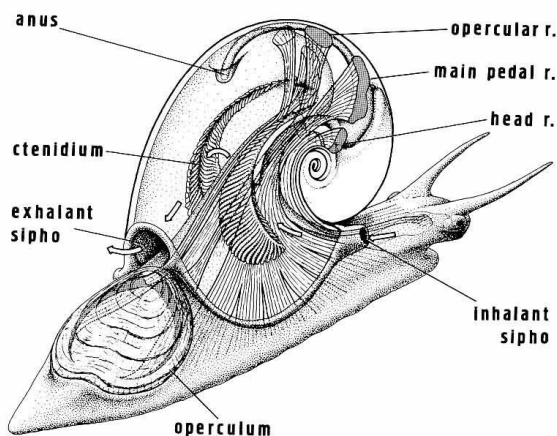
Fig. 2. Sinuitopsis neglecta Perner, 1903, Lower Caradocian of Baltic region; reconstruction of living animal showing tentative interpretation of retractor muscle attachments; conch drawn as transparent, approximately four times enlarged. Arrows indicate the supposed direction of water currents in the pallial cavity.
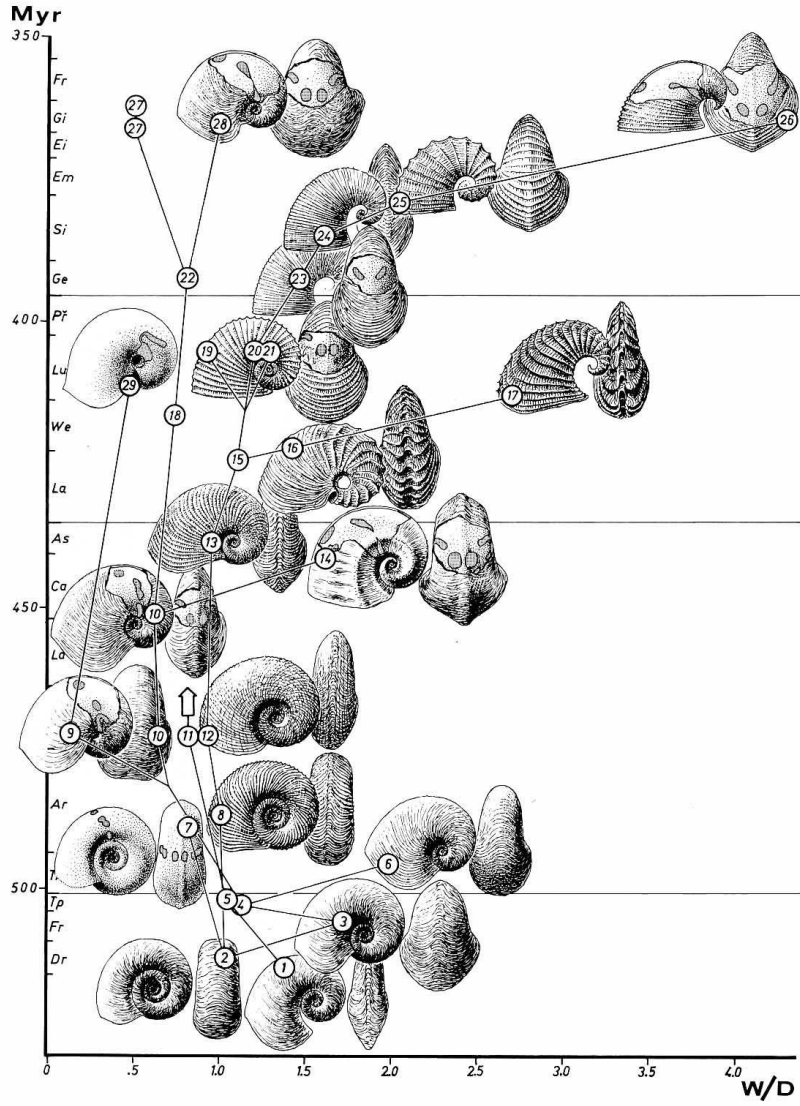
Soft anatomy of *Sinuitopsis*

As indicated above, the distance between the muscle belt and aperture is longer in *S. neglecta* than in Devonian *S. acutilira*. Therefore the mantle cavity must be much longer here (Fig. 2) than in the latter species as reconstructed by Rollins & Batten (1968). Anterolateral apertural sinuses in *S. neglecta* are less distinct than in *S. acutilira* – a feature correlated with the discoidal shape of the shell of the former species. Inhalant siphons were therefore disposed in a somewhat different manner in these species (Fig. 2). As a whole, however, it seems that there are no significant anatomical differences between both these species and other 'cyrtonellid' Monoplacophora.

All known 'cyrtonellid' monoplacophorans have been reconstructed without an operculum (see Rollins & Batten 1968, Horný 1965, Yochelson et al. 1973). This has been done by analogy with Recent *Neopilina* which, similar to all limpet-shaped molluscs, lacks any operculum. The presence of the operculum in hyoliths, archaic groups of Archaeogastropoda, and in ancient cephalopods (Turek 1978, Holland et al. 1978, Dzik 1981) suggests, however, that common ancestors of these groups, i.e. early Monoplacophora with elongated shells, also had opercula. This supposition can be supported by the similarity in the distribution of muscle scars in

hyoliths, 'cyrtonellid' monoplacophorans, and early cephalopods (Dzik 1980, 1981, and in press). Therefore, I reconstruct here the *Sinuitopsis neglecta* animal bearing a symmetrical horny operculum (Fig. 2). By analogy with hyoliths which are suggested to be relatives of Monoplacophora (Marek 1967, Dzik 1978, 1980), I connect the pair of subanal muscles with the operculum. It does not mean that homologues of these muscles must always be treated as opercular retaractors; similar distribution of muscle scars also occurs in limpet-shaped *Archinacella powersi* Ulrich & Scofield, 1897 (see Knight 1941) in which the operculum would be functionless.

Relationships between Cyrtonellida and Bellerophontida

All known 'cyrtonellid' Monoplacophora have a similar pattern of muscle scars to *S. neglecta* (see Fig. 3). They are diversified mostly in the development of separate lateral and dorsolateral (umbonal) muscle scars. The strongest separation of these scars is known in *Multifariites lenaensis* Bialyi, 1973 – the weakest one, in *Archinacella powersi*. The pattern of muscle scars alone cannot be used for dividing 'cyrtonellids' into smaller discrete groups. Its di-

versity is rather low and without any distinct order in time distribution (Fig. 3). The external shape and ornamentation of conchs contain much more information which can be used in phylogenetic reconstructions.

Diversity of the Early Palaeozoic bellerophonts and 'cyrtonellid' monoplacophorans is expressed mostly in the different expansion rate of the whorl, in the degree of conch involution, in the depth of the anal sinus (or slit), and in the presence or lack of longitudinal and/or transverse ornamentation on the conch surface. On the one side of the spectrum of morphological diversity, shells characterized by a high expansion rate and gyroconic shape (like *Cyrtonella*) can be put; on the other one, those with a low expansion rate and deeply involute shell (like *Sinuites*). The use of Raup's (1966) coordinates, i.e. (1) distance from the coiling axis to the generating curve (measured as a ratio between the radii of external and umbonal margins of whorl) and (2) whorl expansion rate (measured as the ratio between heights of subsequent whorls) is very convenient for description of the shape of planispiral shell. When put on a two-dimensional diagram of Raup's coordinates, two extremal types of bellerophontid shells mentioned above are disposed far from each other on the upper left and lower right sides, but the stock of less characteristic forms is distributed in the center. Addition of a third dimension, time, makes the picture rather complex and unclear; this is why, for convenience and clarity, I retained two-dimensional presentation of data (Fig. 3). The ratio of the whorl expansion rate

(W) to the distance of the generating curve from the coiling axis (D) is used as one coordinate, time as the other one. This is partially justified because indexes W and D are, in the case of bellerophontid shells, clearly correlated. The temporal distribution of shell forms, anal sinus and ornamentation characteristics allows connection of all known Bellerophontida and Cyrtonellida through continuous morphological lineages. Monophyly of the whole group including Bellerophontida and Cyrtonellida is strongly suggested.

The Middle Devonian *Cyrtonella mitella* (Hall 1860) with an extremely short shell seems to be an offshoot of the group of longitudinally ornamented Silurian and Early Devonian forms, partially those assigned to Cyrtonellida *(Yochelsonellis;* see Horný 1963b) and to Bellerophontida *(Pharetrolites;* see Rohr et al. 1979). The shallowing of the anal sinus seems to occur during evolution of this group, parallel with shortening of the shell and, as a consequence, the development of a gyroconic shell shape (Fig. 3). Upper Ordovician *Temnodiscus evolvens* Perner, 1903 (see Horný 1963a) may be the ancestor of this branch. *Sinuitopsis acutilira*, diametrically different in conch shape, Middle Devonian representantive of Cyrtonellida, can be derived, through several temporally and morphologically intermediate forms, from the Early Ordovician *Sinuitopsis* and *Sinuitella* species (Fig. 3). The *Sinuitopsis* evolutionary branch continues up to the Upper Givetian without any important changes in the conch shape. Similarly, all other known representantives of Cyrtonellida

Fig. 3. Time distribution of the Early Palaeozoic bellerophonts plotted against conch characteristics. Shape of conchs, sculpture, and, if known, pattern of muscle scars are illustrated. Supposedly related forms are connected by vertical lines. Bellerophonts with a deep anal slit and those with strongly expanded apertures are omitted. W – whorl expansion rate; D – distance of generating curve from coiling axis (see Raup 1966). (1) *Strepsodiscus maior* Knight, Dresbachian, Colorado. (2) *Sinuella minuta* Knight, Upper Dresbachian, Texas. (3) *Anconochilus barnesi* Knight, Lower Franconian, Texas. (4) *Cloudia buttsi* Knight, Trempeleauan, Alabama. (5) *Chalarostrepsis praecursor* Knight, Trempeleauan, Quebec. (6) *Sinuitella norvegica* (Brøgger), *Ceratopyge* limestone, Norway. (7) *Multifariites lenaensis* Bialyi, Arenigian, Sibiria (8) Modestospira polonica (Gürich), Bukówka sandstone, Poland. (9) *Sinuites sowerbyi* Perner, Šárka Formation, Bohemia. (10) *Sinuitopsis neglecta Perner*. Šárka and Chlustina Formations, Bohemia; Backsteinkalk, Baltic. (11) *Tropidodiscus pusillus* (Perner). Šárka Formation, Bohemia. (12) *Gamadiscus nitidus* (Perner), same. (13). *Temnodiscus evolvens* (Perner), Králův Dvůr Formation, Bohemia. (14) *Cyrtolites ornatus* Conrad, Upper Ordovician, Ontario. (15) *Temnodiscus cristatus* (Perner), Liteň Formation, Bohemia. (16) *Pharetrolites pharetra* (Lindström), Wenlockian, Gotland. (17) *Temnodiscus eximius* (Perner), Liteň Formation, Bohemia. (18) *Cyrtolites arrosus* Lindström, Wenlockian, Gotland. (19) *Yochelsonellis planicosta* (Perner), Kopanina Formation, Bohemia. (20) *Y. fallax* (Perner), same. (21) *Y. kokeni* (Perner), same. (22) *Sinuitina spinari* Horný, Dvorce-Prokop Limestone, Bohemia. (23) *Cyclocyrtonella eremita* (Perner), Lochkov Limestone, Bohemia. (24) *Neocyrtolites advena* (Perner), Dvorce-Prokop Limestone, Bohemia. (25) *Pharetrolites vostokovae* Rohr, Boucot & Ushatinskaya, Lower Devonian, Kazakhstan. (26) *Cyrtonella mitella* (Hall), Hamilton Group, New York. (27) *Sinuitina slavinka* Horný, Třebotov Limestone, Bohemia; Świętomarz beds, Poland. (28) *Sinuitopsis acutilira* (Hall), Hamilton Group, New York. Data from Lindström (1881), Knight (1941, 1947b, 1948), Horný (1963a, b, 1965), Bialyi (1973), Yochelson (1962, 1963, 1964), Rohr *et. al.* (1979), Peel (1980), and other sources.

can be derived from bellerophonts using morphological characteristics and time as the basis for phylogenetic reconstruction. The only difference between Cyrtonellida and Bellerophontida is that in the former muscle scars are well developed, whereas in the latter they are not known or only umbonal scars are developed. Data recently presented by Peel (1980) suggest that muscle scar of *Bellerophon*-type (Knight 1947a, Peel 1972) may be homologous with the umbonal scars of *Sinuites* (cf. Peel 1980, Fig. 1). If so, pattern of muscle attachment typical for the Late Palaeozoic typical bellerophonts can be derived from that of Early Palaeozoic *Sinuitopsis*, with *Sinuites* and *Sylvestrosphaera* patterns as morphologically intermediate stages.

Typical bellerophonts with a deep anal slit are not separated from the *Sinuitopsis*-like forms by any morphological break. They are first represented in the fossil record by the Trempeleauan *Chalarostrepsis praecursor* Knight, 1947 which can be derived from slightly older Dresbachian *Strepsodiscus maior* Knight, 1947 with an acute anal sinus. The morphological distance between the latter species and other Cambrian bellerophonts with a shallow anal sinus is not large (Fig. 3). It seems that the presence of a deep anal slit can be diagnostic on levels not higher than the family level. Independent origin of slits from sinuses in several lineages and secondary disappearance of the slit are both fully probable. Koken (1897, p. 131, Fig. 8) in his description of *Tropidodiscus sphenonotus* (Koken, 1897) mentioned: 'auf den Flanken eine Reihe eigenthümlicher Eindrücke'. They are similar to the muscle scars of *Sinuitopsis*. It could mean that at least some of Early Palaeozoic bellerophonts with deep anal slit had muscle attachments of *Sinuitopsis*-type. The lineage of primitive discoidal bellerophonts with a deep slit continues up to the Eifelian. In the Early Llanvirnian several globose forms appear which are the supposed ancestors of later typical bellerophonts (see Horný 1961, Knight 1941).

Larval development of Bellerophontida

Data on the larval development of the Early Palaeozoic monoplacophorans and gastropods are very scarce. Lindström (1884) suggested that a small pit in the apical part of the shell interior of *Pilina* is a remnant of a protoconch. This idea has been accepted by subsequent authors (inter alios, Peel 1977, Yochelson 1977). The shell of primitive molluscs is thickened inside by secretion of pearl matrix during growth, and there is no possibility of retention of the shape of a protoconch on this side of the shell. The true protoconch in the adult shell is infilled with pearl matrix and subsequently damaged during growth of the shell by influence of external factors. If it is preserved in adult shells, it can be observed only on the tip of the external shell surface, as in Recent *Neopilina* and gastropods. The pit inside the shell of *Pilina* probably represents a scar of attachment of an unknown soft organ. It has been suggested that this organ may be homologous with the cephalopod siphuncle (Dzik 1981).

The course of larval development of primitive molluscs can be reconstructed on the basis of minute morphological characters of the protoconch. Particular developmental events are expressed in the retardation of growth and changes of external ornamentation of the protoconch. However there are still several open questions concerning the methodology of inference in this area of investigation (cf. Jablonski & Lutz 1979). Previous efforts in this area of study concern mostly distinction between planktotrophic and lecithotrophic mode of life of larvae (Dzik 1978, Jablonski & Lutz 1979 and in press). They were based on the analogy with Recent mesogastropods, neogastropods and bivalves, in which small embryonic shell (Protoconch I) and larval shell (Protoconch II), well separated morphologically from the remaining shell, indicate presence of planktotrophic veliger stage, while large Protoconch I is characteristic of forms with lecithotrophic free living larva or, if Protoconch II is not developed, with lecithotrophic development within egg covers. This mode of inference was applied to the interpretation of protoconchs of Early Palaeozoic bellerophonts, gastropods, and hyoliths (Dzik 1978, 1980). New data presented by Bandel (1979) and Iwata (1980) show, however, that in the primitive gastropod order Archaeogastropoda (with exception of Neritacea) there is only an embryonic shell developing regardless of whether it was formed in the egg capsule or by the swimming trochophore (Bandel 1979, 55). It seems, therefore, that in primitive fossil molluscs presence of the free living larval stage cannot be inferred from the morphology of the embryonic shell.

Neither is it easy to demonstrate whether the

stage of free-living late veliger was developed in fossil early molluscs. No Palaeozoic gastropod or monoplacophoran having distinctly morphologically separated Protoconch II is known now. The free-living postembryonic larval stage occurs in numerous groups of all molluscan classes. It seems therefore that presence of the free-living late veliger is an original feature of the Mollusca and that the mode of development of the Archaeogastropoda is not necessarily a primitive one. The metamorphosis is not always connected with a strong change in the external ornamentation; for instance, in the early Cephalopoda the boundary between the larval shell and teleoconch is variably developed and often expresses only a slight change in the distribution of growth lines and/or internal thickening of the shell (Erben et al. 1969, Ristedt 1968, Dzik 1981). Some hyolith populations show a sharp peak of mortality at postembryonic stage corresponding in size to gastropod veliger shells. This peak has been interpreted as an effect of metamorphosis and, consequently, as evidence of free-living late veliger stage (Dzik 1978, 1980). It is disputable whether this way of inference could be applied to fossil Monoplacophora.

Protoconchs of two representantives of the Ordovician Bellerophontida have already been described (Dzik 1978): *Kokenospira estona* (Koken 1889) from the Baltic region and *Modestospira* sp. from Poland. *K. estona* has a smooth, relatively large protoconch distinctly separated from the ornamented remaining shell (Fig. 6). Abrupt changes in surface ornamentation can be interpreted as an effect of hatching and/or metamorphosis. This idea is supported by a strong increase in mortality at this stage of development (Dzik 1978), comparable in size with metamorphosing larvae of Recent gastropods. Thus *K. estona* had no free-living late veliger larva. Its protoconch is, however, dissimilar to embryonic shells of Recent archaeogastropods. Instead of having approximately one whorl, typical for Recent Archaeogastropoda (Bandel 1979), it has three whorls, like embryonic shells of Early Palaeozoic pleurotomariaceans (Dzik 1978) and veligers of Recent mesogastropods. *Modestospira* sp. has only the first half of the shell whorl which is smooth (Fig. 4c; Dzik 1978, Fig. 4D). Slightly different morphology of the protoconch is presented by *Sinuitopsis* sp. from the Arenigian of the Baltic region (Fig. 4A,B). The boundary between the embryonic and remaining shells
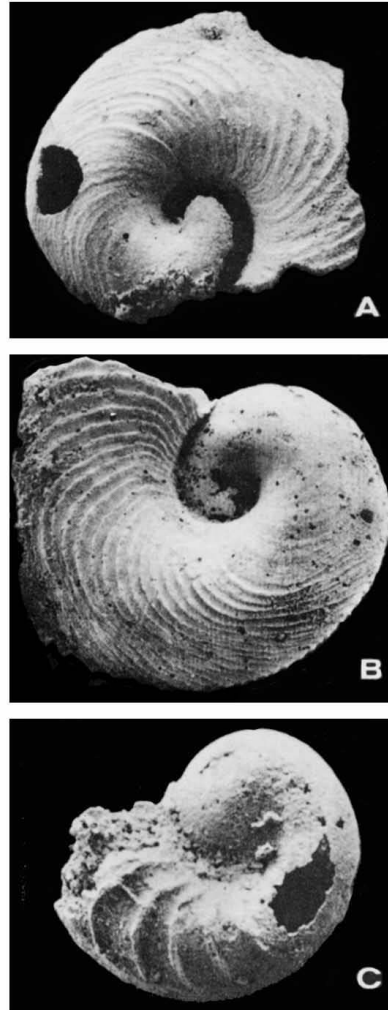

Fig. 4. Natural casts of juvenile (larval?) shells of Ordovician bellerophonts. A, B. *Sinuitopsis(?)* sp., Arenigian (Volkhovian), *Paroistodus originalis* Zone, erratic boulder E-276, Międzyzdroje, Pomerania; lateral views of specimens ZPAL Ga 1/27, 28, respectively, × 66. C. *Modestospira* sp., Llandeilian, *Amorphognathus inaequalis* Zone, sample A-5, Mójcza Limestone, Mójcza near Kielce, Poland; lateral view of incomplete specimen ZPAL Ga 1/29, × 100.

Fig. 5. Internal mould of juvenile (larval?) shell of *Tropidodis-cus(?)* sp., Arenigian (Kundan), Gullhögen quarry, Skövde, Sweden, × 100.

here is indistinct. *Modestospira, Sinuitopsis,* and *Tropidodiscus* (Fig. 5) can be compared with Recent *Haliotis* (Iwata 1980, Pl. 5:3) and possibly had the same mode of development. It must be noted, however, that several dozens of specimens of these genera from various localities consist of approximately two whorls. Because of this increase in mortality, it cannot be excluded that the free-living late veliger stage occurred here. The mode of larval development in the bellerophonts discussed seems to be correlated with their evolutionary advancement (cf. Fig. 3 and 6). The tendency, common to all molluscs, towards expansion of the embryonic stage in early development, is expressed here.

The majority of Palaeozoic molluscan larval shells already described are preserved as internal moulds (cf. Fig. 5). It makes any interpretation of the course of larval development difficult. Morever, several authors have treated these larval shells as adult ones and paid no attention to the marks of metamorphosis or hatching in their morphology. For these reasons it is not known if the earliest known tightly spirally coiled initial parts of shells of Monoplacophora – *Yangtseconus priscus* Yu, 1979 from the Early (?) Cambrian of China and *Protowenella flemingi* Runnegar & Jell, 1976 from the Middle Cambrian of Australia and Bornholm – belonged to larvae

or juveniles. Illustrated specimens (Runnegar & Jell 1976: Fig. 6C) show some marks of growth lines and supposed apertural constrictions, but the significance of these features is uncertain. Attribution of *Protowenella* to Bellerophontida (Runnegar & Jell 1976, Berg-Madsen & Peel 1978) is unreasonable because the spiral shape of the protoconch does not indicate a spiral shape of the adult shell (cf. Recent *Neopilina*). Whatever the true systematic position of *Protowenella* is, it seems more evolutionarily advanced than all known Early Cambrian monoplacophorans and resembles some Ordovician bellerophonts.

A slightly coiled protoconch is known in the Ordovician supposed monoplacophoran with conical shell *?Macroscenella* cf. *M.montrealensis* Billings (Runnegar & Pojeta 1976: pl. 15: 1–4). Most probably other limpet-shaped Palaeozoic Monoplacophora also had a spirally coiled protoconch similar to *Neopilina* or *Macroscenella*. There are, however, several findings of Early Cambrian forms which, as is seen on poor illustrations (Abaimova 1976, Yu 1979), have flat subhemispherical protoconchs. Their relation to Monoplacophora is uncertain. Some of these fossils belong rather to Stenothecoida, which are, in my opinion, not molluscs but rather inarticulate brachiopods with calcareous shells. It is not easy to distinguish monoplacophorans from isolated calcareous shells of Inarticulata if details of musculature are not known. No characteristics in the morphology of stenothecoids unequivocally indicate molluscan affinity; on the contrary, a bilaterally symmetrical bivalve conch (Koneva 1976, 1979), sometimes slightly twisted, and the pattern of mantle canal system (Horný 1957, Yochelson 1969) suggest brachiopod affinity (cf. Cooper 1976). They seem to form one more order of Inarticulata with calcareous shells rather than an early derivative of molluscan stock. Thus, there are to unequivocal data on early molluscs with flat protoconchs, though existence of such forms cannot be excluded.

Data on larval development of both 'cyrtonellid monoplacophorans' and 'bellerophontid gastropods' can be put into the scheme of their relationships based on the external morphological characters (Fig. 3) without any disturbances (cf. Fig. 6). Peculiar larvae of the suborder Jinonicellina Pokorný, 1978 (incertae sedis), represented in the Early Ordovician by *Janospira nodus* Fortey & Whittaker, 1976 and in the
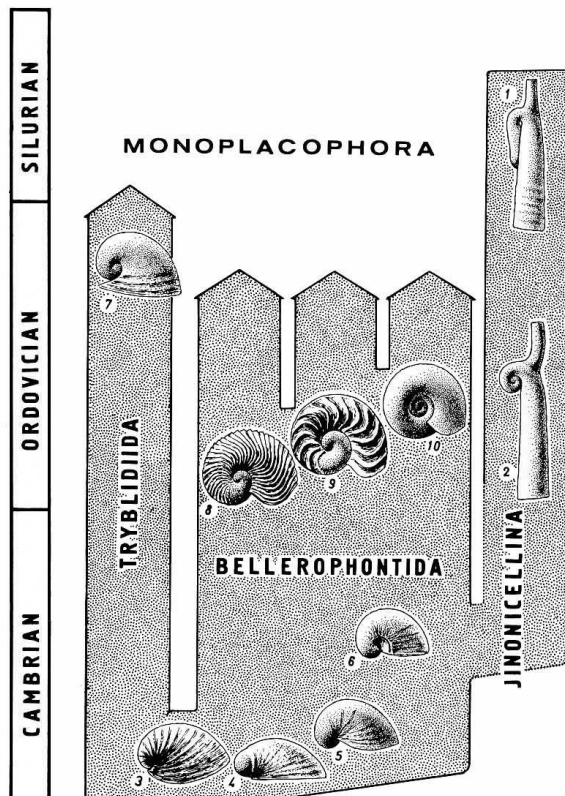
Fig. 6. Initial shell parts (veliger shells?) of Early Palaeozoic Monoplacophora. (1) *Jinonicella kolebabai* Pokorný, Kopanina Formation, Bohemia. (2) *Janospira nodus* Fortey & Whittaker, Valhafonna Formation, Svalbard. (3) *Anabarella plana* Vostokova, Tommotian, Sibiria. (4) *Bemella jacutica* (Missarzhevsky), same. (5) *Yangtseconus priscus* Yu, Huangshadong Formation, China. (6) *Protowenella flemingi* Runnegar & Jell, Coonigan formation Australia. (7) *?Macroscenella* cf. *M. montrealensis* Billings, Chambersburg limestone, Virginia. (8) *Sinuitopsis(?)* sp., Volkhovian, Baltic. (9) *Modestospira* sp., Mójcza Limestone, Poland. (10) *Kokenospira estona* (Koken), Lasnamägian, Baltic. Data partially after Dzik (1978), Fortey & Whittaker (1976), Pokorný (1978), Yu (1979), Missarzhevsky (1969), Runnegar & Jell (1976), Runnegar & Pojeta (1974), and Berg-Madsen & Peel (1978). Enlarged approximately × 25.

Upper Silurian by *Jinonicella kolebabai* Pokorný, 1978, can be derived from that of Bellerophontida with a spirally coiled, smooth embryonic shell. The boundary between the spiral part of the *Janospira* shell and the straight one may be interpreted as corresponding with hatching and/or as a boundary between larval, and adult shell (Fig. 6). Similar anal tubes to

Jinonicellina are developed in embryonic shells of the Middle Cambrian *Yochelcionella* (Runnegar & Jell 1976) and in the Lower(?) Cambrian *Archaeotremaria* (Yu 1979; the Tommotian age of this form and associated ones does not seem to be well documented). Close relationships between these two genera are almost certain, so the family name Archaeotremariidae Yu, 1979

can be applied to both of them, instead of Helcionellidae Wenz, 1938 which should be restricted to less specialized forms. Direct relationships between Archaeotremariidae, characterized by conical or endogastrically coiled embryonic shells, and Jinonicellina, characterized by exogastrically coiled embryonic shells, suggested by Runnegar (1977), seem doubtful.

Conclusions

The new data presented above on the musculature and larval development of the Baltic Cyrtonellida and Bellerophontida support the view that both of these groups are closely related to each other. Review of the time distribution of known Early Palaeozoic representantives of these orders shows that they are artificially separated groups and that they both contain fragments of the same evolutionary lineages. Those species of spirally coiled Monoplacophora in which muscle scars are known have been previously assigned to Cyrtonellida; remaining ones have been left in Bellerophontida. I postulate that these two names should be synonymized. The order Bellerophontida (incl. Cyrtonellida) could be joined with the suborder Jinonicellina incertae sedis, into a single superordinal taxon (the name Amphigastropoda Simroth, 1906, may eventually be used for it). Elevation of Jinonicellina to the ordinal rank needs some data on the morphology of adult animals. If this taxonomic assignment of bellerophonts were accepted, then the class Monoplacophora would consist of three subclasses: Tergomya Horný, 1965. Amphigastropoda Simroth, 1906 (=Cyclomya Horný, 1965), and Coniconchia Ljashenko, 1955.

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