Evolution of ‘small shelly fossils’ assemblages of the Early Paleozoic

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The allegedly sudden appearance of skeletal fossils at the beginning of the Cambrian is a preservational artifact. The most characteristic earliest Cambrian fossil assemblages are calcareous fossils with secondary phosphatic envelopes. Such preservation, although less and less abundant, continued to occur throughout the whole Early Paleozoic. A high organic productivity, low sedimentation rate, and shallow bioturbation controlled their distribution. It is proposed that the evolutionary diversification and ecologic expansion of infaunal detritus feeders resulted in extinguishing the ‘small shelly fossils’ benthic environments. Gradual replacement of the Cambrian coeloscleritophoran-monoplacophoran associations by Ordovician machaeridian-gastropod and then by Silurian and later bivalve-gastropod dominated ones is evident in the series of the Meishucun-, Mójcza-, and Kok-type faunas. This is followed by a reduction in diversity of associated organisms, starting with the anabaritids (possibly of trilobozoan or nemathelminthan affinities), through tommotiids (possible machaeridians), palaeoscolecid priapulids, hyoliths (with monoplacophoran-cephalopod relationships), octactinellid and receptaculitid sponges, and then the septemchitonid polyplacophorans.

Key words: taphonomy, Cambrian, Ordovician, Silurian, molluscs, sponges, problematica.

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Introduction

The term ‘small shelly fossils’ was coined by Matthews (in Matthews & Missarzhevsky 1975) to characterize the assemblages of minute fossils, originally phosphatic or secondarily phosphatized, that were recovered from early Cambrian limestones by etching them in acetic acid (Rozanov *et al.* 1969; Rozanov & Zhuravlev 1992). Since those pioneer studies on acid resistant microfossil assemblages from the earliest Cambrian of Siberia much additional data have been assembled, and several monographs on similarly preserved Cambrian fossils have been published (i.a. Runnegar & Jell 1976; Qian & Bengtson 1989; Bengtson *et al.* 1990). It is now clear that the 'small shelly fossils' assemblages are not restricted to the rocks of the early Cambrian but they occur not only in later Cambrian strata but are widespread also in the Ordovician, Silurian, and even Devonian. Phosphate-coated microfossils are sometimes abundant enough to develop a well-defined lithofacies; the rock may then by devoid of any macrofossils (Dzik *et al.* 1994). The question which still remains to be solved is why they were so common in the early Paleozoic, becoming more and more restricted geographically till virtually absent in strata of post-Paleozoic age.

It is apparent that those abundant occurrences of phosphate-coated minute skeletal fossils resulted from action of highly specific taphonomic factors in spatially and temporally restricted environments (Dzik *et al.* 1994). The allegedly sudden appearance of skeletal fossils at the beginning of the Cambrian is thus a preservational artifact. They were especially widespread at the beginning of the Tommotian transgressive event, but had occurred also much earlier during the Manykayian stage that, together with the Tommotian, covers a time span comparable in duration with the rest of the Cambrian (Bowring *et al.* 1993). By no means was the appearance of 'small shelly fossils' sudden. Presumably, owing to generally shallower bioturbation of sediments in shelf areas of the early Paleozoic, shelly detritus was then exposed long enough to enable extensive phosphatization. Especially in temperate climate regions close to upwellings, with high biological productivity, the action of microorganisms releasing phosphate ions resulted in frequent development of phosphatic coatings around skeletal grains. Such strata with 'small shelly fossils' developed over geographically wide areas of the sea floor along margins of some early Paleozoic continents (Brasier 1992).

In this review particular assemblages of phosphatized fossils of different geological ages will be compared quantitatively with each other. It can be inferred from the basic features of phosphate deposition that the development of phosphate-coated skeletal remains within the sediment required very specific environmental conditions. Identification of biologically significant changes in structure of those assemblages may allow to reach a rarely available target: to trace the evolution of a discrete community type. For clarity, the data on 'small shelly fossils' from the Cambrian of Yakutia, Ordovician of the Holy Cross Mountains and the Baltic area, Silurian of the Carnic Alps, as well as the Devonian of the Holy Cross Mountains and Carboniferous of Westfalia (Herholz 1992) are here arranged according to (1) similarity in their preservation and (2) presumably corresponding ecological role in communities.

Early Cambrian assemblage

The somewhat unfortunate decision to place the base of the Tommotian, originally intended to correspond to the Precambrian/Cambrian boundary, at a sedimentary discontinuity surface in the stratigraphically condensed section Ułachan-Suługur at the Aldan River, Siberia (see Rozanov & Sokolov 1984), has resulted in a subsequent heated debate on the exact meaning of the unit in offshore Cambrian sections of the Siberian Platform (Valkov 1987; Missarzhevsky 1989; Rozanov 1992; Khomentovsky & Karlova 1993). Radiometric data suggests that a considerable time span corresponds to the condensed strata between the top of the Vendian algal limestones and the base of relatively continuous sequence of the Tommotian in Siberia (Bowring *et al.* 1993). It is now apparent that the distribution of fossils in different sections is under strong facies control (Rozanov 1992) and that the diversity of fossil assemblages increases more significantly upwards in beds of the Lena river sections, of relatively shallow-water origin, than in the deeper-water Yudoma-Olenek River facies belt.

The Early Cambrian limestones of the Lena River section of Yakutia are rich in originally phosphatic fossils, the tubes of *Torellella*, minute 'buttons' of the palaeoscolecid *Hadimopanella* (Bengtson 1977), and ornate sclerites of *Camenella* (Bengtson 1970) being the most abundant. These fossils do not form a restricted assemblage and can be found in a variety of rocks. What is usually meant by the term 'small shelly fossils' assemblage includes also internal phosphatic molds of *Chancelloria* 'spicules', anabaritid tubes and hyolith conchs, as well as other phosphatized originally calcareous fossils.

In the Lena River section assemblages with significant numbers of secondarily phosphatized fossils are mostly restricted to a single horizon in the type Tommotian. These are beds surrounding the first small archaeocyath buildups in the area. The strata are well exposed in two places: in the mouth of the Tiktirikteech creek and in the gorge of the Bydjangaia stream. The latter locality is next to the classic Isyt' section. The most fossiliferous bed is a dark red glauconitic limestone, typical of the Piestrocvietnaja svita (which means 'variegated formation' in Russian), about 2.2 m above the base of the lithologic unit 10 in this section (see Rozanov & Sokolov 1984: p. 30, Fig. 11) and 2.8 m above the characteristic bed of glauconitic limestone with numerous burrows marking an apparent discontinuity at its top. Probably the same discontinuity surface, followed 2.6 m above by a bed rich in large monoplacophorans in proximity of archaeocyathid buildups, occurs in the Tiktirikteech locality (Rozanov *et al.* 1969: p. 31; Dzik 1991a: Fig. 6). Few secondarily phosphatized fossils occur above this horizon, although macrofossils are locally numerous. A sample of a red limestone with accumulations of *Allatheca* hyoliths collected 0.5 km to the west from the Tiktirikteech stream mouth (Tt-6), probably located a few meters higher, yielded only originally phosphatic fossils, among them a lot of tommotiid sclerites.

Even in the richest phosphatized microfossils sample from Bydjangaia the acetic-acid-resistant residue shows a high contribution of originally phosphatic tubes. Among total number of 5144 microfossils 1547 specimens (30.1 per cent) are phosphatic tubes and sclerites. Conical, lanceolate in cross section tubes of *Torellella* (Bengtson *et al.* 1990: p. 191 classify apparently identical tubes as *Byronia*? sp.) contribute 43.8 per cent to this class of fossils. The remaining are straight (43.6 per cent) or sinuous (10.1 per cent) tubes of *Hyolithellus*. Sclerites of *Camenella* are rather subordinate (1.4 per cent) and only a single conical *Lapworthella* sclerite has been found.

The other abundant kind of preservation of microfossils are phosphatic steinkerns (1699 specimens). Here, tubes of the anabaritid *Spinulitheca billingsi* are the most numerous: 398 specimens, which gives 23.4 per cent among specimens of similarly preserved fossils. Second in number are disintegrated rays of chancelloriid spicules (16.7 per cent), caps (3.9 per cent) and spines (2.3 per cent) of *Sachites proboscideus*, and other halkieriids (2.9 per cent). Hyoliths are also very common (together 18.1 per cent), being dominated by a form probably conspecific with *Turcutheca crasseocochlia* (203 conchs), *Allatheca* (72 conchs), *Ladatheca* (9 conchs), *Conotheca* (6 conchs), orthothecids (4 conchs), and the oldest hyolithids *Burithes* (14 conchs).

Although among the 1750 secondarily phosphatized calcareous shells the same groups of fossils are represented as among nuclei, they occur in different numerical proportions. The most common in this class are the chancelloriids, halkieriids being also common, but the number of phosphatized anabaritid tubes and mollusc conchs is surprisingly low. Ad hoc invoked causes, like different original mineralogical composition or preservational differences related to shape of fossils, appear difficult to convincingly substantiate by the available evidence.

Some of the secondarily phosphatized, or transformed into calcite, sponge spicules occurring in the Tommotian glauconitic limestones were probably originally siliceous. Remarkably, such spicules became more abundant higher in the Lena section, where discontinuity surfaces, indicative of very slow sedimentation, disappear. Especially rich in spicules are some samples from the Atdabanian of Aččagy Tuoidach (*Pagetiellus anabarus* Zone; bed G at the river shore). These are devoid of glauconite and phosphate limestones and contain a lot of calcitic and calcitized fossils. The bed with abundant hyoliths and ahtioconchids about 2.5 below the top of the Piestrocvietnaja Formation in this locality (*Judomia* Zone; bed 17) gives an insight into a more advanced molluscan assemblage than the Tommotian one, with *Yochelcionella* bearing a fully developed snorkel. In these and in strata of corresponding age in the Ułachan Kyyry Taas section, 7.2 m below the top of the Piestrocvietnaja Formation, the first echinoderm sclerites have also been encountered in abundance.

Even more obviously linked with the rock matrix is the distribution of agglutinated skeletons. In the Lena section the first foraminifers appear together with fine quartz in the Piestrocvietnaja Formation (Žurinskij Mys, sample at the river bed, probably higher part of the *Dokidocyathus regularis* Zone). Perhaps availability of the building material controls also distribution of agglutinated tubes in generally clastic sections of the Cambrian. This is obvious in the case of *Onuphionella*, constructing its spectacular tubes with mica flakes. Its distribution must be limited to clayish strata containing muscovite.

The spectrum of 'small shelly fossil' assemblages in the early Cambrian may thus range from those composed exclusively of originally phosphatic skeletal remains (i.e. sample Tt-6 from Tiktirikteech), through mixed with domination of phosphorite internal moulds and addition of phosphatized calcareous fossils, to acid-resistant residues containing virtually all skeletal detritus enveloped in calcium phosphate linings. The Chinese Meishucun fauna is the classical example of the last.

Below, the present knowledge of possible biological affinities of the most important fossils of the Siberian Tommotian is discussed, with references to published evidence from elsewhere. Alas, little more than just an 'educated guess' is possible in most cases.

Sponges

Phosphatized or calcitized sponge spicules, mostly hexactines, sporadically occur together with other phosphatized Tommotian fossils but they are of minor importance. They became more abundant in the Atdabanian part of the Lena section, where they are associated with non-phosphatized shelly fossils. Especially unusual in their symmetry are spicules with five to eight horizontal and two vertical rays of same length, showing thus typically octactinellid patterns when six horizontal rays are present (Fig. 1A–D). A peculiar dissolution at the ray bases suggests secondary calcitization, and these are more likely originally siliceous derived hexactinellid sponge spicules.

Undoubted, originally calcitic octactinellid spicules of *Eiffelia araniformis* (Missarzhevsky 1981) occur also in the Atdabanian of Siberia, although they are not especially abundant.

Archaeocyathids. — Phosphatized pieces of archaeocyathid cups are common fossils in Bydjangaia. In other Tommotian localities with 'small shelly fossils' archaeocyathids occur abundantly as phosphorite internal moulds of small cups but in true archaeocyathid buildups phosphatized fossils are missing. Phosphatization may preserve the network of archaeocyathid cup walls in great detail and its spiny appearance at the earliest stages of calcification is especially impressive (Fig. 2C). This can be used as an additional evidence in support of poriferan affinities of the archaeocyaths (see Debrenne *et al.* 1990; Debrenne & Zhuravlev 1992). Later in histogeny (and perhaps phylogeny) all these details became obliterated.

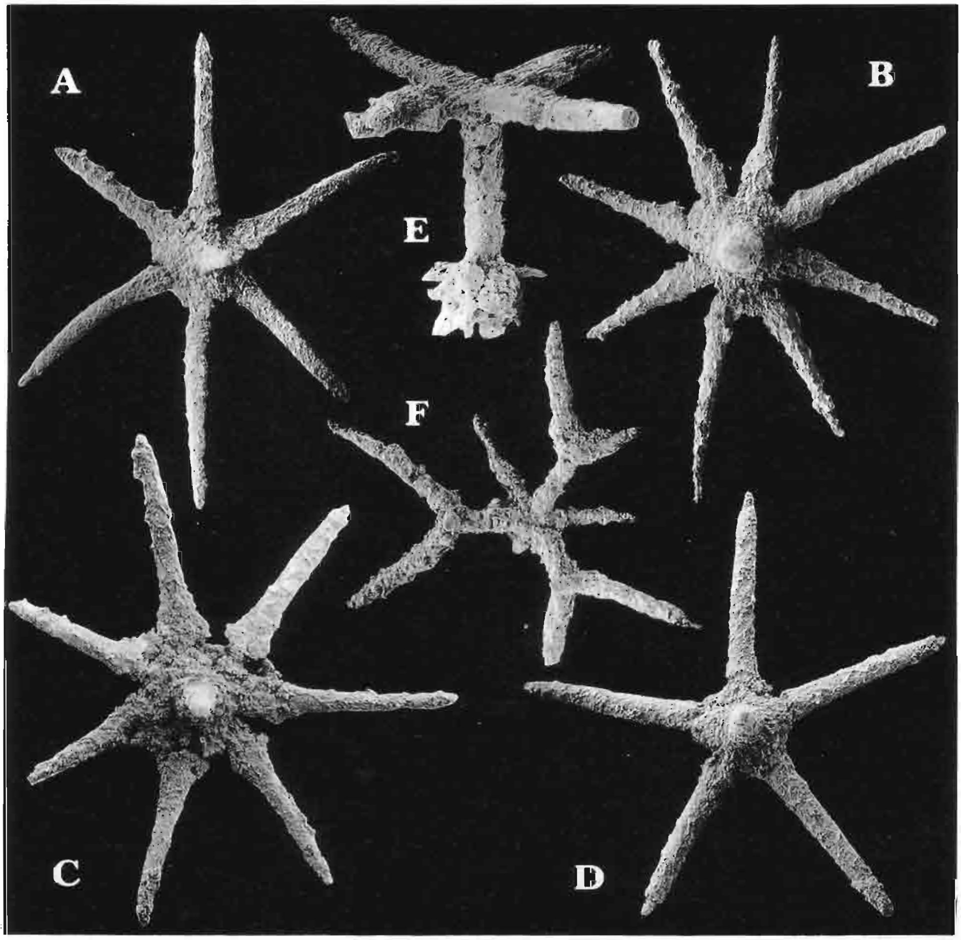

Fig. 1. Cambrian sponge spicules from the Atdabanian upper Piestrocvietnaja Formation at Aččagy Tuoidach, Yakutia; now calcitic, originally perhaps siliceous. ❑A–D. Octactinellid-like spicules (*Heterostella*?) with variable number of horizontal rays, sample AT-C taken at the river bank. ❑E. Hexactinellid(?) rooted pentactin, from the bed with hyolith opercula higher in the cliff close to the top of the formation; × 100. ❑F. Another type of hexactinelli(?) spicules; same sample × 130.

Phosphatic tubes

Two kinds of phosphatic tubes commonly occur in the early Paleozoic rocks: the circular in cross section hyolithellids and the lenticular torellellids. Their host organisms were hardly closely related to each other.

Very little in the morphology and internal structure of *Hyolithellus* tubes can be found that could help to restrict the number of possible relationships. The only feature that seems unique to this Cambrian fossil is the presence of punctation on the inner side of large sinuous tubes of *H. vladimirovae* (Fig. 3E), which are suggestive of some muscular attach-

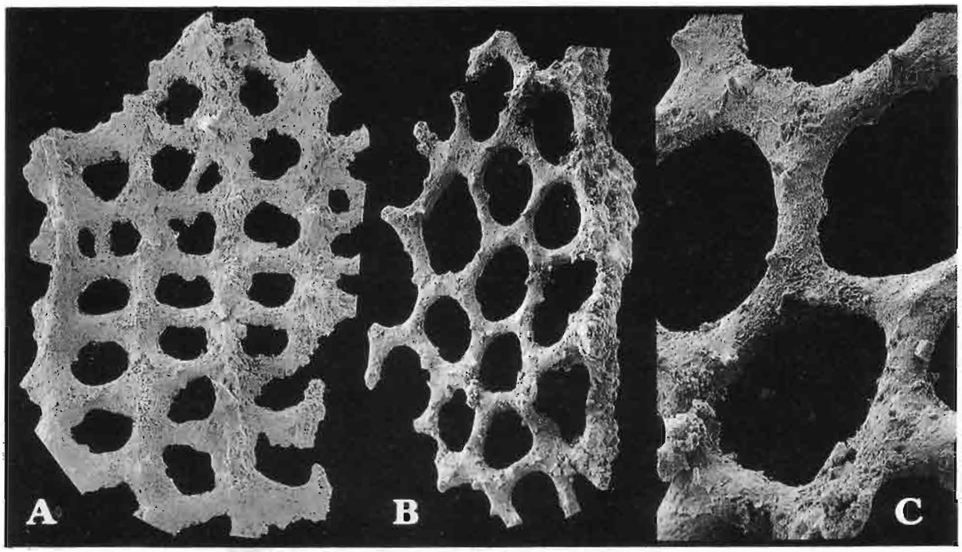

Fig. 2. Phosphatized walls of archaeocyathid cups from the Tommotian *Dokidocyathus regularis* Zone of Bydjangaia, Yakutia; a primitive organization of highly porous radial walls suggests *Aldanocyathus*. ☐A. External wall seen from inside; × 66. ☐B–C. Radial wall; note spinosity of the network; × 66 and 200, respectively.

ments. Similar tubes are known to occur as high in the stratigraphic column as the late Permian (Malzahn 1968). The attachment discs of *Hyolithellus* (Fig. 3F; Meshkova 1974: Pl. 19: 11), if properly identified, would imply that the tube secretion started long after the settlement of the larva, when the animal reached reasonable size. These enigmatic fossils surely deserve ordinal rank as the Hyolithellida Syssoiev 1957.

The tubes of *Torellella* are less indifferent morphologically, being lenticular in cross section and bearing a swelling at the base that may have functioned as an attachment disc (Missarzhevsky & Mambetov 1981: Pl. 4: 9, 11; Bengtson *et al.* 1990: Fig. 126B–C). Such tubes occur actually in the whole Paleozoic, being usually classified as *Sphenothallus* (for their attachment discs the name *Phosphannulus* is available). Possibly the Sinian *Diaoyapolites* was ancestral for the lineage (see Chen & Xiao 1992). At least until the exact relationships of the early Cambrian type species of *Byronia*, *B. annulata* Matthew 1899 are elucidated the name Byroniida Bischoff 1989 has to be used to these fossils with much caution.

Calcareous tubes

Anabaritids. — Owing to discoveries of well-preserved phosphatized anabaritid tubes in the Parara Limestone, the morphology and ontogeny of these fossils is known now well enough (Bengtson *et al.* 1990) to dismiss several earlier interpretations of their relationships, among the most foolish being my own (Dzik 1986a). Along with the clear triradial symmetry

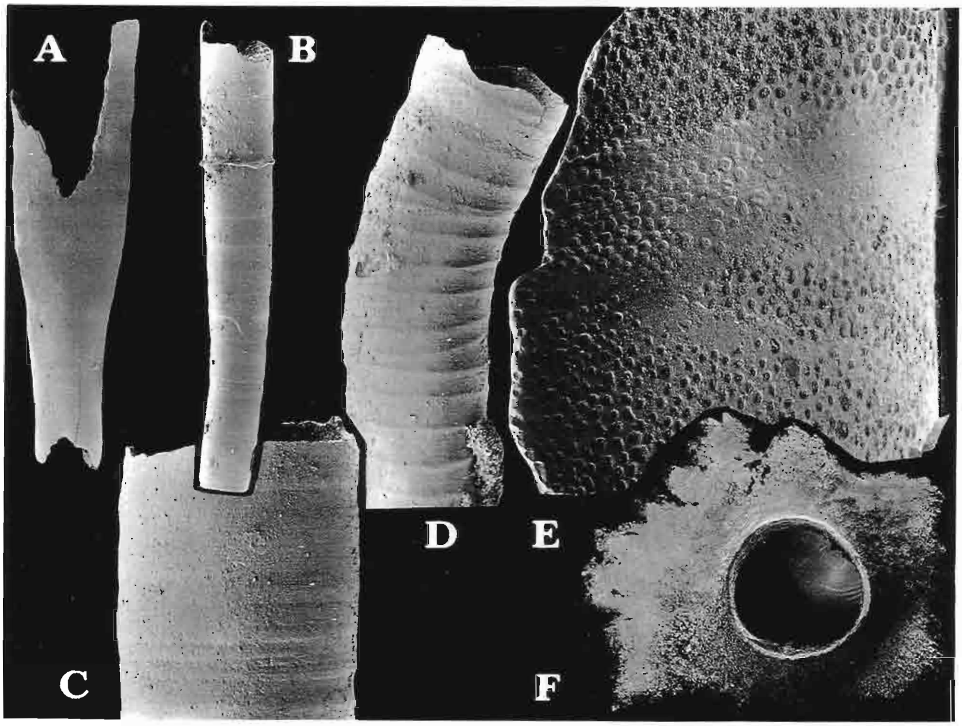

Fig. 3. Cambrian phosphatic tubes from the Tommotian *Dokidocyathus regularis* Zone of Bydjangaia, Yakutia; all × 35. ❑A. *Torellella lentiformis* Syssoiev 1962, lateral view of the tube, acute margins on both sides. ❑B–C. *Hyolithellus tenuis* Missarzhevsky 1966, juvenile and somewhat older ontogenetically tubes, respectively. ❑D–F. *Hyolithellus vladimirovae* Missarzhevsky 1966, medium size tube in lateral view (D), interior of broken large tube with pitted ornament (E), and possible attachment disc with etched calcitic callus around the base of phosphatic tube (F).

of the originally aragonitic (Bengtson & Runnegar 1992) *Anabarites* tubes, their swollen initial parts with an apical opening and, appearing later in ontogeny, transverse collars characterize the group. The internal moulds of *Spinulitheca billingsi* tubes from Bydjangaia show that they had apices of the same kind (Fig. 4H). Phosphatized tubes of the species are annulated in a way similar to that of typical anabaritids. The transverse section of *Spinulitheca* is not strictly circular but roundly triangular. Its anabaritid nature seems thus very likely. *Spinulitheca* is the most common Tommotian fossil, being a rock-building fossil in some horizons. It appears that not only in the pre-Tommotian but also in middle Tommotian strata of Siberia the anabaritids dominate in some environments.

Despite a lot of morphologic data and taxonomic diversity of the anabaritids, their zoological relationships remains elusive. They share triradial symmetry with the famous Ediacaran *Tribrachidium*, but whether this is a trait of evolutionary connection between these organisms or just a constructional similarity remains disputable. The larval(?) part of the

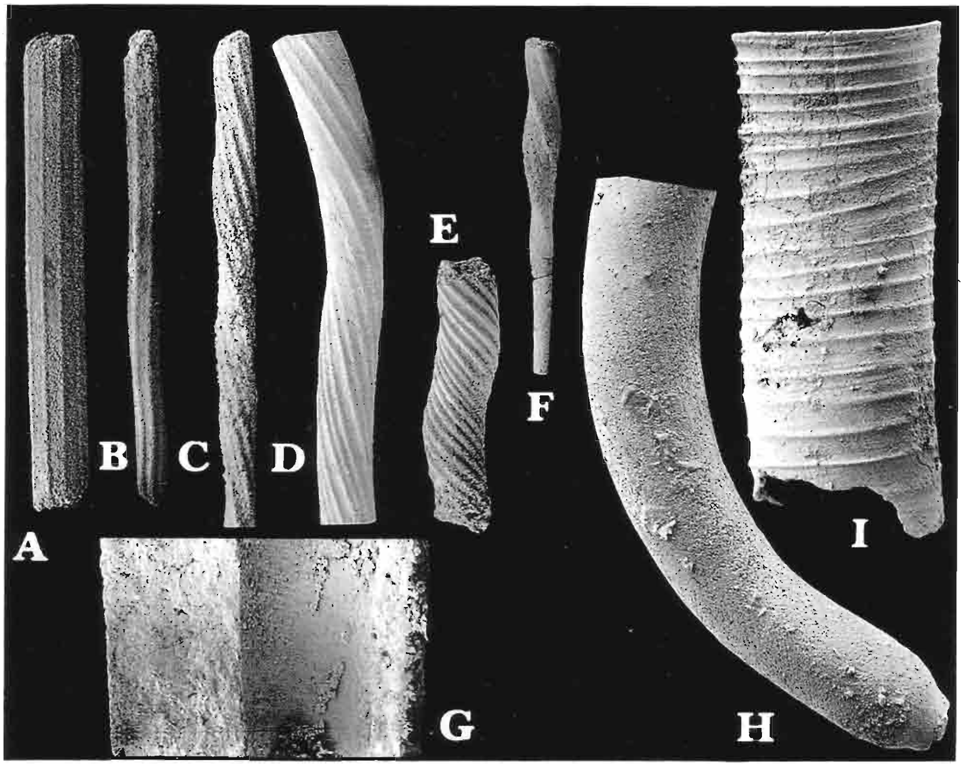

Fig. 4. Cambrian calcareous tubes from the Tommotian *Dokidocyathus regularis* Zone of Bydjangaja, Yakutia. ❑A–G. Problematic *Coleoloides trigeminatus* Missarzhevsky 1969. A–F. Variation in shape and number of helically coiled internal furrows as visible on phosphatic internal moulds; × 37. G. Empty space after removal of the nucleus illustrated in C showing smooth external surface of the tube; × 150. ❑H–I. Anabaritid *Spinulitheca billingsi* (Sysoiev 1962); nucleus of the tube apex (H; × 75), with opening diagnostic for the anabaritids, and apertural part of phosphatized tube (I; × 35).

anabaritid tube somewhat resembles priapulid loricae in having an apical perforation. The apical opening may have served to hold a larval attachment organ.

Another enigmatic calcareous tube, which remotely resemble *Anabarites* in having longitudinal internal ribs, belongs to *Coleoloides*. The exterior of its cylindrical tube is smooth, perhaps with indistinct growth lines (Fig. 4G). Internally the longitudinal ribs tend to be helically coiled in very variable ways (Fig. 4A–F). In some environments *Coleoloides* tubes occurred gregariously, vertically embedded in the sediment (Brasier & Hewitt 1979; Landing 1993).

Phosphatic dermal sclerites

Palaeoscolecids. — In some Atdabanian localities of the Lena River section the most numerous phosphatic fossils are button-like minute

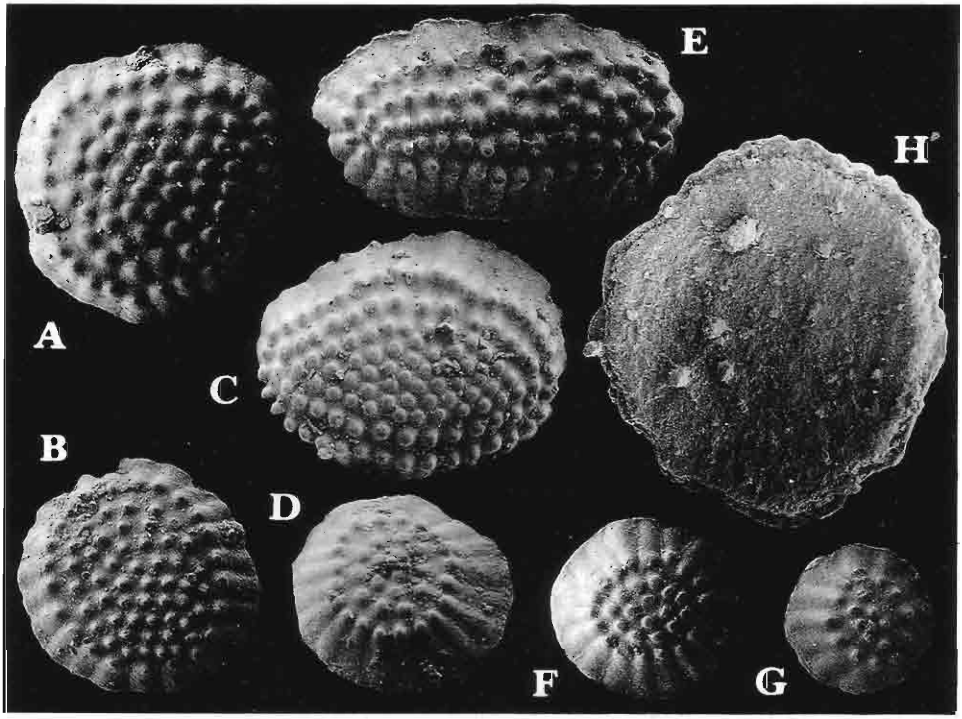

Fig. 5. Phosphatic sclerites of the Cambrian palaeoscolecid *Hadimopanella knappologica* (Bengtson 1977) from the Atdabanian of Aččagy Kyyry Taas, bed 21, set III, Yakutia. ❑A–G. Variation in shape and number of tubercles; × 180. ❑H. Basal side with the boundary between the external hyaline in inner spongy layers; × 350.

sclerites of the palaeoscolecid *Hadimopanella knappologica* (Bengtson 1977) (Fig. 5). The apparent structural discontinuity between the external cup layer and the basal porous tissue of these sclerites suggests an analogy or even homology with vertebrate dermal scales (Bengtson 1977; Dzik 1986b); in fact, in material described somewhat earlier, partially articulated specimens from the late Cambrian, increments indicative of growth from outside were reported (Müller & Miller 1976). As a result, the search for affinities of these sclerites was directed in a totally wrong direction, as in several other problematic Cambrian groups. Subsequently, larger fragments of dermal covers were discovered with well preserved sclerites proving the palaeoscolecid affinities of *Hadimopanella* and its Ordovician successors (Kraft & Mergl 1989; Hinz *et al.* 1990; Müller & Hinz-Schallreuter 1993). The general morphology and internal anatomy of the palaeoscolecids, well known for some time owing to complete specimens preserved on the rock bedding plane, strongly support their priapulid affinities (see Dzik 1993 for review).

Conodonts. — The true affinities of the earliest Tommotian conodont-like conical denticles *Fomitchella* remain enigmatic. *Fomitchella* has an internal organization similar to that of advanced latest Cambrian cono-

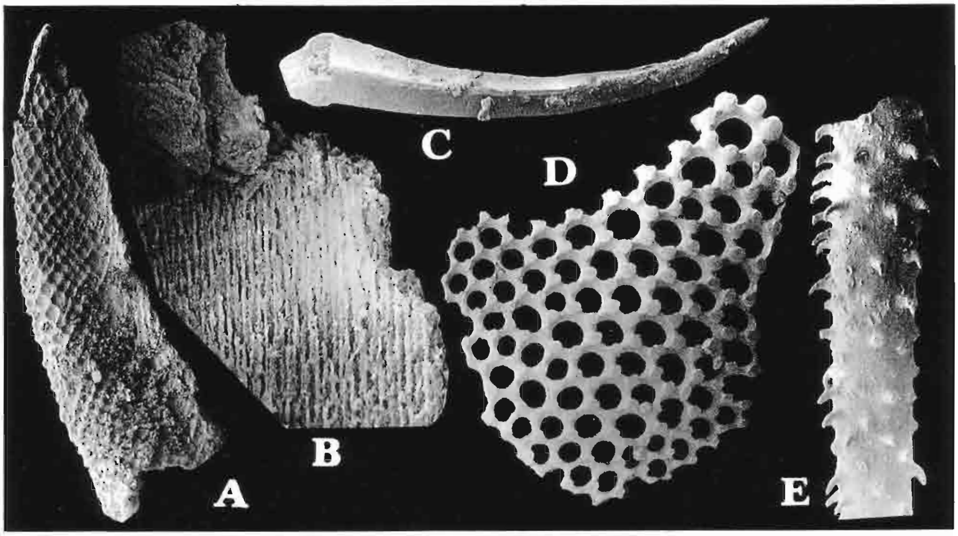

Fig. 6. Cambrian phosphatic fossils, with possible secondary additional phosphatization, from the Atdabanian Pieriechodnaja Formation at Ułachan Kyyry Taas, set IV (associated with a lingulid and an acrotretid) or Aččagy Kyyry Taas, bed 21, set III, Yakutia. ❑A–B. Problematic *Rhombocorniculum* sp., Ułachan Kyyry Taas; external view and internal structure exposed at the apex, × 80 and × 800, respectively. ❑C. Possible chaetognath grasping spine *Protohertzina* sp., Aččagy Kyyry Taas; × 80. ❑D. Lateral plate of the xenusiid lobopodian *Microdictyon*, Ułachan Kyyry Taas (see Bengtson *et al.* 1986 for more complete specimens); × 80. ❑E. Spinose tube from Ułachan Kyyry Taas; × 60.

donts but not to the Middle Cambrian westergaardodinids ('paraconodonts'; Bengtson 1983).

Equally difficult to place in the phylogenetic tree are phosphatic spines of *Protohertzina* (Fig. 6C; Bengtson *et al.* 1990), closely resembling phosphatized grasping spines of late Cambrian chaetognaths (Szaniawski 1982). Unlike the chaetognath 'protoconodonts' of the late Cambrian Orsten pelagic assemblages (note that according to Müller & Walossek 1991 they were meiofaunal), the latest Vendian/early Cambrian *Protohertzina* was apparently not a member of any planktic association which could be compared with Recent chaetognath-copepod-dominated oceanic communities. Thus, if really related to the Chaetognatha, *Protohertzina* may represent earlier pre-pelagic stage in the evolution of the group, and was thus of different anatomical organization, which can hardly be inferred from the available scarce evidence.

Scaly armors

Tommotiids. — The ornate, pyramidal phosphatic sclerites of the tommotiids are among the most characteristic fossils of the early Cambrian and were the first to receive treatment adequate to their probable evolutionary importance (Bengtson 1970). Their surface is sometimes or-

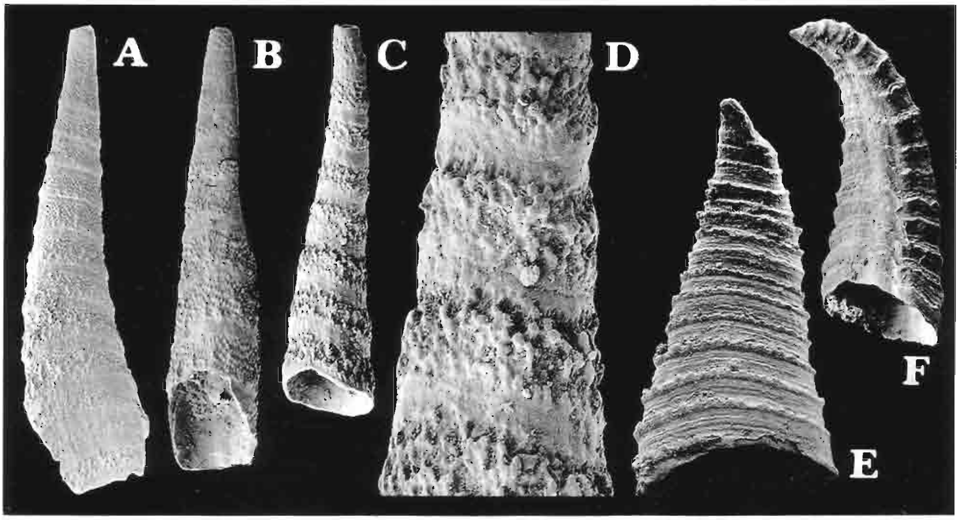

Fig. 7. Cambrian phosphatic sclerites of *Lapworthella* from Siberia. ❑A–D. *Lapworthella tortuosa* Missarzhevsky 1966, Tommotian of Tiktirikteech, sample Tt-6, *Dokidocyathus regularis* Zone; A × 30, B × 40, C × 45, D portion of C enlarged to × 110. ❑E–F. *L. bella* Missarzhevsky 1966, Atdabanian of Aččagy Kyyry Taas, bed 21, set III, × 40.

namented with imprints of epithelial cells, analogous to that in the cuticle of arthropod carapaces (Laurie 1986; Conway Morris & Chen 1990). In Bydjangaia, the tommotiids are subordinate members of the assemblage, which probably corresponds to their actual role in the original community. High conical sclerites of *Lapworthella tortuosa* Missarzhevsky 1966, forming continuous morphological series within the scleritome, probably represent the most primitive morphology in the group (Fig. 7A–D). Small sample size does not allow to state with certainty whether the Bydjangaia population of *Camenella* is conspecific with *C. garbowskae* Missarzhevsky 1966, known from other localities (Fig. 8).

Not only the tommotiid affinities but even the exact composition of their scleritome remain unknown. In the first monographic account of the group, Bengtson (1970) noticed that the tommotiid sclerites form mirror-image pairs and that there are two kinds of such paired sclerites in the scleritome, the more pyramidal mitrate and strongly concave sellate ones. His conclusions were based on 126 specimens of a Baltic *Camenella* species. The most reasonable reconstruction of the armor would thus be with four longitudinal rows of scales, the sellate sclerites forming two dorsal rows and mitrate ones bordering them laterally. The tommotiid body armor would then closely resemble that of primitive plumulitid machaeridians, being different mostly in the mineralogical composition of the skeleton.

The general applicability of this model of the tommotiid scleritome organization has been subsequently undermined by identification of strictly symmetrical sclerites in some Australian and Antarctic species, where also numerical proportions (largest sample of 348 specimens)

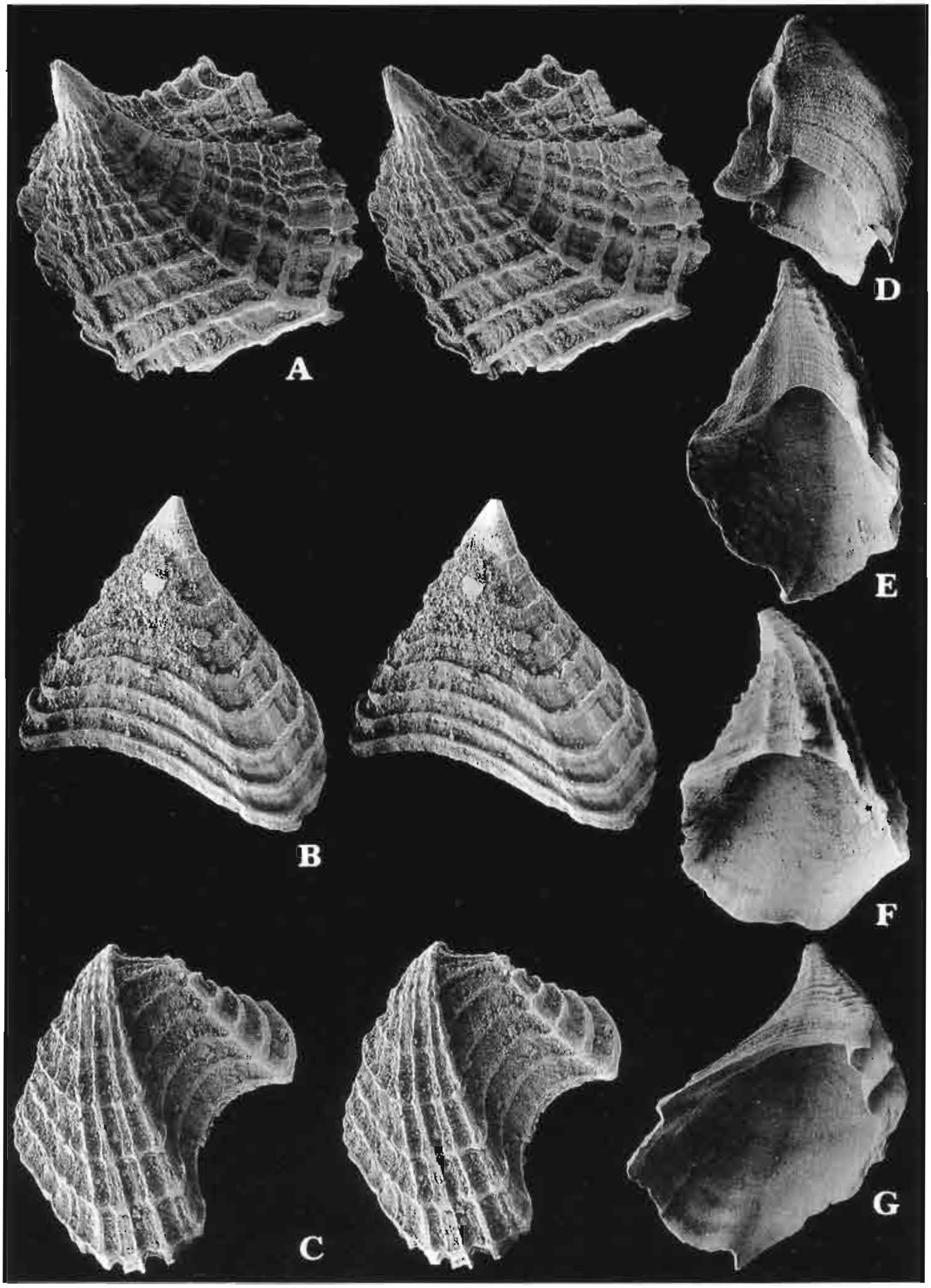

Fig. 8. Tommotiid *Camenella garbowskae* Missarzhevsky 1969 from Tiktirikteech, sample Tt-6, *Dokidocyathus regularis* Zone. ☐A–C. Stereopairs of external surfaces of mitrate (A, × 60), planiform (B, × 45), and sellate (C, × 60) sclerites. ☐D–G. Interiors of various mitrate sclerites, × 60.

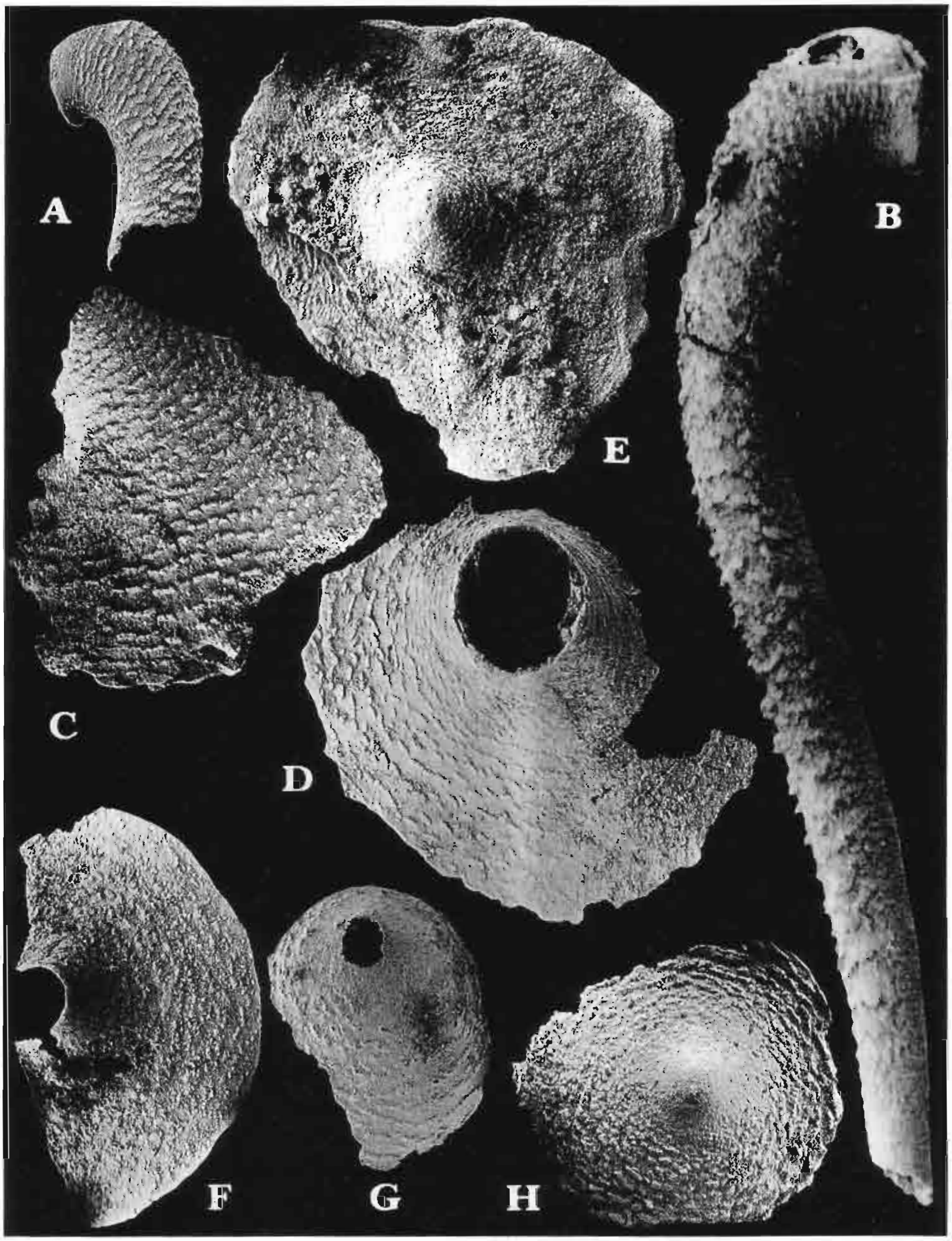

Fig. 9. Phosphatized originally aragonitic 'coeloscleritophoran' sclerites of the sachitid *Sachites proboscideus* Meshkova 1969 from the *Dokidocyathus regularis* Zone of the Tommotian of Bydjangaja, Yakutia. ❑A–B. Tubular sclerites; A × 30, B × 60. ❑C–H. Coniform sclerites; C, E × 35, D, F × 30, G × 55, H × 70.

between sclerite types are hard to reconciliate with their arrangement in four rows (Evans & Rowell 1990). Sclerite type C of these authors, which could be homologized with the sellate type of Bengtson (though they rather

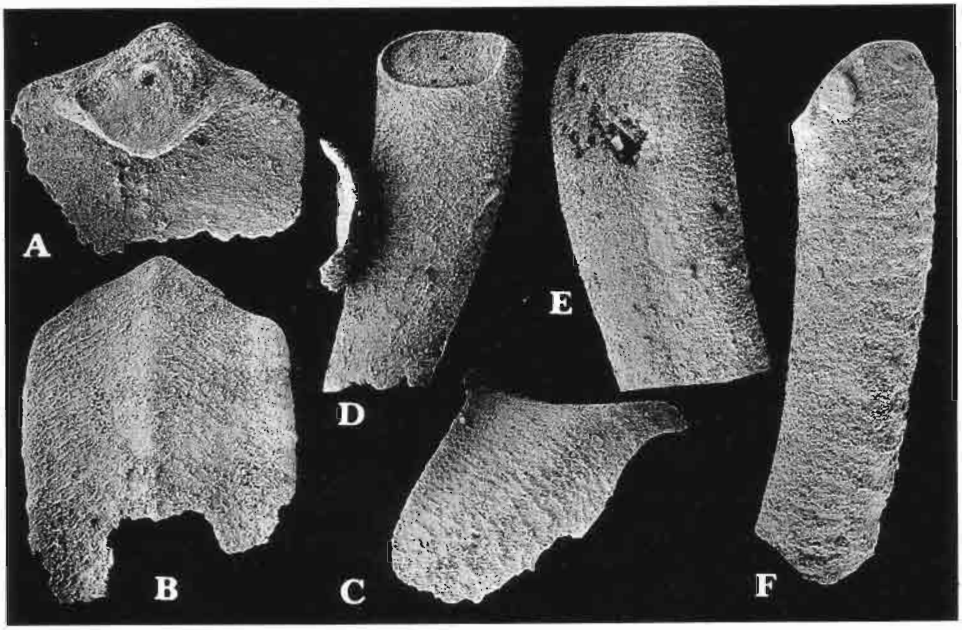

Fig. 10. Phosphatized originally aragonitic 'coeloscleritophoran' sclerites of the advanced sachitids from the *Dokidocyathus regularis* Zone of the Tommotian of Bydjangaja, Yakutia; all × 60. ❑A–C. *Halkieria* sp.; semisymmetrical (A–B) and asymmetrical (C) palmate sclerites. ❑D–F. *Hippopharangites* sp. n., semisymmetrical (D–E) and asymmetrical (F) sclerites.

resemble planiform mitrate sclerites of *Camenella*), contributes about 80 per cent to the sample. The symmetrical sclerites, representing only 4 % of the sample, have thus been interpreted as located medially in the dorsal body armor, in its anterior part.

The largest sample at my disposal, of the Siberian tommotiid *Camenella* from Tiktirikteech (Tt-6), consists of 501 specimens. 209 (39 per cent) of them represent the sellate type, which is clearly separated morphologically from other element types, with no transitional morphologies. The mitral sclerites show a great morphologic variability, with an intergradation between sclerites with various numbers of lateral ribs (Fig. 8A–B, D–G). Relatively few intermediates connect typical mitral (pyramidal) sclerites (represented by 247 specimens) with their flat planiform variety (45 specimens; Fig. 8B), characterized by weakly developed lateral ribs. Similar proportions have been reported for these element types in a Mongolian sample of *Camenella* by Bengtson (1986; sample size 30 specimens). Although in this case numerical proportions of element types do not contradict Bengtson's model of the scleritome so strongly, some uncertainty remains. The number of sellate sclerites is significantly lower than expected. Several of them are also smaller in size than associated mitrate sclerites. If, despite these difficulties, the machaeridian-style scleritome organization is accepted, the extensive variation in morphology of the mitral sclerites would be consistent with strongly polarized morphologic variability of lateral sclerites in *Plumulites*. Perhaps even the presence of a rare, morphologically distinct planiform subtype of the mitrate sclerites might find its place in the *Plumulites* model as the 'head' lateral sclerites.

One has to be aware, however, that the exact range of variation within particular species is not well established in the tommotiids because of usually low sample sizes. It is by no means certain that all samples are monospecific and that they are not 'contaminated' with sclerites of other sympatric species.

Sachitids. – Isolated sclerites of these enigmatic organisms occur widely in Cambrian strata. Reports by numerous authors with basically different methodological backgrounds resulted in much nomenclatorial confusion, only partially resolved by Bengtson *et al.* (1990). The order Sachitida He 1980 includes several lower-rank units, the central position being occupied by the oldest known genus, *Halkieria*.

Halkieriid sclerites are common in Bydjangaia, both as phosphatic internal moulds and with phosphatized walls of their originally aragonitic (Bengtson *et al.* 1990) sclerites. At least six sympatric sachitid species are present (Figs 9–10).

The recent discovery of articulated halkieriid scleritomes in the early Cambrian of Greenland presented quite unexpected morphologic features (Conway Morris & Peel 1990). It appeared that in the body armor two oval shells were incorporated, the anterior one being strongly convex and annulated, resembling at least superficially conchs of the helcionellid *Bemella* (see Dzik 1991a), while the posterior one is flat, operculum-like and ornamented with a reticulate pattern.

Isolated shells with reticulate ornamentation formed by ridges on the concave side (thus unlike true mollusc conchs) commonly cooccur with leafy halkieriid sclerites (i.a. *Marocella* and *Maikhanella*; see Evans 1992; Bengtson *et al.* 1990), and they may represent posterior shells of various halkieriids (Bengtson 1992). Some of them are composed of basally open papillae, proposed by Bengtson (1992) to be modified, minute sclerites incorporated in a plate.

The Middle Cambrian probable halkieriid relative *Wiwaxia* does not have any large plates in its scleritome, but its particular sclerites reach a remarkable size (Conway Morris 1985; Bengtson & Conway Morris 1984). The *Wiwaxia* sclerites bear some resemblance to annelid setae (Butterfield 1990), but this does not seem to contradict a descent from the halkieriids, which seems likely. The lack of shells could then be secondary.

Presumably the early Tommotian *Sachites* is the most primitive member of the group. It had long, tubular sclerites, which are associated in several Siberian samples with large funnel-like sclerites exhibiting the same surface ornamentation (Fig. 9). Some other halkieriid sclerites occur in association with elaborately ornamented *Archaeopetasus*-like caps (Kerber 1988; Bengtson *et al.* 1990). The inner surface of these sclerites is smooth. If these were homologues of the halkieriid posterior shell it would develop by increase in size of a single sclerite, not by fusion of numerous

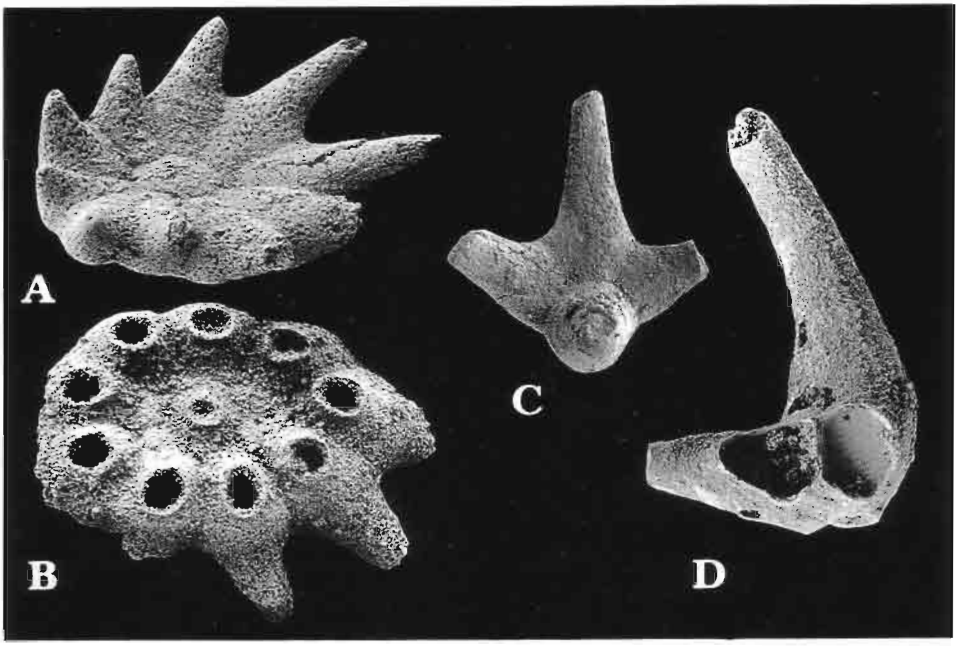

Fig. 11. Phosphatized originally aragonitic chancelloriid 'coeloscleritophoran' sclerites with empty interiors from the *Dokidocyathus regularis* Zone of the Tommotian of Bydjangaja, Yakutia. ❑A–B. *Ginospina araniformis* Missarzhevsky 1989; specimens in oblique external (A, × 40) and basal (B, × 60) views. ❑C–D. *Archiasterella* sp; specimens with three and four horizontal rays, external and lateral views, respectively; both × 40.

small ones, as proposed by Bengtson (1992). However, their homology with the posterior shells of *Maikhanella-Marocella*-type is by no means certain. An alternative explanation can be proposed that they armed low conical protuberances on the animal body, representing an initial stage in development of halkieriid sclerites.

Despite the abundance of spine-like and cap-like sclerites of *Sachites* in Bydjangaia, it is difficult to identify possibly associated anterior (and posterior) shells. The only associated fossils that resemble shells of the Greenland species are conchs of *Bemella* and related helcionellids. They show early development closely similar to other associated molluscs, with flat circular embryonic shell clearly separated from the teleoconch but with distinct growth lines suggestive of fully planktotrophic larval development (Fig. 12A).

Chancelloriids. — The chancelloriids, although originally identified as sponges, had their spinose sclerites filled with soft tissue which secreted the mineral wall over its whole surface; their organization appears thus incompatible with such a taxonomic attribution. They shared with the halkieriids calcareous composition and empty interiors of their sclerites with a small round opening at the base of each unit. This similarity led Bengtson & Missarzhevsky (1981) to unify both groups in the single taxon Coeloscleritophora.

Bengtson *et al.* (1990) proposed *Eremactis* to be a connecting link between *Chancelloria* and *Sachites*. The similarity is really striking, and on purely morphologic ground it would not be difficult to derive 'spicules' of the chancelloriid by fusion of bunches of halkieriid sclerites, as interpreted by Bengtson (in Bengtson *et al.* 1990). The only problem is the basic difference in body plans of the halkieriids and chancelloriids. No doubt the halkieriid animal was bilaterally symmetrical, dorso-ventrally flattened, possibly with a molluscan sole (Bengtson & Conway Morris 1984) and at the same time articulated chancelloriid specimens (Rigby 1978) with sclerites covering opposite body walls (Bengtson *et al.* 1990: p. 45) show that the animal had a radial organization and was probably sedentary.

At least three species of chancelloriids occur in Bydjangaia, represented by four distinct kinds of 'spicules'. The species with multirayed sclerites (Fig. 11A–B), named *Ginospina araniformis* by Missarzhevsky (1989) differs from species of *Chancelloria* (see Bengtson *et al.* 1990) in having a button-like central unit. In the sample it is represented by 227 phosphatized specimens and 35 internal moulds. *Archiasterella* with smooth sclerites bearing five or four arched radii counts 38 (32) and 272 (87) phosphatized specimens and internal moulds, respectively. Large three-rayed 'spicules' of *Elkanospina trispinata* Missarzhevsky 1989 with strongly reclined radii, are represented by 39 phosphatized specimens and 125 internal moulds.

Polyplacophorans. — As commented above, findings of articulated halkieriids with the anterior shell resembling low conical conchs of the helcionellid *Bemella*, generally accepted to be a monoplacophoran, introduces some uncertainty into classification of the earliest fossil molluscs. Possibly the halkieriids, molluscan affinities of which are likely (Bengtson 1992), are offshoots of earliest conchiferan molluscs with secondarily lost protective function of their conchs and opercula (Dzik 1993). The suggestion by Bengtson (1992) of iterative homology between the sclerite cover and at least posterior shell of the halkieriids interestingly complements Runnegar & Pojeta's (1974: p. 316) idea that the conchiferan conch may be homologous to the polyplacophoran valves. Perhaps fossil material to test these ideas is already available, but one is not able to use it properly because of difficulties with interpreting isolated valves and distinguishing them from conchs and opercula.

Some of the flat Cambrian 'conchs' may actually represent polyplacophoran valves, but until articulated specimens are found it is impossible to prove such suspicions. In the Early Cambrian several fossils intermediate between *Latouchella*-like conchs on the one hand and the flat merismoconchids on the other (Kerber 1988) are known, which show at the same time some similarity to later chelodid polyplacophorans. The Tommotian *Rugaeconus* (Vassiljeva 1990) is perhaps the oldest merismoconchid. These similarities of unknown evolutionary meaning once again exposes the difficulties with identification of isolated skeletal parts in paleontology.

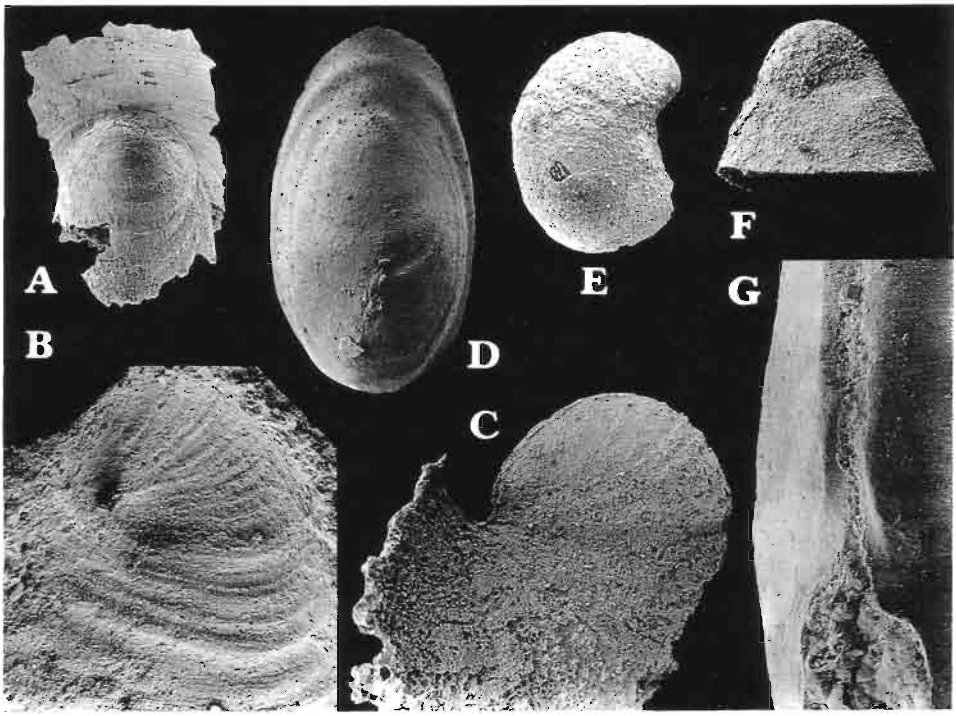

Fig. 12. Larval stages of Cambrian molluscs from the Tommotian (A–E, G) and Atdabanian (F) of Yakutia; all × 70 except G which is × 150). ❑A. Phosphatized conch probably belonging to the helcionellid *Bemella jacutica* Missarzhevsky 1969, adults of which occur in the same bed, *Dokidocyathus regularis* Zone of Bydjangaja. ❑B–C. *Latouchella korobkovi* (Vostokova 1962); negative impression of the external apex surface in phosphorite (B) and phosphatized crushed conch (C). ❑D. *Isitella recta* (Missarzhevsky 1989); phosphatic nucleus showing distinct change from flat embryonic to high conical adult conch shape (the end oriented up represents proposedly posterior elongation). ❑E. *Barskovia* sp.; Tiktirikteech. ❑F. Undetermined rostroconch; Aččagy Tuoidach, bed with hyolith opercula, note much smaller diameter of the embryonic hemispherical conch than in Tommotian helcionellids. ❑G. *Watsonella sibirica* (Missarzhevsky 1974), Tiktirikteech Tt-6, phosphatic nucleus showing the apex split into two valves from the beginning of shell ontogeny.

The halkieriids themselves, if Bengtson's (1992) model of the origin of their plates is accepted, may represent the amphineuran branch of the early molluscs.

Mollusc conchs

Monoplacophoran molluscs. — Well-preserved phosphatized apices of various mollusc conchs from Bydjangaia and other Siberian localities show that the Tommotian helcionellids had a distinct but uniform style of larval development. Their sharply delimited embryonic conchs are convex but not hemispherical, being thus like those in the Recent limpet-like monoplacophorans. The prominently irregular growth lines on their external surface (Fig. 12A) suggest rather planktotrophic early develop-

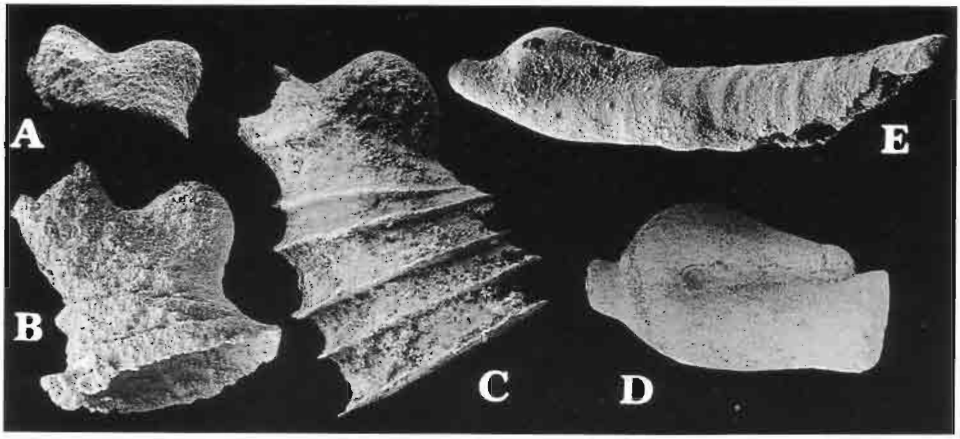

Fig. 13. Early Paleozoic snorkel-bearing minute molluscs; × 75. ❑A–C. *Yochelcionella* sp. from the bed with opercula at Aččagy Tuoidach, Atdabanian. Ontogenetic series of conchs, now calcitic. ❑D. *Jinonicella* sp. n. from early Caradoc sample 129s of Lesieniec 1 borehole, eastern Poland; phosphatized conch with partially exfoliated wall. ❑E. *Jinonicella kolebabai* Pokorný 1978 from the Ludlow Kok Formation of Cellonetta Lavinerinne, Carnic Alps, Austria; phosphatic envelope of the conch.

ment. Brooding in oviducts up to the stage of creeping juvenile characterizes at least some of the Recent monoplacophorans, which then have rather smooth external surface of the embryonic shell with delicate, regularly distributed growth increments (see Waren & Hain 1992: Fig. 22). There is no unequivocal evidence of muscle attachment scars in these mollusks, thus their direct relationship to later limpet-like Monoplacophora remains open to question. The adult conch size is relatively large, up to 25 mm in diameter in a species of *Bemella* and 15 mm in *Latouchella* (Dzik 1991a). This contradicts the commonly held opinion that the oldest conchiferan molluscs were of microscopic sizes (e.g. Chaffee & Lindberg 1986).

Two kinds of laterally compressed conchs of clear rostroconch affinities are associated with typical helcionellids in Bydjangaia. In both the protoconchs are relatively flat, oval, with distinct growth lines visible also on internal moulds. As in associated *Bemella*, their growth was more intense along the anterior margin which made the protoconch slightly spiral. After this stage a conical teleoconch developed with a slight curvature developing somewhat later and disappearing again.

The more generalized of these early rostroconchs (Fig. 12D) is high conical, with slightly curved apex. It is probably conspecific with *Isitella recta* (Missarzhevsky 1989). After reaching about 1.5 mm length, its conch aperture developed a posterior elongation with a deep sinus. The other seems ancestral to *Yochelcionella pelmani* Vassiljeva 1990, the type population of which derived from a slightly higher horizon at Tiktirikteech. It developed, rather late in ontogeny a wide 'snorkel' with drop-like section (see Vassiljeva 1990: Pl. 1: 1, 2). All specimens in Bydjangaia (even those of a size comparable with fully grown *Y. pelmani*) in place of the snorkel have an extension similar to that in associated *Isitella*, also open ventrally but developing much earlier in the ontogeny — immediately after the larval stage. Like typical rostroconchs, the conch of *Yochelcionella* grew after metamorphosis in such a way that the lateral sides of the aperture met ventrally leaving only more or less cylindrical openings at the conch ends, the larger one for the foot and the narrower one for the exhalant siphon (Pojeta & Runnegar 1976). The only difference was that in *Yochelcionella* the meeting margins were completely unified. As a result, a kind of scaphopod-like morphology developed, as in several other rostroconch lineages (Pojeta & Runnegar 1979; Peel 1991).

The snorkel of *Y. pelmani* was separated dorsally from the conch cavity by a short inner transverse shelf (pegma), a feature typical of ribeiriid rostroconchs (MacKinnon 1985; Peel 1991). Although only two phosphatized specimens of each species have been found in the Bydjangaia sample, 42 and 40 phosphorite internal moulds, respectively, give some insight into their morphologic distinctions.

In Atdabanian and later members of the *Yochelcionella* lineage, the tube of the snorkel closes much earlier than in *Y. pelmani*. A complete series of ontogenetic stages is represented by numerous calcitic conchs from Aččagy Kyyry Taas (extracted from the rock in buffered acetic acid; Fig. 13A–C). The embryonic conch was much smaller than in Tommotian predecessors, hemispherical, without distinct growth lines. This suggests that the early development was no longer planktotrophic and took place within egg covers. The teleoconch developed secondarily an exogastric curvature.

Conchs of *Latouchella* (139 internal moulds) are very common in Bydjangaia, though also in this case phosphatized specimens (Fig. 12C) are rare (only 3 in number). Although superficially resembling later bellerophontids, the Tommotian *Latouchella* had its early ontogeny identical with associated helcionellids, and its relationship to the true bellerophontids seems remote.

Bivalves. — The lineage leading to the bivalves seems to be represented in Bydjangaia sample by rare *Watsonella sibirica* (Missarzhevsky 1974). Distinct growth increments indicate its molluscan, not the repeatedly evoked arthropod nature, and shape is suggestive of ribeiriid affinities. However, unlike rostroconchs, its apical part, corresponding to the embryonic stage, shows a medial furrow suggestive of hinge (Fig. 12G). A hinge-like structure was thus developed prior to metamorphosis. Fully developed bivalve features characterize slightly younger Atdabanian *Pojetaia*, late Early Cambrian *Fordilla*, and Middle Cambrian *Tuarangia* (Pojeta 1978; Berg-Madsen 1987; Bengtson *et al.* 1990).

Gastropods. — Two kinds of asymmetrically coiled mollusc conchs, suggestive of a gastropod internal organization, occur in the oldest ‘small shelly fossils’ assemblages of Siberia and Newfoundland: the widespread, gracile *Aldanella* and the sinistrally coiled *Barskovia*, more robust in appearance. Both are represented by rare specimens in Bydjangaia. Although available specimens are not well preserved, it is clear from the morphology of their apical parts that the embryonic conchs were different from each other. In *Barskovia* it was hemispherical in shape (Fig. 12E) and without distinct growth lines (in associated rostroconchs easily visible even on nuclei). The protoconch of *Aldanella* is completely different from those of the associated helcionellids and rostroconchs; it is of the type represented by excellently preserved *Pelagiella* from the Atdabanian Parara Limestone of Australia (Bengtson *et al.* 1990: Fig. 167H).

It is unclear whether this difference is of any phylogenetic value or just reflects more elongated conical appearance of the teleoconchs. Anyway, it is easier to construct a complete morphologic series connecting the spirally coiled earliest gastropods with the hyolith *Turcutheca*, via *Ceratoconus* and *Hamusella* (see Valkov 1987), than with the helcionellids.

Hyoliths. — Among the six hyolith species occurring in Bydjangaia, the laterally compressed conchs with oval, slightly drop-like, cross section are the most common. Their embryonic shells were high hemispherical and ornamented with prominent growth lines in a way resembling associated monoplacophorans, as shown by the single phosphatized specimen with partially preserved apex (Fig. 14A; the second one, more complete, was broken while mounting on a SEM stub) and numerous phosphoritic internal moulds. This is suggestive of planktic life of the corresponding larval stage. The change from embryonic to later stage in most specimens is marked by a more or less distinct constriction (Fig. 14D–E). Generally, growth lines in this species are prominent and with common irregularities, sometimes apparent repairs of broken conch margin. As in other hyoliths, apices of larger conchs are commonly cut off with diaphragms, sometimes with peripheral thickenings similar to that in Australian *Actinotheca* (see Bengtson *et al.* 1990). On larger conchs internal moulds the center of the septum shows an irregular small callus (Fig. 14C). The species may be conspecific with *Turcutheca crasseocochlia* Syssoiev 1962, as interpreted by Missarzhevsky (in Rozanov *et al.* 1969), but published illustrations do not allow to discriminate it from the other associated species with only slightly less compressed conchs but different curvature and much smaller protoconchs (Fig. 14I).

None of the secondarily phosphatized calcareous hyolith opercula co-occurring in the same samples with the more compressed *Turcutheca* conchs can be safely matched with them. Perhaps the operculum of this species was unmineralized. Some strongly convex calcareous opercula found in a loose block in Tiktirikteech agree in their outline with the less compressed species, conchs of which dominate in this sample. In Bydjangaia such conchs are less numerous (only 17, when compared with 229 of *Turcutheca*); perhaps they belong to a species of *Ladatheca*. Its type species, *L. annae* Syssoiev 1959, has a straight adult conch, and the Bydjangaia specimens of a diameter larger than 0.75 mm are invariably straight. Adults of *L. cylindrica* (Grabau 1900) from the Tommotian of

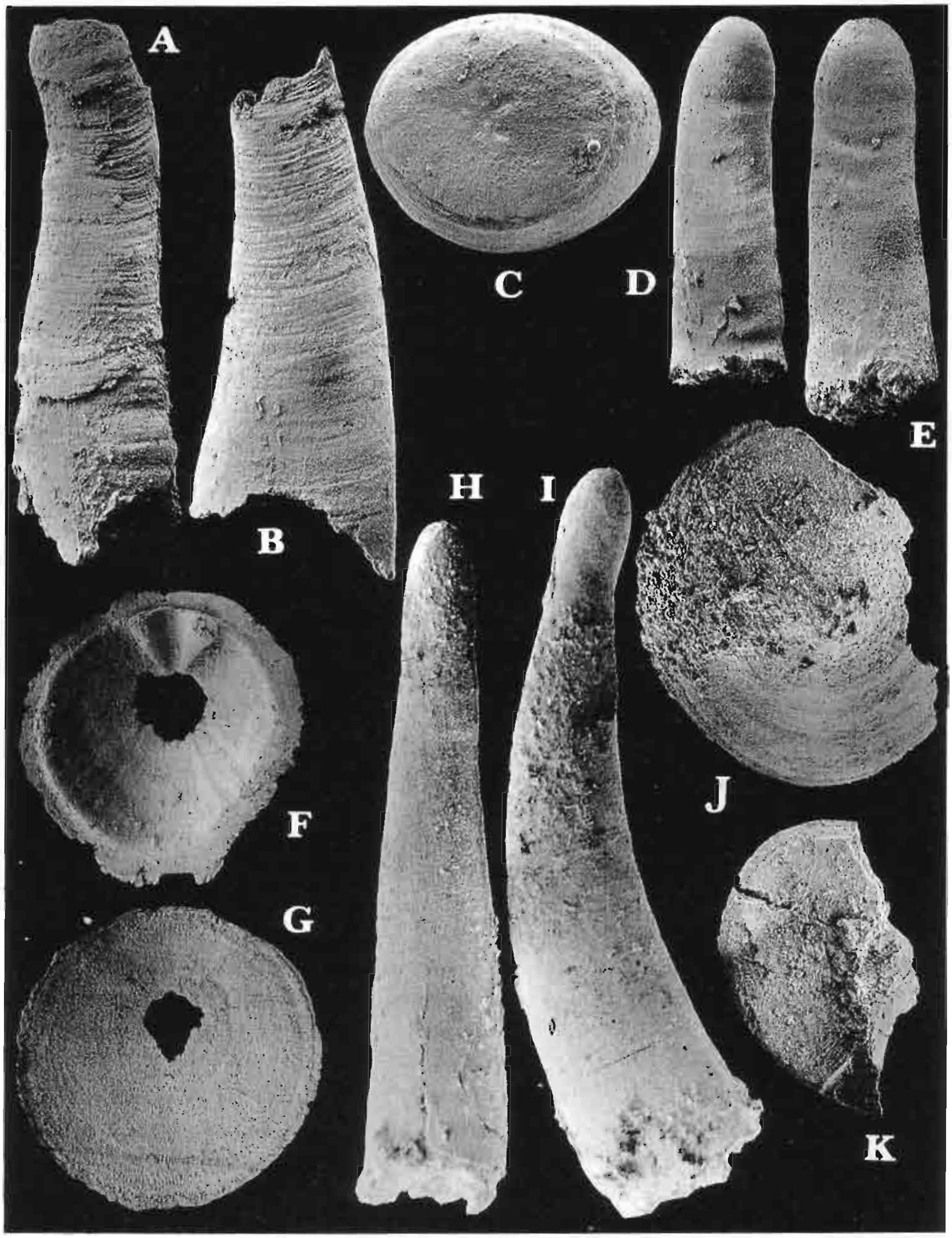

Fig. 14. Cambrian circothecid hyoliths from the Tommotian *Dokidocyathus regularis* Zone of Bydjangaja, Yakutia; all × 70. ❑A–E. *Turcutheca crasseocochlia* Syssoiev 1962, phosphatized apical parts (A, B) of the conch, phosphatic internal moulds (D–E) in lateral views (D,E) and nucleus of a diaphragm (C). ❑F–H. *Conotheca* sp., internal and external surfaces of phosphatized juvenile opercula (F–G) and phosphatic nucleus of a juvenile conch (H). ❑I–K. *Ladatheca*? sp., phosphatic nucleus of a juvenile conch (I), external and internal views of phosphatized juvenile opercula (J–K). Adult conchs of *L. annae* (Syssoiev 1959), the type species of the genus, are straight.

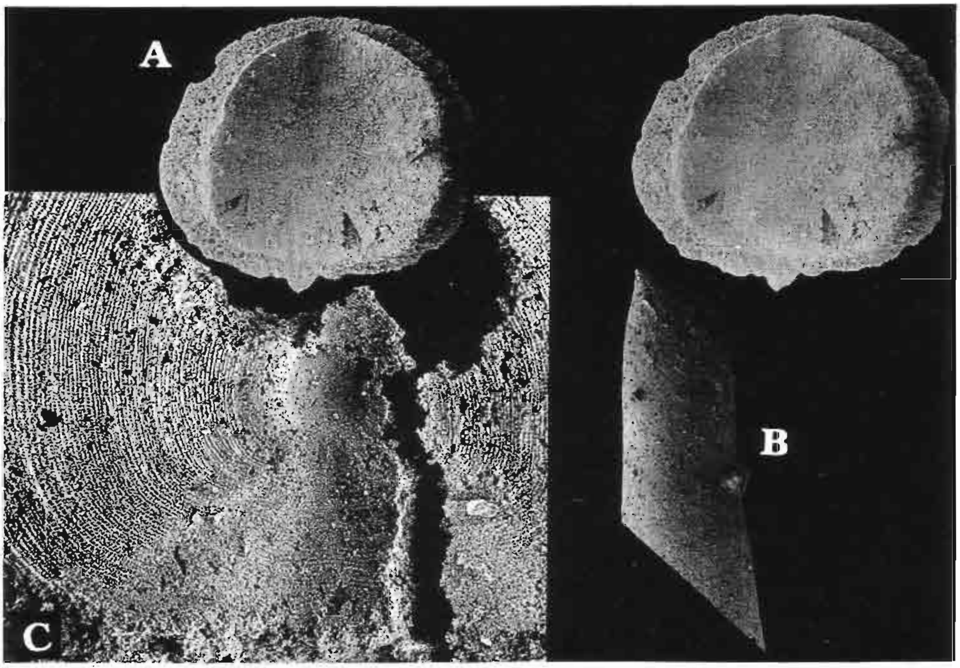

Fig. 15. Cambrian orthothecid hyoliths from the Tommotian *Dokidocyathus regularis* Zone of Bydjangaja, Yakutia; all × 70. ❑A–B. *Allatheca*, stereopair of internal surface of a phosphatized juvenile operculum (A) and phosphatic nucleus of the apex of a conch tentatively identified as belonging to the species. ❑C. negative imprint of external operculum surface in phosphorite.

Newfoundland were partially infaunal, with the conch submerged in the sediment apex-down, sometimes encapsulated by stromatolites (Landing 1993).

The internal surface of the presumed *Ladatheca* operculum is smooth (Figs 14K, 16A). An incipient depression bordered by radially aranged slight thickenings may be homologous to the cardinal processes of more advanced hyoliths, although it remains unclear which is the ventral margin. The associated conchs show clearly hyolith apices and there is nothing in the morphology of the operculum that would contradict such an affiliation of *Ladatheca*. Opercula of this kind have been also found in Małyj Karatau, Kazakhstan, by Missarzhevsky & Mambetov (1981: Fig. 15: 2–3). Another ovally shaped operculum, but with prominent cardinal processes, was attributed with question mark to *Turcutheca* by Landing *et al.* (1980: Pl. 1: 23–24); it probably represents a more advanced circothecid genus. The circular opercula of *Conotheca*, common in Bydjangaia (7, in association with 23 conchs) and other Siberian localities of the Tommotian (Fig. 14F–G) have well recognizable cardinal processes and radial ribs — incipient clavicles (see also Bengtson *et al.* 1990).

The most significant differences between the opercula discussed above and those of orthothecid hyoliths are the central to centro-dorsal (instead

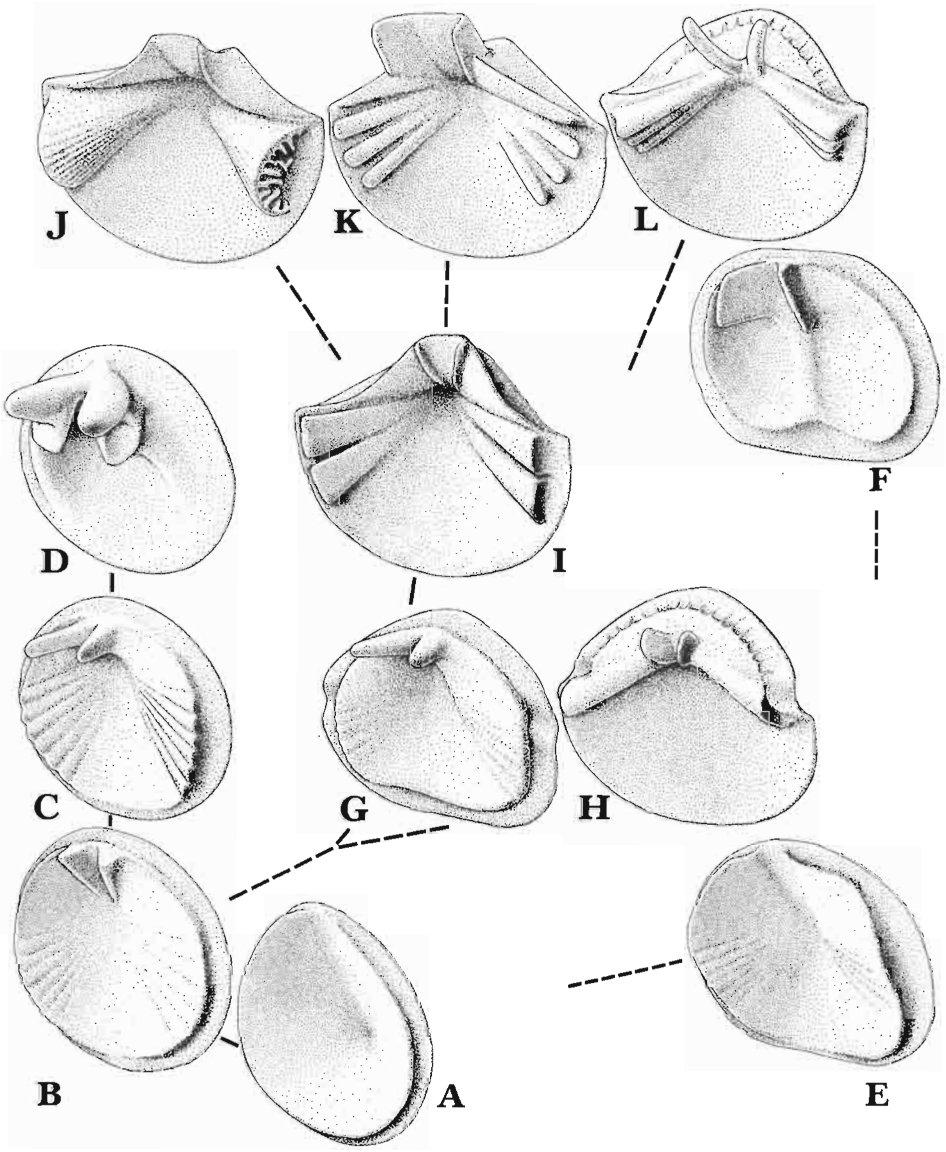

Fig. 16. Representative morphologies of hyolith opercula arranged according to their stratigraphic order of appearance; these are oblique internal views of juvenile opercula not to scale. Cardinal processes are presumed to be attachments of main operculum retractor muscles — they match with paired dorsal scars close to the conch aperture. Clavicles may have held muscles retracting some pedal tentacles. Broken lines indicate suggested relationships; partially based on Bengtson *et al.* (1990) and Kruse (1990). Circothecida: ❑A. *Ladatheca*? sp., Tommotian ❑B. *Conotheca* sp., Tommotian. ❑C. *C. australiensis* Bengtson 1990, Atdabanian. ❑D. *Guduguwan hardmani* (Etheridge 1890), Ordian-Templetonian (Middle Cambrian). Orthothecida: ❑E. *Allatheca* sp., Tommotian. ❑F. *Bactrotheca* sp., Llanvirn. Hyolithida: ❑G. *Hyptiotheca carraculum* Bengtson 1990, Atdabanian. ❑H. *Parkula bounites* Bengtson 1990, Atdabanian. ❑I. *Nganki wumirri* Kruse 1990, Ordian-Templetonian. ❑J. *Carinolithes* sp., Caradoc. ❑K. *Leolites* sp., Caradoc. ❑L. *Recilites* sp., Caradoc.

of centro-ventral) location of apices and high cardinal processes in the orthothecids. These characters, well developed also in the late Cambrian *Circotheca* and Ordovician *Bactrotheca* (Fig. 16F; see Marek 1963; Dzik 1980), can be used to differentiate members of the hyolith order Circothecida Syssoiev 1968.

Allatheca, the hyolith common in the Siberian Tommotian with ventrally flattened conch suggestive of orthothecid affinities, has its operculum with a prominent marginal flange broken only at the ventral depression (Figs 15A, 16E; Missarzhevsky 1989: Pl. 3: 12). Presumably in its ventral part the flange is homologous to cardinal processes and to clavicles in the dorsolateral part. Some large specimens attributed to this genus have well recognizable clavicular ribs (Rozanov *et al.* 1969: Pl. 11: 4). The opercula of *Allatheca* still had a primitively subcentral apex but it is possible to derive organization of Ordovician orthothecids from it.

Prominent cardinal processes developed even further than in *Conotheca* in some early hyolithids (see Marek 1963, 1967; Bengtson *et al.* 1990), presumably including also the Tommotian *Burithes* (only external surfaces of its opercula are well recognizable in my material).

Morphologically elaborated clavicles associated with small cardinal processes characterize the typical hyolithids. Atdabanian *Parkula* from the Parara Limestone (Fig. 16H; Bengtson *et al.* 1990) seems to be the oldest typical hyolithid, and early Cambrian opercula of even more advanced hyolithid morphology have been illustrated by Qian & Zhang (1983).

The question of the zoological identity of the hyoliths is still disputed (see Yochelson 1988 for the most recent review). New evidence (Bengtson *et al.* 1990) has made it unlikely that the apical morphology of the hyolith conchs described by myself (Dzik 1978, 1980) is a preservational artifact, as has been claimed by Bandel (1986). The hyolith embryonic conchs are always swollen, either mucronate with growth lines, or smooth and subspherical. The variation seems to correspond to differences in early development, either free, or within egg covers (Dzik 1978).

The apical part of the adult hyolith conch is usually filled with periodically secreted diaphragms, and the muscle scars may show a serial distribution in thick-shelled conchs. The dorsal conch scars probably connected with the cardinal processes and could work in the same way as the columellar muscles attached to processes on the neritid opercula. The function of the ventral sets of muscle attachments inside the conch is less apparent but they can be interpreted as being rooted in the foot (Dzik 1981b).

The style of embryonic and larval development of the hyoliths is closely similar to that of primitive early Paleozoic conchiferan molluscs. Nothing in their morphology is incompatible with the mollusk nature of the group (Marek & Yochelson 1976). The long, folded gut filled with sediment and enigmatic flattened appendages (helens) are unique features (apomorphies) of the orthothecids and hyolithids, respectively, which cannot at present be used to disprove their molluscan affinities. The serial distribution of muscle scars, proposed to express an internal segmentation by Runnegar *et al.* (1975), developes also in cephalopods, in result of a stadial growth connected with formation of septa.

Turcutheca, with its mixture of monoplacophoran and hyolith characters, has an important phylogenetic position. Its laterally compressed, elongated but slightly curved conch and the fact that the operculum of its close relative *Ladatheca* was still lacking any specializations typical of more advanced hyoliths, make it a better candidate than the true conical monoplacophorans for the ancestor of the earliest ellesmeroceratid nautiloids. Although the apical part is missing in all the known specimens of late Cambrian cephalopods, the minute size of conch fragments of the oldest known nautiloid, *Plectronoceras* (Webers & Yochelson 1989: Fig. 3), shows that it had small embryonic and larval conchs, as had better known early Paleozoic orthoceratids (Dzik 1981b). The crucial point in understanding cephalopod origin is why the soft tissue remained attached to the wall of embryonic conch long after metamorphosis, when the diaphragms develop in the apical part of the conch. It has been proposed that this was due to extension of the pelagic mode of life of the larva to later stages (Dzik 1981b). The cephalopod ancestor must have had a high conical, laterally compressed adult conch, and a primitive hemispherical embryonic conch (Dzik 1981b; Bandel 1982; Dzik 1993). These requirements are not met by the Late Cambrian monoplacophoran *Knightoconus*, proposed by Yochelson *et al.* (1973) to represent the direct ancestor of the cephalopods. Its strongly curved apex (Webers & Yochelson 1989: Fig. 2c) is suggestive of typically monoplacophoran organization.

It can be thus concluded that the hyoliths are most likely related both to the monoplacophorans and to the cephalopods, having their evolutionary roots in forms transitional between these classes. Whether the Tommotian *Turcutheca* was already pelagic at postlarval stages remains unknown. The close lithological similarity between Cambrian *Turcutheca*-bearing strata and later cephalopod limestones provides a weak argument in favor of such a possibility.

Echinoderm sclerites

The first isolated echinoderm sclerites appear in Siberia in the late Atdabanian (Rozhnov *et al.* 1992). The Atdabanian echinoderm assemblage along with standard epispire-bearing and brachiolar eocrinoid plates, contains more problematic winged plates with more or less convex external surface and transverse ridges on their internal side. In the later Early and Middle Cambrian, echinoderms reached significant diversity and since that time their phosphatized sclerites contribute to ‘small shelly fossils’ assemblages.

Middle Ordovician assemblage

Phosphatized minute fossils commonly occur in the Ordovician strata of the East European Platform, beginning from the late Tremadoc *Ceratopyge* limestone and ranging up at least to early Caradoc age equivalents of the Dalby Limestone. In the stratigraphically highly condensed Ordovician strata of the Małopolska Massif of south-eastern Poland, this kind of preservation of small shelly fossils continues up to the end of the Caradoc (Dzik *et al.* 1994). In all these strata phosphatic internal moulds of juvenile or larval molluscs usually dominate, but sometimes the original aragonitic conchs are replaced with calcium phosphate, or at least thin phosphatic linings preserve their original surface morphology.

Phosphatized small shelly fossils are especially abundant and diverse in the Mójcza Limestone of the Małopolska Massif, cropping out in the Holy Cross Mountains. They have recently been the subject of monographic description (Dzik *et al.* 1994). Similar Baltic assemblages were studied by several authors, but the only comprehensive description of a whole assemblage is that by Hynda (1986), based mostly on samples from the boreholes Piszcza 16 in Volhynia, Ukraine, as well as Novosielki 29 and Vysokoje 1 from the Brest Litovskij depression, Byelarus. The same formations continue across the state boundary, being recovered in several boreholes near the south-western margin of the East European Platform.

Hynda (1986: Tab. 1) published numerical data on distribution of particular groups of phosphatized fossils in the borehole Piszcza 16. When percent contributions in particular samples are counted (Fig. 17), it appears that in samples containing mostly phosphatic internal moulds, the dominant kinds of fossils are either pelmatozoan echinoderms or bryozoans. These two main groups of early Paleozoic filter feeders were probably typical of different environments, as their abundances are at least to some degree negatively correlated. Some large-scale phylogenetic factor may also be involved. In the Early Ordovician 'small shelly fossils' assemblages only few primitive paleotubuliporinid bryozoans occur, whereas in the Late Ordovician the bryozoans were very diverse in these environments, with numerous species of rhabdomesines and of phyllodictyid and fenestellid cryptostomes (Dzik 1993). At the same time diversity of cystoids and crinoids in the Baltic area decreased.

No obvious correlation between frequency of either bryozoans or echinoderms and typical 'small shelly fossils' is visible. Instead, the most diverse 'small shelly fossils' assemblages with phosphatized conchs occur in samples with low contribution of both echinoderms and bryozoans (in the early Llanvirn of the Piszcza 26 borehole). The same relationship has been observed in Mójcza and in boreholes in the Polish part of the Platform. One of the most productive samples that I have had occasion to study is the earliest Caradoc (*Baltoniodus variabilis* Subzone of the *Amorphognathus tvaerensis* Zone) sample 129s, Lesieniec borehole, depth 1337

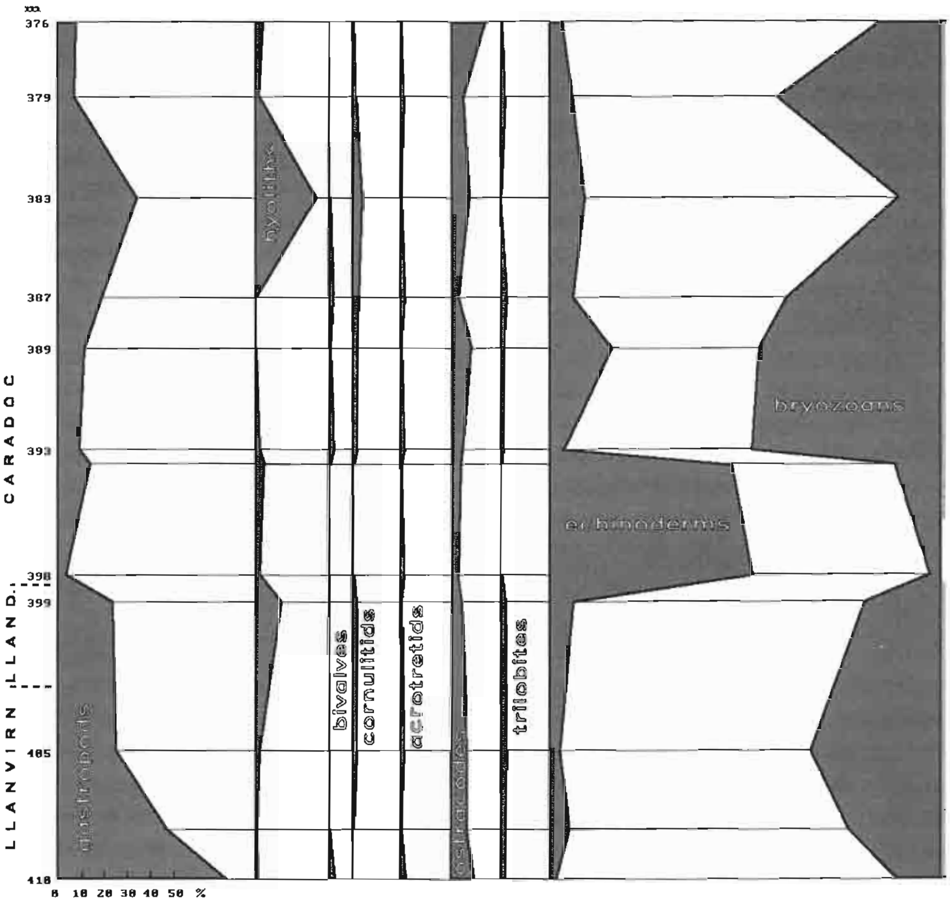

Fig. 17. Logs of per cent contribution of particular groups of phosphatic and phosphatized microfossils to samples taken from the core of Piszcza 26 borehole, Volhynia, Ukraine (based on data of Hynda 1986).

m. The rock matrix is closely similar to that of the Baltic *Orthoceras* limestone, though no macrofossils were identified in the sample.

The most important groups of fossils in typical Ordovician 'small shelly fossils' assemblages are, in order of abundance: molluscs, echinoderms and/or bryozoans, machaeridians, and ostracodes. Subordinately acrotretid brachiopods, calcitic cornulitids, phosphatic tubes of *Sphenothallus*, and conulariids may occur. Among molluscs, the gastropods and bellerophontid monoplacophorans invariably dominate (in Volhynian Novosielki 29 borehole up to 74.4 % of the assemblage). Hyoliths are important, although their contributions vary (in Piszcza 16 up to 25.0 %). Bivalves are rare in the Ordovician 'small shelly fossils' assemblages, with contributions below one per cent. In some samples septemchitonid polyplacophorans, ribeiriid rostroconchs, and *Jinonicella* are common, though they never compete in number with the main groups.

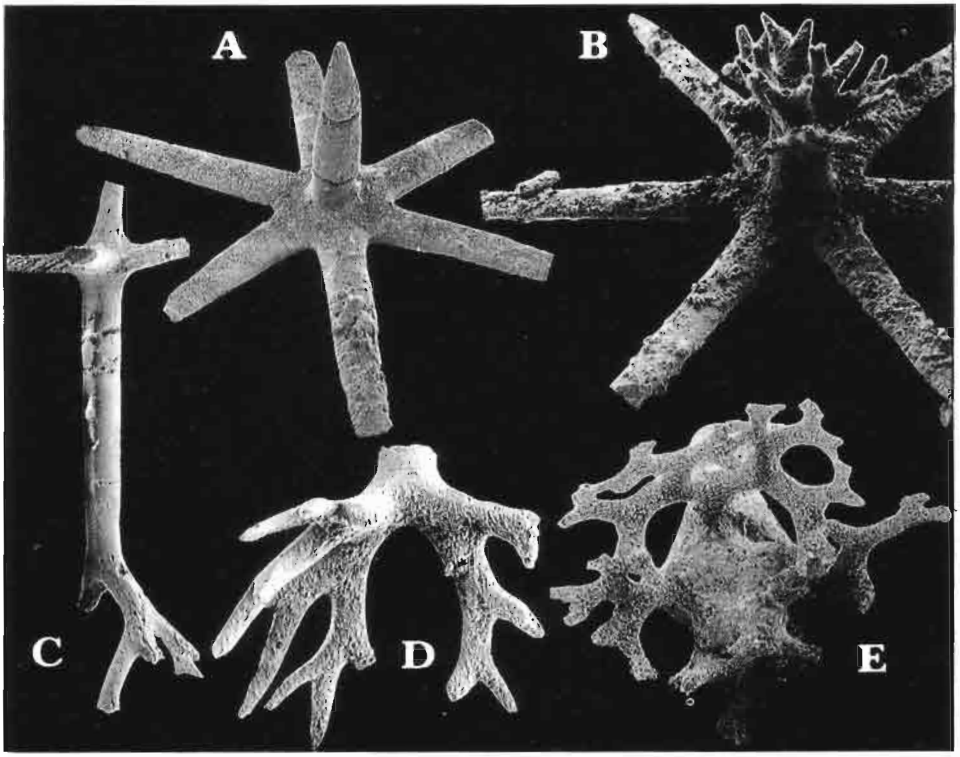

Fig. 18. Ordovician octactinellid spicules with preserved original calcitic composition from Baltic erratic boulders. ❑A–B. Oblique view of spicules with sharp (A, boulder E-326, Llanvirn; × 30) or root-like (B, E-090, Ashgill; × 40) vertical rays. ❑C. Spicule with sharp pointed external ray and dichotomously branching tip of internal ray, E-326, × 35. ❑D. More complete roots from the same sample × 75. ❑E. Anastomosing roots forming a network, E-085, Llanvirn; × 45.

Below particular groups of Ordovician 'small shelly fossil' are reviewed with reference especially to the sample 129s from Lesieniec 1 borehole, chosen as representative for this period.

Sponges

Octactinellids. — Calcitic spicules of octactinellids are common in cephalopod limestones of the Baltic area, sometimes associated with spicules of less certain affinities (Reif 1968). In Mójcza they are commonly enveloped in phosphatic linings (Dzik *et al.* 1993). The octactinellid species occurring in the Baltic Llanvirn has ramified inner ray of its spicules. In some cases they form a basal network (Fig. 18E), presumably delimiting the paragaster wall of the sponge. Such 'arboral' terminations of the main axis have been identified also in Devonian octactinellids (Langner 1991). The surface of well-preserved spicules is completely smooth, and their common occurrence in beds where all aragonitic shells were dissolved,

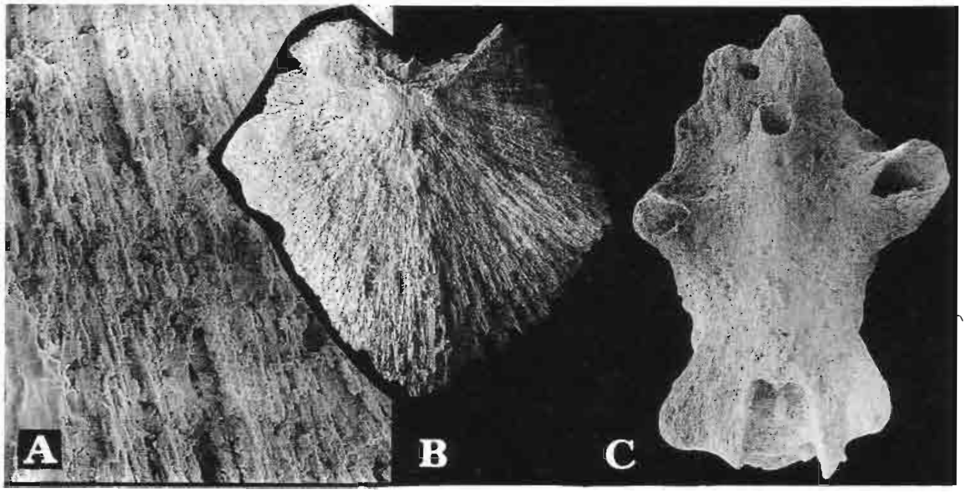

Fig. 19. Phosphatized meroms of the Ordovician receptaculite *Tetragonis murchisoni* Eichwald 1840 showing originally aragonitic radial acicular structure; borehole Lesieniec 1, eastern Poland, sample S-129s, early Caradoc. ❑A–B. Corroded head plate from inner side, × 225 and 45, respectively. ❑C. Head from internal side with partially preserved bases of horizontal spines; × 60.

instead of being transformed into calcitic sparite, suggests original calcitic composition. Relationships between the octactinellids, known since the Atdabanian, and the radiocyathids, probable ancestors of the receptaculites (Nitecki & Debrenne 1979), seem likely. If so, this would require development of more orderly distribution of rays in the course of the evolution, which is a common feature in the phylogeny of sponges.

Receptaculites. – The surface of originally aragonitic receptaculitid meroms was also glossy (Dzik 1992: Fig. 6.3B). In Mójcza and some Baltic boulders, more or less completely phosphatized meroms of *Tetragonis* are common. The phosphatized tissue distinctly shows original radial arrangement of aragonitic acicules in the merom head (Fig. 19A–B). The external surface of the merom head in *Ischadites*, as in many other receptaculitids, bears clear growth lines (Dzik *et al.* 1994), which indicates that the body was not permanently covered with secreting tissue from outside. Although exact affinities of the receptaculitids remain unknown, they are rather zoological, and calcareous sponges are the best candidates for their relatives. It has to be kept in mind, however, that the similarity of the receptaculitid meroms to known sponge spicules is rather superficial. The organization of meroms is not radial, and the subdivision into head, axis, and roots, shared with the octactinellid spicules, may only express similarities in the body plans. Not much support is offered by this new structural evidence on receptaculitids to the idea that they are successors of the radiocyathids (Nitecki & Debrenne 1979), as there is still some controversy regarding the original mineralogy of the latter (see Zhuravlev 1986).

Phosphatic tubes

Sphenothallus. — In their lenticular cross section and laminar phosphatic structure (Schmidt & Teichmüller 1956, 1958) the *Sphenothallus* tubes are closely similar to *Torellella*. Although no longer as common as in the early Cambrian fossil assemblages, these phosphatic tubes are frequent fossils not only in the Ordovician but also in the late Paleozoic (Brood 1988; Van Iten *et al.* 1992). In Ordovician 'small shelly fossils' assemblages only pieces of thickened corners of the tubes and attachment discs ('*Phosphannulus*') are usually found.

Conulariids. — Although some fossil phosphatic tubes of apparently tetraradial symmetry have been reported from strata as old as the early Cambrian in age (Qian & Bengtson 1989; Conway Morris & Chen 1992), undoubted conulariids are only known beginning with the Ordovician. Fragments of their prominently ornamented tests are common fossils in Ordovician 'small shelly fossils' assemblages, but their most typical occurrences are related more to shaly facies.

Calcareous tubes

Cornulitids. — Calcitic tubes of the cornulitids are common fossils in the Ordovician cephalopod limestones and their phosphatic internal moulds form significant parts of 'small shelly fossils' assemblages of this period (Hynda 1986; Dzik *et al.* 1994). The characteristic feature of the cornulitids is the presence of serially arranged internal concentric folds, directed proximally. Such folds are typical also of the tentaculites, which share with the cornulitids calcitic shell microstructure, external ornamentation (with longitudinal striae and transverse annulation), and swollen embryonic parts. The main difference consists in the sessile, cementing mode of life of the cornulitids (instead of freely lying on soft bottoms). They precede tentaculites in time, and the origin of the tentaculites from cornulitids is very likely.

The minute Ordovician cornulitid *Cornulitozoon* has been proposed to be an ancestral solitary bryozoan (Dzik 1991b). If this was really the case, then all these tubular organisms were lophophorates.

Phosphatic dermal sclerites

Palaeoscolecids. — Ornate scales of *Milaculum*, a relative of the Cambrian *Hadimopanella*, with more elaborated external ornamentation and highly ordered pattern of collagen strands in the base (Dzik 1986b), are widespread in Baltic cephalopod limestones, but their contribution is invariably very low and decreasing upwards through the geological time scale. In some samples significant portions of the dermal covers of Ordovician palaeoscolecids may be preserved as the result of extensive secondary phosphatization (Boogaard 1988).

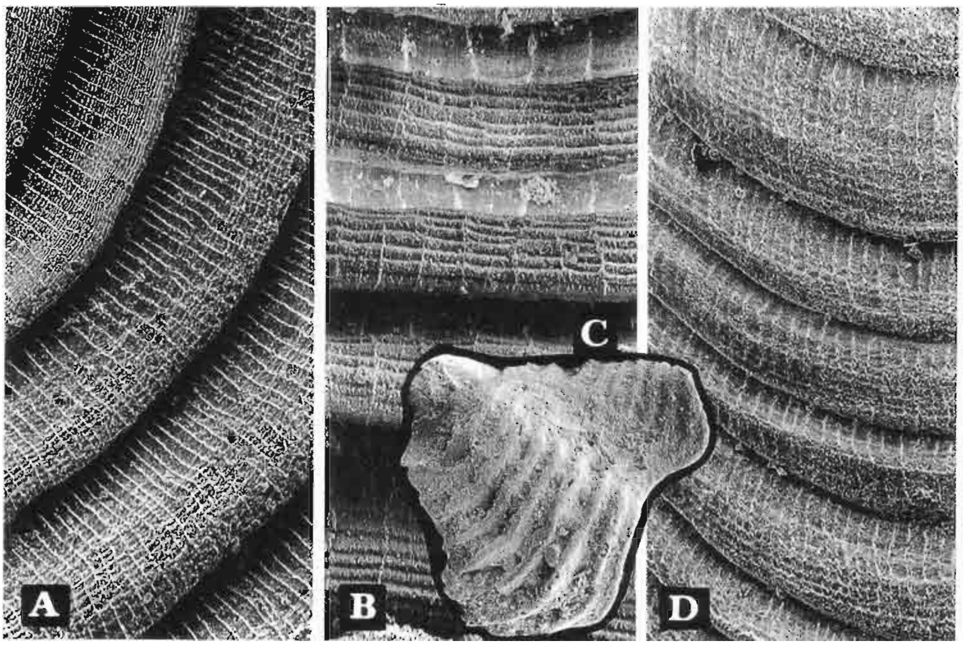

Fig. 20. Sclerite ornamentation of Ordovician machaeridians from Mójcza, Holy Cross Mountains, Poland; interiors of exfoliated phosphatic linings showing the sculpture in negative (A, C–D; × 200) and complete specimen with intact phosphatic lining seen from outside (B; × 50). ☐A. *Deltacoleus* cf. *crassus* Withers 1926, sample MA-99, Late Caradoc. ☐B–C. *Mojczalepas multilamellosa* Dzik 1986, sample MA-85, Middle Caradoc. ☐D. *Aulakolepos elongatum* Dzik 1994, sample MA-99.

Conodonts. — Isolated conodont elements belong to the most important contributors to Ordovician pelagic assemblages, and also among 'small shelly fossils' they are diverse and numerous. However, in the strata most abundant in phosphatized fossils within the Mójcza Limestone, as well as in correspondingly rich Baltic horizons, the contribution of conodonts is relatively low, and some exotic, probably less cold-water elements appear. Low percentage of conodonts in phosphate-rich strata may partially be an effect of increased volume of the acid-resistant residue which masks otherwise rich conodont assemblages.

Scaly armors

Machaeridians. — Calcitic machaeridian plates are among the most numerous microfossils of the Ordovician cephalopod limestone of the Baltic region (Dzik 1986a). They frequently became phosphatized, allowing the observation of details of the external ornamentation on the interior of phosphatic linings (Fig. 20; Dzik *et al.* 1994). Remarkably, along with a distinct rugation and concentric growth lines, the machaeridian sclerites show very characteristic radial striation, which is represented by delicate fissures. I am unable to find any analogue of this kind of ornamentation in other fossil groups.

The only source of information that may allow taxonomic placement of the machaeridians remains the general plan of the armor and the mode of secretion of the plates in the most primitive members of the group. In *Plumulites*, which is definitely the form closest to pre-Ordovician ancestors of the group, the sclerites are very thin and have serially arranged tubular extensions at their apical end. Apparently the thin calcified sclerite enveloped leaf-like body protuberances from its dorsal side and at least marginally from the ventral side (Dzik 1986a). The sclerites were arranged in four longitudinal rows, but the two first body segments had only the median pair of sclerites. The subsequent three 'head' segments had complete sclerite sets but the lateral sclerites were morphologically different from those on the following 'thoracic' segments (Jell 1979). As discussed above, the data on numerical proportions between particular sclerite types in the Cambrian tommotiids suggest similar body organization. If one accepts this model of the tommotiid scleritome their relationships to the true machaeridians would be also consistent with the flat conical initial shape of *Plumulites* sclerites. The problem of the zoological affinities and ancestry of the machaeridians would then be transferred to the earliest Cambrian and could be solved by identifying the tommotiid ancestry.

Soft-anatomy evidence on the Machaeridia (as well as on the tommotiids) is lacking, and there seems to be no way to make a choice between the alternative interpretation of their organization as being related either to the articulates or molluscs (Dzik 1986).

Polyplacophorans. — The earliest undoubted polyplacophorans are represented by two branches: the chelodids with flat, uniformly convex, subtriangular valves, and the septemchitonids with angularly bent, roof-shaped valves. Both groups were already present in the Late Cambrian (Runnegar *et al.* 1979). The overlapping apical parts of the valves of *Chelodes* show distinct growth lines, and their whole external surface is ornamented with minute tubercles (Fig. 21A; Dzik *et al.* 1994) similar to, although less prominent than, those in the septemchitonids (Fig. 21C).

In the oldest well known septemchitonid polyplacophoran, *Matthevia*, each of the pyramidal valves had two internal cavities separated by a thickening of the wall (Runnegar *et al.* 1979). That this was an archaic feature is suggested by its gradual disappearance in the septemchitonids, where it occurs in a clearly recognizable form solely in tail valves of the early Ordovician *Sarkachiton* (Dzik 1986a; Dzik *et al.* 1994). The biologically most significant changes concerned, however, the general shape of the body. In *Matthevia*, the body, with evidently a wide foot, presumably had eight dorsal humps, each armed with a massive valve. There were no such humps in *Septemchiton*, and all the eight plates were roof-like, with flat lateral surfaces (Rolfe 1981). Further evolution led towards an increasingly narrower body and progressively thinner plate-like armor. In the Late

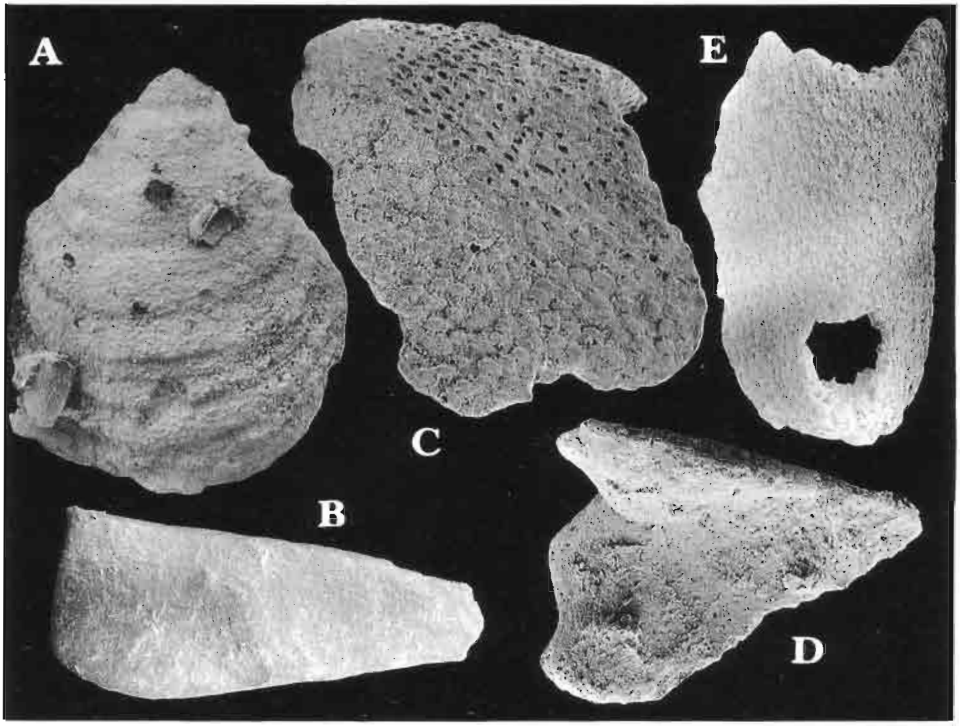

Fig. 21. Phosphatized valves of Ordovician polyplacophorans; all × 50 except B which is × 40. ☐A. *Chelodes* sp. late Caradoc of the Mójcza Limestone, Holy Cross Mountains, Poland, sample MA-4, note surface granulation. ☐B. Solenocaridid *Bursata santacrucensis* Dzik 1994 from latest Caradoc of the Mójcza Limestone, sample MA-99, lateral view of tail valve. ☐C–E. Septemchitonid *Sarkachiton kielcensis* Dzik 1994 from MA-99 (C) and early Caradoc of the Lesieniec 1 borehole, eastern Poland, sample 129s, thoracic (C–D) and tail (E) valves; note spinose appearance of the valve surface.

Ordovician *Bursata* (Fig. 21B) the valves became inversely U-shaped in transverse section, leaving only a narrow ventral fissure for the foot. The process continued further in *Solenocaris* and Silurian *Carnicoleus*.

The polyplacophorans contributed significantly to the 'small shelly fossils' assemblages throughout the early Paleozoic. The Late Caradoc samples of the Mójcza Limestone contain at least four sympatric species of the polyplacophorans. Also in the sample Lesieniec 129s, used here as the model 'small shelly fossils' assemblage of the Baltic Ordovician, 24 valves of an advanced, relatively thin-valved *Sarkachiton* have been found. The same, or closely related species occurs commonly in somewhat older, Llanvirn glacial erratic boulders of Baltic origin and in sections of the Island of Öland.

Mollusc conchs

Both in the Piszcza and Lesieniec Llandeilo and early Caradoc, larval mollusc conchs dominate (Fig. 37). Almost all of them are gastropods and bellerophontids. Among 1358 specimens two species of each of these groups dominate, the bellerophontid *Pharetrolites*(?) contributing 29.8 per cent and platyceratid the *Holopea*(?) *pusilla* 29.4 per cent. In all 18 mollusc species have been identified. Bivalves are virtually absent in this sample, and in all Ordovician samples studied by myself they are very rare, though sometimes well-preserved specimens can be found. Except for sinistrally coiled *Mimospira*, which in this sample contributes 6.6 per cent (being more common in some others), no gastropod species is more common than 4 per cent.

Gastropods. — Although both larval and adult gastropod conchs are common in the Baltic Ordovician, it is extremely difficult to match them with particular species. Apparently most of the larvae represented in pelagic cephalopod limestones had their adults living in much more near-shore environments. Ordovician gastropod larvae had much less diversified morphologies than those of Recent gastropods. Few characters diagnostic for adults are recognizable in the larvae.

The most striking feature of virtually all Ordovician larval gastropods is their loosely coiled first whorl (Figs 22B–C, 23P–Q). The apical, hemispherical part presumably corresponding to the trochophore stage is sometimes separated from the subsequent stages by a slight constriction. The following first coil shows invariably a smaller or larger umbilical perforation in all the bellerophontids (Dzik 1981a) and dextrally coiled Ordovician gastropods (Fig. 23). The remarkable exception are the sinistrally coiled clisospirids (Fig. 22F), with a tight first coil (Dzik 1983) suggestive of lecithotrophic early development, perhaps within egg covers.

Although at least 17 species of gastropods and bellerophontids are represented in the Lesieniec 126s sample, only two make up much more than five per cent of the assemblage. These are a discoidal bellerophontid (Fig. 23F) and the platyceratid *Holopea* (Fig. 23L). This bellerophontid species, named *Tropidodiscus minutus* by Hynda (1986), contributes 29.8 per cent. Juvenile conchs closely similar to the dominant *Holopea* (contributing 29.4 per cent) were described from the early Llanvirn by Hynda 1986 as *H.*? *pusilla.*

Some of the gastropods with a large umbilical perforation had a completely straight initial part of their protoconchs, and the first whorl is much more loosely coiled than the following ones (Fig. 22A, G). Several such forms were illustrated by Bockelie & Yochelson (1979) from the Valhallfonna Formation of Spitsbergen, where they cooccur with *Janospira*. The largest straight protoconch was typical of the Early Ordovician *Eccyliomphalus* and related primitive gastropods with almost planispiral conchs. The eccyliomphalids were traditionally placed close to the straparollids in classification, the idea consistent with the presence of carrier shells among loosely coiled eccyliomphalids (Rohr 1993), but the completely different larval conch morphology contradicts this. Instead, they are more likely to be successors of early pleurotomariids, as proposed by Yochelson (in McLean 1981).

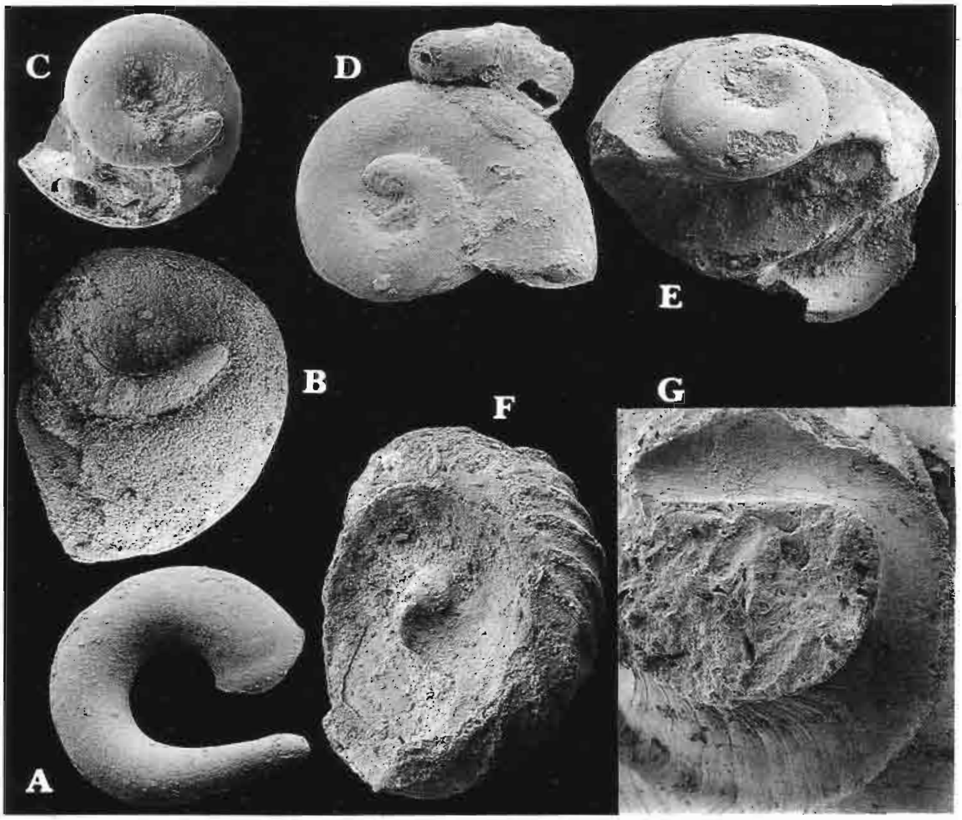

Fig. 22. Juvenile stages of Ordovician gastropods; all × 60 except G which is × 35. ❑A. *Subulites*(?) sp., phosphatic nucleus of veliger(?) conch from Baltic erratic boulder E-175. ❑B. *Subulites*(?) sp. 7, coarsely phosphatized conch from the early Caradoc of Lesieniec borehole, sample 129s. ❑C. Pyritized(?) pleurotomariid conch from boulder E-231. ❑D. Pleurotomariid(?) *'Holopea' obscura* Hynda 1986 from Lesieniec 1 sample 129s. ❑E. *'Holopea'* sp. 5 (aff. *H.? pusilla* Hynda 1986), same sample. ❑F. *Mimospira* sp., same sample. ❑G. *Eccyliomphalus* or *Pararaphistoma* sp. negative impression at the top of phosphatic nucleus of conch umbilicus, boulder E-326; note extremely large umbilical perforation, straight conical larval conch, and sudden appearance of coiling with prominent growth lines developing somewhat later.

Paradoxically, closely similar larval stages have been also identified in the most high-spiral Ordovician gastropod *Subulites* (see Bockelie & Yochelson 1979: Fig. 5C). It appears thus that the eccyliomphalids and subulitids are closely related to each other but not to the straparollids or loxonematids which had completely different larvae (see Figs 23N, 30F *versus* 30G, 35E and Bandel 1991).

Apart from the clisospirids, the only gastropods that show morphologically separated early developmental stages are the trochonematids. The first half-coil is smooth, relatively tightly coiled, with very small umbilical perforation and relatively large apex. Well preserved specimens from the Mójcza Limestone show that the spiral ornamentation appears suddenly,

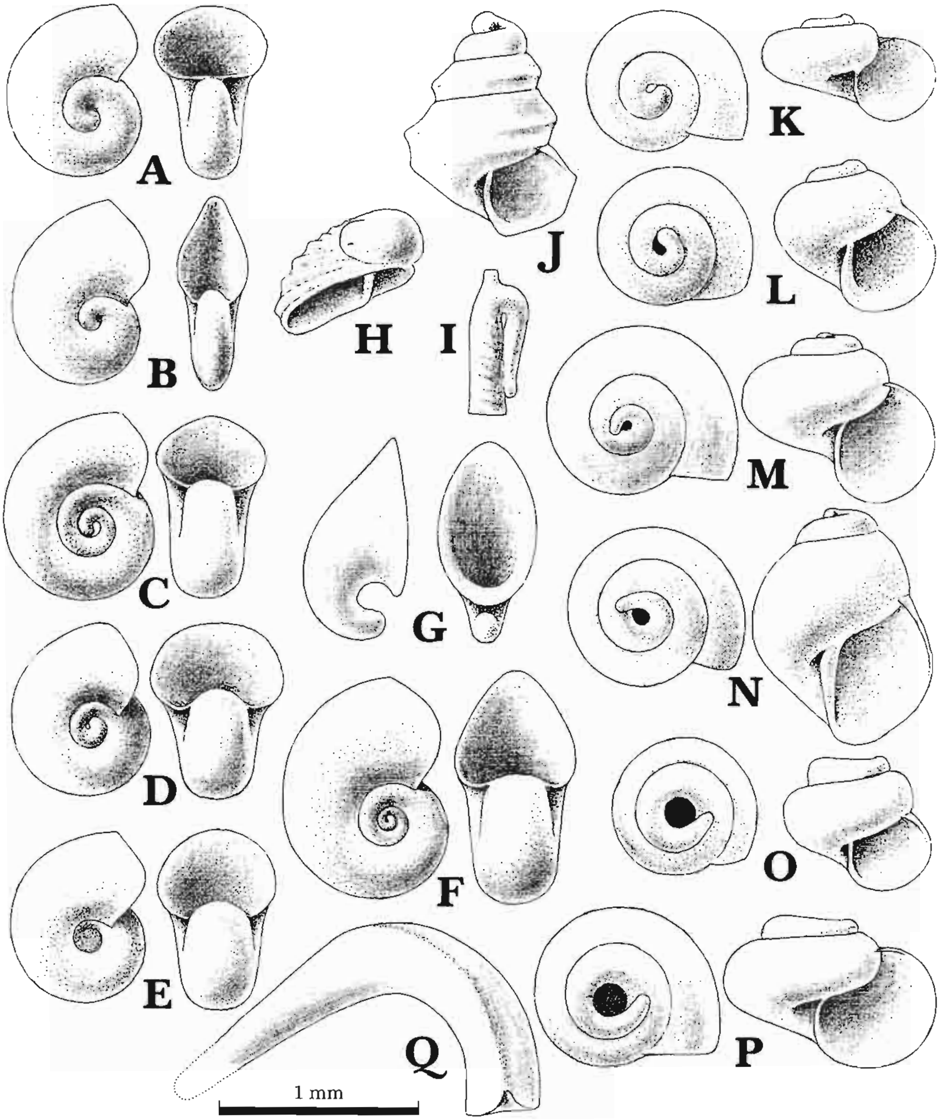

Fig. 23. Diversity of larval and early postlarval gastropod and bellerophontid conchs in sample 129s taken at depth 1337 of the Lesieniec borehole, eastern Poland; early Caradoc, *Baltoniodus variabilis* Subzone. Semidiagrammatic presentation based on camera lucida drawings of phosphatized conchs; growth lines are rarely discernible in the Lesieniec material. ❑A. *Severynella trochlearis* Hynda 1983 (3.9 per cent of the assemblage). ❑B. *Temnodiscus disciformis* Hynda 1983 (3.2). ❑C. cf. *Bucania christianiae* (Koken 1925) (2.6). ❑D. *Kokenospira*? sp. aff. *K. subglobosa* Hynda 1983 (3.8). ❑E. *Sinuites* sp. (0.1). ❑F. *Tropidodiscus (Peruniscus) minimus* Hynda 1983 (29.8). ❑G. *Archinacella*? sp. (0.9). ❑H. *Mimospira* sp. (6.6). ❑I. *Jinonicella* sp. n. (0.8). ❑J. *Trochonema* sp. (2.6). ❑K. '*Straparollus*' sp. (2.9). ❑L. *Holopea*? sp. aff *H.? pusilla* Hynda 1986 (29.4). ❑M. '*Naticonema*' sp. (2.7). ❑N. *Subulites* cf. *revalensis* Koken 1925 (0.8). ❑O. Subulitid similar to PMO NF 3207/5, 4 in Bockelie & Yochelson (1979: Fig. 5F–H) (2.5). ❑P. *Clathrospira*? *obscura* (Hynda 1986) (3.1). ❑Q. *Eccyliomphalus*, *Leseurilla* or *Pararaphistoma* sp. (4.3).

together with distinct growth lines (Dzik *et al.* 1994). This may suggest early development within egg covers. The Ordovician trochonematid protoconchs are coiled in a plane which is slightly oblique to the following whorls.

The remaining gastropod larvae are more difficult to interpret. The most common gastropod group in the Lesieniec sample, also the most diverse taxonomically in the Mójcza Limestone, are the holopeids, ancestral to the late Paleozoic platyceratids.

It would be strange if among the phosphatized juvenile gastropods so abundant in the Baltic cephalopod limestones the pleurotomariid *Clathrospira elliptica* (Hisinger 1839), most common as adults, is missing, although the choice that I made identifying its larvae (Dzik 1978) may not be the proper one. Even if some other protoconch morphology represented in the associated 'small shelly fossils' assemblage belongs to this species, the early stages of the Ordovician pleurotomariids were apparently very close to those of coeval holopeids, presumably members of the trochid branch, as suggested by similarities with late Triassic trochoids (Bandel 1993). All this is in contradiction with ontogenetically late calcification of gastropod protoconchs proposed by Bandel (1982) to be phylogenetically ancient.

Rostroconchs. — Rostroconchs were diverse in the early Paleozoic of Gondwana. Neither bivalves nor rostroconchs were common in the Baltic area before the Late Ordovician warm period. There were only few episodes of significant contribution of the rostroconchs to fossil assemblages of those ages, the most significent being the early Late Cambrian, when the problematic *Tuarangia* invaded Baltica (Berg-Madsen 1987), the early Llanvirn Kundan age with *Eopteria* (Dzik 1992: Fig. 7.2A–D), and finally the early Late Ordovician 'reef' assemblages. Incidentally, these were also epochs of increased bivalve abundance. The only Ordovician 'small shelly fossils' assemblage known to me with abundant rostroconchs is from the Kundan red cephalopod limestones of Gullhögen in Västergötland, Sweden, where *Eopteria* and ribeiriid juveniles occur (Fig. 24D–G). Coeval glauconite limestones of Öland and erratic boulders contain well preserved phosphatized juvenile bivalves and also adults.

Janospira from the Llanvirn of Spitsbergen, with spiral larval shell, and *Jinonicella*, known from the Llandeilo, with straight, only adaperturally coiled larval shell (Fig. 13D), are possible successors of Cambrian *Yochelcionella* (Runnegar 1977; Pokorný 1979). The Lesieniec 129s sample yielded 11 specimens of *Jinonicella*, common also in coeval strata of Volhynia, Ukraine (Hynda 1986).

Bivalves. — Until the Late Ordovician, bivalves are of minor importance in 'small shelly fossils' assemblages. Some of the rare specimens are well preserved and show a rather simple course of early ontogeny with a hardly discernible embryonic or larval stage (Fig. 24A). It seems that larvae were free-living and planktotrophic and did not undergo profound anatomical transformations in metamorphosis.

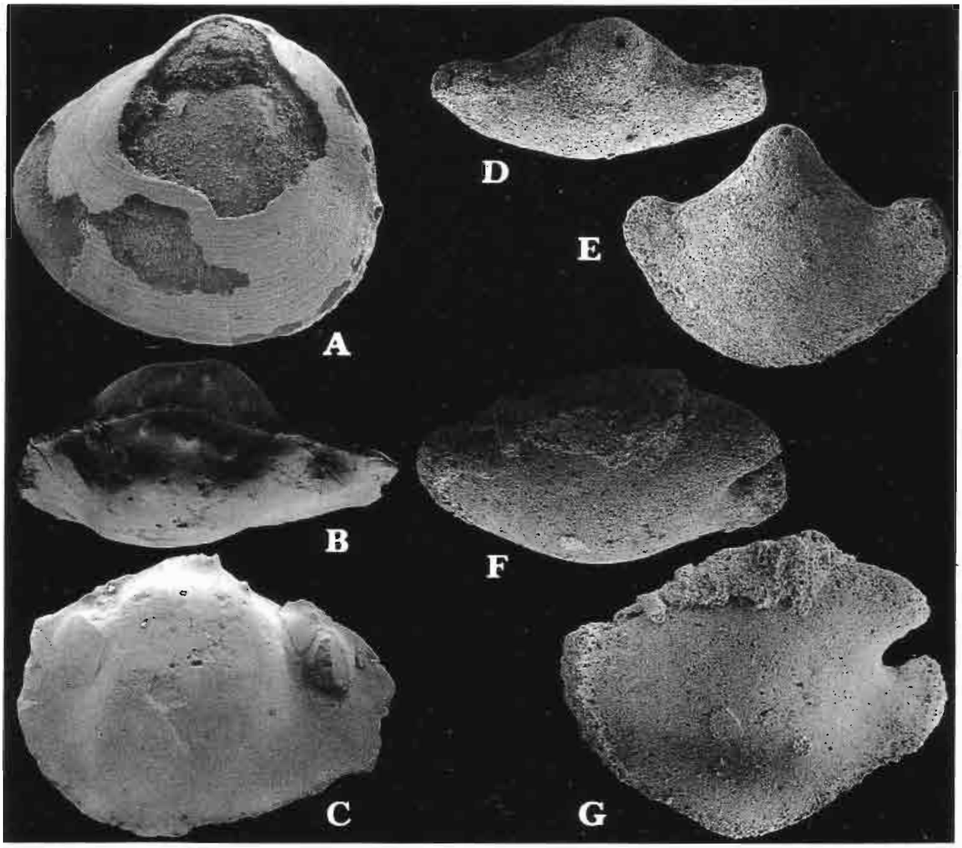

Fig. 24. Juvenile stages of Ordovician bivalves and rostroconchs from the Baltic early Llanvirn (late Kundan). ❑A–C. Primitive nuculid from erratic boulder E-079, external view of phosphatized shell (A, × 45) and phosphatic nucleus in oblique dorsal and lateral views (B–C, × 30) with prominent replicas of muscle scars. ❑D–E. *Eopteria* sp., phosphatic(?) shell nucleus from Gullhögen quarry, Västergötland, Sweden, note hemispherical embryonic part; × 35. ❑F–G. Undetermined ribeiriid from the same sample; × 30.

Hyoliths. – In the Baltic Ordovician hyoliths are second to gastropods in abundance among phosphatized 'small shelly fossils', though ratios between these two fossil groups vary (Fig. 17). In environments producing phosphatic internal moulds, the fossilization potential of larval conchs is obviously much higher than that of opercula, but in some samples, with calcareous fossils entirely replaced by calcium phosphate, opercula may dominate (Dzik *et al.* 1994). In the sample Lesieniec 129s, 62 conch internal moulds were associated with 61 opercula. Although the dominant conch species of *Recilites* is represented by opercula (13 specimens; Fig. 25A), opercula of *Carinolites* dominate, which is of secondary importance among conchs (only 7 specimens; Fig. 25C). Together at least six hyolith species occurred in this sample, which is by no means unusual (see Dzik *et al.* 1994).

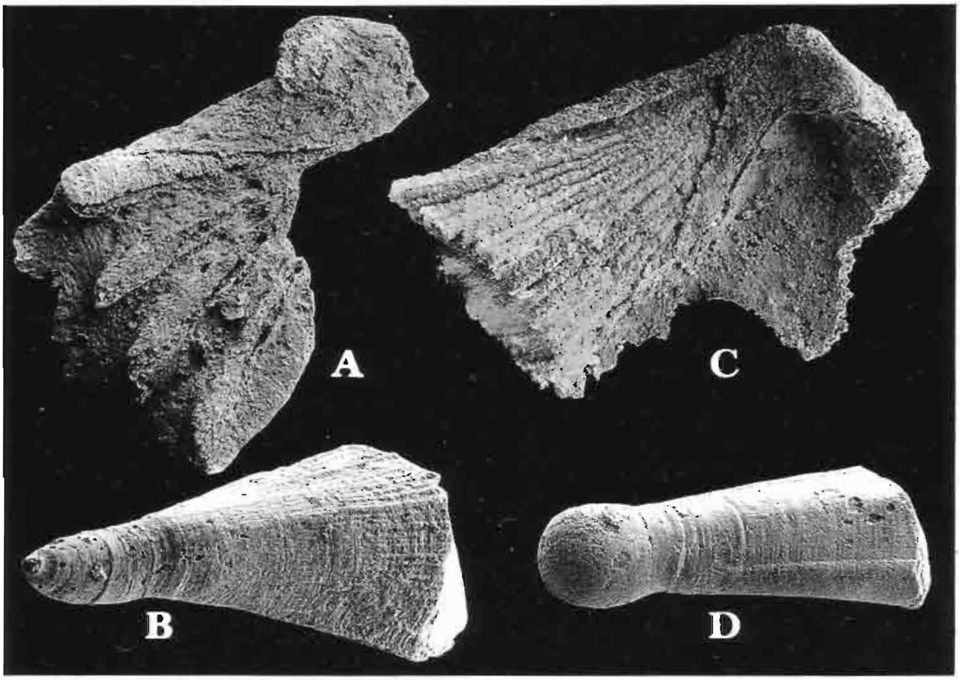

Fig. 25. Ordovician hyolithid opercula from the early Caradoc sample 129s of the Lesieniec 1 borehole, eastern Poland and probably congeneric larval conchs (increased mortality at this size class suggests metamorphosis) from the Baltic erratic boulder E-113, late Llanvirn *Eoplacognathus robustus* Zone; all × 70. ❑A–B. *Leolites* sp. ❑C–D. *Carinolithes* sp.

Ordovician hyoliths are much more diverse than their early Cambrian relatives in respect to various modes of larval development and internal organization of opercula. Whereas virtually all Cambrian hyoliths had relatively small, mucronate protoconchs, in the Ordovician there also occur those with subspherical, smooth apices of large size (Fig. 25B, D; see Dzik 1978, 1980). Very sophisticated patterns of cardinal processes and clavicles are represented among hyolithid opercula of Ordovician age (see Marek 1963, 1967).

The role of hyoliths in the Ordovician small shelly fossils assemblages seems thus only slightly less important than in the Tommotian, although the hyolithids with elaborated opercular morphology dominate there instead of circothecids (which continued at least till the end of the Ordovician).

Late Silurian assemblage

The Silurian 'small shelly fossils' assemblages discussed below was recognized in a loose block of cephalopod limestone collected at the Cellonetta Lavinerinne in the Carnic Alps, Austria, derived from the Ludlow part of the Kok Formation. Although several more samples were taken from the exposure, the exact bed (see Walliser 1964) from which the boulder originated has not been identified. The only macrofossils recognizable in the block are orthoconic nautiloids. All the Kok Formation 'small shelly fossils' assemblages assemblage have structures different from those of the Ordovician, not only from the Baltic region and the Holy Cross Mountains, but also from Siberia and the North American Midcontinent. A randomly selected portion of 368 phosphatic fossils from the Cellonetta sample revealed the following: along with echinoderm sclerites (41.0 per cent) and gastropods (16.3 per cent), which are also numerous among the Ordovician 'small shelly fossils', there are abundant juvenile bivalves that outnumber other molluscs (33.4 per cent). The relation between larval gastropods and bivalves in pelagic environments above the sediments rich in 'small shelly fossils' was thus reversed during their evolution between the late Ordovician and late Silurian. This corresponds to an increase in diversity of the bivalves in the corresponding time span (Fig. 37).

In addition the contribution of the machaeridians to the Silurian assemblage is much lower (only 2.2 per cent and single a species) than is usual for the Ordovician samples, and hyoliths, although present, are not significant members of the assemblage. Other groups encountered already in the Ordovician, like trilobites, ostracodes, *Sphenothallus* tubes, conulariids, calcareous sponge spicules, and receptaculites, continue in low numbers but have a steady presence. The only completely new group of fossils are phosphatized telson spines and mandibles of archaeostracan Crustacea (see Dzik 1979).

Sponges

Octactinellids. — Spicules closely similar to those of *Anomaloides reticulatus* Ulrich 1878 from the Maysvillian of Kentucky and Malongulli Formation of New South Wales, which is probably identical with *Vaccipraticola ypsilon* of Nilsson & Bengtson (1982) from the Ashgill of Scania (Webby & Trotter 1993), are common fossils in the Kok Formation (Fig. 26C–D). Their three flattened horizontal rays, each with a medial furrow, and rudimentary ones in between, meet in the center with sharply pointed vertical rays. This allows derivation from typically developed octactinellid spines but definitely not from the receptaculitid meroms, as suggested by Rigby (in Webby & Trotter 1993). The *Anomaloides* spicules were most likely calcareous, perhaps calcitic in composition, like those in the octactinellids.

Receptaculites. — Least common phosphate-coated spicules of the Kok Formation are probable receptaculitid meroms without head plates (Fig. 26A–B). As in other receptaculitids, which in the Siluro-Devonian are typical of shallow-water reefal environments, the upper and lower of the vertical rays are not in the same line, and the transverse rays are flattened.

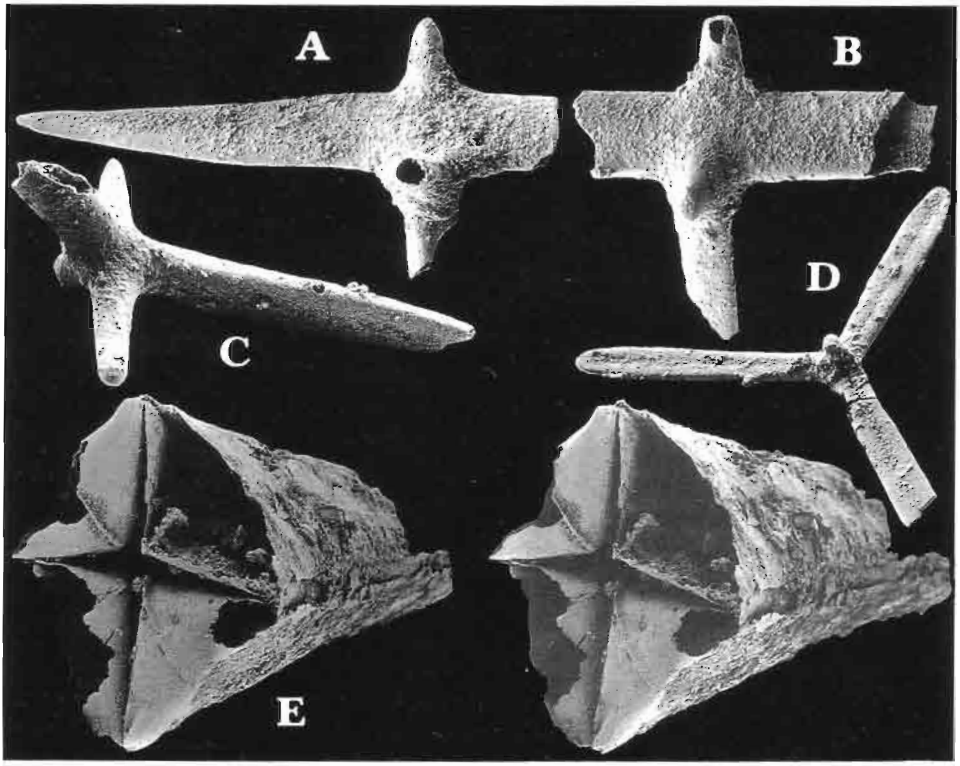

Fig. 26. Phosphate-coated meroms of an unnamed receptaculitid (A–B), octactinellid(?) sponge *Vaccipraticola* (=*Anomaloides*) cf. *reticulata* (Ulrich 1878) (C–D), and stereopair of a juvenile conulariid (E) from the Ludlow of the Kok Formation of Cellonetta Lavinerinne, Carnic Alps, Austria; A–C × 75, D–E × 45.

Such a morphology is suggestive of a secondary reduction of the skeleton in this unnamed Silurian receptaculitid.

Along with sponges, the assemblage from Cellonetta contains also delicate ramose bryozoans (fenestellids), but their role is less important than in corresponding Ordovician assemblages.

Phosphatic tubes

Sphenothallus. — Problematic *Sphenothallus* tubes and their isolated attachment discs ('*Phosphannulus*') are common Silurian fossils (i.a. Brood 1988; Van Iten *et al.* 1992) although, as in the Ordovician, they are rarely as abundant as their ancestors, torellellids, in the Cambrian. In Cellonetta they contribute only 1.0 per cent to the assemblage.

Conulariids. — Of similar low importance are the conulariids. Among the few specimens found in Cellonetta are also weakly phosphatized juveniles, one specimen preserving its closed aperture (Fig. 26E). Usually only well mineralized, serrated transverse ridges are preserved, both in articulated macrofossils and as isolated pieces among 'small shelly fossils'.

The thin organic or phosphatic tests of the conulariids owe their square cross section to a special mode of closure of their apertures (Kowalski 1935), an analogue of which can be found in the Japanese art of folding paper — origami. To produce this kind of aperture closure contraction of the muscles attached to four points at the margin of the test was necessary. As a result, the adapertural part of the test was folded inside to form a kind of box. Tri-, penta-, or hexagonal conulariid tests are known which require respective number of muscle sets. The tests of ancestral conulariids, before they developed the mechanism of 'origami' closure, were apparently cylindrical, with tetraradial symmetry expressed only in the number of internal septa. Such an organization is actually known in the circoconulariids of Bischoff (1978).

It appears thus that the tetraradial symmetry of the conulariids by itself does not provide conclusive evidence of their allegedly scyphozoan affinities. The radial internal organization is also typical for the nemathelminthes and especially the tests of the Cambrian hexaconulariids (see Conway Morris & Chen 1992) show some similarity to those of larval priapulids although their distinctly separated larval parts were closed apically which indicates either lack of an anus or a U-shaped gut.

Some functional problems arise, however, if other than coelenterate nature of the conulariid animal would be accepted. The 'origami' folding of the aperture must have resulted in a significant decrease in volume of the test, so that a certain amount of water had to be released. This could be done easily only if the animal had a large water-filled gastric cavity, thus being rather of coelenterate than nemathelminthan organization.

Phosphatic dermal sclerites

Conodonts occur in all the samples of the Kok Formation with phosphatized fossils, and the most common species are typical for rather offshore environments. Although in coeval shallow-water environments of the Baltic area and elsewhere thelodonts and acanthodian fish and scales are abundant, they have not been encountered in the Carnic Alps assemblages of 'small shelly fossils'. The reason may be both deeper sea and colder climate.

Scaly armors

Machaeridians. — Machaeridians continued to be diverse and common fossils in the Silurian although their diversity seems to be lower than in the Ordovician. In the Cellonetta assemblage excellently preserved secondarily phosphatized plates of *Aulakolepos* occur. Their surface ornamentation is preserved in detail, nicely showing the presence of radial minute fissures intersecting the concentric annulations (Fig. 27), earlier recognized in congeneric Ordovician sclerites (Fig. 20D). Near the posterior margin of the plate a kind of terrace lines developed along these fissures.

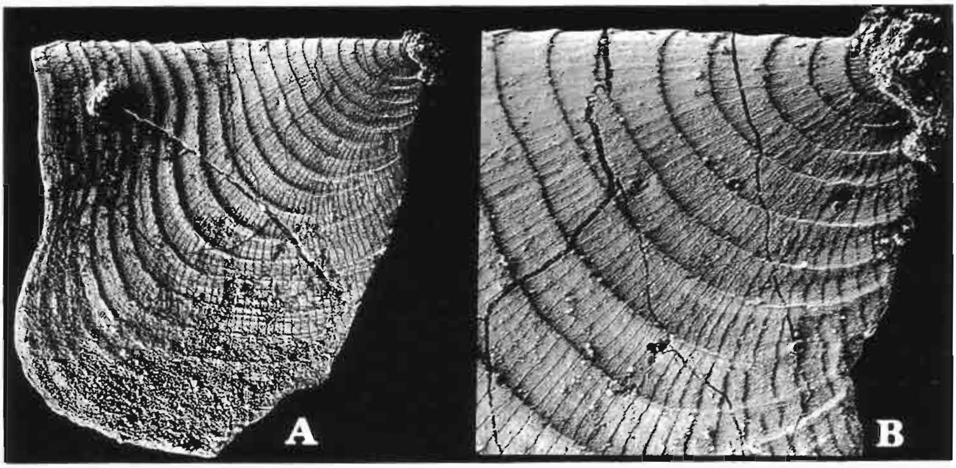

Fig. 27. Silurian machaeridian *Aulakolepos* from the Ludlow of the Kok Formation of Cellonetta Lavinerinne, Carnic Alps, Austria; dorsal sclerite coated with phosphate in lateral view (A, × 70) and magnified apex (B, × 200).

Polyplacophorans. — Although the chelodid polyplacophorans were not uncommon as macrofossils in the Silurian, their once diverse relatives, the septemchitonids, left only one highly derived lineage, represented in Cellonetta by *Carnicoleus* (Dzik 1993). Like the septemchitonids in the Ordovician cephalopod limestones, the Silurian *Carnicoleus* occurs in low numbers in the Kok Formation samples being dominated by associated lepidocoleid machaeridians. The first identified *Carnicoleus* specimens (Dzik 1986a) from a sample collected in the Rauchkofel Süd locality (near Valentin Törl) represented halves of two large thoracic valves. In their asymmetrically sinusoidal cross section (Fig. 26H) they closely resemble complete sclerites of *Aulakolepos*. The difference consists in pseudoporous walls and lack of any adductor muscle attachments, otherwise typical of the machaeridians, in *Carnicoleus*. That it was not a machaeridian is proven by the presence of juvenile thoracic valves of the same wall structure and external ornamentation (Fig. 28C) in a sample taken from the Cellonetta Lavinerinne.

The Cellonetta specimens are smaller than those from Valentin Törl, and their width is smaller than height. The body was thus more or less laterally flattened. The degree of flattening is inversely correlated with size (Fig. 26E–G). Except for a single specimen of a juvenile tail valve, in which lateral margins leave a narrow gap along the venter thus giving an inversely U-shaped cross section, all the complete specimens from Cellonetta have the ventral margins of their valves merging ventrally (Fig. 28E). All this suggests that only at the earliest ontogenetic stages was the armor of *Carnicoleus* opened ventrally and was able to grow by free marginal accretion. After the margins met each other at the midline, some plastic deformation of the dorsal part of the valve appeared necessary so as to accommodate the geometric constraints. To enable growth, a kind of

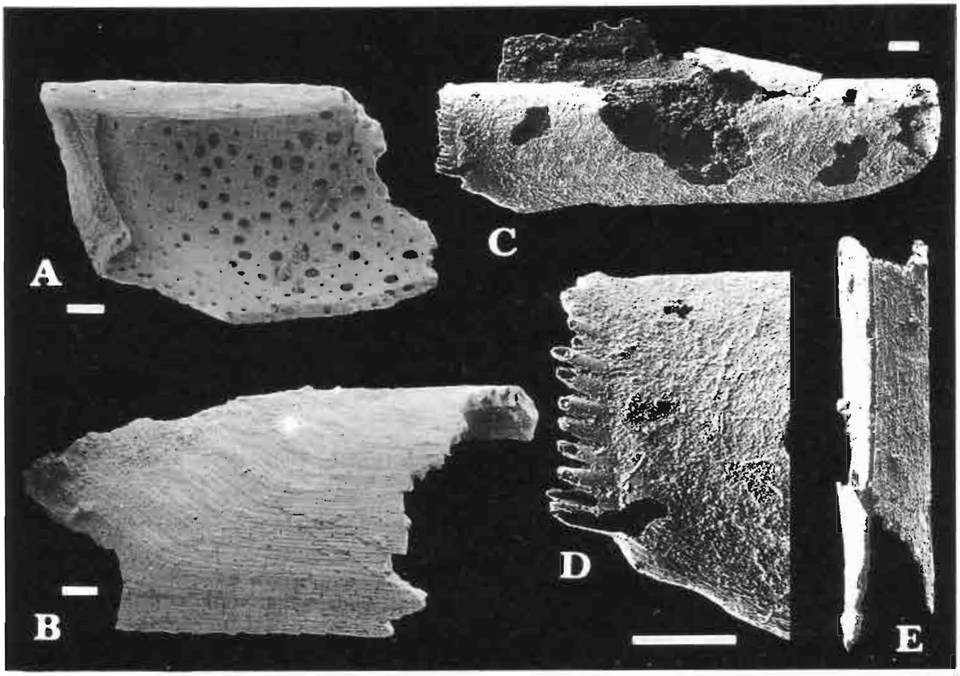

Fig. 28. Phosphatized thoracic valves of the Silurian septemchitonid *Carnicoleus gazdzickii* Dzik 1986 from the Ludlow of the Kok Formation of the Carnic Alps, Austria. ☐A–B. Adult valves split in halves from Rauchkofel Süd, interior and external surface; × 50. ☐C–D. Juvenile valve from Cellonetta Lavinerinne in lateral view (note exfoliated external phosphatic lining showing surface ornamentation in negative; × 40) and magnification of marginal spines; × 140. ☐E. Juvenile valve from the same locality in ventral view, note ventral margins in touch; × 50.

imperfect dorsal ligament had thus to develop medially, in a similar manner to that of the rostroconchs (Pojeta & Runnegar 1976). Subsequent growth resulted in a gradual increase in the width of valves and finally their dorsum developed a longitudinal concavity (Fig. 29H). The 'ligament' area was evidently weaker than the rest of the valve and this is the probable cause of the common presence of medially split larger valves, and the reason of their *Aulakolepos*-like appearance.

The only known juvenile tail valve has its external phosphatic coating exfoliated. The tail valve was evidently very elongate, perhaps even more than here reconstructed (Fig. 26A–B), and probably the armor had proportions similar to the Ordovician probable septemchitonid *Solenocaris*. The single valve which is not completely tubular in appearance and widely gapes anteroventrally is provisionally interpreted here as the second in the armor, although its slightly more robust ornamentation makes the specific identification uncertain. If properly identified, the morphology of this valve suggests the presence of an anteriorly directed rudimentary foot.

The differences in transverse section of valves of various size in Caradoc *Bursata* from the Mójcza Limestone (Fig. 26I–K) and their fre-

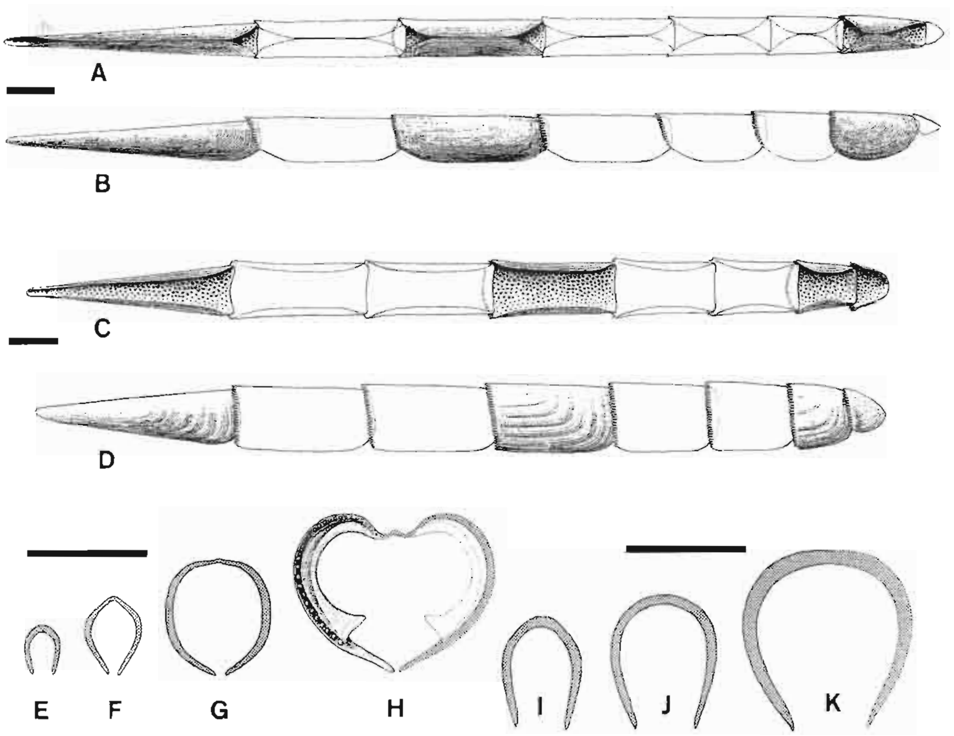

Fig. 29. Reconstruction of body armors of early Palaeozoic solenocaridid Septemchitonida in ventral and lateral views, and camera lucida based cross sections of sclerites of various sizes. Bar scales 500 µm. □A–B, E, H. Silurian *Carnicoleus gazdzickii* Dzik 1986 from the Ludlow of the Carnic Alps, Austria. Specimens E–G from Cellonetta Lavinerinne, H from Rauchkofel Süd. □C–D, I–K. Ordovician *Bursata santacrucensis* Dzik 1994 from the latest Caradoc of the Holy Cross Mountains, Poland.

quent medial splitting also suggest an incipient bending zone along the dorsum. The pseudopores of *Bursata* and *Carnicoleus* are likely to be homologous to the polyplacophoran esthetes, which can be expected to occur in all primitive chitons. If *Carnicoleus* is a successor of typical septemchitonid polyplacophorans of the Ordovician, *Bursata* being the connecting link, the change from inversely V-shaped cross section of Early Ordovician septemchitonid valves, through U-shaped section in *Bursata*, to valves ventrally closed in *Carnicoleus* can be reasonably interpreted as an expression of progressive reduction of the foot.

There is thus a clear time polarity in the subsequent appearance of increasingly narrower body proportions of the septemchitonids, from the robust Late Cambrian *Matthevia*, through elongated *Sarkachiton* (Llanvirn), subcylindrical *Bursata* (Caradoc), to complete closure of the ventral foot openings in *Carnicoleus* (Ludlow). All stages were associated with changes in the valve structure making them thinner and more flexible, at least along the dorsum. These peculiar organisms, possibly ancestral to the Recent solenogasters, convergently to the machaeridians developed body organization of a 'segmented clam' and convergently to the rostroconchs a dorsal 'proto-hinge', enabling modification of the valve shape during its growth. If the trend is extrapolated further a body organization of the solenogasters can be produced, with a thick elastic cuticle armed with spines, both mantle folds merging ventrally along the foot fissure and openings at the anterior and posterior ends of the cylindrical body. It is not clear whether the spines arming the valves in *Carnicoleus* are incorporated mantle spicules or are newly developed structures, analogous to spines arming the machaeridian plates.

This fossil material may offer a solution to the long dispute as to which of the aplacophorans are the most primitive. It seems to show that the solenogasters are direct successors of the septemchitonid polyplacophorans.

There is no good reason to assume that the oldest mollusks were similar to the Recent wormlike plateless aplacophorans, as accepted by most zoologists (see Haszprunar 1992).

Mollusc conchs

Monoplacophorans. — Although the tryblidiid monoplacophorans are not common fossils in the Silurian at least two species are represented in the Cellonetta sample. Their protoconchs are disc-shaped (Fig. 30A), as in their Recent successors.

Unlike the Ordovician assemblages of a similar kind, the bellerophontids are rare in Cellonetta. Subsphaerical typical bellerophontids and disc-shaped forms are represented among juveniles, but their species-level classification remains a difficult undertaking.

Gastropods. — The overwhelming majority of gastropod juveniles from Cellonetta belong to *Naticopsis*-like platyceratids with narrow umbilicus (Fig. 30H–I). At least two species are represented, being different in whorl expansion rate and height of spire. The higher-spire species is relatively rare. Perhaps the genus *Platyceras* itself may be represented by juveniles with larger apex and more loosely coiled first whorl (Fig. 30D). Another kind of juvenile, low-spire and with open umbilicus, may be conspecific with adults identified as *Umbospira nigricans* by Heritsch (1929) from the same strata (Fig. 30B).

Two kinds of Cellonetta gastropods are of Ordovician aspect. One of them has a small apex and large umbilical opening and may be of subulitid or pleurotomariid affinities (Fig. 30F). The second bears a strong resemblance to the eccyliomphalids (Fig. 30E) and may correspond to adults identified as *Lytospira subuloidea* by Heritsch (1929).

Some high-spired gastropods are also present in the assemblage. The very narrow, almost fusiform larval shells almost certainly represent some of the Kok Formation loxonematids (Fig. 30G), which is consistent with the apex morphology in Carboniferous and Triassic members of the group illustrated by Herholz (1992) and Bandel (1992). Affinities of the more robust form remain uncertain.

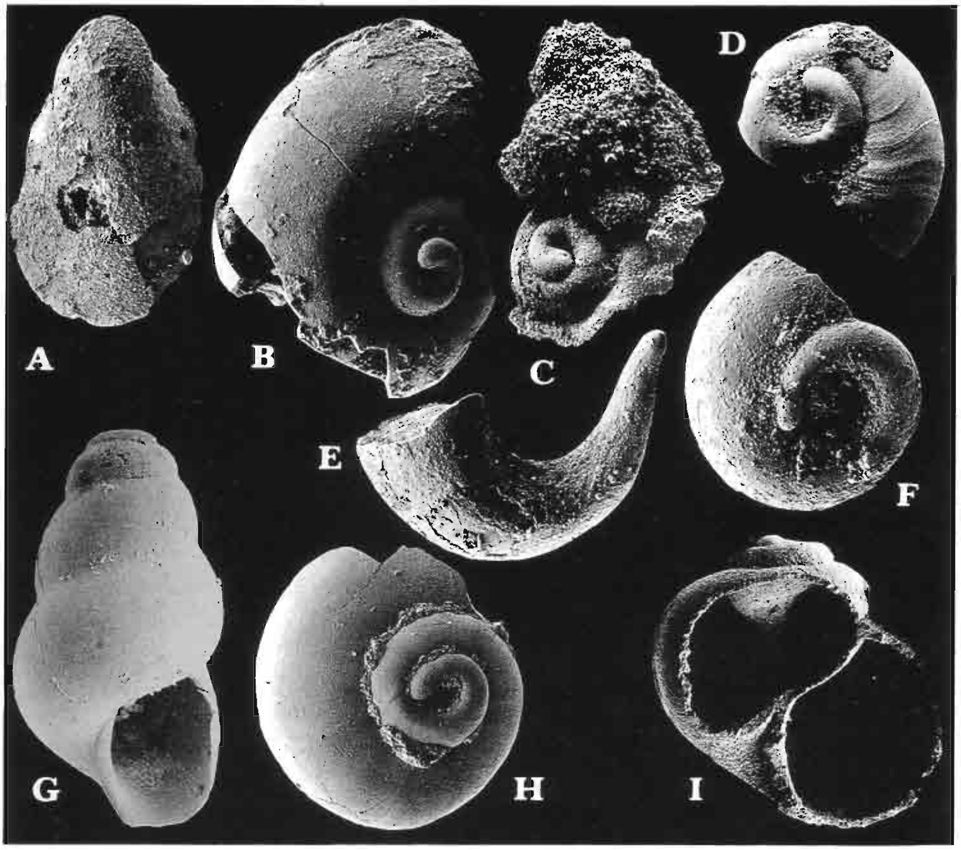

Fig. 30. Juvenile Silurian monoplacophoran and gastropod conchs from the Ludlow of the Kok Formation of Cellonetta Lavinerinne and Rauchkofel Süd (G), Carnic Alps, Austria; conchs preserved as phosphatic linings or pyritized; all × 60. ☐A. Monoplacophoran *Pilina* sp., note typically tryblidiid flat embryonic conch. ☐B–C. Open umbilicate gastropod possibly conspecific with *Umbospira nigricans* as understood by Heritsch (1929). ☐D. '*Platyceras otiosum*'. ☐E. '*Lytospira subuloidea*'. ☐F. Undetermined pleurotomariid. ☐G. *Loxonema propinquum* or *Holopella trochlearis* of Heritsch (1929). ☐H–I. '*Naticopsis plicatula*'.

Rostroconchs. — True rostroconchs in the Silurian are generally confined to shallower environments, and they are missing in the Kok Formation.

Of much interest is the occurrence of well preserved, though rare, specimens of *Jinonicella kolebabai* Pokorný 1978 (Fig. 13E). It differs from the Ordovician species of Hynda (1986) in that its initial part more tightly adheres to the tube. Although the phosphatic envelope is too thick to express fine details of the external ornamentation, it is clear that the strong growth lines developed immediately after completion of the coiled part of the shell. It seems thus probable that the initial part, 'creeping' over the tube, was the larval conch, and the snorkel at the end of tubular adult conch developed after metamorphosis. The mode of early development was thus analogous, though rather not homologous, to that in the eccyliomphalid gastropods. The spire of the Ordovician *Janospira* can be interpreted in the same way but, if the jinonicellids are successor of *Yochelcionella*, much change in larval development had to take place between the Middle Cambrian and Early Ordovician. A similarity of *Jinonicella* to early postlarval stages of scaphopods (Engeser *et al.* 1994) is remarkable.

Bivalves. — Larval and early postlarval shells of the bivalves dominate the Silurian 'small shelly fossils' assemblages of the Kok Formation (Fig. 37). Among 906 completely preserved bivalve shells selected from the Cellonetta sample, 64.0 per cent are those of a species with relatively flat, oval valves (Fig. 31L). Larval hinge with numerous minute teeth along the dorsal valve margin and a series of slightly larger teeth below the beak show some cyrtodontid affinities but do not allow more precise taxonomic placement. Specimens more triangular in shell outline (Fig. 31H–I) may represent related species. Similar affinities are also possible for flat shells with high umbo, contributing only 0.7 per cent to the whole assemblage. Some rare high-triangular valves are characteristic in having very weak crenulation along the posterodorsal margin ond only a few teeth below the beak (10) (Fig. 31J–K).

Less numerous (13.5 per cent) is a more definitely cyrtodontid species with much more robust and convex valves and stronger central teeth series (Fig. 31B, E). The external surface of its valves is ornamented with concentric rugae.

Similar but even stronger rugation characterizes globular, *Paracyclas*-like shells with less prominent hinge teeth (Fig. 31A, C), representing the third most abundant species (8.6 per cent) of the same group. It appears thus that more than 85 per cent of the bivalves in this assemblage are anisomyarians and perhaps also early heterodonts.

An important large group of bivalves in the Cellonetta assemblage are thin-shelled forms resembling the cardiolids. They represent 8.4 per cent of the sample. Their larval shells are more or less smooth, and the metamorphosis is prominently expressed in a sudden change of ornamentation from concentric growth lines to a complex reticulate pattern (Fig. 32A). The early postlarval hinge is composed of taxodont teeth more or less uniform in size (Fig. 32C). This is consistent with the presence of adult taxodont hinge in the cardiolid *Slava* from the Ludlow of Bohemia (Křiž 1985: Pl. 10: 7–9) and strongly suggests their palaeotaxodont nature. The most common species in its almost circular outline of the larval shell resembles juvenile stages of a cardiolid from the Wenlock of the Carnic Alps named by Křiž (1974) *Carnalpia rostrata*, but may just represent a generalized cardiolid larvae (Fig. 32A; see i.a. Křiž 1979: Pl. 10: 2, 14: 3).

Two more possible cardiolid species are present in the sample, both showing a change to a rhomboidal shape after metamorphosis (Fig. 32B), which makes them closely similar to early postlarval stages of *Butovicella* as described by Křiž (1969, Křiž & Serpagli 1994; according to him the genus is fairy closely related to the modiomorphids). The species differ

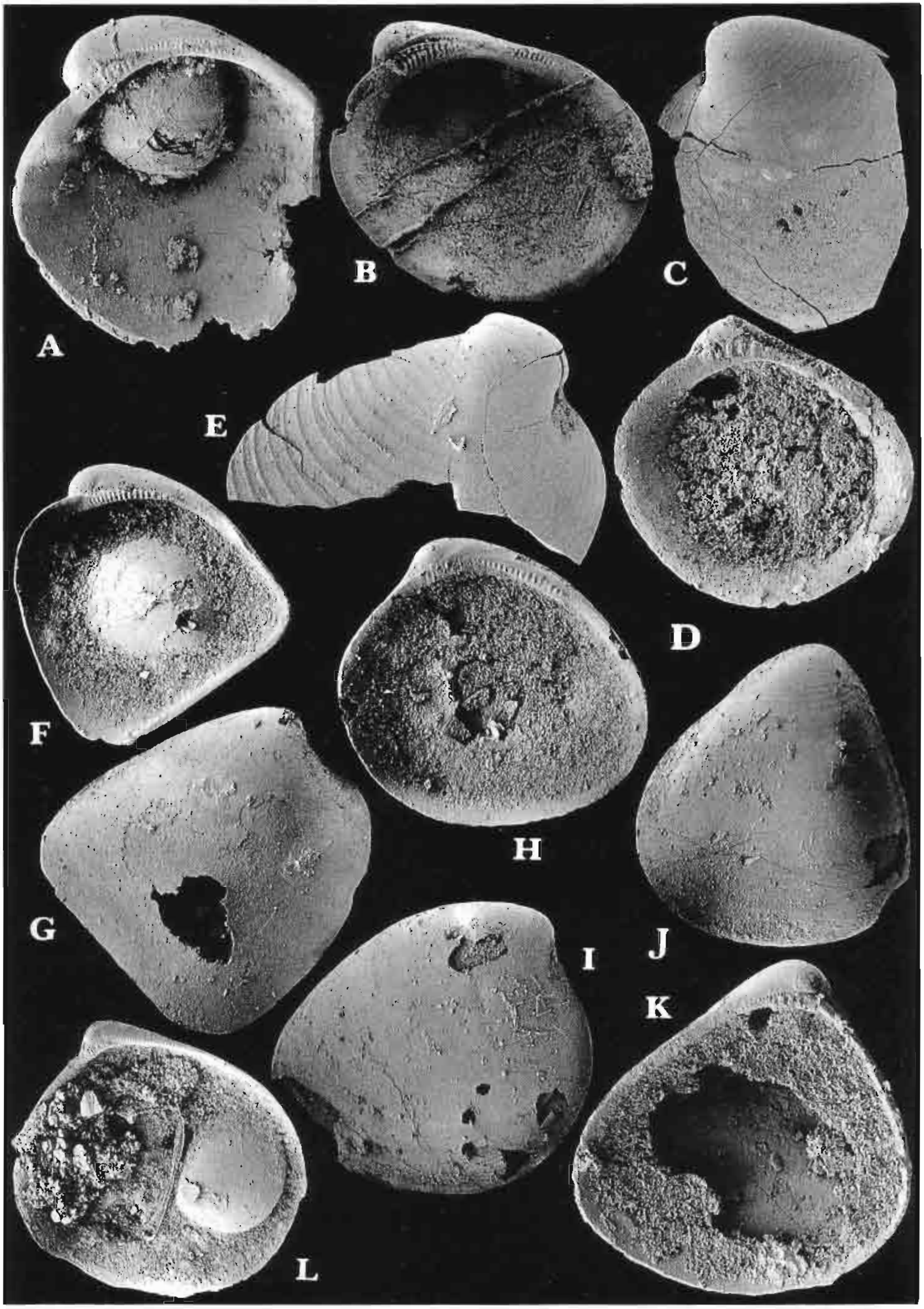

Fig. 31. Silurian cyrtodontid and related bivalves from the Ludlow of the Kok Formation of Cellonetta Lavinerinne and Rauchkofel Süd (B), Carnic Alps, Austria; valves preserved as phosphatic linings or pyritized. ❑A, C–E. Cyrtodontid sp. 6, A and C × 45, D × 90. ❑B, E. Cyrtodontid sp. 5; × 60. ❑F–G. *Spanila*? sp. 1; × 60 and × 45, respectively. ❑H–I. Gen. indet. sp. 8a; × 60. ❑J. Gen. indet. sp. 8; × 35. ❑K–L. Gen. indet. sp. 10; × 54 and × 60, respectively.

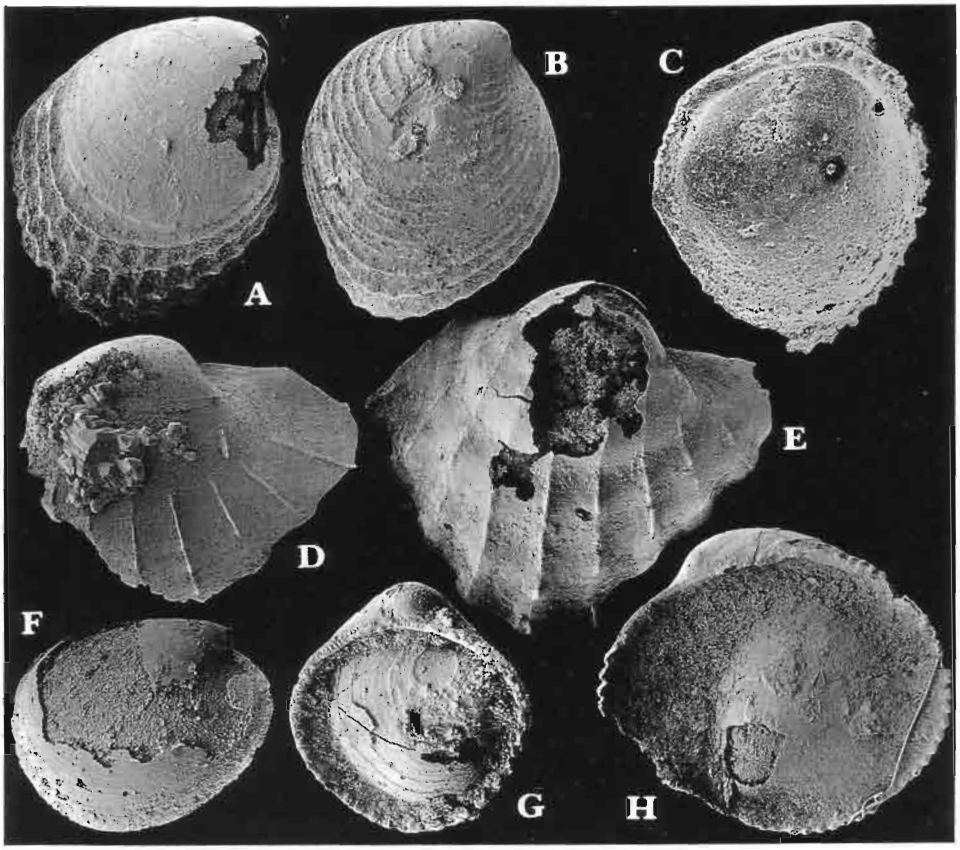

Fig. 32. Probable cardiolids and related bivalves from the Ludlow of the Kok Formation of Cellonetta Lavinerinne, Carnic Alps, Austria; valves preserved as phosphatic linings or pyritized; × 60 except A and B which are × 45. ❑A, G. *Butovicella* cf. *migrans* (Barrande 1881), early postlarval shell with metamorphosis distinctly expressed by change in ornamentation. ❑B–C. *Butovicella galemmu* Kříž 1994. ❑D–E. *Praecardium*? sp. ❑F–H. *Dualina*? sp. 4.

from each other in the almost smooth or strongly rugate surface of the larval shell.

Not so common (1.2 per cent), but highly informative, are early praecardiids (Fig. 32D–E). In this case the metamorphosis is recognizable only in the appearance of a few low radial blades at the shell surface and development of cardiolid-like concentric annulation. Otherwise the shells are almost completely smooth, with only indistinct growth lines. The hinge is reduced to a few teeth.

The clear boundary between the larval stage and crenulation of the valve margins is shared with the cardiolids by juvenile conchs possibly belonging to *Dualina*, which contribute 1.5 per cent to the bivalve assemblage (Fig. 32H). Immediately after the metamorphosis these shells developed an asymmetric fold at the posterior(?) end. No hinge teeth are present.

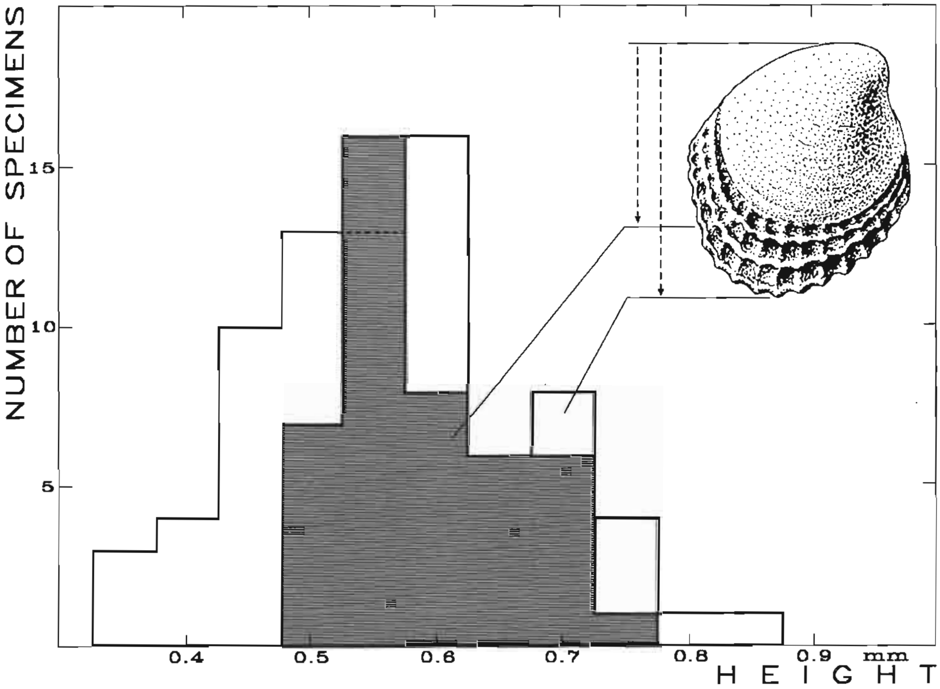

Fig. 33. Size frequency distribution of height of *Butovicella* valves in randomly selected part of the Cellonetta Lavinerinne sample and height of prodissoconchs in the whole sample (shadowed). Note that modal values of both histograms are closely similar (although with opposite skeweness) which indicates mortality peak exactly at the metamorphosis. At least three species of the cardiolids are represented but they do not differ significantly in size of their prodissoconchs.

Somewhat isolated morphologically is a species represented by larval shells with irregularly quadrangular outline and only one series of hinge teeth posterior of the beak (Fig. 31F–G; 2.0 per cent of the sample).

Some rare shells slightly resemble in outline Silurian *Janeia* (Liljedahl 1984), others may be ctenodontids.

The most striking feature of all those larval bivalves is the similarity in hinge organization. The hinge is composed of two series of small teeth, variously expressed. The more prominent but less numerous teeth arm the area below and somewhat anterior of the beak. The other series of minute denticles extends along the whole dorsal area posterior of the beak and may partly overlap with the main series running slightly above it. In species of possible cyrtodontid affinities at early postlarval stages, the posterior series tends to be transformed into a crenulated longitudinal ridge, whereas the main series becomes stronger. Such larval hinges may represent a status close to the ancestral one in bivalves, from which various hinge patterns of post-Cambrian bivalves developed.

Hyoliths. — At least four species of hyoliths are represented in the Cellonetta assemblage, which is rather surprising as hyoliths are very rare

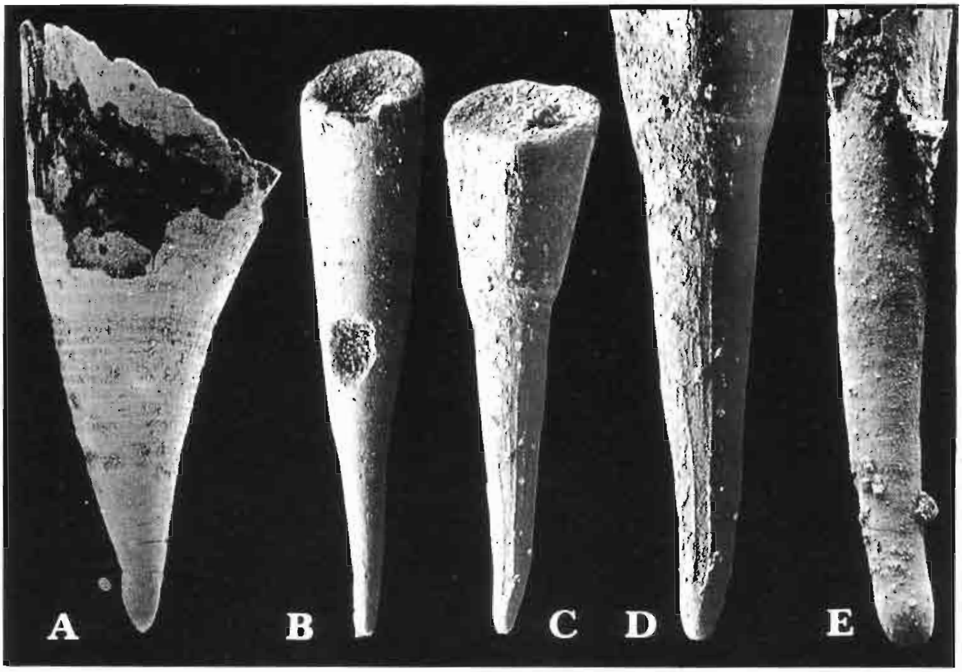

Fig. 34. Silurian hyoliths from the Ludlow of the Kok Formation of Cellonetta Lavinerinne, Carnic Alps, Austria; conchs preserved as phosphatic linings. ❑A. Unnamed orthothecid (perhaps a nautiloid with extremely small embryonic conch?), lateral view; × 60. ❑B. Unidentified carinolitid with external shell wall missing in the apical part; × 50. ❑C–D. Unnamed pauxillitid with similarly exfoliated apex; × 60 and 100, respectively. ❑D. *Circotheca* sp.; × 100.

in Silurian macrofossil assemblages. Although it is well known that several hyolith lineages continued from the Ordovician to the Silurian, only the most conservative *Circotheca* shows typical hyolith early ontogenetic stages among the Cellonetta species (Fig. 34E). In two hyolithid species, cooccurring with it, the apical part, separated by an abrupt constriction, does not show any growth lines or protoconch at the apex (Fig. 34B–D). This morphologically distinct part of the conch corresponds in size to that of the larval conch as inferred from distribution of mortality among Ordovician hyolithis (Fig. 25B, D; Dzik 1978). Probably the larval conch of the Silurian hyolithids was weakly mineralized, and only a secondary filling of the conch apex is preserved. Perhaps also in the evolution of hyoliths, parallel to some gastropods, a loss of ability to calcify larval conchs took place.

The most unusual of the Cellonetta hyolith-like conchs have an apex closely resembling typical Ordovician hyoliths, but at the same time show prominent septation, breviconic appearance and exogastric curvature, all suggestive of cephalopod affinities (Fig. 34A). Also here ornamentation of the conch changes slightly at the stage corresponding to proposed maturation of the hyolithid (and early cephalopod) larvae. Although most of the orthoceratids have much larger apices (including associated phosphatized specimens), the Carnic Alps Silurian yielded species with very small mucronate protoconchs and larval stages with shape and ornamentation similar to that of the problematic specimen from Cellonetta. Namely, *Hemicosmorthoceras laterculum* Ristedt 1968 from the Kok Formation at Cellonetta had extremely small mucronate protoconch 0.25 mm in diameter (Ristedt 1968). As the septal surface of my specimen is too roughly preserved to reveal the presence of the siphuncle, its affinities must remain questionable.

Youngest 'small shelly fossils' assemblages

Phosphatization is a common phenomenon also in late Devonian cephalopod limestones of the Holy Cross Mountains, Poland, though usually its effects are restricted to archaeostracan cuticle (Dzik 1979). Some horizons, however, contain also assemblages of phosphatized fossils similar to those reviewed above. Especially well preserved phosphatized and pyritized mollusc conchs occur in strata bordering the sedimentary discontinuity between *Palmatolepis marginifera* and *P. trachytera* Zones of the Famennian in the classic Łagów locality, famous for its goniatites. Preservation is similar as in the Kok Formation, but pyritized microfossils, subordinate in the Carnic Alps, dominate in the Holy Cross Mountains. With some reservation, the Łagów fossils may be considered as representative of a residual late Devonian 'small shelly fossils' assemblage.

Calcareous sponge spicules and phosphatic tubes of *Sphenothallus* are missing in the Łagów assemblage, although they are known from coeval strata of different facies. Among phosphatic dermal sclerites, conodonts are as common as before being supplemented by teeth and scales of the acanthodians, paleoniscids, and sharks. Apparently they were able to penetrate offshore pelagic environments more successfully than Silurian agnathans and early acanthodians.

Benthic molluscs in Łagów are similar to those from Cellonetta. There are some low- and higher-spire platyceratids (Fig. 35A, D), much taller possible loxonematids (Fig. 35E), but also more advanced gastropods. *Neritopsis*-like possible neritids (Fig. 35H) were still not similar in early development to Recent or even Triassic neritids. In not having a tightly coiled prodissoconch these Devonian gastropods are close to Ordovician and Silurian gastropods of *Naticonema*-like conch morphology (reviewed above). Either this Paleozoic group is not related to the neritids or the type of larval conch typical for the neritids developed later, though before their first undoubted occurrence in the Late Triassic as proven by larval shells (Bandel 1992). Paradoxically, the alleged Triassic platyceratids of Bandel (1992) are much more similar to coeval neritids than to probable platyceratids from the early Paleozoic illustrated here.

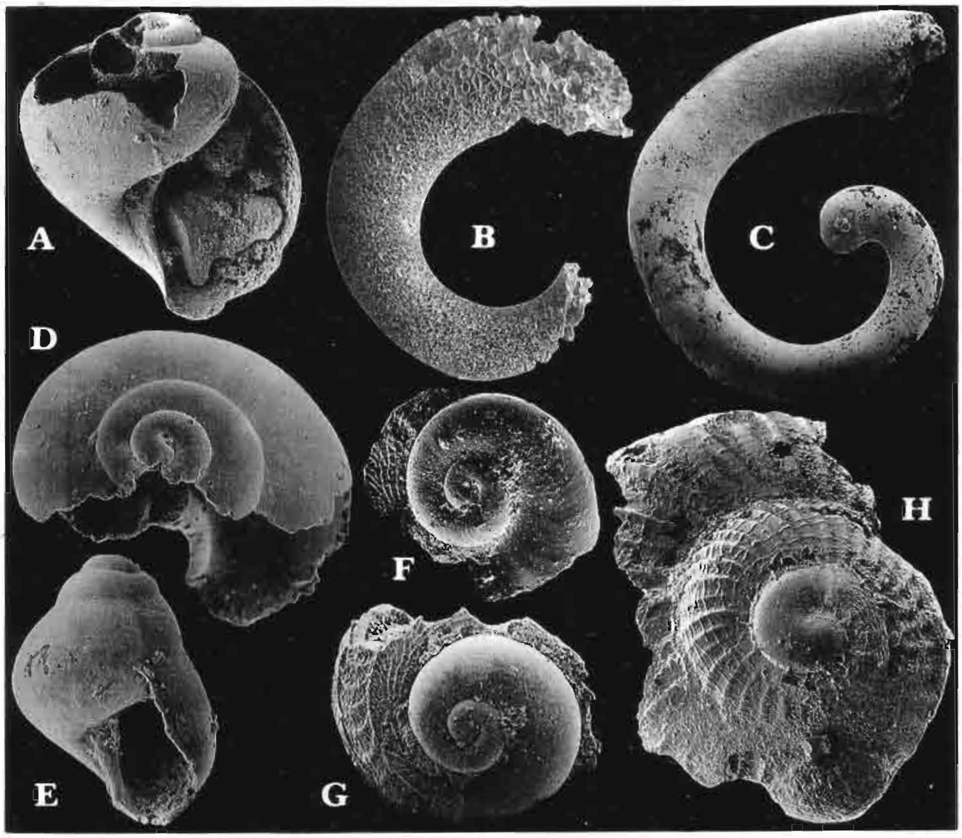

Fig. 35. Devonian juvenile gastropods from the Famennian Łagów beds of Łagów-Dule, Holy Cross Mountains, Poland; all × 60. ❑A, D. Undetermined platyceratid, pyritized conchs. ❑B–C. *Serpulospira crassitesta* (Tietze 1870); conch wall preserved as a spongy siliceous fabric, an effect of diagenetically late infilling with silica of boundaries between calcite crystals (B) and phosphatic nucleus (C); note that despite superficial similarity to early Paleozoic *Lytospira*, the conch apex is quite different. ❑E. Undetermined loxonematid. ❑F–G. Pleurotomariid *Mourlonia* sp., two views of the same specimen to show growth lines on relatively smooth larval conch and prominently ornamented teleoconch with the selenizone developing suddenly in metamorphosis (G also in Dzik 1978). ❑H. *Naticopsis* sp.; teleoconch with neritid traits but embryonic conch much more primitive than in true members of the group (new picture of the specimen illustrated in Dzik 1978).

Of Paleozoic appearance are also late Devonian pleurotomariid larval shells, with a small apex and more than two smooth whorls ornamented only with growth lines (Fig. 35F–G). These growth lines provide evidence of early calcification and secretion of calcareous larval shell by mantle. The sudden appearance of prominent ornamentation and the selenizone is a modern aspect of these pleurotomariids. In this respect they are dissimilar to the late Triassic pleurotomariid *Wortheniella*, with very small sharply delimited protoconch, and the selenizone and conch ornamentation developed gradually (Schwardt 1992). *Wortheniella* had thus the same style

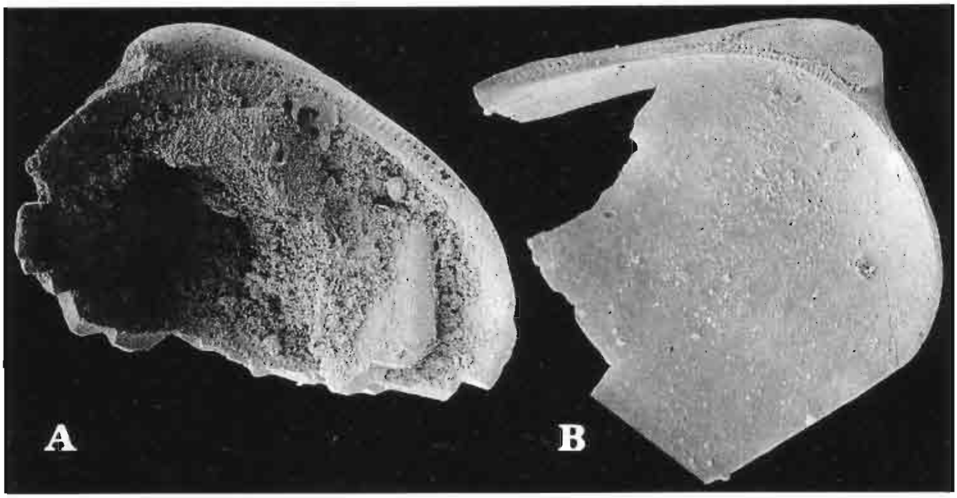

Fig. 36. Devonian juvenile bivalves from the Famennian Łagów beds of Łagów-Dule, Holy Cross Mountains, Poland; both × 60. ☐A. Pyritized valve of unidentified cyrtodontid(?). ☐B. Phosphatized valve of *Guerichia* sp.

of larval development as the Devonian *Neritopsis* or Ordovician trochonematids, which is probably primitive for all these groups.

Bivalves occur also in Łagów, the most common being probably the thin-shelled *Guerichia*. Its rudimentary hinge (Fig. 36B) suggests anisomyarian affinities.

An assemblage of pyritized juvenile mollusc shells closely resembling that from the Famennian of Łagów is also known from the Katharina marine horizon at the boundary of Westfalian A and B in western Germany (Herholz 1992). There minute gastropod and bivalve shells are most diverse and numerous in pelagic strata with ammonites, conodonts, and thin-shelled bivalves. The gastropod larval-conchs assemblage from the Katharina horizon along with generalized forms resembling those from Łagów and Cellonetta contains also some more advanced loxonematids with swollen first coil (‘*Bulimorpha germanica*’) and heterostrophic possible architectonicids. Judging from data of Herholz (1992: Fig. 4), higher contributions of agglutinating foraminifers and ostracodes are negatively correlated with the abundance of pyritized juvenile molluscs in the core section. All this suggests that also pyritization (perhaps connected with earlier phosphatization) took place in conditions of a low sedimentation rate, without any supply of coarse terrigenous material, apparently during the maximum of a brief transgressive event.

A different kind of assemblage is represented by phosphatized ostracodes which occur together with fish teeth and scales in the Visean cephalopod limestones of Ostrówka in the Holy Cross Mountains. In this case a resemblance to the early Paleozoic ‘small shelly fossils’ assemblages is remote, if any.

I am not aware of any phosphatized 'small shelly fossils' assemblage from strata younger than Carboniferous, although several kinds of Mesozoic cephalopod limestones were dissolved in acids in our laboratory. It seems thus reasonable to conclude that this kind of preservation of minute fossils is almost completely restricted to the early Paleozoic and that 'small shelly fossils' assemblages gradually disappeared after the Ordovician. The reason of this disappearance seems to be rather taphonomic than evolutionary, as most of the fossil groups that occurred in early 'small shelly fossils' assemblages continued to be represented even in much younger strata of other facies.

Preservation of 'small shelly fossils'

Contrary to widely held opinions, the organisms with originally phosphatic skeleton were subordinate in early Paleozoic 'small shelly fossils' assemblages of high diversity, and their contribution did not change significantly during the early Cambrian (Bengtson & Runnegar 1992) and later. In the Cambrian the tommotiids, palaeoscolecids, and inarticulate brachiopods were most abundant in non-condensed strata devoid of secondarily phosphatized fossils. Phosphatic tubes, when abundant, were transported there from other environments, as their attachment structures are extremely rare. The majority of 'small shelly fossils' were originally calcareous. Similarly, in the Ordovician and Silurian the groups of organisms with originally phosphatic skeleton (acrotretids, conulariids, conodonts, and fish) are not the most abundant in association with phosphatized fossils. The factor controlling distribution of the discussed assemblages was thus phosphatization alone.

Virtually all phosphatized 'small shelly fossils' originated by developement of thin phosphate linings covering their surface and penetrating internal cavities. Such epitaxial crystallization of calcium phosphate is especially efficient at substrates which offer good crystal lattice matches. This provides a catalytic effect by reducing the critical supersaturation at which a rapid increase of nucleation occurs (Nancollas 1989: p. 163). The process of precipitation, which requires anoxic conditions, was shown experimentally to initiate as soon as after two weeks in normal temperature (Briggs & Kear 1993).

Because of the crucial role of the substrate, phosphatization is usually rather selective. Generally, aragonitic fossils more easily underwent phosphatization than calcitic ones. In the Silurian Kok Formation sample from Valentin Törl, aragonitic mollusc conchs are phosphatized whereas calcitic ostracodes and trilobites are silicified.

The time and space distribution of 'small shelly fossils' was clearly controlled by the availability of phosphate ions in sea water and long enough exposure of calcareous detritus to their action. This seems consistent with the observed patterns in occurrence of such assemblages.

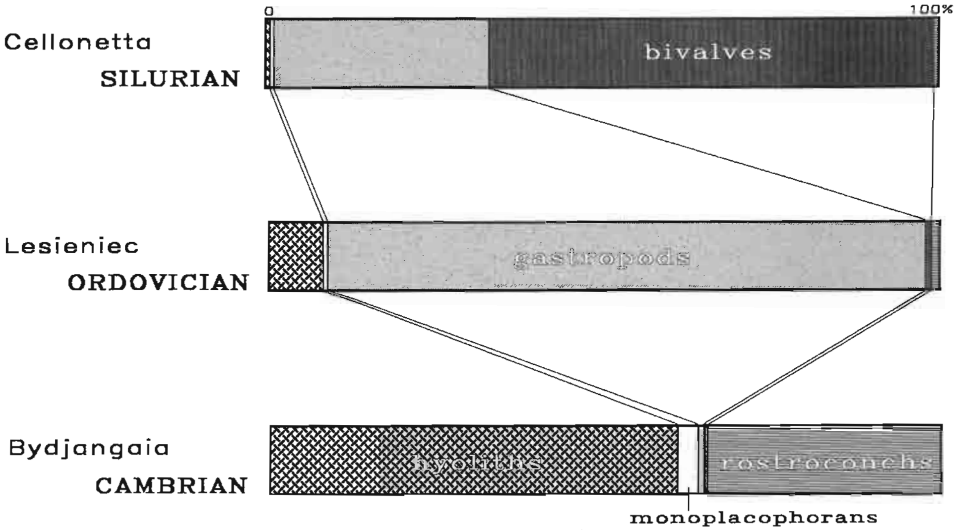

Fig. 37. Structure of conchiferan mollusc assemblages in representative samples of 'small shelly fossils' discussed in the text.

Modern phosphatic sediments develop mostly along west oceanic coast margins, where dynamic upwelling of nutrient-rich waters enhances primary productivity, and the presence of well-defined oxygen minimum zone favors accumulation of organic-rich sediments and consequent phosphogenesis, and along current-dominated margins, where low bulk sediment accumulation rates permit intense biogenic mixing of surficial sediments, and favor physico- and biochemically induced super-saturation of porewaters in respect to apatite (Föllmi *et al.* 1991). Apatite precipitation is frequently mediated by microbial activity (e.g. Southgate 1986). Phosphate-coated skeletal grains are widely known in strata from the Cambrian (Southgate 1986) to Tertiary (Föllmi *et al.* 1991).

Only preliminary paleogeographic reconstructions for the crucial period of time near the Vendian/Cambrian boundary are now available (McKerrow *et al.* 1992) and it would be premature to interpret the distribution of phosphate deposits (see Cook 1992) in terms of oceanic water circulation. Perhaps the Siberian Platform in its drift from low to somewhat higher latitudes incidentally went into the field of increased phosphate precipitation at the moment when the basal Cambrian transgression was initiated. A somewhat better fit with the phosphogenesis model is provided by the paleogeographic and paleoclimatic evidence on the Ordovician of the Holy Cross Mountains. In its migration from southern polar regions the Małopolska microcontinent, with the Holy Cross Mountains at its tip, was in temperate climatic zone and close to the western shore of the Baltica continent during high stand of the sea level in the Middle Ordovician (Dzik *et al.* 1994). Probably the Gondwana related Carnic Alps reached similar position in the Silurian. Westerly exposed to the open sea, in respect to the main shallow shelf areas, was also the Łagów region in the Holy Cross Mountains in the early Famennian, which was the time almost immediately after extinction of warm-water reefal ecosystems.

Conclusion

A striking feature of the 'small shelly fossils' assemblages of post-Cambrian age is the abundance of molluscan larvae. That these are really larvae (Dzik 1978) and not dwarf adults is clearly shown by the pattern of mortality in Silurian cardiolid bivalves (Fig. 33). After the Ordovician they gradually become virtually the sole members of the assemblages. Apparently, the sedimentation of their rock matrix took place in environments with increased mortality at the time of metamorphosis. Such mass occurrences of larval shells (but not phosphatized) are known also in younger strata (e.g. Conti & Monari 1991). In case of the Jurassic Kimmeridge Clay bivalve prodissoconchs covering bedding planes it has been proposed that larval shoals failed to settle and metamorphose due to anoxic bottom conditions (Oschmann 1991: p. 571). Similarly difficult was settlement of bryozoan larvae during the deposition of the Ordovician Mójcza Limestone where some horizons are unusually rich in juvenile colonies. They were apparently unable to continue their growth on a substrate not stable enough to anchor safely larger erect colonies. In effect juvenile colonies were susceptible of being overthrown and covered with sediment (Dzik *et al.* 1994).

Phosphate richness in the sediment is a result of high biological productivity and low non-organic sedimentation rate. The environment in which 'small shelly fossils' originated was really characterized by extremely slow sedimentation. Such environments, generally corresponding to the cephalopod limestone facies, were also widespread in ancient seas after the early Paleozoic, so this alone does not explain the disappearance of 'small shelly' fossils from the fossils record. To enable phosphatization, the calcareous detritus has to be exposed long enough to phosphate-rich water. In modern marine environments of high organic productivity it is unlikely to prevent bioturbation which hides calcareous particles within the sediment before phosphatization can be completed and oxygenates the sediment. The sedimentary features of the strata extremely rich in phosphatized skeletal detritus from the Ordovician of the Holy Cross Mountains suggests that the very shallow depth of bioturbation of the sediments was the main factor which controlled the distribution of 'small shelly fossils' assemblages.

An interesting question is the increase in contribution of pyritized conchs in the 'small shelly fossils' assemblages from the Silurian to Devonian, and its apparent complete domination in younger strata. This may either express some change in sedimentation processes in the same environment or perhaps a shift of basically the same conditions of fossilization to somewhat different zones of the sea bottom.

Both these two factors, low sedimentation rate and shallow bioturbation, had to coincide to produce the Meishucun, Mójcza, and Kok types of preservation of skeletal fossils. It has been proposed that sediment bioturbation was generally shallower in the early Paleozoic (Thayer's bulldozer theory; Thayer 1983) and the environments in which the 'small shelly fossils' were produced were probably the last to which the bioturbating mud-eaters invaded probably not earlier than after the early Paleozoic. It follows thus that the evolutionary diversification and ecologic expansion of the sedentary polychaetes, eleutherozoan echinoderms, and other infaunal detritus feeders resulted in extinguishing the 'small shelly fossils' bottom environments.

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Streszczenie

Niezbyt udatny termin „small shelly fossils" (drobne skamieniałości skorupkowe) utrwalił się w literaturze paleontologicznej jako określenie masowych nagromadzeń mikroskopijnych skamieniałości pozyskiwanych przez rozpuszczenie skał wapiennych w kwasie octowym. Opisane po raz pierwszy z kambru Jakucji, w największej obfitości skamieniałości tego typu występują w chińskim stanowisku Meishucun. Są one jednak znane nie tylko z wczesnego kambru, jak się często przywykło sądzić. Identycznie zachowane (dzięki pierwotnie fosforanowemu składowi szkieletu lub wtórnym fosforanowym otoczkom) zespoły skamieniałości znane są m.in. z ordowiku Mójczy w Górach Świętokrzyskich i z sylurskiej formacji Kok w Alpach Karnijskich.

Charakterystyczną cechą wszystkich tych wystąpień „small shelly fossils" jest nadzwyczaj duży udział młodocianych, wczesno-postlarwalnych stadiów rozwojowych. Jest to zapewne wyraz szczególnych warunków środowiska skrajnie powolnej sedymentacji, umożliwiającej wtórną fosfatyzację drobnych szczątków szkieletowych ale utrudniających, bądź uniemożliwiających, stabilny rozwój bentosu. Rzecz jasna, zespoły z różnych epok geologicznych różnią się od siebie zdecydowanie składem taksonomicznym, nie wydaje się jednak by udział skamieniałości o szkielecie pierwotnie fosforanowym był większy w kambrze niż później. Ilościowe porównanie zespołów ukazuje ich stopniowe przekształcenia, np. wśród larw mięczaków w kambrze dominują hyolity, w ordowiku ślimaki a w sylurze małże.

Ani masowe pojawienie się zespołów „small shelly fossils" nie było nagłe (poprzedziła je długotrwała manykajska epoka sporadycznego ich występowania) ani też ich zanik nie był skutkiem nagłych przekształceń biocenoz czy środowiska. W trakcie starszego paleozoiku stawały się one coraz rzadsze aż do zupełnego zaniku. Można domniemywać, że pozostawało to w związku z ekspansją bioturbatorów do skrajnych środowisk.