Silurian retiolitids of the East European Platform

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Late Llandovery to late Ludlow isolated retiolitid assemblages from deep boreholes drilled in the Polish part of the East European Platform are used to restore phylogeny of the group. The process of reduction of the network skeleton (reticulum and clathria), as well as reduction of the transverse rods and change of virgula position started in the Wenlock. All Ludlow retiolitids have a central virgula and reduced rhabdosomes. Colonies of the *Gothograptus* lineage with finite growth, related to reduction in the number of thecae, first appeared in the Late Wenlock and continued in the Ludlow. Their evolution leads either to development of finite rhabdosomes with few thecae (*Holoretiolites*) or to almost complete reduction of clathria and reticulum (*Plectodinemagraptus* gen. n. of the *Plectograptus* lineage). The latter homeomorph of the Ordovician abrograptid *Dinemagraptus* is the last known retiolitid of late Ludlow age (*Cucullograptus hemiaversus* / *C. aversus* Zone). The family Retiolitidae consists of five separate lineages. *Sokolovograptus polonicus* sp. n., *Neogothograptus* gen. n., *Holoretiolites atrabecularis* sp. n., *Semiplectograptus urbaneki* gen. et sp. n., *Plectodinemagraptus gracilis* gen. et sp. n. are proposed. *S. polonicus* from the *Cyrtograptus murchisoni* Zone has a strongly reduced rhabdosome.

K e y w o r d s : graptolites, retiolitids, Silurian, Poland, East European Platform, deep borings, Baltic erratic boulders, phylogeny.

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Introduction

Silurian graptoloids of the Retiolitidae Lapworth 1873 have rhabdosomes with a heavily reduced cortical layer of the periderm. The rhabdosome is composed of a network of lists of microfuselli and bandaging, developed from the sicula, nema, and thecal walls (thecal framework), and by bifurcation of virgella (ancora sleeve); the sicular and thecal walls are not

usually preserved. Some retiolitids have a well developed prosicula, initial parts of interthecal septa (transverse rods) and traces of incremental periderm (Bates & Kirk 1992; see also Urbanek & Rickards 1974). Because of strong reduction of the colony skeleton, the relationships of the retiolitids to regular graptolites are not clear. The ancestors of the retiolitids may be the petalograptids, as proposed by Rickards *et al.* (1977) and also by Bates & Kirk (1984).

Mitchell (1987) proposed a homology of the proximal ancoral structure of the petalograptids, which appears by bifurcation of virgella (ancora), with that of the retiolitids. The oldest ancora structures are known from Llandovery petalograptids in such species as *Petalograptus obuti* (Rickards & Koren' 1974), *P. ovatoelongatus* Kurck 1882, *P. insectiformis* (Nicholson 1868) (Fig. 1) and *P. minor* (Elles 1897). The development of the ancora may lead to the appearance of an ancora umbrella (Fig. 11B), and later at its distal end the reticulum and clathria framework termed the ancora sleeve by Bates & Kirk (1984, 1987) 'secreted as a cortical bandages onto a sleeve or jacket of incremental periderm' (Bates 1990) (Fig. 11A).

The Ordovician archiretiolitids and abrograptids earlier and independently developed an organisation of the rhabdosome similar to that of the retiolitids. However, they did not develop any proximal ancora structures, and the colony's outer skeleton was formed of lists connected to virgellar and antivirgellar spines, to the lateral spines from the nema, and thecal spines. In both groups fusellar periderm of the early stages of growth is preserved forming the metasicula in the abrograptids and the metasicula and initial parts of the first thecae in archiretiolitids.

The evolution of skeleton in the Silurian retiolitids and in their Ordovician analogue resulted in several homeomorphies. The Ordovician *Reteograptus geinitzianus* Hall 1859 (Abrograptidae) superficially resembles the Silurian *Plectograptus macilentus* Törnquist 1887 (Plectograptinae) (see Mitchell 1990) and the Ordovician *Dinemagraptus warkae* Kozłowski 1952 (Abrograptidae) is similar to *Plectodinemagraptus gracilis* gen. et sp. n. (Plectograptinae) (Fig. 2). Such a repetitive development of similar patterns in overall morphology of rhabdosomes in Ordovician and Silurian graptolites, in spite of their different structural foundations (reclined and scandent biserial types with ancora sleeve respectively) was probably related to the similar adaptive type they represented.

The Ordovician archiretiolitine graptolites disappeared from the fossil record with the Late Ordovician crisis. It is generally believed that during the Early Silurian graptoloids radiated into vacant niches developing new rhabdosome constructions, analogous to those of Ordovician retiolitids.

It has been proposed that evolution of specific retiolitids was connected with a hydrochemical crisis, which happened several times in the Silurian (Wilde *et al.* 1991; Quinby-Hunt *et al.* 1990). Only those planktonic organisms that lived in well oxygenated, thin upper photic layers

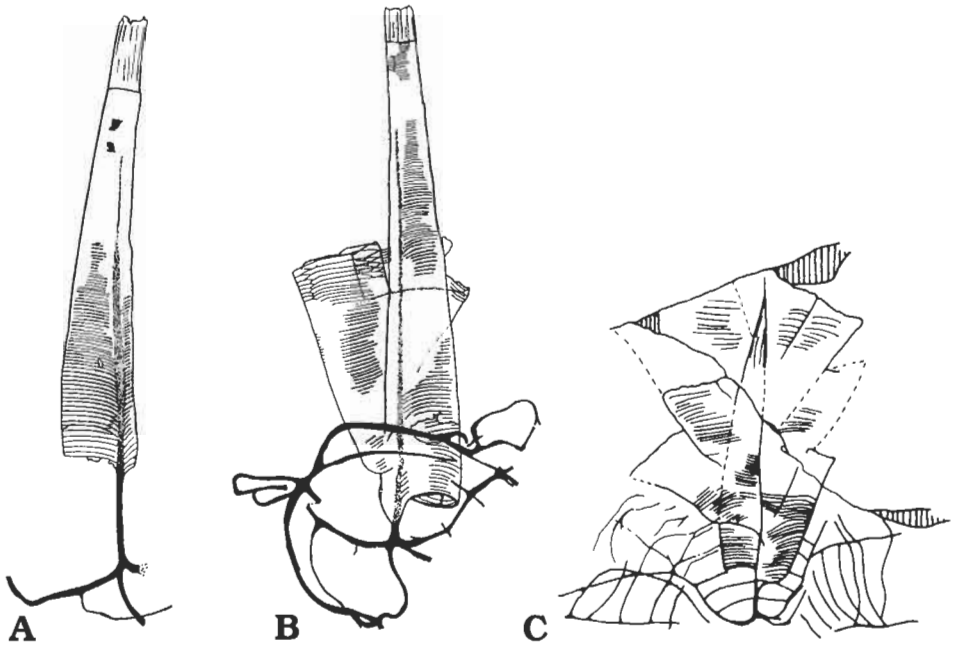


Fig. 1. Ancora structures in the petalograptids — probable ancestors of the retiolotids. ❑A–B. *Petalograptus insectiformis* (Nicholson 1868), early growth stages, *Coronograptus gregarius* Zone. A × 30, B × 35 (after Hutt *et al.* 1970). ❑C. *Petalograptus obuti* (Rickards & Koren' 1974), with well developed ancora umbrella, *Coronograptus cyphus* Zone × 10 (after Rickards & Koren' 1974).

had a chance of surviving such a condition. The retiolitids, using proteins more economically to build the skeleton, had an evolutionary advantage over graptolites with massive periderm living in a low productivity open sea. The mass occurrence of species of the Plectograptinae, in contrast to those of the Monograptinae, during the Late Silurian crisis has been noted by Koren' (1991).

The ancora umbrella and sleeve were apparently adaptations to pelagic life. In Kirk's (1990: fig. 10) opinion, the ancora sleeve construction allowed the canalization of efferent currents of water, which improved the nutrition of the colony and possibly its automobility. This increased the ability of the young colonies to disperse and simultaneously provided a protective function (Bates & Kirk 1992). Such an organization of the colony may have assured evolutionary success for the retiolitids.

In this paper, being a modified version of my doctoral thesis presented in 1993 at the Institute of Palaeobiology Polish Academy of Sciences, the succession of retiolitid species with complex astogeny from deep boreholes in the Polish part of the East European Platform and from Baltic erratic boulders is described. These new data will be used to discuss relationships among species of the subfamily Plectograptinae.

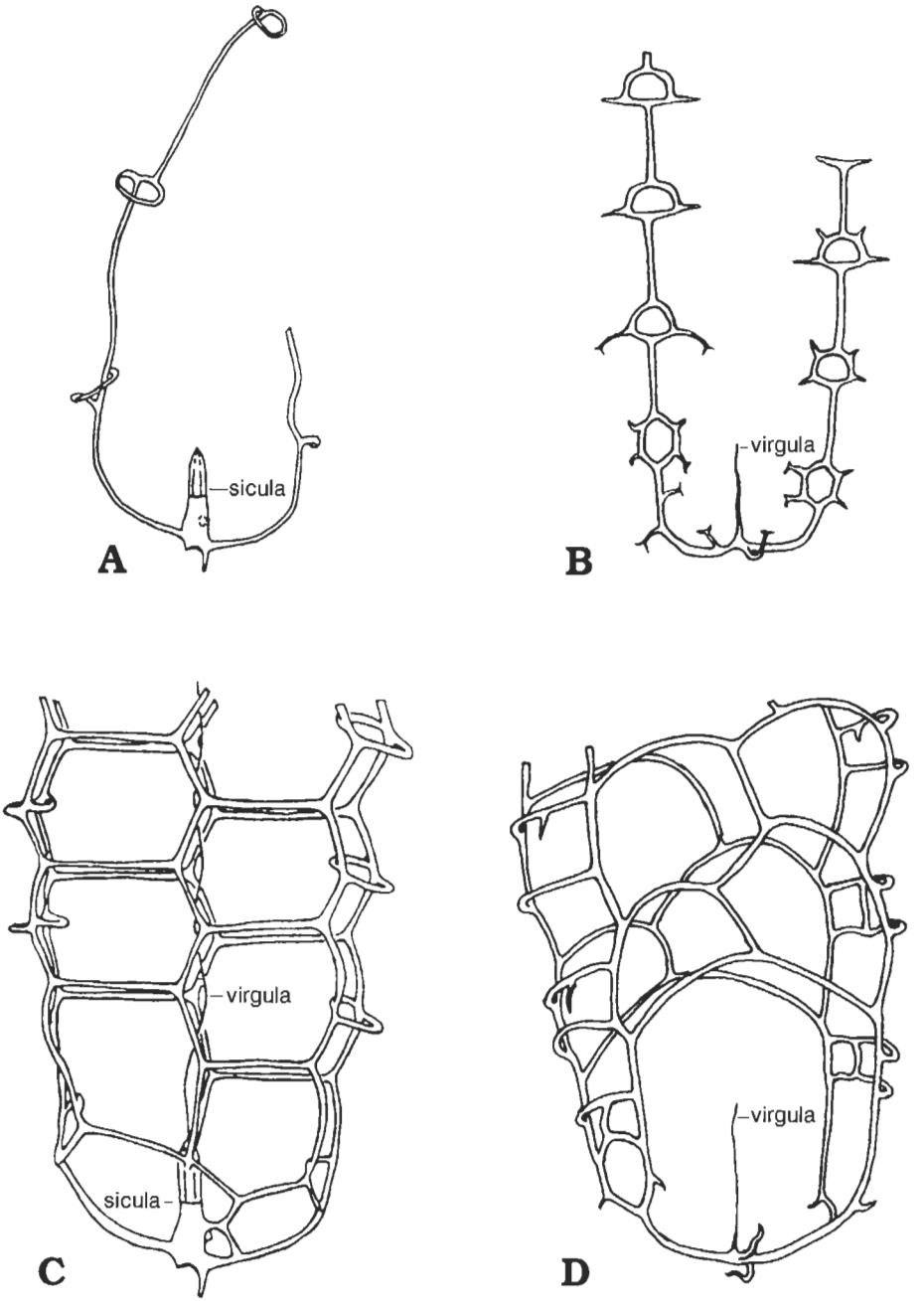
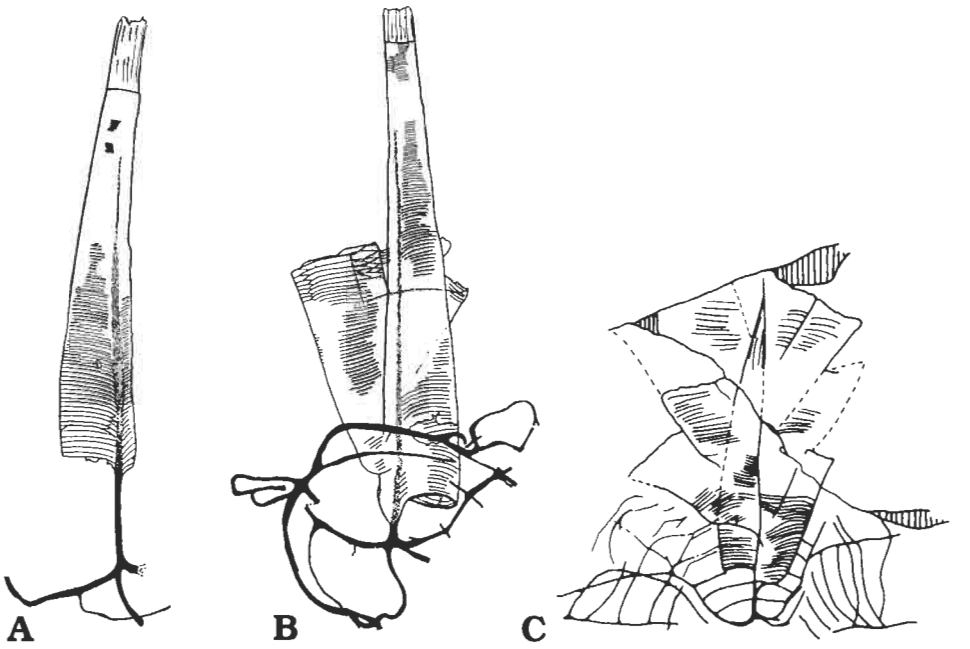


Fig. 2. Homeomorphy of Ordovician abrograptids (A, C) with Silurian plectograptids (B, D). ❑A. *Dinemagraptus warkae* Kozłowski 1951; ordovician erratic boulder from Warka of Poland (after Kozłowski 1951). ❑B. *Plectodinemagraptus gracilis* gen. et sp. n., *Cucullograptus aversus/C. hemiaversus* Zone, Mielnik borehole. ❑C. *Reteograptus geinitzianus* Hall 1859; Llandeilo-Caradoc from (after Finney 1980). ❑D. *Plectograptus macilentus* Tornquist 1887, *Lobograptus parascanicus* Zone, Mielnik borehole.



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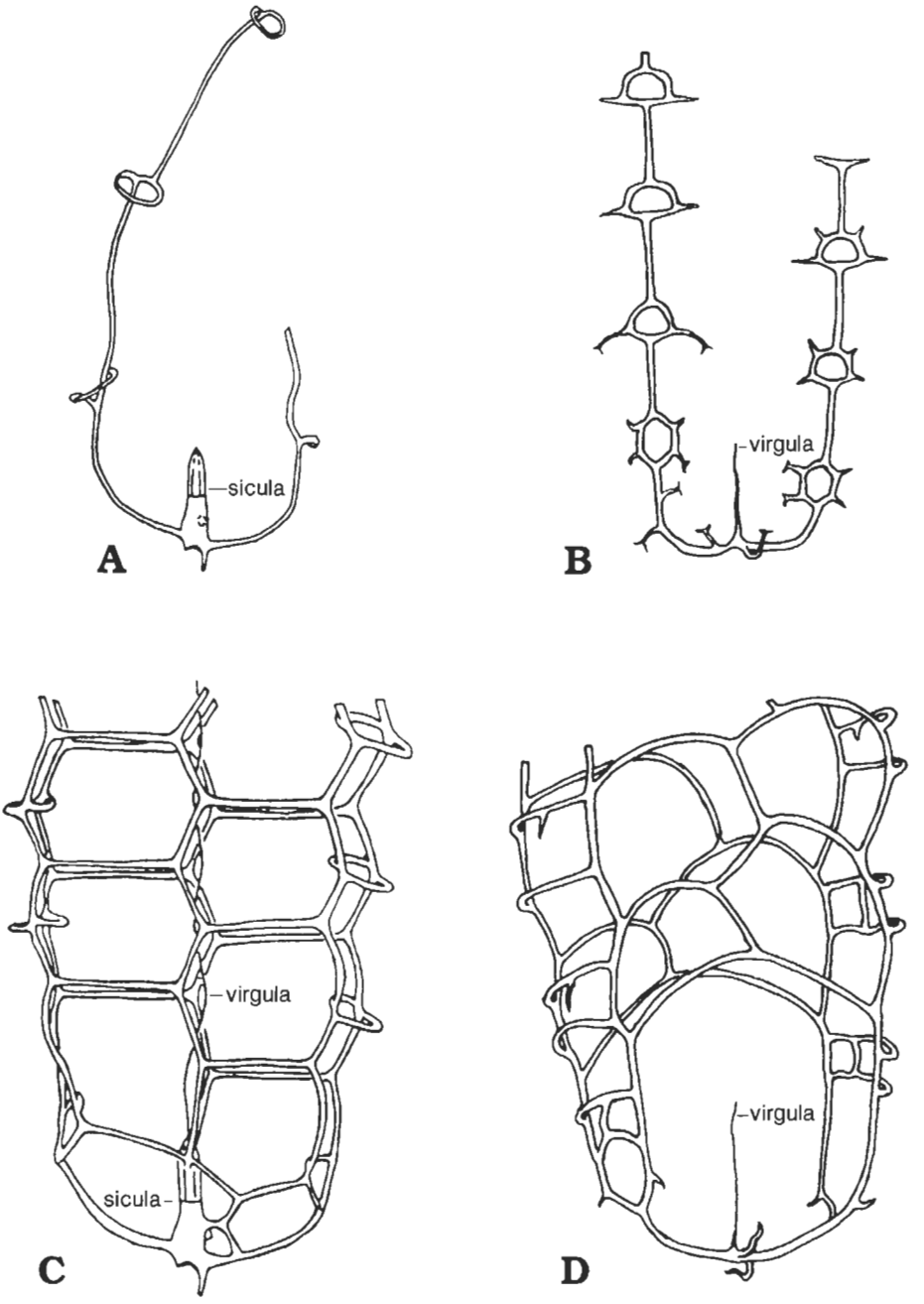

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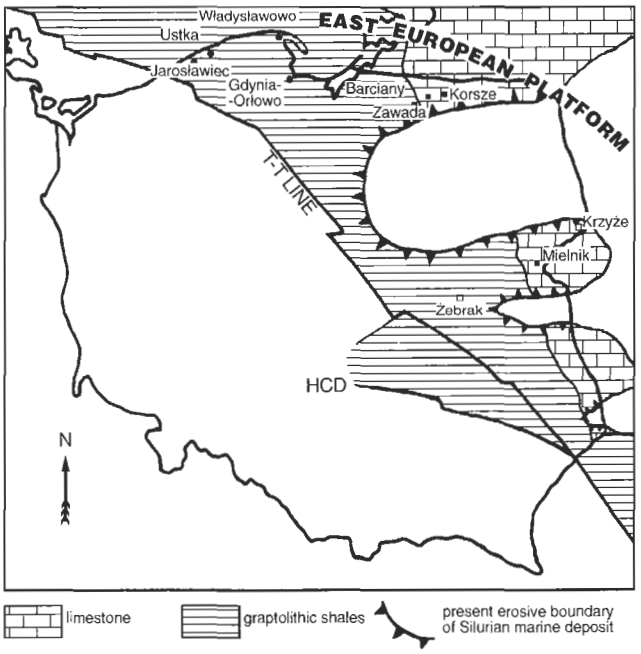


Fig. 3. Facies distribution in the late Wenlock and early Ludlow of NE Poland (after Tomczyk & Tomczykowa 1994) with locations of boreholes that yielded retiolitids by black squares, erratic boulders by black circles, and other boreholes by white squares. Abbreviations: T–T LINE — Teisseyre — Tornquist line, HCD — Holy Cross Mountains dislocation.

Material

The investigated material comes from deep boreholes drilled in the Polish part of the East European Platform and from erratic boulders collected from the Baltic Coast. Boreholes Zawada 1, Barciany 4, and Korsze 1 are in the eastern part of the Peribaltic Syncline, and Mielnik IG 1 borehole in the eastern part of the Podlasie Depression (Fig. 3).

Material studied is stored in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (abbreviated ZPAL).

Stratigraphic position of strata with retiolitids. — The Silurian of the north-eastern part of the Peribaltic Syncline has been penetrated by numerous boreholes (Teller 1968, 1976, 1986; Tomczyk 1962, 1964, 1968, 1979). The Llandovery is represented by nodular limestones, merging into black shale claystones with intercalations of a green marl with high carbonate content. In the Wenlock, light-grey, carbonate clays with a graptolite fauna and with rare intercalations (up to 20 cm) of grey limestones dominate. The Ludlow is represented by grey clays with graptolites but the latest Silurian strata were removed by erosion before the Late Permian transgression.

The thickness of the Silurian in the Zawada 1 borehole is 196.0 m (1673.5–1477.5 m). Middle and Late Llandovery black claystones, partly laminated with pyrite, intercalated with green marls, occur between

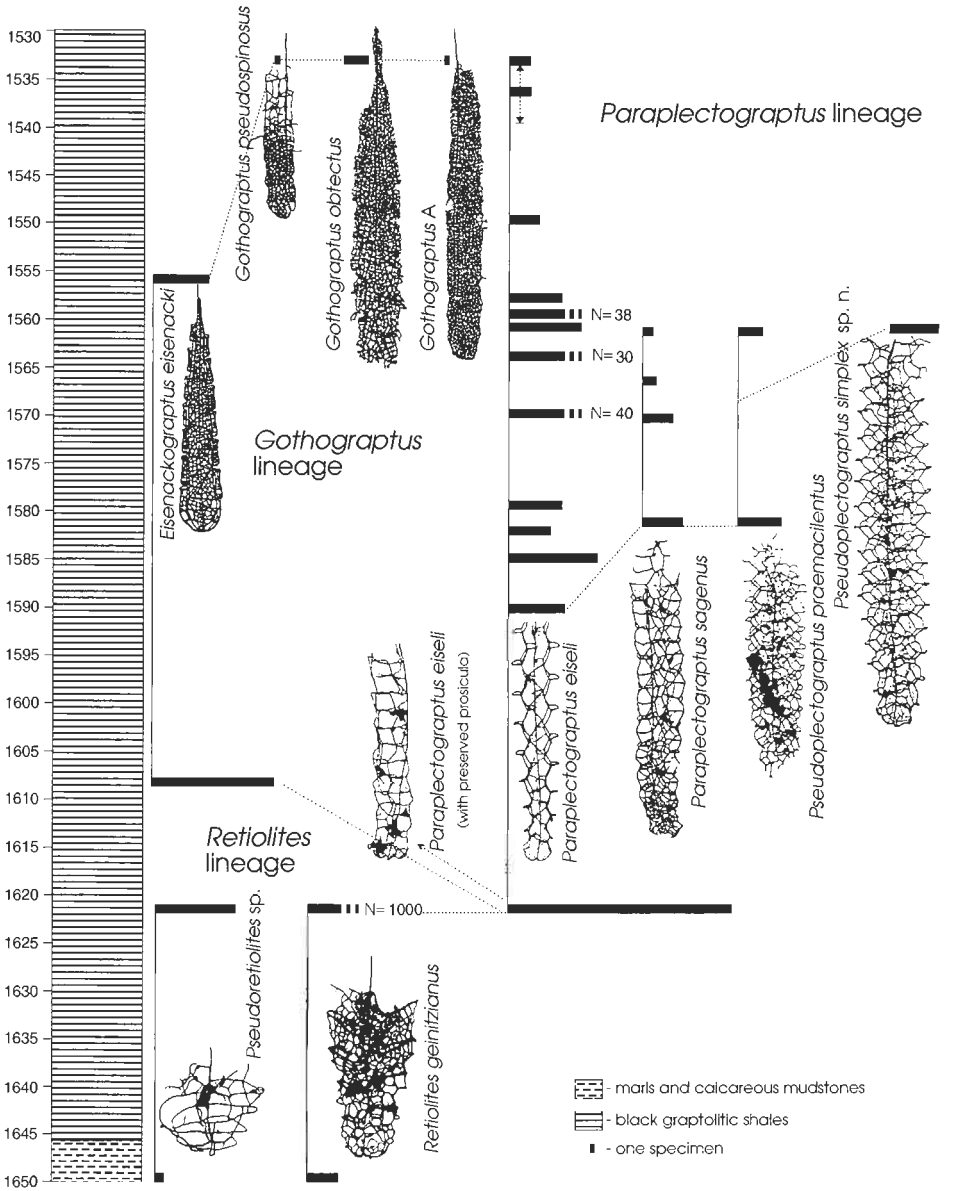


Fig. 4. Stratigraphic ranges and proposed evolutionary connections (stippled line) between species of *Retiolites*, *Paraplectograptus* and *Gothograptus* lineages; based on Zawada 1 borehole.

depths of 1657.8–1646.7 m (Fig. 4). The age determinations are based on graptolites (according to Lech Teller's unpublished data): *Monograptus priodon* (Bronn 1835), *Spirograptus spiralis* (Geinitz 1842), *Rastrites approximatus* Perner 1897, and *Monoclimacis vomerinus* (Nicholson 1872).

The Wenlock (depth 1646.7–1533.3 m) is represented by light-grey calcareous claystone with rare intercalations of up to 20 cm of light-grey marly

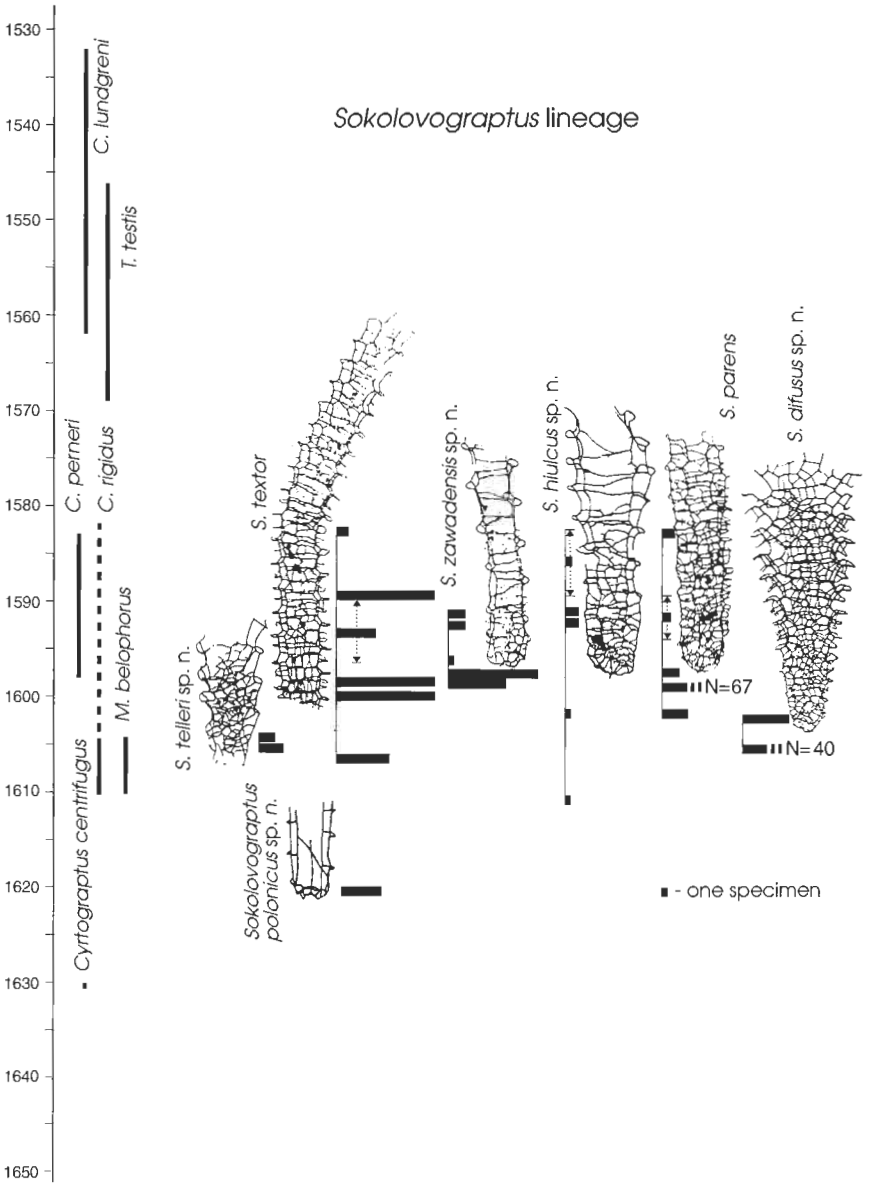


Fig. 5. Stratigraphic ranges of species of *Sokolovograptus* lineage; based on Zawada 1 borehole.

limestones; it contains a typical Wenlockian graptolite fauna (according to Teller 1976 and his unpublished data): *Cyrtograptus lundgreni* Tullberg 1883, *C. radians* Törnquist 1887, *C. hamatus* (Baily 1862), *C. murchisoni* Carruthers 1867, *C.* cf. *insectus* Bouček 1931, *C. urbaneki* Teller 1976, *C. perneri* Bouček 1933, *Monograptus testis* (Barrande 1850), *M. flemingi* (Salter 1852), *M. flexilis* Elles 1900, *M. flexuosus* (Tullberg 1883), *M. anten-*

nularius (Meneghini 1857), *Monoclimacis vomerinus* (Nicholson 1872), *Monoclimacis flumendosae* (Gortani 1922), *Monoclimacis zawadensis* Teller 1986. Retiolitids from the Zawada borehole are illustrated on Figs 4, 5.

The lithology of the Korsze 1 borehole is similar to that of Zawada 1, which is located nearby. At depths of 1589.4–1595.9 m only *Paraplectograptus eiseli* (Manck 1917) has been identified.

The core of Barciany 4 borehole is similar to the two boreholes described above. The only retiolitid, *P. eiseli*, occurs at depths of 1562.0–1568.0 m, together with *M. testis, M. flemingi, C. lungreni, Pristiograptus* ex. gr. *dubius* (Suess 1851). They represent the *C. lundgreni* Zone.

In the area of the Podlasie Depression claystone a facies with graptolites is dominant in the western part (the Żebrak borehole near Siedlce, Okuniew, and others), gradually changing in to carbonates to the east (the Krzyże borehole: Tomczyk 1962) (Fig. 3). In the Mielnik borehole there are mostly carbonates, making chemical isolation of graptolites easier.

The lithology and stratigraphy of the Mielnik borehole (Fig. 6) is documented by Tomczyk (1964, 1968, 1979). Urbanek (1963, 1966, 1970) published a detailed analysis and description of its isolated graptolite fauna (without retiolitids).

The Silurian sequence in the Mielnik borehole is 536.5 m thick. A stratigraphical gap includes all the Llandovery, and calcareous claystones of the *C. murchisoni* Zone lie directly on Late Ordovician rocks.

The Ludlow, occuring at depths from 1080.0 to 932.0 m, is represented by calcareous and marly claystones with occasional lenses of limestone (Tomczyk 1962). At depths of 1035.0–1045.0 m the *N. nilssoni* Zone is indicated by the graptolites *Neodiversograptus nilssoni* Lapworth 1876, *Colonograptus colonus* (Barrande 1850), *Saetograptus* cf. *chimaera* (Barrande 1850), and *M. uncinatus* Tullberg 1883. The late Ludlow ranges from 1035.0 to 932.0 m. The graptolite fauna is variable. From 1035.0 m to 1003.0 m *N. nilssoni, Lobograptus scanicus parascanicus* (Kühne 1955), *L. progenitor* Urbanek 1966, *L. expectatus* Urbanek 1960, *Colonograptus colonus, S. chimaera cervicornis* Urbanek 1958, *Monoclimacis micropoma micropoma* (Jaekel 1889), *P. dubius, Bohemograptus bohemicus* (Barrande 1850) and *'Barrandeograptus' operculatus* Münch 1938 occur.

At depths of 970.0–1003.0 m *L. imitator* Urbanek 1966, *L. scanicus scanicus* (Tullberg 1883), *L. scanicus parascanicus, L. expectatus, Cucullograptus pazdroi* Urbanek 1954, *N. beklemishevi* Urbanek 1963, *S. chimaera cervicornis* Urbanek 1958, *M. micropoma micropoma, P. dubius* have been identified. At depths of 960.0–970.0 m grey calcareus claystones contain graptolites described by Urbanek (1966): *L. invertus* Urbanek 1966, *L. scanicus amphirostris* Urbanek 1966, *N. beklemishevi, S. chimaera cervicornis, S.* cf. *leintwardinensis* (Hopkinson 1880), *P. dubius tumescens* (Wood 1900) and *B. bohemicus* (Barrande 1850). At depths of 941.0–960.0 m *L. cirrifer* Urbanek 1966, *L. expectatus bicornis* Urbanek 1966, *C. hemiaversus* Urbanek 1960, *C.* cf. *aversus* (Eisenack 1942), *N.*

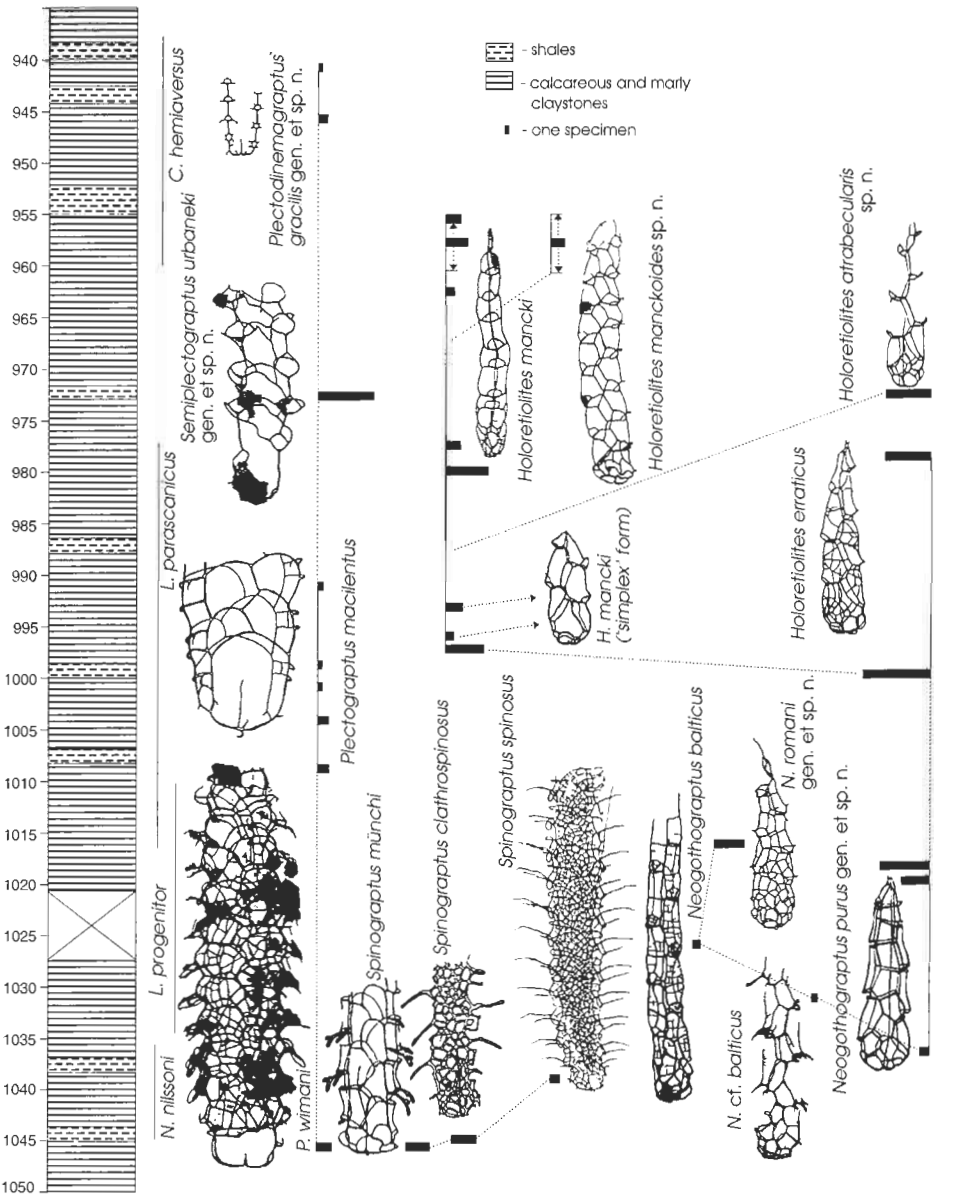


Fig. 6. Stratigraphical ranges and proposed conections between species of *Gothograptus* and *Plectograptus* lineages; based on the Miclnik borehole.

beklemishevi, *S. chimaera salvei* (Hopkins 1880) and *P. dubius* have been identified. Retiolitids from the Melnik borehole are illustrated on Fig. 6.

Erratic boulders from the Baltic Sea area. — Most of the Silurian boulders of graptolite limestone from the Baltic Sea area include graptolites of the early Ludlow age. The oldest graptolite fauna is that with *M. priodon* (Bronn 1834) (see Urbanek 1966). The youngest age is do-

cumented by the presence of *Cucullograptus aversus rostratus* Urbanek 1969, in a characteristically scant assemblage (without saetograptids), also found immediately above *S. leintwardinensis* Zone in boreholes. The assemblage with *C. aversus rostratus* is correlated here with the earliest Ludfordian (Siedlce beds) in the Polish lowlands (Urbanek 1966).

The Retiolitids from erratic boulders described herein form the following associations:

Jarosławiec 22: *B. bohemicus*, *C. pazdroi*, *L. scanicus parascanicus*, *N. beklemishevi*, *P. dubius*, *S. chimaera*, *Plectograptus macilentus* (Törnquist 1887), *Neogothograptus purus* gen. et sp. n., and *Holoretiolites mancki* (Münch 1931). This assemblage may represent the *L. scanicus* Zone.

Jarosławiec 25: *'B.' operculatus*, *L. progenitor*, *P. dubius*, and *P. macilentus*.

Jarosławiec 45: *L. progenitor*, *L. scanicus parascanicus*, *N. beklemishevi*, *P. dubius*, and *Neogothograptus romani* gen. et sp. n.

Jarosławiec 145: *L. scanicus scanicus*, *S. chimaera cervicornis*, *N. purus* gen. et sp. n., and *H. mancki*.

Graptolites from boulders J. 22, J. 25, J. 45 and J. 145 represent the *L. progenitor*/ *L. scanicus* Zone.

Jarosławiec 147: *Gothograptus kozlowskii* Kozłowska-Dawidziuk 1990.

Jarosławiec 149: *S. chimaera cf. salweyi*, *L. expectatus*, *'Bar.' operculatus*, and *N. purus*. This probably represents the *L. scanicus*/*invertus* Zone.

Jarosławiec 228: *S. chimaera*, *P. dubius*, *B. bohemicus*, *L. scanicus parascanicus*, *N. romani*, and *H. erraticus* (Eisenack 1951). This assemblage represents the early part of the *L. scanicus* Zone.

Władysławowo 128: *L. scanicus scanicus*, *S. chimaera*, and *H. mancki*. These forms represent the *L. scanicus* Zone.

Gdynia-Orłowo 134: *H. manckoides* sp. n.

Ustka 137: *L. scanicus parascanicus*, *S. chimaera cervicornis*, *P. dubius*, *B. bohemicus*, and *H. mancki*. These forms occur in the early part of the *L. scanicus* Zone.

Phylogeny of the retiolitids

In discussing phylogenetic relationships among graptolites of the family Retiolitidae both the stratigraphical data (Figs 4–6) and morphological characters of the rhabdosome (Figs 7–11) are used.

It is still not possible to indicate unequivocally the retiolitid ancestors (see Fortey & Cooper 1986; Loydell 1992). This makes identification of plesiomorphic characters of the group difficult. The uniqueness of retiolitid rhabdosomes testifies to their monophyly. Lenz & Melchin (1987) divided family Retiolitidae into subfamilies Retiolitinae and Plectograptinae based on the different ornaments on the surface on the cortical bandages: in the Retiolitinae this is formed of longitudinal strations, in the Plectograptinae the pustulose.

Mitchell (1987) recognised the following characters as typical of the family Retiolitidae (his subfamily Retiolitinae): (1) ancora incorporated into clathria, (2) thecae elongate with great overlap and (3) fusellar periderm reduced to clathria. Mitchell (1987) proposed three generic groups: the petalograptids, retiolitids, and plectograptids. The last two groups corre-

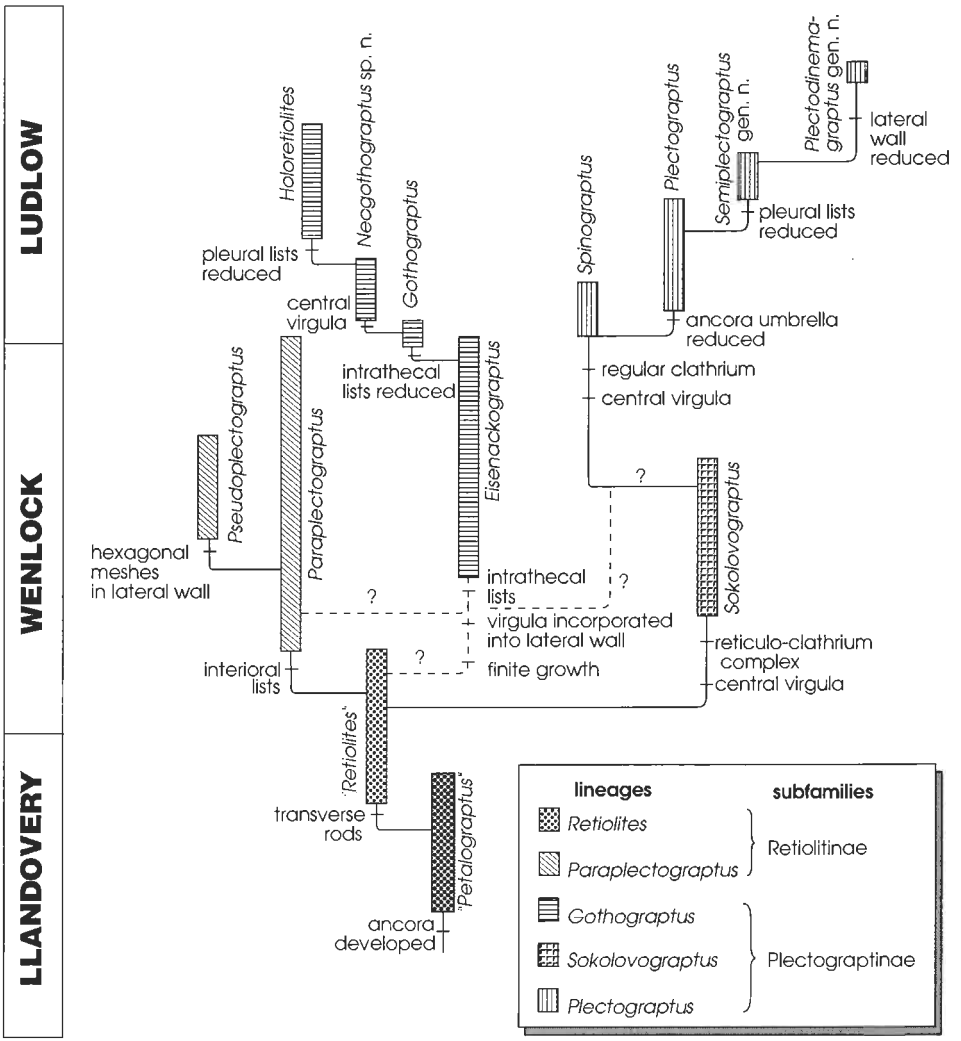


Fig. 7. Phylogenetic lineages of the Retiolitidae and the '*Petalograptus*' lineage.

spond to the subfamilies Retiolitinae and Plectograptinae *sensu* Bouček & Münch (1952), and are here also regarded as subfamilies. The present study is focused on the subfamily Plectograptinae, which is especially well represented in the studied material.

The presence of well developed transverse rods (corresponding with character 7, after Mitchell 1987) distinguishes the subfamily Retiolitinae from the Plectograptinae (Fig. 7). The presence of the interioral lists, the type of transverse rods, a reticulum partially separate from the clathria (external common canal) and the virgula connecting with parietal lists link the genera *Paraplectograptus* and *Pseudoplectograptus* with the *Retiolites* lineage. The lack of a connection between the subapertural lists and the transverse rods

(character 10) seems to be a new character, unique to *Paraplectograptus* and *Pseudoplectograptus*. The arrangement of the lists of the lateral walls of the clathria, and the presence of transverse rods are joint characters of the genera *Pseudoplectograptus*, *Paraplectograptus*, and *Retiolites*. The *Sokolovograptus* lineage occupies a separate place because it differs from the other plectograptids in the presence of a reticulo-clathria complex in the lateral walls. The central position of the virgula and lack of transverse rods links it with the *Plectograptus* lineage. A reticulum (sometimes reduced) entirely dependent on the clathria seems to be a new characters in the plectograptids. These characters suggest a common origin of the *Plectograptus* and *Gothograptus* lineages. A regular clathria pattern with a combination of sub- and supraapertural, medial, pleural, and parietal lists is a common characters of the genera in the *Plectograptus* lineage.

The position of the *Gothograptus* lineage seems doubtful, because of the presence of the transverse rods in its oldest representative *Eisenackograptus eisenacki*. This character is lacking in other species of the *Gothograptus* lineage. Assuming that the intrathecal lists are homologous with the transverse rods, which is suggested by their position, *E. eisenacki* would be related to the *Retiolites* lineage. On the other hand, if the origin of these lists was independent of the transverse rods, the *Gothograptus* lineage can be more closely connected with the *Plectograptus* lineage, because of the presence of a reticulum dependent on the clathria and the development of the ventral orifices.

Succession of the Wenlock retiolitids in Zawada borehole

***Retiolites* lineage**. — The oldest species of the group occur below the *Cyrtograptus centrifugus* (Figs 4, 5). These are *Retiolites geinitzianus* and *Pseudoretiolites* sp. These species differ in the construction of the ancora umbrella. The lists of *R. geinitzianus* ancora form regular hexagonal meshes (Fig. 13G), whereas rectangular meshes occur in *Pseudoretiolites* sp. (Fig. 12C). The construction of the clathria of young rhabdosomes is similar. The transverse rods prolonging into subapertural lists are very similarly developed in both species (Fig. 12).

***Paraplectograptus* lineage**. — *Paraplectograptus eiseli* together with *R. geinitzianus* and *P.* sp. occur above *C. centrifugus*. The range of *P. eiseli* overlaps the upper part of occurrence of *C. lundgreni* (Figs 4, 8). *Paraplectograptus sagenus* has been found (Fig. 4) in the upper part of the *C. rigidus* range and continues up to the appearance of *M. testis*.

The rhabdosome of *P. eiseli* is built of a regular clathria, without reticulum. The parietolateral wall consists of parietal lists forming almost triangular meshes (Fig. 8). In *P. sagenus* a reticulum is present in the ventral and lateral walls.

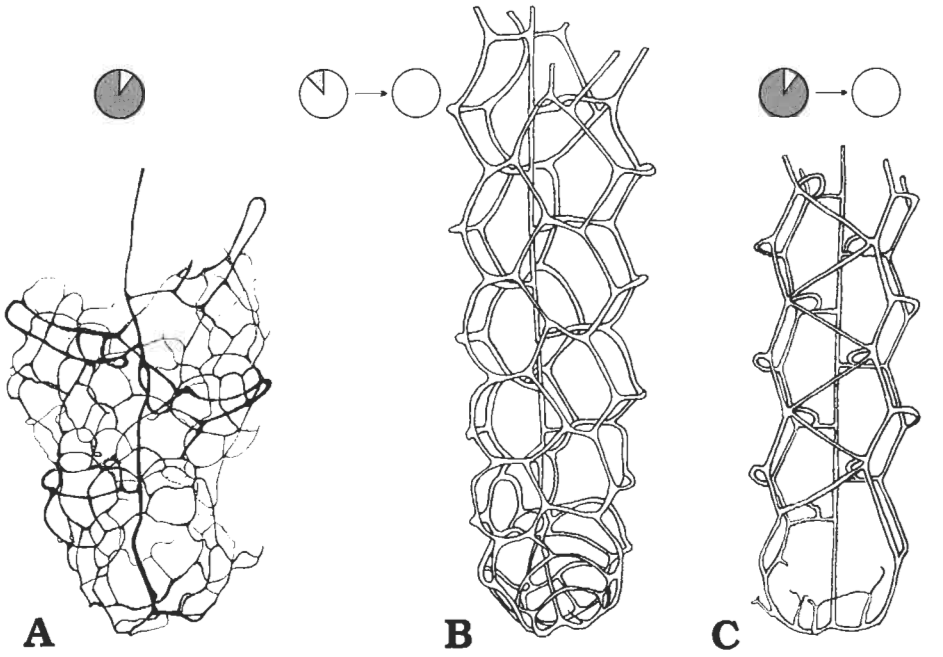


Fig. 8. Rhabdosome morphologies typical for lineages of the Retiolitinae: ❑A. *Retiolites* lineage. ❑B–C. *Paraplectograptus* lineage, including (B) *Pseudoplectograptus* and (C) *Paraplectograptus*. Grey areas show the approximate density of reticulum.

Pseudoplectograptus praemacilentus, occurring in the lower part of range of *M. testis* (Fig. 4), is considered to belong to the *Paraplectograptus* lineage. The lateral walls of *P. praemacilentus* are constructed of parietal and dorsal lists forming hexagonal meshes, which can be disorderly arranged in the reticulum, especially in the middle part of the wall. This species differs from *P. simplex* sp. n. in the construction of ventral wall. *P. praemacilentus* possesses two apertural lists, but *P. simplex* has only one. The latter shows also a trend towards prominent thickening of the virgula in the distal part of the rhabdosome (Fig. 4).

The representatives of the *Retiolites* and *Paraplectograptus* lineages possessing interioral lists-type of transverse rods, occurred in the early Wenlock. Paraplectograptids with their advanced characters of smaller size and reduced reticulum survived into the late Wenlock.

***Sokolovograptus* lineage**. — The first sokolovograptid occurs below the range of *M. belophorus*. This is *S. polonicus*, which represents a maximum simplification of the rhabdosome in this lineage. The rhabdosome is formed of a simple ancora umbrella (Figs 5, 26), pleural and subapertural lists in the ventral walls and sometimes relatively few parietal lists in the lateral walls. *M. belophorus* occurs together with *S. telleri*, in which the reticulo-clathria of the lateral walls are quite well developed (Figs 5, 25), whereas the ventral walls are strongly reduced, as in *S. polonicus*.

Much complication in the construction of the rhabdosome is shown by the two species, *S. textor* and *S. parens*, occurring in the higher parts of the borehole. They differ from *S. telleri* in having a more complicated arrangment of the ventral walls. Presumably *S. telleri*, characterised by the most reduced ventral walls, derived from *S. textor*, which is known from the late Llandovery of Arctic Canada (Lenz & Melchin 1987). *S. textor* occurs in most samples studied herein from the lower part of the range *of M. belophorus* to the uppermost part of the range of *C. perneri* (Fig. 5).

S. textor occurs from depths of 1607.1 to 1582.9 m (Fig. 5) and possesses a rather narrow rhabdosome, slightly widening towards the distal end. The reticulo-clathria complex is uniformly developed along the total length of the rhabdosome.

The rhabdosome of *S. hiulcus* widens towards the distal end, where simultaneously the reticulo-clathria complex is reduced to horizontal parietal lists (Figs 5, 18C, I), and the supraapertural lists are reduced. This species occurs at depths from 1609.1 to 1582.9–1590.6 m. At a depth of 1599.7 m there are few forms with a strong contraction above the corona, and sometimes also in the medial parts of the rhabdosome.

S. zawadensis occurs at depths from 1599.7 to 1580.5 m (Fig. 5). The rhabdosome narrows to the distal end. A reduction of lists in lateral walls is marked, whereas in the distal parts only parietal ones are developed. In the ventral wall subapertural and supraapertural lists are present.

The range of *S. parens* is similar to that of *S. textor*. This species occurs at depths from 1606.1 to 1582.9–1590.6 m (Fig. 5). The basic difference between this species and *S. textor* is in the arrangement of the ventral walls. In *S. parens* the ventral wall is more complicated, being formed by subapertural and supraapertural lists and a reticulum, which is absent in the ventral wall in *S. textor*. Two species, *S. parens* and *S. diffusus* sp. n. can be distinguished. *S. parens* occurs at depths of 1603.1 to 1582.9 m (Fig. 5), and is characterised by a rhabdosome gently widening distally and with the uniform meshes and thickness of the reticular lists. *S. diffusus* sp. n. occurs between 1603.1 and 1609.1 m (Fig. 5). These rhabdosomes are very wide distally, with great variability of size of the reticular meshes and thickness of these lists.

Thus the first member of the *Sokolovograptus* lineage, the early Wenlock *S. polonicus*, shows a simple rhabdosome morphology which is much less complicated than in later species (*S. telleri, S. textor, S. parens*). This may be a case of evolution proceeding in the opposite direction to that shown in most retiolitids.

***Gothograptus* lineage**. — *Eisenackograptus eisenacki* occurs in the middle part of the range of *M. belophorus* and in lower part of the range of *C. lundgreni* (Fig. 4). The number of thecae in the finite rhabdosome of specimens studied ranges from 15 to 20. The virgula has a central position in the proximal, and medial parts of the rhabdosome, but in the distal part it is incorporated into lateral wall and also extends along the appendix.

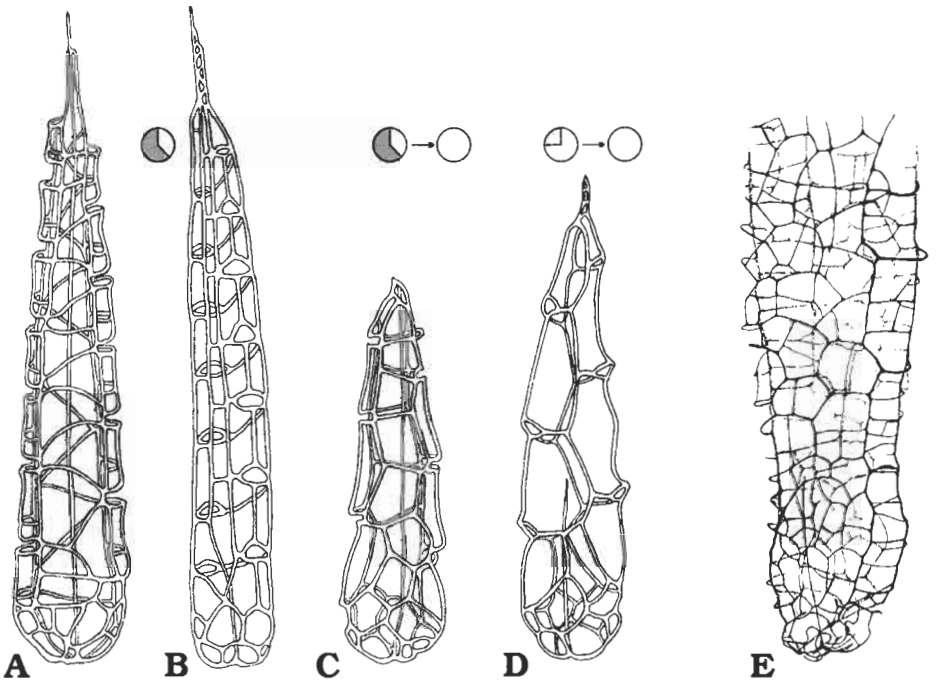


Fig. 9. Rhabdosome morphologies typical for lineages of the Plectograptinae. ❑A–D. *Gothograptus* lineage, including (A) *Eisenackograptus*, (B) *Gothograptus*, (C) *Neogothograptus* gen. n., (D) *Holoretiolites*. ❑E. *Sokolovograptus* lineage. Grey areas show the approximate density of reticulum.

Later species of the *Gothograptus* lineage are *G. pseudospinosus*, *G. obtectus* and *G.* sp. A. These species occur in the middle and upper part of the range of C. *lundgreni* (Kozłowska-Dawidziuk 1990). Their virgula is incorporated into the lateral wall in the proximal part of the rhabdosome, and they possess a distal tubular appendix similar to that of *E. eisenacki*, with the virgula in its wall. Species variability in *Gothograptus* is partially expressed in various apertural processes. Simple spines occur in *G. pseudospinosus*, whereas complex, reticulate veils cover the apertures and thecae of *G. obtectus*, and thecal hoods cover the apertures of *G. nassa.*

The first representative of the gothograptids, *E. eisenacki*, shows the most primitive characters, especially by possessing transverse rods, equivalent to the initial development of the interthecal septa. Its similarity to the other gothograptids is expressed in finite growth of the colony, ending with an appendix, and the virgula incorporated into lateral wall. In *Eisenackograptus* the virgula is incorporated into the distal part of rhabdosome, in contrast to the youngest, late Wenlock *Gothograptus* (*G. kozlowskii, G. pseudospinosus, G. nassa, G. obtectus*), where it is incorporated in the proximal part of rhabdosome and runs in the lateral wall along a rhabdosome devoid of any intrathecal lists. But only one late Wenlock *Gothograptus* — the *G. chainos* (Lenz 1993: pl. 7: 2) possesses free virgula

that reaches the appendix, similar to the *E. eisenacki*. The complete separation of the virgula from lateral wall in early Ludlow members of the lineage, *Neogothograptus* gen. n. and *Holoretiolites*, seems to indicate a very rapid transition from the former construction – *Gothograptus* with the virgula in the lateral wall for almost total length (Figs 6, 9).

Succesion of the Ludlow retiolitids in the Mielnik borehole

***Plectograptus* lineage.** — The first representatives of the Ludlow retiolitid fauna belonging to the plectograptids, *Plectograptus wimani* and *Spinograptus munchi*, occur below the range of *Lobograptus nilssoni* (Fig. 6).

P. wimani appears to be closely related to *P. macilentus*, having a very similar arrangement of clathria and similar size of rhabdosome. *P. wimani* possesses a well developed reticulum and apertural apparatuses shaped like reticulate hoods, which are different from the simplified, reticulum-free and apertural apparatuses of the rhabdosome of *P. macilentus*.

The rhabdosome of *Semiplectograptus urbaneki*, which occurs above the range of *L. parascanicus* (Fig. 6), is similar to *P. macilentus*, but narrower (about 1 mm) and lacks any pleural lists (Fig. 10).

The next stage of simplification in the arrangement of the clathria is represented by the rhabdosome of *Plectodinemagraptus gracilis*, which is thought to be descended from *Semiplectograptus urbaneki*, and occurs in the upper parts of *C. hemiaversus* range (Fig. 6) in Mielnik borehole. The width of the rhabdosome of *P. gracilis* is about one milimetre smaller than that of *S. urbaneki*, and lacks any lists in the lateral walls (Fig. 10). These lists (Fig. 27D) are extremely reduced to slight processes that project from the apertural lists. The rhabdosome of *P. gracilis* is the most reduced among all the known retiolitids.

Morphological changes due to reduction of the ancora umbrella, reticulum, apertural apparatuses, clathria and decrease of sizes of rhabdosome occurring in the stratigraphical sequence of species *P. wimani, P. macilentus, S. urbaneki*, and *P. gracilis* are consistent with the general evolutionary tendency among the retiolitids.

Spinograptus munchi occurs slightly below the range of *L. nilssoni* (Fig. 6) and is the first representatives of the genus in the Mielnik borehole. The rhabdosome of *S. munchi* shows the most reduced form of ancora sleeve among species of the genus, and lacks a reticulum. This species is also characterised by the widest branching of apertural processes. A well developed reticulum is present in the higher occurring *S. clathrospinosus* (Fig. 6), which in contrast to *S. munchi* possesses very narrow and strongly longitudinal apertural processes of clearly visible reticulofusellar form, similar constructed to all species of *Spinograptus*. In Arctic Canadian material Lenz (1993: pl. 3: 1.4–5.7) described *S. clathrospinosus* form with 'club shaped or spatulate' apertural processes.

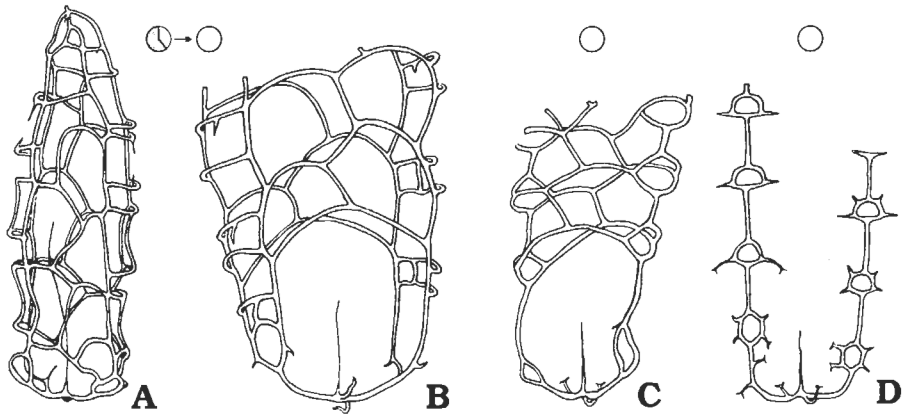


Fig. 10. Rhabdosome morphologies in *Plectograptus* lineage of the Plectograptinae including: (A) *Spinograptus*, (B) *Plectograptus*, (C) *Semiplectograptus* gen. n., and (D) *Plectodinemagraptus* gen. n. Grey areas show the approximate density of reticulum.

The densest reticulate network and also the most reduced apertural processes are found in the rhabdosome of *S. spinosus*, which occurs above the other species of this genus (Fig. 6), co-occurring in this borehole with *N. nilssoni*.

The morphological changes of species of the *Spinograptus* deviate from the general pattern of evolution of the retiolitids concerning the development of reticulum in stratigraphicaly younger forms. All specimens of the genus possess a reticulofusellar structure of apertural processes, which in the youngest form, *S. spinosus*, is limited to the distal parts of spines.

***Gothograptus* lineage**. — The *Gothograptus* lineage is known from Late Wenlock to Ludlow, where it is very diverse. The first local representative is *Neogothograptus purus*, occuring in the upper part of *L. nilssoni* range and in the higher part of the range of *L. progenitor* (Fig. 6). This species differs from Wenlock forms of the lineage in the central position of the virgula. *N. purus* also differs in having a simple form of rhabdosome, lacking a reticulum and apertural apparatuses (Fig. 9).

N. balticus occurs in the lower part of the range of *L. progenitor* (Fig. 6) being different from the above mentioned species in the presence of reticulum, apertural apparatuses forming single, reticular, and narrow hoods growing from the supraapertural lists. One specimen showing finite growth of the rhabdosome with thick lists has fine, additional lists under the ancora, named here the outer ancora.

N. romani is known from the upper part of the range of *L. progenitor* (Fig. 6). It differs from *N. purus* in the presence of a reticulum in the lateral walls and a smaller number of thecae in finite rhabdosomes.

Successive simplification of the clathria in *Gothograptus* lineage continues up to reduction of the pleural lists, typical of *Holoretiolites*. The first representative of the genus, *H. erraticus*, occurs in the middle part of the range of *L. parascanicus* (Fig. 6) and possesses a reticulum (Fig. 17C). In

a few specimens additional lists form a outer ancora (Fig. 28), similar to that in *N. balticus*.

H. mancki occurs slightly below *H. erraticus*, also in the upper part of the range of *L. parascanicus* and in the lower part of the range of *C. hemiaversus* (Fig. 6). The rhabdosome of *H. mancki* is longitudinal, cylindrical in shape with a long, reticulate appendix, and lacks both a reticulum and apertural processes. The number of thecae in the finite rhabdosome is commonly 10–12. In the lower part of the occurrence of *Holoretiolites mancki* (Fig. 6) in this borehole, there occurs the form described earlier as *H. simplex*. It has a rhabdosome of conical shape, 4–5 thecae and vestigial appendices formed of only 2 or 3 lists. This form is considered herein as *H. mancki*.

In the lower part of range of *C. hemiaversus*, *H. mancki* occurs together with *H. manckoides* (Fig. 6), which is almost twice as wide, being otherwise similar to *H. mancki*. The number of thecae is up to 16, and no appendix has been observed. The new species possesses subapertural lists two times as long as in *H. mancki*, while medial lists in both species are of similar length.

Holoretiolites atrabecularis, occurring in the upper part of the range of *L. parascanicus* (Fig. 6), shows a reduction of the medial lists distal of the corona. They appear as thin processes or only as denticles on subapertural lists (Fig. 29C). The finite rhabdosomes are free of a reticulum and the appendices are commonly very short. The number of thecae in the finite rhabdosome is usually 6. This is the most evolutionarily advanced *Holoretiolites*.

The Ludlow representatives of the *Gothograptus* lineage possess greatly reduced rhabdosomes when compared with the late Wenlock forms, with the central position of the virgula and progressive reduction of the reticulum and clathria and also a diminution in size of finite rhabdosomes. However, some departures from this general direction of evolutionary changes occur for example, when simple and, supposedly, evolutionary advanced forms, are succeeded by more primitive forms (e.g *N. balticus*, *H. erraticus* and *H. manckoides*)

Systematic description

Terminology

In the retiolitid rhabdosome descriptions the terminology used by Bulman (1970), Bates & Kirk (1984, 1991, 1992), Kozłowska-Dawidziuk (1990) and Lenz (1993) is applied, with several new terms added. Those most frequently used are defined below (Fig. 11):

ancora	structure formed by diverging tip of virgella at early growth stage of petalograptids and retiolitids.
ancora sleeve	distal prolongation of ancora, forming an additional wall above that of the thecae, composed by meshwork of lists (clathria and

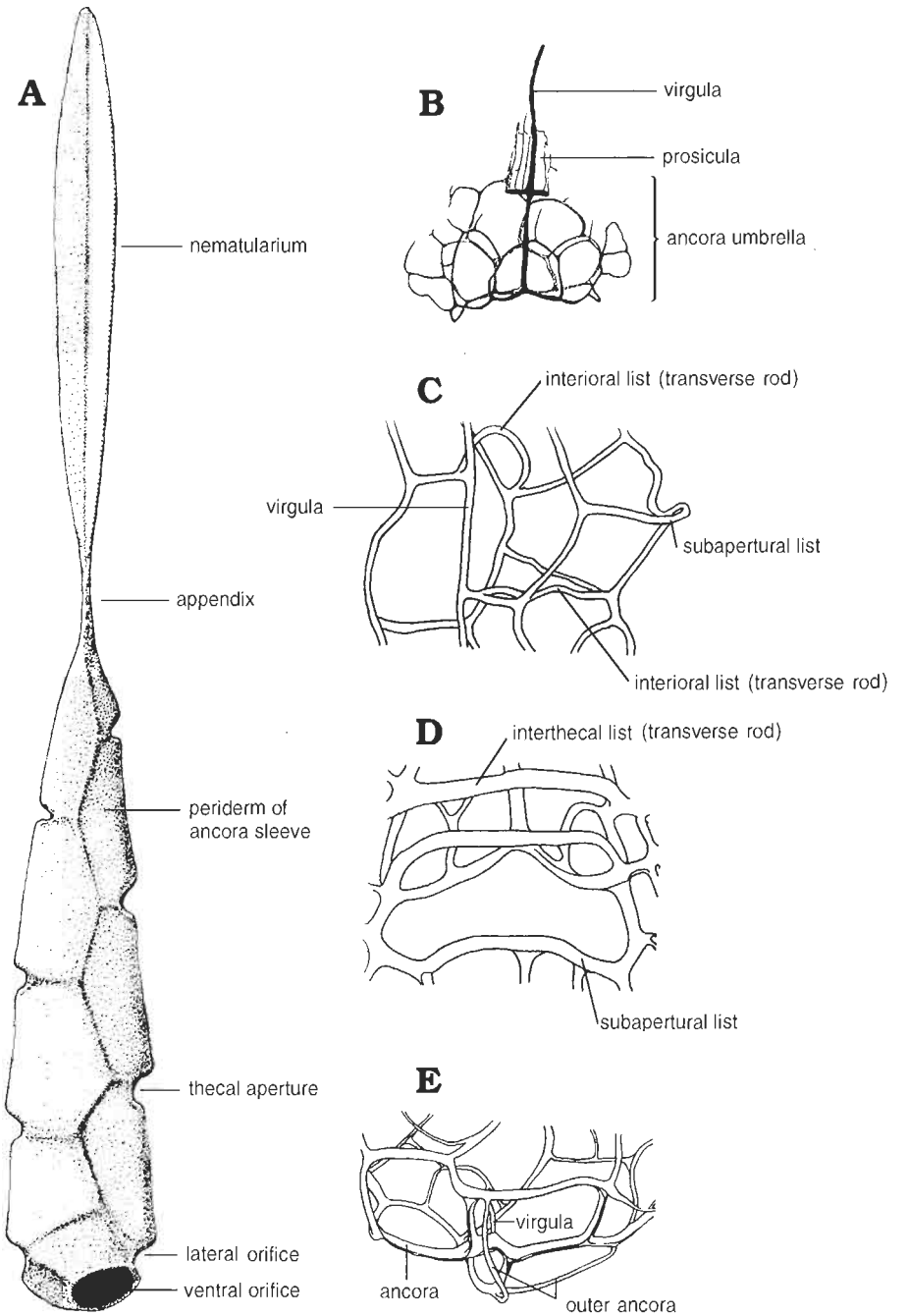


Fig. 11. Presentations of terminology. ❑A. Hypothetical *Holoretiolites* with nematularium and preserved incremental periderm of the ancora sleeve. ❑B. Young stage of growth of *Retiolites geinitzianus* Barrande 1850. ❑C. Fragment of *Paraplectograptus eiseli* (Manck 1917). ❑D. Inside view of aperture of theca of *Eisenackograptus eisenacki* (Obut & Sobolevskaya 1965). ❑E. Outer ancora of *Holoretiolites erraticus* Eisenack 1951.

	reticulum, or reticulo-clathria complex, and periderm between them but without elements of thecal framework, e.g. transverse rods),
ancora umbrella	early stage growth of ancora sleeve proximal of thecae,
clathria	thicker than reticulum lists of rhabdosome, with typical pattern for given groups; especially pronounced in mature plectograptines,
outer ancora	additional lists, connect with ancora, that follow the course to ancoral lists,
finite rhabdosome	rhabdosome of terminated growth, usually ending with appendix,
intrathecal list	the list situated below aperture inside of theca, bound with pleural lists, known in *Eisenackograptus eisenacki*-type of transverse rods,
interioral list	the list running from parietal to pleural lists, and bound with parietal lists between apertural lists, occurs in *Paraplectograptus* lineage-type of transverse rods (Fig. 8),
orifices	lateral or proximal ventral apertures, do not being apertures of the thecae,
reticulum	thin lists forming meshwork, situated between clathrial lists,

Family Retiolitidae Lapworth 1873

Subfamily Retiolitinae Lapworth 1873

Discussion. — Lenz (1993) divided the subfamily Plectograptinae into two informal subgroups: (1) *Paraplectograptus* group (*Gothograptus, Holoretiolites, Paraplectograptus, Spinograptus*, and *Balticograptus*) and (2) *Plectograptus* group [*Plectograptus* (*Plectograptus*), *Plectograptus* (*Sokolovograptus*), and possibly *Agastograptus*]. His division is based on the position of the virgula: 'those with the virgula attached throughout or to the distal part of the rhabdosome, and those in which the virgula is totally free beyond its ancoral attachment'.

This division would be different had the construction of the rhabdosome of *Paraplectograptus* been correctly interpreted. Actually, the edges of interthecal septum that are present in this rhabdosome (herein called transverse rods) and regarded earlier as aboral lists, connect at their ends to the pleural lists (see Bouček & Münch 1952: fig. 11h). The presence of the transverse rods has been noticed by Bates & Kirk (1984: fig. 4h), in a specimen assigned by them to *Retiolites* sp., which is here identified as *Pseudoplectograptus praemacilentus*, closely related to *Paraplectograptus*.

Because of the above observation the genus *Paraplectograptus* is here moved to the Retiolitinae (from *Plectograptinae*), together with *Pseudoplectograptus*. Thus two lineages are here recognised within the subfamily Retiolitinae: the *Retiolites* and *Paraplectograptus* lineages, and the subfamily Plectograptinae is divided into three lineages: *Sokolovograptus* (*Sokolovograptus*), *Plectograptus* (*Plectograptus, Semiplectograptus* gen. n., *Plectodinemagraptus* gen. n., and *Spinograptus*) and *Gothograptus* (*Eisenackograptus, Gothograptus, Neogothograptus* gen. n., *Holoretiolites*) (Fig. 7).

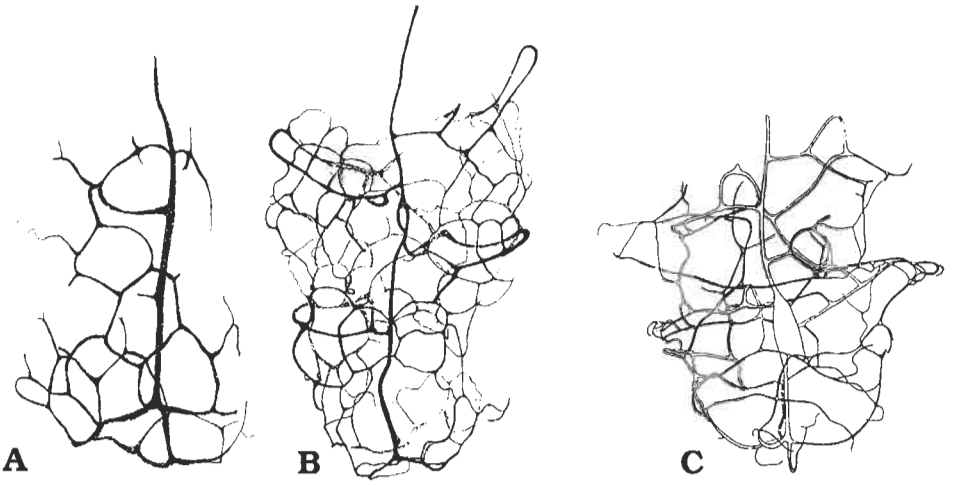


Fig. 12. Young growth stages. ❑A–B. *Retiolites geinitzianus* Barrande 1850. ❑C *Pseudoretiolites* sp.

Genus *Retiolites* Barrande 1850

Type species: *Gladiolites geinitzianus* Barrande 1850.

Species included. — Only type species.

Retiolites geinitzianus Barrande 1850

Figs 12A–B; 13.

Retiolites (vel *Gladiolites*) *geinitzianus* Barrande; Barrande 1850: pp. 18–25, pl. 4: 16–19, 24, 33; non pl. 4: 20–23.

Retiolites geinitzianus Barrande; Holm 1890: pp. 18–25, pl. 2: 2–5.

Material. — About 1000 immature and mature specimens, commonly flattened ZPAL G. XVI/1928–2927, borehole Zawada 1 depths 1621.7 m and 1651.4 m.

Description. — The longest rhabdosome reaches 22 mm. The width of the proximal part of rhabdosome is 0.7–1.2 mm. Maximum width about 3.8 mm. Young stages are represented by prosiculae, ancora stage, ancora umbrella formed by hexagonal meshes, and rhabdosomes of several thecae. The first transverse rod to theca 1/1 starts below the apex of the prosicula. The proximal lateral orifices are on both sides of the rhabdosome. The clathrial lists of the immature specimens are very fine (Fig. 12C), in contrast to the very thickened lists of mature rhabdosomes.

Remarks. — The mature rhabdosomes in the investigated material are difficult to study because of flattening and and the presents of sediment. It is therefore difficult to designate subspecies. The width of the rhabdosome reaches 3.8 mm, corresponding to that of *Retiolites geinitzianus angustidens* Elles & Wood 1908.

Genus *Pseudoretiolites* Bouček & Münch 1944

Type species: *Retiolites perlatus* Nicholson 1868.

Species included. — *P. perlatus*, *P. dentatus* Bouček & Münch 1944, *P. decurtatus* Bouček & Münch 1944, and *P. rete* Richter 1853.

Pseudoretiolites sp.

Figs 12C; 15A.

Material. — 20 immature rhabdosomes, ZPAL. G. XVI/121–139, borehole Zawada 1, depths 1621.7 m and 1651.4 m.

Description. — The length of the biggest rhabdosome, at the growth stage of second pair of thecae is 3.5 mm. All specimens possess prosiculae, and sometimes several fuselli of the metasicula (length about 0.38 mm). Apertural ring of the sicula possesses a small dorsal lobe, developed into the dorsal spine of length to 0.2 mm, which is not always preserved (Fig. 15A). Ancora umbrella possesses spiral and radial lists (Fig. 12C). The lists of the first theca in contact with the last ancora umbrella list (Fig. 12C). Transverse rods are linked to apertural processes of thecae by add detail of processes. The zigzag parietal lists in the lateral wall are connected to transverse rods.

Remarks. — The specimens of *Pseudoretiolites* represent only young astogenetic stages of the rhabdosome, and it is difficult to assign them a to species. The apertural processes are similar to processes of *P. perlatus* and *P. decurtatus* (Bouček & Münch 1944: figs 8a–e, 9a–d). The material of Bouček and Münch is not isolated and represents mature rhabdosome, so it is difficult to make comparisons with either species. The sicula and proximal end are similar to those in *P.* cf. *decurtatus* of Lenz & Melchin (1987: pl. 1: 4, 5).

Genus *Paraplectograptus* Bouček & Münch 1948

Type species: *Retiolites eiseli* Manck 1917.

Emended diagnosis. — The edges of the interthecal septa link virgula and parietal lists. The parietal lists form almost triangular meshes. The reticulum may be present or absent. The angle between pleural lists of successive thecae is obtuse. The ventral wall is formed by subapertural and pleural lists. The prosicula is rarely present.

Species included. — *P. eiseli* (Manck 1917) and *P. sagenus* Lenz 1993.

Paraplectograptus eiseli (Manck 1917)

Figs 14; 15D–E.

Paraplectograptus eiseli sp. n.; Manck 1917: p. 338–340, fig. 1–5.

Retiolites tenuis Eisenack; Eisenack 1951: pp. 131–134, pl. 21: 1–13, pl. 22: 1, 2.

Paraplectograptus eiseli Eisenack; Lenz & Melchin 1987a: p. 168, pl. 3: 4.

Emended diagnosis. — The reticulum may be represented by single lists or may be absent. The clathria are regular.

Material. — About 1000 flattened specimens, the most of them representing immature rhabdosome, ZPAL G. XVI/140–1330, Zawada 1 borehole, depths 1621.7 m and 1592.6–1533 m, Barciany borehole depth 1562.0–1568.0 m and Korsze 1 depth 1589.4–1595.9 m.

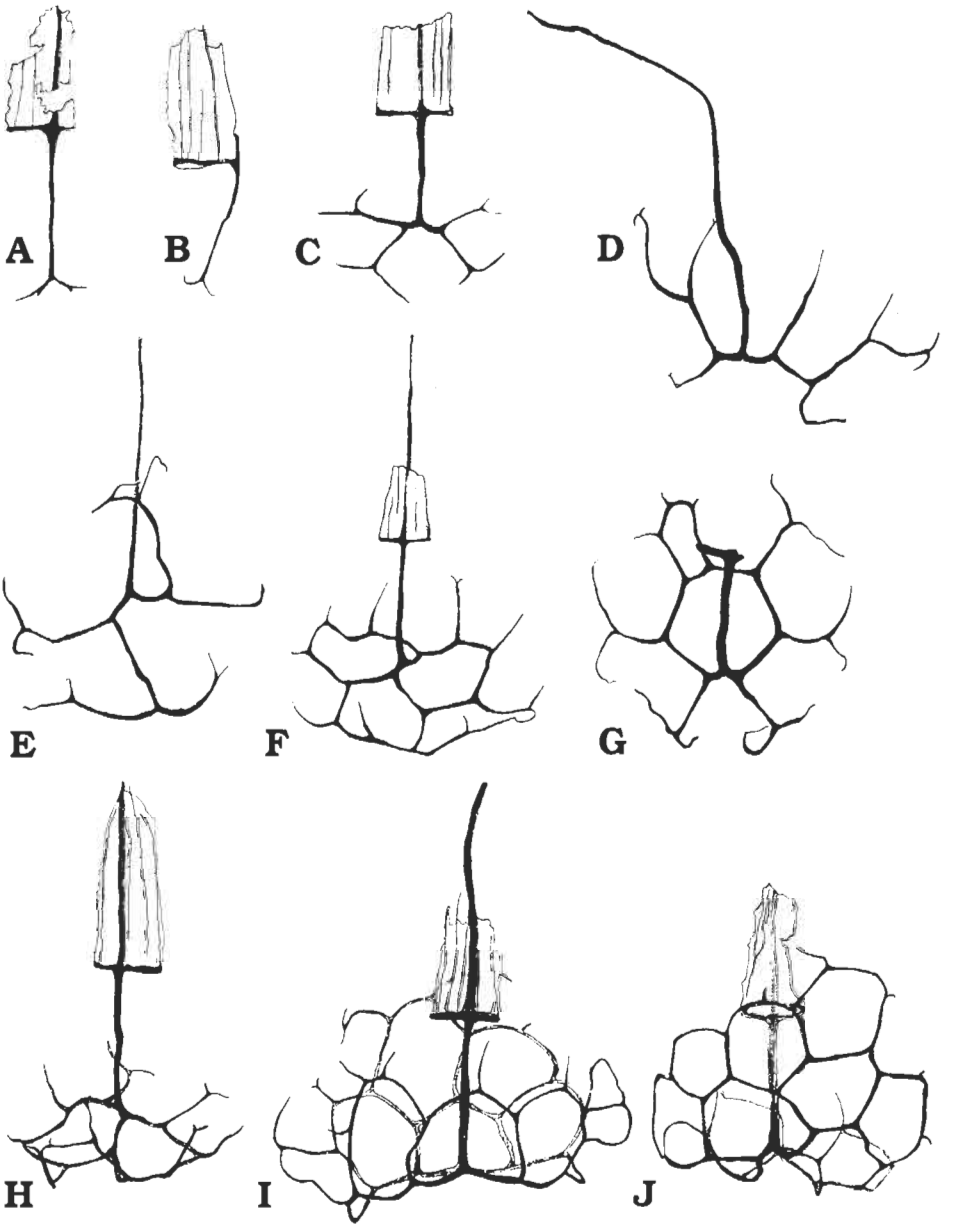


Fig. 13. Succesive early astogenetic stages of *Retiolites geinitzianus* Barrande 1850, *C. murchisoni* Zone, Zawada borehole.

Description. — The length of the rhabdosome is up to 19 mm. The corona always narrow about 0.7–0.9 mm. Rhabdosome widens distally to 1.3–1.6 mm. Thecal spacing of 7–7.5 in 10 mm. The longest rhabdosome possesses 18 pairs of thecae. The coronal lists are fine and well developed. The pleural

lists may be curved in this middle part (Fig. 15D). The immature specimens represent ancora stages and rhabdosomes with several thecae (Fig. 14).

Variability. — Several specimens possess single reticular lists in lateral wall, which make not regular pattern of parietal lists. The prosicula is present in 9 specimens (depth 1621.7 m) whith several pairs of thecae. The clathria of these specimens are slightly irregular. Several mature rhabdosomes possess considerably thickened clathrial lists.

Remarks. — This material corresponds in dimensions with the holotype. They are wider than those described by Lenz & Melchin (1987) being about 0.5 mm in width. *P. eiseli* is very abundant both as immature and mature rhabdosomes. It ranges from Late Wenlock to *C. lungreni* Zone (Fig. 4). In the Canadian material *P. eiseli* is less common (Lenz & Melchin 1987) but ranges from the late Llandovery to late Wenlok *C. lungreni/M. testis* Zone (Lenz 1993).

Paraplectograptus sagenus Lenz 1993

Fig. 15C.

Paraplectograptus sagenus sp. n.: Lenz 1993: p. 22, pl. 15: 1–9, 16: 1–8.

Material. — 10 immature and mature specimens, ZPAL G. XVI/1331–1340, Zawada 1 borehole, depths 1581.9–1559.5 m.

Description. — Rhabdosome length up to 12.0 mm. The width of the corona is up to 1.2 mm, lateral wall up to 1.2–1.9 mm. The distance between apertural lists is about 0.8 mm, but is shorter in the proximal region (Fig. 15D). Thecal spacing of 7 thecae in 10 mm.

Variability. — Specimens differ from each other in the density of the reticulum.

Remarks. — The dimensions of *P. sagenus* are similar to *P. eiseli*. The substantial difference between them is the presence of the reticulum in the former. The reticulum in the Canadian forms is better distinguished in ventral walls.

Genus *Pseudoplectograptus* Obut & Zaslavskaya 1983

Type species: *Plectograptus praemacilentus* (Bouček & Münch 1952).

Emended diagnosis. — The virgula and connected parietal lists are close to the lateral wall, which is formed of a reticulum, or they form this wall, when the reticulum is absent. Parietal and dorsal lists form hexagonal meshes, which may be replaced by reticulum which then builds the lateral wall. The pleural lists and one or two apertural lists form the ventral wall, where the reticulum is less common. The pleural lists bend at almost right angles. The thecal spacing 8–9 in 10 mm.

Remarks to emended diagnosis. — The genus was established for two species described originally as *P. praemacilentus* Bouček & Münch 1952 and *P. lejskoviensis* Bouček & Münch 1952. The diagnosis of *Pseudoplectograptus* by Obut & Zaslavskaya (1983) states that the virgula has a central position in the rhabdosome. The investigations of Lenz & Melchin (1987a) and Lenz (1993) had shown that the virgula is incorporated into

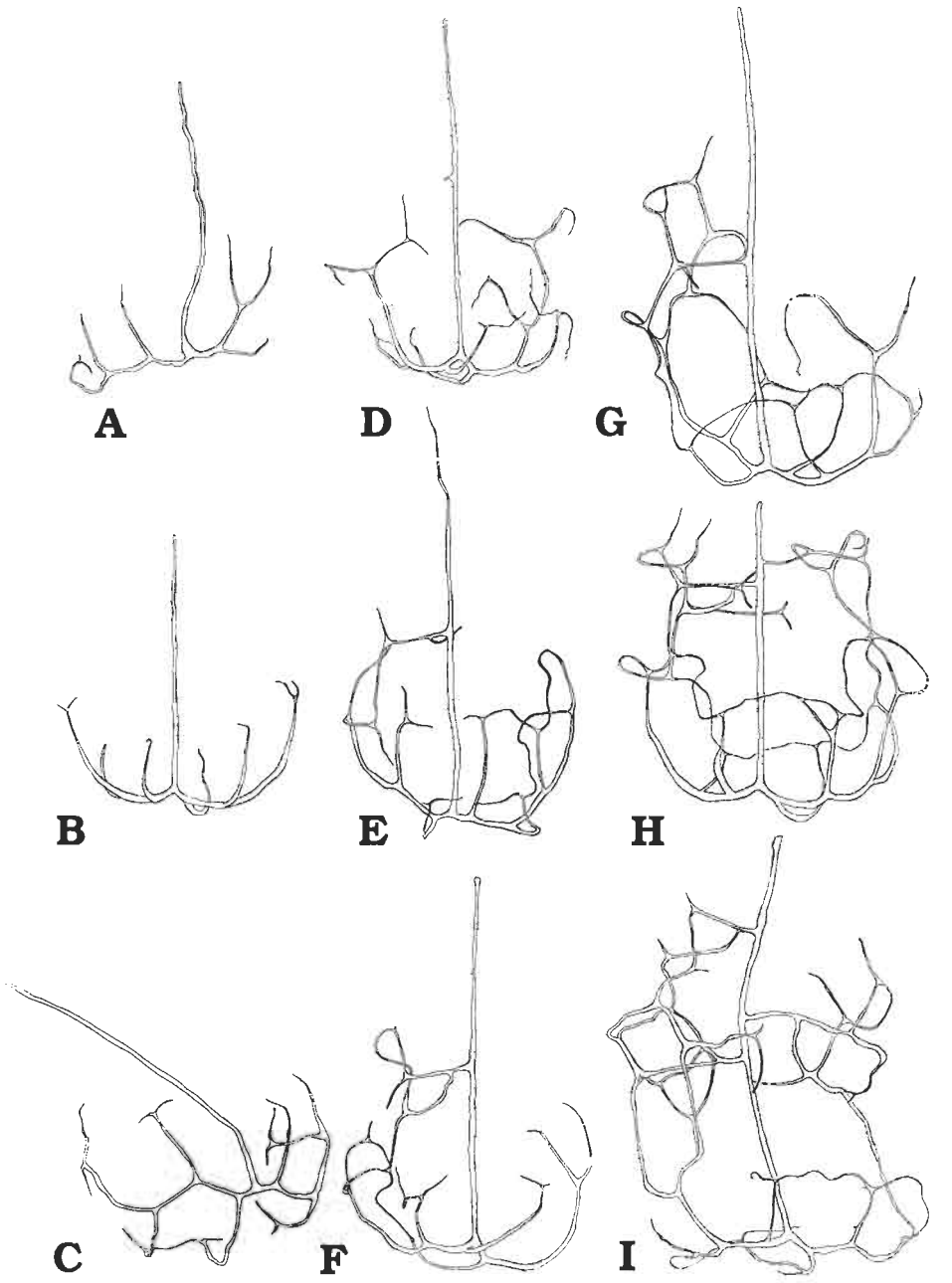


Fig. 14. Succesive early astogenetic stages of *Paraplectograptus eiseli* (Manck 1917), *C. lungreni* Zone, Barciany borehole.

the skeletal structure. The virgula in specimens from Zawada is located near the lateral wall, as in *R. geinitzianus*. Only in case of the *P. areticulatus* sp. n., where the reticulum is absent, may we maintain that the virgula

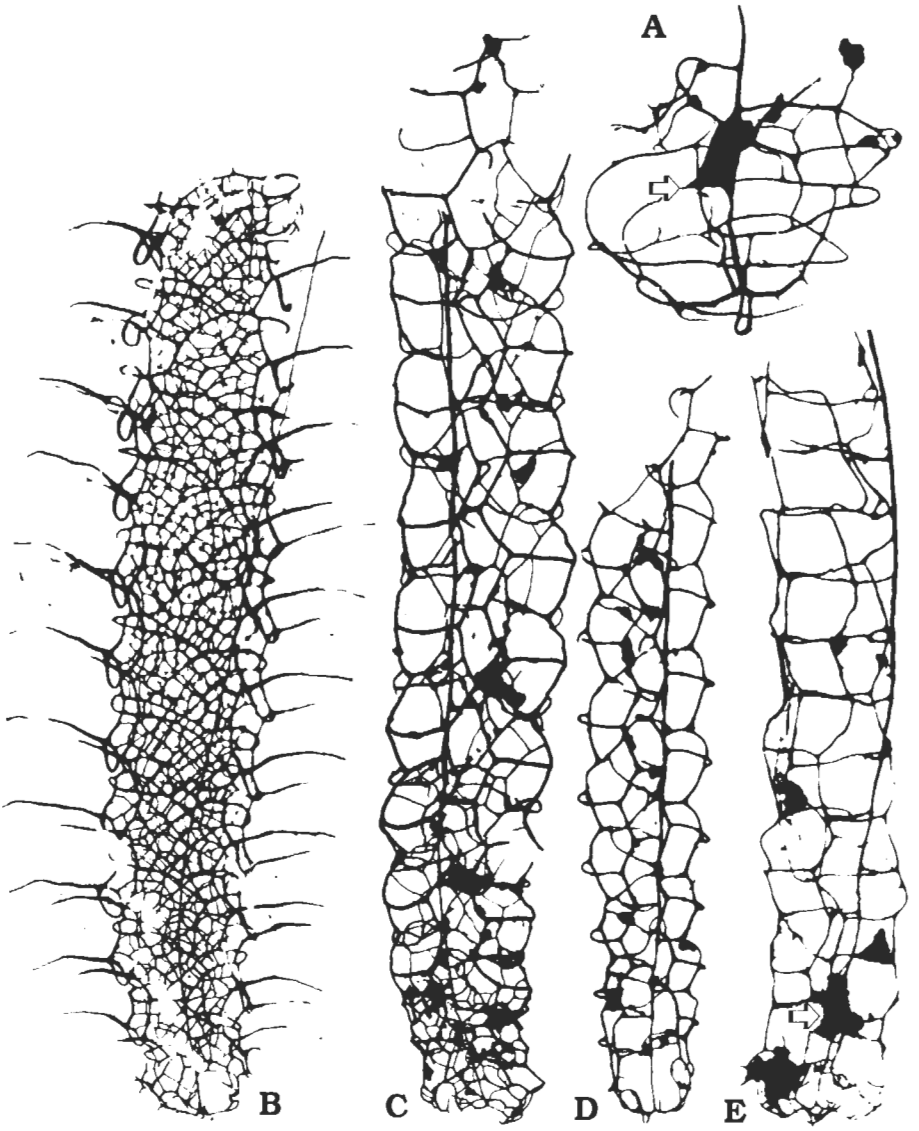


Fig. 15. ❑A. *Pseudoretiolites* sp., young stage of growth with dorsal lobe on prosicula (arrowed). ZPAL G. XVI/122, Zawada 1646.0–1652.0 m; × 16. ❑B. *Spinograptus spinosus* (Wood 1900), finite rhabdosome ZPAL G. XVI/1904, *N. nilssoni*. Zone Mielnik 1038.0 m; × 9. ❑C. *Paraplectograptus sagenus* Lenz 1993; finite rhabdosome, ZPAL G. XVI/1335, Zawada 1562.0–1568.0 m; × 12. ❑D–E. *Paraplectograptus eiseli* (Manck 1917). D. Fragment of mature rhabdosome, ZPAL G. XVI/200, Zawada 1546.5–1552.0 m; × 8. E. Rhabdosome with prosicula (arrowed); × 12.

forms the lateral wall together with the parietal lists. Lenz & Melchin (1987a) removed *P. praemacilentus* to the *Paraplectograptus*.

Species included. — *P. praemacilentus* (Bouček & Münch 1952), *P. simplex* sp. n., and *P. areticulatus* sp. n.

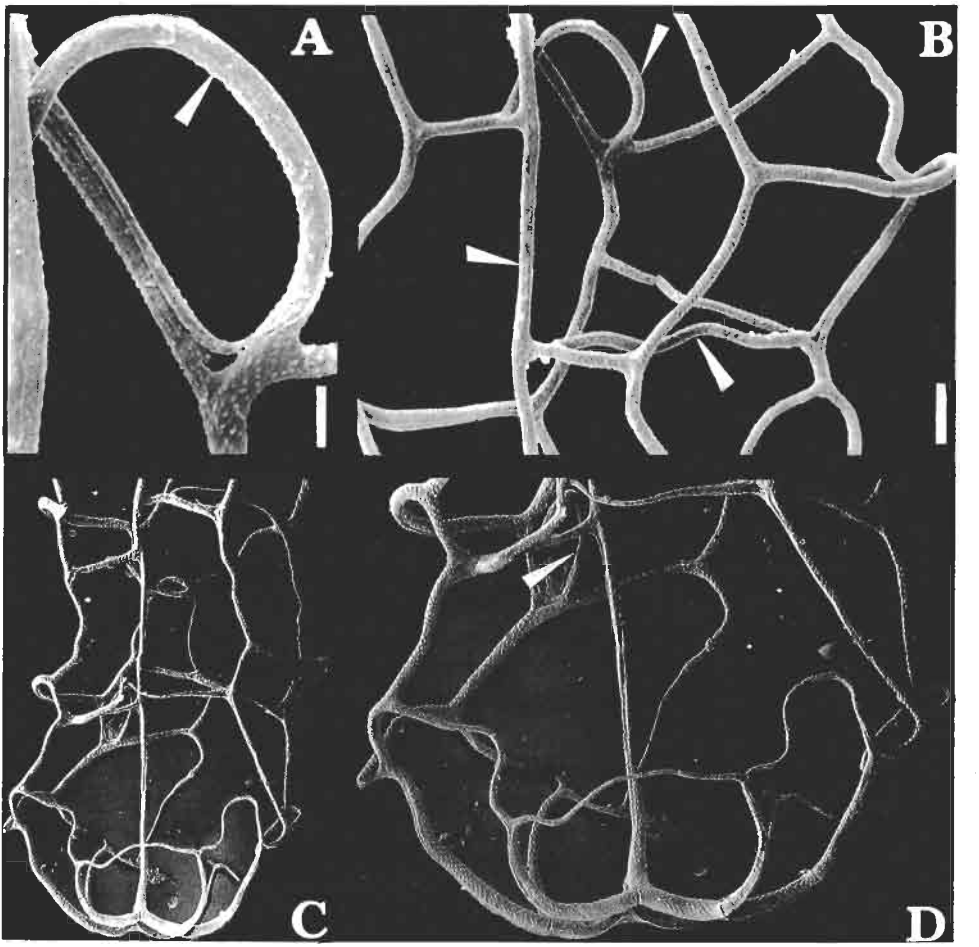


Fig. 16. *Paraplectograptus eiseli* (Manck 1917) fragment of mature specimen, ZPAL G. XVI/1244; Barciany 1562.0–1558.0 m. A. Interioral list (arrowed). B. Medial part with virgula and interioral lists arrowed, bar scale 100 μm. C. Proximal part of rhabdosome; × 24. D. Ancora umbrella with first interioral list arrowed; × 45.

Pseudoplectograptus praemacilentus (Bouček & Münch 1952)

Fig. 17B–C.

Emended diagnosis. — Supraapertural lists may be absent.

Plectograptus praemacilentus sp. n.; Bouček & Münch 1952: pp. 26–28, pl. 1: 5; fig. 8a, c, d; non fig. 8b, c.

Paraplectograptus praemacilentus Bouček & Münch; Lenz & Melchin 1987a: p. 168, pl. 3: 2, 3, 5, 9.

Emended diagnosis. — Supraapertural lists present.

Material. — 12 mature rhabdosomes, slightly flattened, ZPAL G. XVI/1615–1623; borehole Zawada 1, depth 1580.5 and 1559.5 m.

Description. — Maximum length of the rhabdosome up to 10 mm. The longest specimen has 13 pairs of thecae. The width of the rhabdosome in

coronal part up to 1.2 mm, in lateral and medial parts to 1.9–2.2 mm. Coronal lists are very fine. The rhabdosome narrows slightly distally. The distance between subapertural lists is about 0.6–0.7 mm. Clathrial and reticular lists thickness similar. Virgula commonly increases in thickness distally. Reticular meshes situated near the pleural lists are bigger than those situated in the middle of lateral wall. Every thecae possess supraapertural lists (Fig. 17B–C). Thecal spacing 7–8 per 5 mm.

Variability. — Seven fragments of rhabdosome (depth 1580.5–1582.9 m) possessing the diagnostic characters of *Pseudoplectograptus praemacilentus* differ from the holotype by having a narrower rhabdosome, about 0.9 m, thus 1/3 the width of typical specimens of the species. The proximal width of the rhabdosome of these forms is similar (1.2 mm) to that of the holotype. The reticulum of the ventral walls may be absent in narrow forms, but the thickness of the reticular and clathrial lists of the lateral wall is similar. Such width is typical rather of the *Paraplectograptus* rhabdosomes.

Pseudoplectograptus simplex sp. n.

Fig. 17A, D–F.

Plectograptus praemacilentus Bouček & Münch; Bouček & Münch 1952: pp. 26–28: fig. 8b.

Paraplectograptus sp.; Lenz & Melchin 1987a: p. 168, pl. 3: 7.

Paraplectograptus praemacilentus Bouček & Münch; Lenz & Melchin 1991: pp. 216–217, fig. 15G, M–O.

Holotype: ZPAL G. XVI/1623.

Type horizon and locality: Wenlock, *C. radians* Zone, Zawada 1 borehole, 1559.5–1560.5 m, Poland.

Diagnosis. — One apertural list is present in ventral wall.

Material. — 9 mature rhabdosomes, including fragments, slightly flattened, ZPAL G. XVI/1623–1631, borehole Zawada 1, depth 1559.5–1560.5 m.

Description. — The maximum length of a rhabdosome possessing 15 pairs of thecae is 12.9 mm. The width at the corona is about 1.0–1.2 mm, in the proximal part of the rhabdosome up to 1.6 mm, in medial part to 2.3 mm, and tapering towards the distal end to 1.9 mm. The widths of reticular and clathrial lists are similar. The reticulum is best developed in middle part of the rhabdosome in the lateral wall. The virgula widens considerably towards the distal end (Fig. 17E–F).

Variability — Five fragments of rhabdosomes possess the diagnostic characters of *P. simplex*, but differ in having narrow rhabdosomes, about 0.6 mm wide. In addition the reticulum in the proximal parts of this form has smaller-meshes. The length of the proximal part of this narrow form is about 1.0 mm. Some reticular lists may be present on supraapertural lists, making about 3 to 4 meshes. This phenomenon is similar to that described above in *P. praemacilentus*. Canadian forms of the *P. simplex* are wider than these morphs, about 1.6 mm.

Remarks. — The fundamental difference between *Pseudoplectograptus simplex* and *P. praemacilentus* is the presence of two apertural lists and a reticulum in the ventral wall of the latter *P. praemacilentus simplex* from

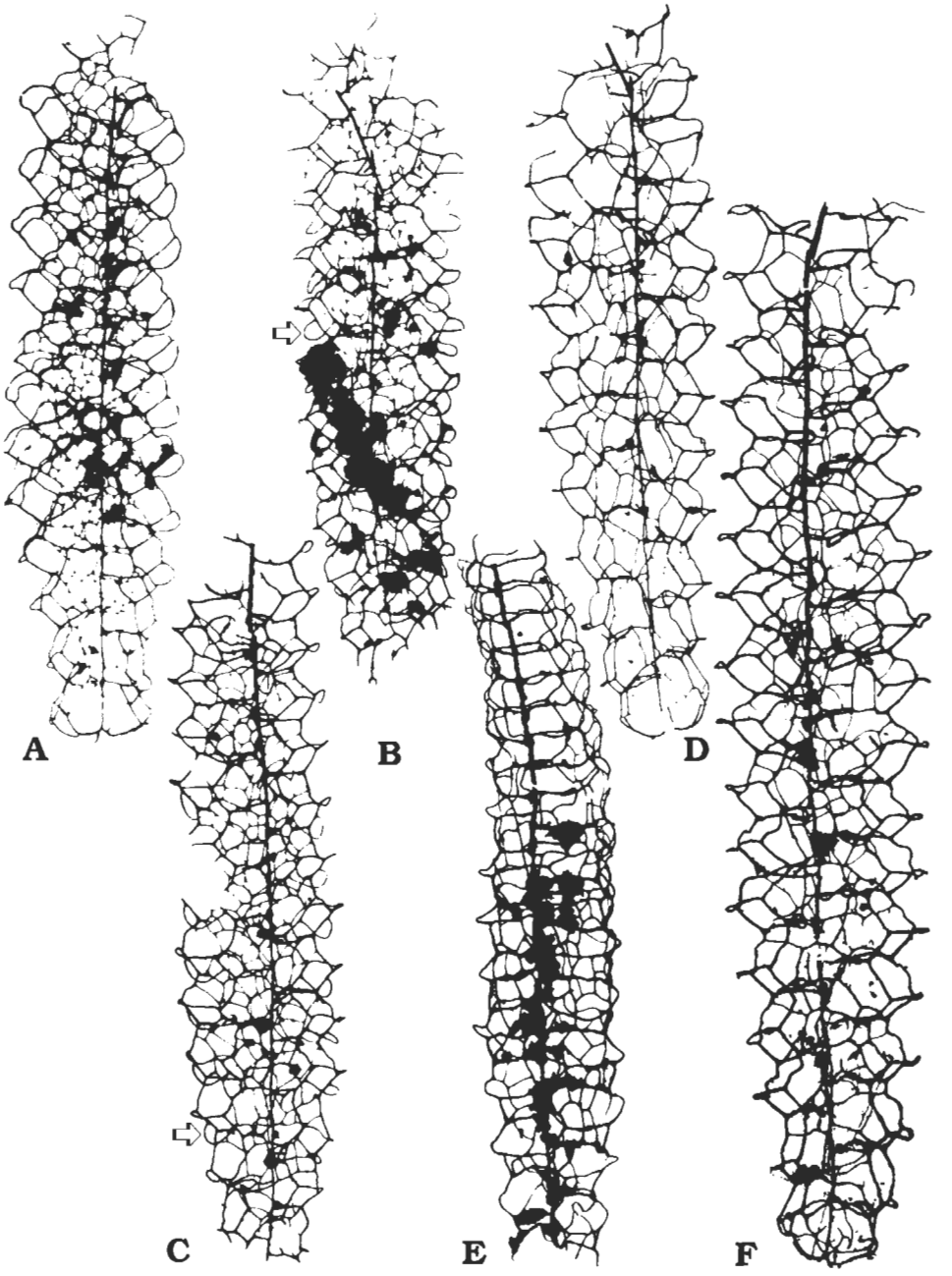


Fig. 17. ❑A, D–F. *Pseudoplectograptus simplex* sp. n., mature rhabdosomes. ZPAL G. XVI/1623–1626, Zawada 1555.5–1562.0 m. ❑B–C. *Pseudoplectograptus praemacilentus* (Bouček & Münch 1952), mature rhabdosomes, supraapertural lists arrowed, ZPAL G. XVI/1615 Zawada 1555.5–1562.0 m. A–C, E–F × 9; D × 10.

Canada is wider than the recovered forms, about 0.9 mm, and also possesses less reticulation. Polish forms are present in the late Wenlock *M. testis* Zone and *C. lundgreni* Zone, but the Canadian forms range from the late Llandovery to late Wenlock.

Pseudoplectograptus areticulatus sp. n.

Paraplectograptus praemacilentus Bouček & Münch; Lenz & Melchin 1987a: p. 168, pl. 3: 2.

Holotype: GSC 78441, pl. 3: 2.

Type horizon and locality: late Wenlock, *C. lundgreni*/*M.testis* Zone, Rookery Creek, Canada.

Diagnosis. — Reticulum absent. One apertural list in ventral wall.

Remarks. — *Pseudoplectograptus areticulatus*, described by Lenz & Melchin (1987: pl. 3: 2) as *Paraplectograptus praemacilentus* is distinguished here because of the total lack of the reticulum. A similar phenomenon appears in the closely related *P. eiseli*. This species occurs in Canada from the *M. turriculatus* Zone to *G. nassa* Zone.

Subfamily Plectograptinae Bouček & Münch 1951

Emended diagnosis. — The tendency to the reduction of the transverse rods and their general absence, virgula incorporated into lateral wall tending to occupy central position, lateral and ventral orifices in corona, generally regular clathria and tendency to reduction of reticulum, tendency to the finite growth of rhabdosome, sometimes with appendix.

Discussion. — In this study the revision of genera belonging to the subfamily Plectograptinae (plectograptid group of Mitchell 1987) is based on the following morphological criteria: presence or absence of transverse rods, position of virgula, arrangement of corona (e.g. in *Plectograptus* lineage the reduction of ancora umbrella), construction of clathria (present or absent pleural, medial or parietal lists) and shape of rhabdosome (Figs 9, 10). Diagnostic criteria used for the recognition of species are: degree of reticulation, construction of apertural apparatuses, and proportions of length of clathrial lists. At the species level the astogeny of the colony is also considered. In previous divisions of the Retiolitidae criteria applied herein at the species level were used for recognition of genera: for example, Obut & Zaslavskaya (1983) considered the presence of a reticulofusellar apertural apparatus a diagnostic character for their genus *Agastograptus*.

Genus *Sokolovograptus* Obut & Zaslavskaya 1976

Type species: *Plectograptus* (?) *textor* Bouček & Münch 1952.

Diagnosis. — Subapertural, supraapertural and pleural lists are present in ventral wall; occasionally looping lists also present. Reticulo-clathria complex developed in lateral wall, very rarely in ventral wall; parietal lists may be distinguished in the distal part of the rhabdosome.

Species included. — *S. textor* (Bouček & Münch 1952), *S. zawadensis* sp. n., *S. hiulcus* sp. n., *S. parens* (Obut & Zaslavskaya 1976), and *S. diffusus* sp. n.

Sokolovograptus textor (Bouček & Münch 1952)

Figs 18A–B; 24D–E.

Plectograptus ?textor sp. n.; Bouček & Münch: pp. 29–31, pl. 9a–e.
Plectograptus ?textor; Bouček & Münch 1952: p. 31, pl. 9a–c.
Plectograptus ?bouceki; Rickards 1967: pp. 243–245, fig. 13 d–e.
Plectograptus (Sokolovograptus) textor; Lenz & Melchin 1987a: p. 168, pl. 3: 10.
Plectograptus (Sokolovograptus) textor; Lenz 1993: p. 14, pl. 2: 2.
non *Plectograptus (Sokolovograptus) textor*; Lenz & Melchin 1987a: p. 168, pl. 1: 9, pl. 3: 13.
Plectograptus (Sokolovograptus) textor; Lenz 1993: p. 14, pl. 2: 1, 3–8.

Emended diagnosis. — Supraapertural and looping lists and reticulum in ventral walls occasionally in proximal part of rhabdosomes. Tendency to the reduction of reticulo-clathria to the only parietal lists in lateral walls.

Diagnosis. — Rhabdosome slightly wider distally.

Material. — 38 slightly flattened fragments of rhabdosome, ZPAL G. XVI/1652–1667, borehole Zawada 1, depth 1607.1 to 1582.9 m.

Description. — Maximum length of rhabdosome is about 5.5 mm, with 16 pairs of thecae (Fig. 18B). Maximum width of rhabdosome measured between pleural lists is about 0.97 mm proximally and to 1.3 mm distally. Reticulo-clathria are finer in proximal part of rhabdosome, but very often meshes increase clearly distal of fourth theca. Subapertural lists are almost horizontal. First thecal pair developed very thin longitudinal lists linking looping and subapertural lists. Virgula is central, extends approximately to the level of third thecal pair.

Variability. — The rhabdosomes display a variation in density of reticulation along their length. The curving of pleural lists is variable, and probably depends on postsedimentation deformation.

Remarks. — *Sokolovograptus textor* from the Zawada borehole is similar to the type material described by Bouček & Münch (1952) in respect of construction and dimension. A Canadian form illustrated in Lenz & Melchin (1987a: pl. 3: 10) also corresponds to the material described here. However, *Plectograptus ? bouceki* Rickards 1967 has the same type of construction of the ventral wall as *S. textor*, and possesses only subapertural and looping lists. The differences to *S. textor*, pointed out by Rickards (1967) are minor, because the angle between the pleural lists and the virgula is small and variable, from 0–15 degrees in both species. The species described by Rickards (1967) possesses the same diagnostic characteristics as *S. textor*, so it is included herein within that species.

Sokolovograptus zawadensis sp. n.

Fig. 18D–H, J.

Holotype: ZPAL G. XVI/1668.

Type horizon and locality: Wenlock, *C. perneri* Zone, Zawada 1 borehole, depth 1598.6–1599.7 m, Poland.

Derivation of the name: from the villagae of Zawada, locality of the borehole.

Diagnosis. — Rhabdosome slightly tapering in medial and distal parts. Pleural and subapertural lists in ventral walls, parietal lists distinct in

lateral walls. Pleural lists parallel to virgula. Reticulo-clathria of lateral wall reduced in middle and distal parts of rhabdosome.

Material. — About 40 slightly flattened fragments of rhabdosome, ZPAL G. XVI/1668–1707, borehole Zawada 1, depth 1599.7–1590.0 m.

Description. — Maximum length of rhabdosome of 8 thecal pairs is up to 6.1 mm. Width of rhabdosome (measured between pleural lists) ranges from 0.64 mm to 0.97 mm proximally counts 0.6 mm at 4th thecal pair, 0.8–1.0 mm distally. Reticulo-clathria are formed of large irregular meshes to the level of the second thecal pair. Parietal lists appear in lateral walls towards the distal part of rhabdosome under subapertural lists, slightly oblique proximally, at level of 4th thecal pair being almost horizontal. Reticulo-clathria reduced beyond 3rd thecal pair in most specimens, possibly indicating immaturity. Specimen ZPAL G. XVI/1671 possesses considerably coarser pleural and subapertural lists (Fig. 18J).

Variability. — The meshes of reticulo-clathria complex show differences in density, especially in proximal parts of the lateral walls.

Remarks. — Rhabdosomes of *S. zawadensis* taper in distal parts of rhabdosome, in contrast to *S. textor*, where the distal part is wider. In both these subspecies the reticulo-clathrial complex is reduced in the ventral and lateral walls, while other elements of the skeleton are similar. They also differ in the width of the rhabdosome, and the shape of the pleural lists, although they may be distorted by diagenetic processes. These lists are curved in *S. textor* but in *S. zawadensis* are almost straight.

Sokolovograptus hiulcus sp. n.

Fig. 18C, I.

Plectograptus (Sokolovograptus) textor; Lenz & Melchin 1987a: p. 168, pl. 1: 9.

Holotype: ZPAL G. XVI/1707.

Type horizon and locality: Wenlock, *C. perneri* Zone, Zawada 1 borehole, 1582.9 1609.1 m, Poland.

Derivation of the name: from the Latin *hiulcus* meaning obtuse.

Diagnosis. — Rhabdosome widens towards distal end. Subapertural and looping lists are present in ventral wall. Sometimes these lists are connected by fine, single lists. Reticulum sometimes reduced distally so that only lists remaining are subapertural lists ventrally and horizontal parietal lists in lateral walls.

Material. — 6 incomplete rhabdosomes, slightly flattened, ZPAL G. XVI/1707–1712, borehole Zawada 1, depth 1582.9–1609.1 m.

Description. — Maximum length of rhabdosomes is 14.8 mm, with 10 thecal pairs. Width of rhabdosome (measured between pleural lists) proximally about 0.97 mm, rhabdosome widening distally to a maximum width of 1.9 mm across 7th thecal pair of thecae (Fig. 18C). Reticulum of lateral walls is very sparse distally, with only parietal lists present (Fig. 18I). Distal ventral wall with subapertural, looping and longitudinal lists reduced distally and only subapertural lists remaining. The distance be-

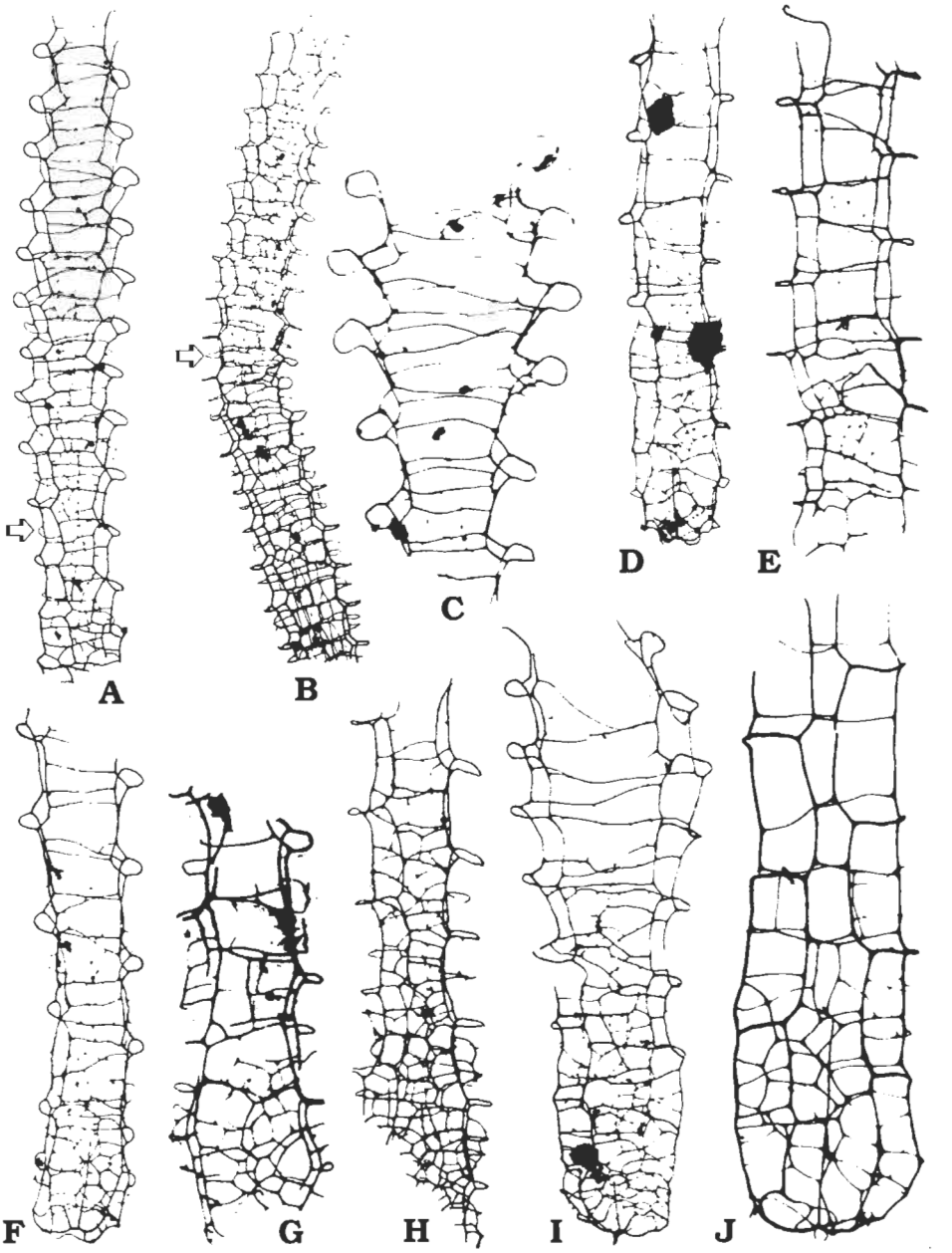


Fig. 18. ❑A–B. *Sokolovograptus textor* (Bouček & Münch 1952), fragments of mature rhabdosome with looping lists arrowed, ZPAL G. XVI/1652, 1653; Zawada 1577.5–1582.9 m, ZPAL G. XVI/1719, 1720, Zawada 1597.7–1603.1 m. ❑C, I. *Sokolovograptus hiulcus* sp. n.; C. Distal part of rhabdosome ZPAL G. XVI/1707, Zawada 1582.9–1590.6 m. I. Mature rhabdosome; ZPAL G. XVI/1709, Zawada 1582.9–1590.6 m. ❑D–H, J. *Sokolovograptus zawadensis* sp. n. fragments of rhabdosome; ZPAL G. XVI/1668–1671, Zawada 1577.7–1582.9 m, ZPAL G. XVI/1719, 1720, Zawada 1597.7–1603.1 m. A, F × 7; D, E × 11; G × 12; H × 10; J × 20; C, I × 14.

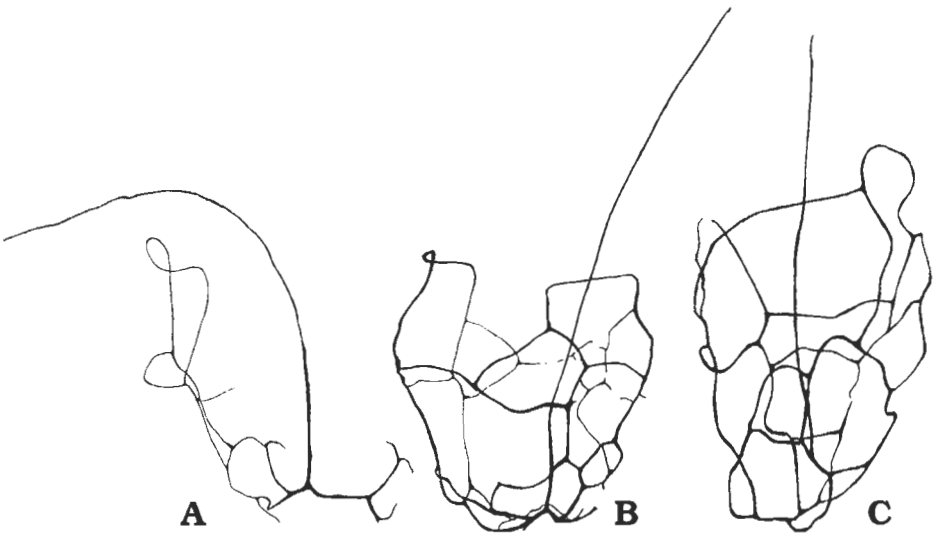


Fig. 19. Young stages of growth of *Sokolovograptus*, Zawada 1597.7–1603.1 m.

tween subapertural lists of adjacent thecae is variable, about 0.7 mm to 0.97 mm.

Variability. — There are differences in density of reticulum, and slight difference in width of the rhabdosome, especially in the distal parts.

Remarks.— *S. hiulcus* is most similar to *S. zawadensis*, but its rhabdosome is considerably wider distally.

Sokolovograptus parens Obut & Zaslavskaya 1976

Figs 20A, 1; 21.

Sokolovograptus parens (Obut & Zaslavskaya); Obut & Zaslavskaya 1976: pp. 123–126, pl. 3: 1–8.

Emended diagnosis. — Subapertural and finer supraapertural lists linking with reticulum; looping lists present.

Remarks. — Obut & Zaslavskaya (1976) did not consider in their diagnosis the reticulum and looping lists in the ventral wall. This character distinguishs *S. parens* from *S. textor*.

Diagnosis. — Rhabdosome 1.1 mm wide proximally to 1.6 mm distally. Reticulation reduced distally.

Material. — About 90 slightly flattened specimens, ZPAL G. XVI/1730–1819, borehole Zawada 1, depth 1603.1–1581.9 m.

Description. — Maximum rhabdosome length is 13.5 mm, with 15 thecal pairs. Width (measured between pleural lists) is 0.7 mm proximally, 1.1 mm medially, and 1.5–1.6 mm distally. Rhabdosome sometimes narrows again distally. The density of reticulum meshes may increase distally (Fig. 20A). In exceptional cases reticulum may be reduced.

Variability. — Insignificant differences in width and reticulation can be observed in the distal part of the rhabdosome.

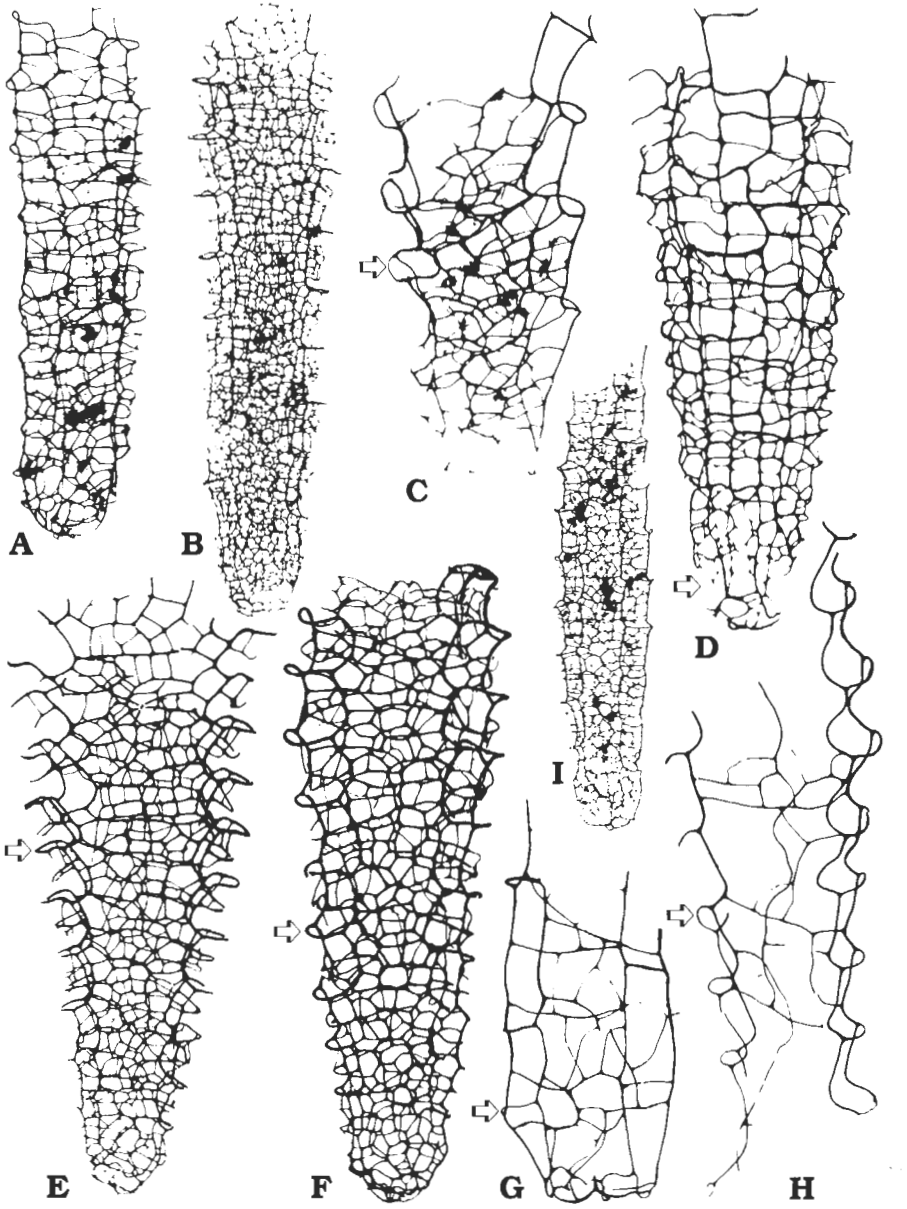


Fig. 20. ❑A–B. I. *Sokolovograptus parens* Obut & Zaslavskaya 1976. A. Dorso-lateral side of mature rhabdosome, ZPAL G. XVI/1730, Zawada 1597.7–1603.1 m. B. Lateral side of mature rhabdosome, ZPAL G. XVI/1835, Zawada 1603.1–1609.1 m, × 9. I. dorso-lateral side of mature rhabdosome, ZPAL G. XVI/1836; Zawada 1603.1–1609.1 m, × 7. ❑C, G, H. *Sokolovograptus telleri* sp. n.; dorso-lateral sides of fragments of rhabdosomes, subapertural lists arrowed, ZPAL G. XVI/1875–1877; Zawada 1603.1–1609.1 m, C × 10, G × 16, H × 4. ❑D–F. *Sokolovograptus diffusus* sp. n.; mature rhabdosomes, D. Ventral side, ventral orifice arrowed, ZPAL G. XVI/1822; Zawada 1603.1–1609.1 m. E. Lateral side, ZPAL G. XVI/1829, Zawada 1603.1–1609.1 m. F. Dorso-lateral side ZPAL G. XVI/1824, Zawada 1603.1–1609.1 m, subapertural lists arrowed. A, D–F × 13.

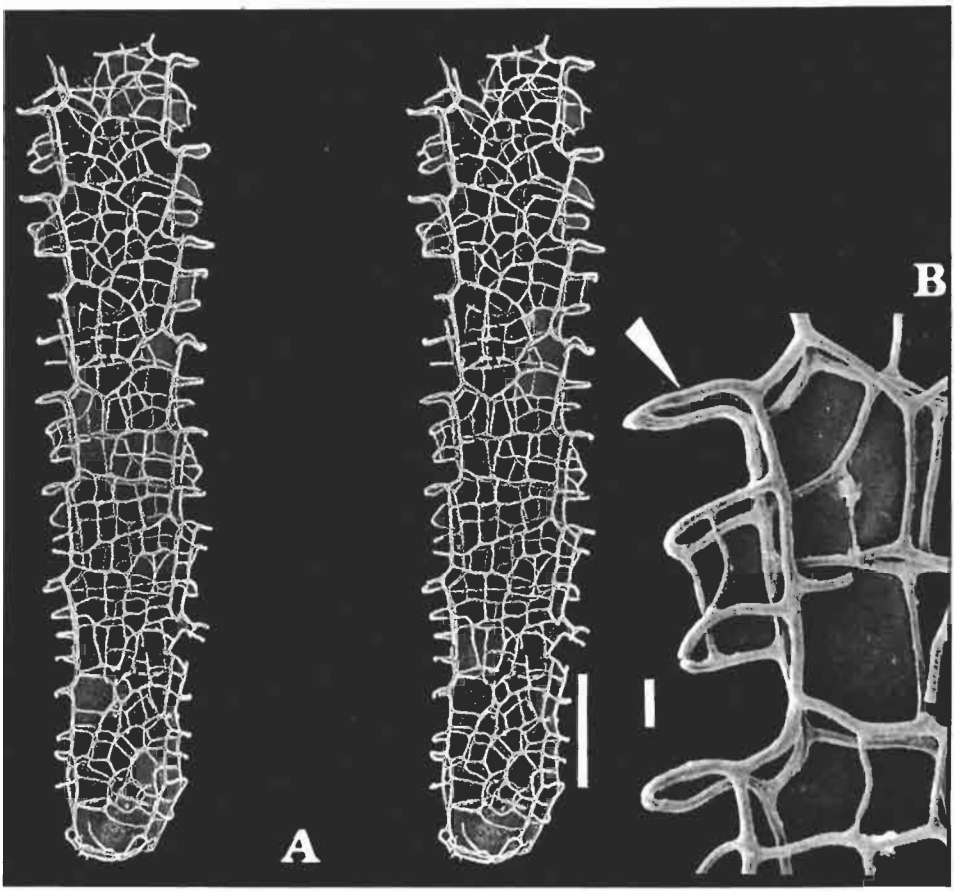


Fig. 21. *Sokolovograptus parens* Obut & Zaslavskaya 1976. A. Stereopair of mature rhabdosome, bar scale 1 mm. B. Fragment of medial part with subapertural list (arrowed), ZPAL G. XVI/1819, Zawada 1597.7–1603.1 m, bar scale 100 μm.

Remarks. — The specimens of *S. parens* from Zawada 1 borehole are closely comparable to the material from a borehole in the Kaliningrad region described by Obut & Zaslavskaya (1976).

Sokolovograptus diffusus sp. n.

Figs 20B, D–F; 22; 23.

Holotype: ZPAL G. XVI/1820.

Type horizon and locality: Wenlock, *M. flexilis* Zone, borehole Zawada 1, depth 1606.1 m.

Derivation of the name: from Latin *diffusus*, meaning broad, expansible.

Diagnosis. — Rhabdosome 0.9–1.0 mm wide proximally, 1.6 mm medially and 1.9 mm distally. Well developed reticulo-clathrial complex throughout. Lists forming rhabdosome may be thin or thick.

Material. — 50 rhabdosomes, slightly flattened, well preserved, ZPAL G. XVI/1820–1869, borehole Zawada 1, depth 1603.1–1606.1 m.

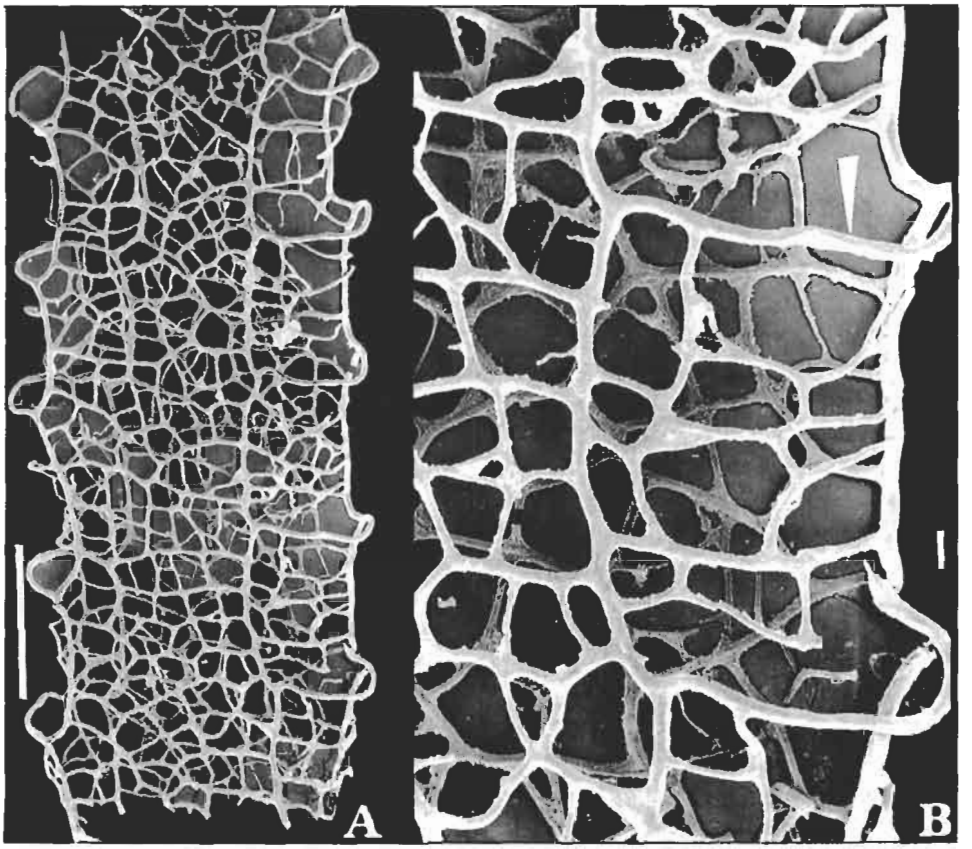


Fig. 22. *Sokolovograptus parens* Obut & Zaslavskaya 1976. A. Fragment of medial part of mature rhabdosome, ZPAL G. XVI/1869, Zawada 1597.7–1603.1 m, bar scale 1 mm. B. Theca with subapertural list arrowed, bar scale 100 μm.

Description. — Maximum length of rhabdosome is 10.3 mm, with 12 thecal pairs. Width (measured between pleural lists) ranges from 0.9–1.0 mm proximally to 1.6 mm medially and 1.9–2.9 mm distally. The shape of rhabdosome is conical, increasing considerably in width to 4th thecal pair (Fig. 20E). Lateral orifices are well developed (Fig. 20D). Reticular meshes are polygonal, rather large. Thecal shapes are distinctly marked by the presence of reticulum. Subapertural lists are longer and thicker than supraapertural lists. Looping lists are well developed.

Variability. — About one third of the specimens possesses very thin lists, forming small meshes in the reticulo-clathria (Fig. 22), the rest of specimens having lists and bigger meshes in the reticulo-clathria (Fig. 23A).

Remarks. — *S. diffusus* differs from *S. parens* by having a wider rhabdosome and also greater variation of the thickness and spacing of the lists of reticulo-clathria. The presence of a reticulum in the lateral wall makes the shape of the thecae similar to that of the plectograptids. The lateral orifices

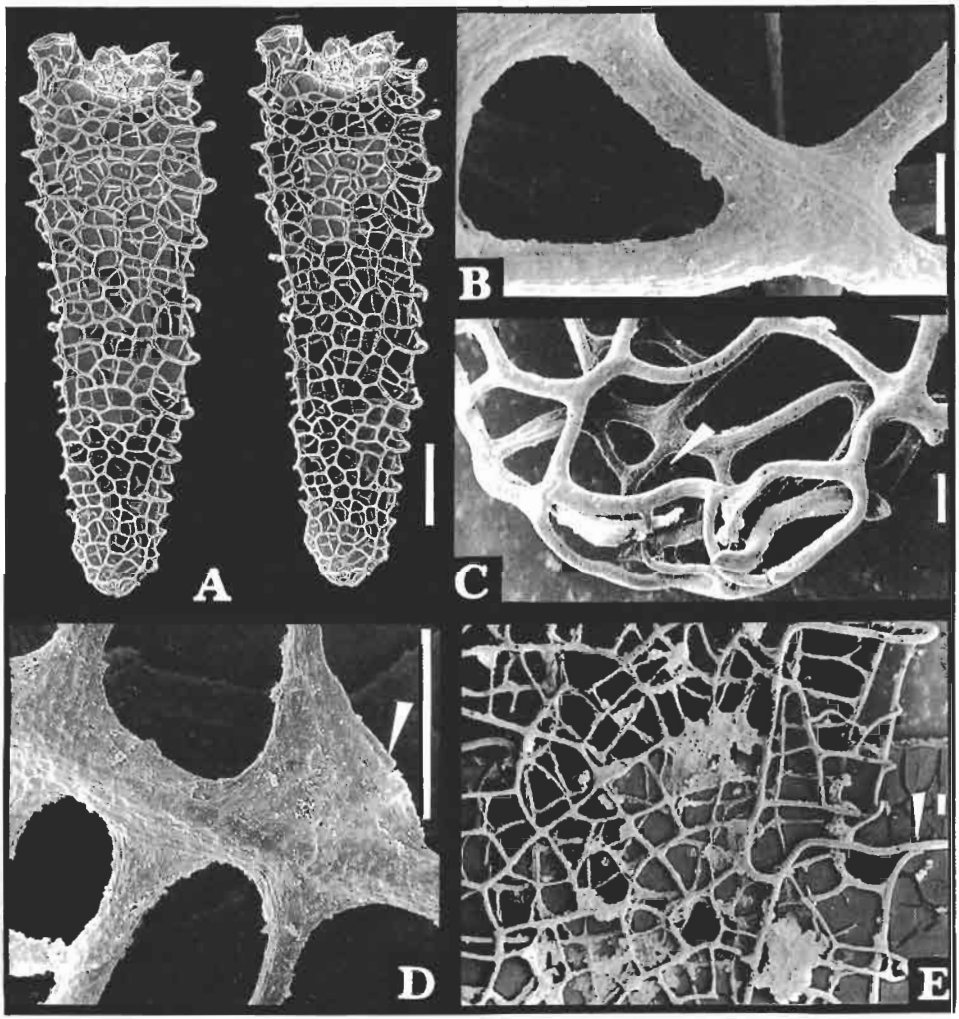


Fig. 23. ❑A–C. *Sokolovograptus diffusus* sp. n. Mature rhabdosome ZPAL G. XVI/1824, Zawada 1603.1–1609.1 m. A. Steropair, bar scale 1 mm. B. Surface of lists of lateral wall seen from the outside, bar scale 500 μm. C. Proximal part with lateral orifice arrowed, bar scale 100 μm. ❑D–E. *Sokolovograptus parens* Obut & Zaslavskaya 1976, ZPAL G. XVI/1869, Zawada 1597.7–1603.1 m, dorso-lateral side of mature rhabdosome. D. Surface of list of lateral wall with periderm In angle between lists, bar scale 100 μm. E. Subapertural list arrwed ZPAL G. XVI/1868, Zawada 1597.7–1603.1 m, bar scale 100 μm.

are distinct in proximal parts in rhabdosome (Fig. 20D), due to the density of the reticulum.

Sokolovograptus telleri sp. n.

Figs 20C, G, H; 24B–C; 25.

Holotype: ZPAL G. XVI/1870.

Type horizon and locality: Wenlock, *M. flexilis* Zone, borehole Zawada 1, depth 1603.1–1609.1 m.

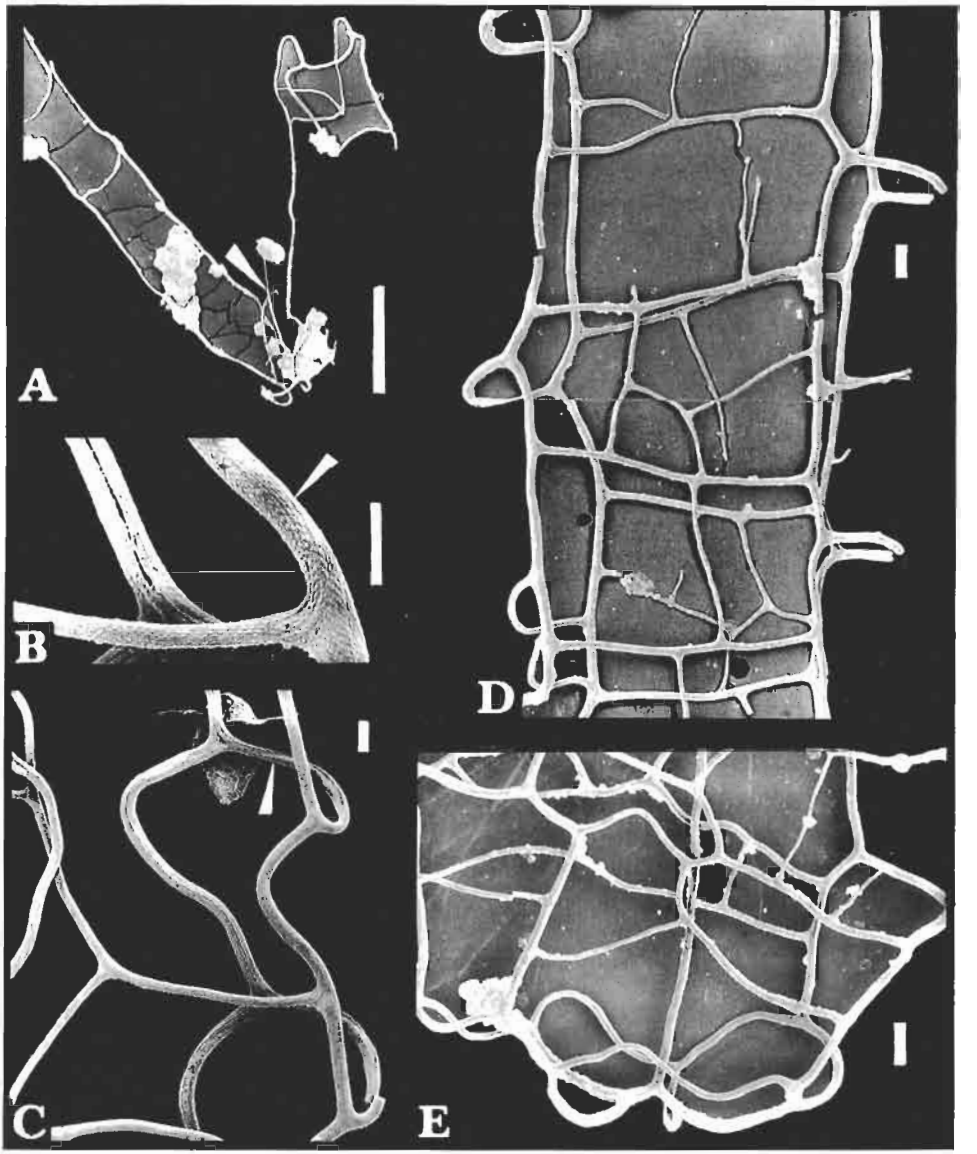


Fig. 24. ❑A. *Sokolovograptus polonicus* sp. n., deformed immature rhabdosome with virgula arrowed, ZPAL G. XVI/1902 m; bar scale 1 mm. ❑B–C. *Sokolovograptus telleri* sp. n. ZPAL G. XVI/1875, Zawada 1603.1–1609.1 m, bar lines 100 µm. B. Pleural list arrowed with nodules on the surface. C. Fragment of medial part of mature rhabdosome, subapertural list arrowed. ❑D–E. *Sokolovograptus textor* (Boucek & Münch 1952). D. Fragment of medial part of mature rhabdosome specimen ZPAL G. XVI/1661; Zawada 1590.6–1597.1 m, bar scale 100 µm. E. Ancora umbrella of mature specimen ZPAL G. XVI/1662, Zawada 1590.6–1597.1 m, bar scale 100 µm.

Derivation of the name: honouring Lech Teller, Polish graptolite specialist.

Diagnosis. — Ventral walls formed of subapertural and pleural lists, without reticulum. Meshes of reticulo-clathria of lateral walls large.

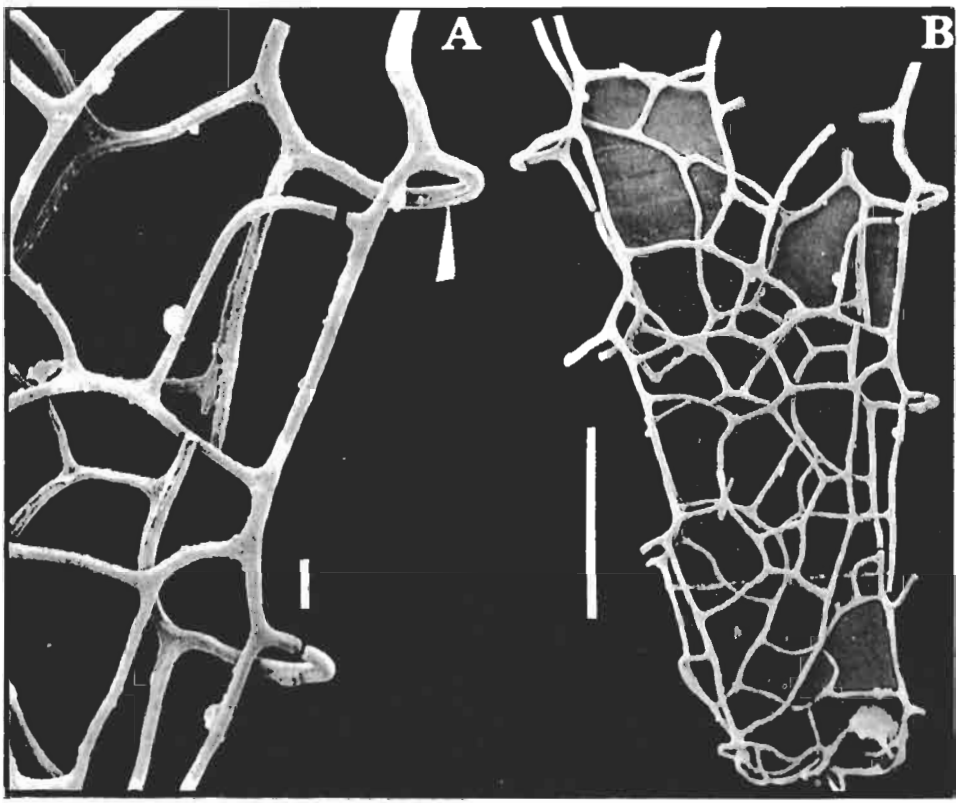


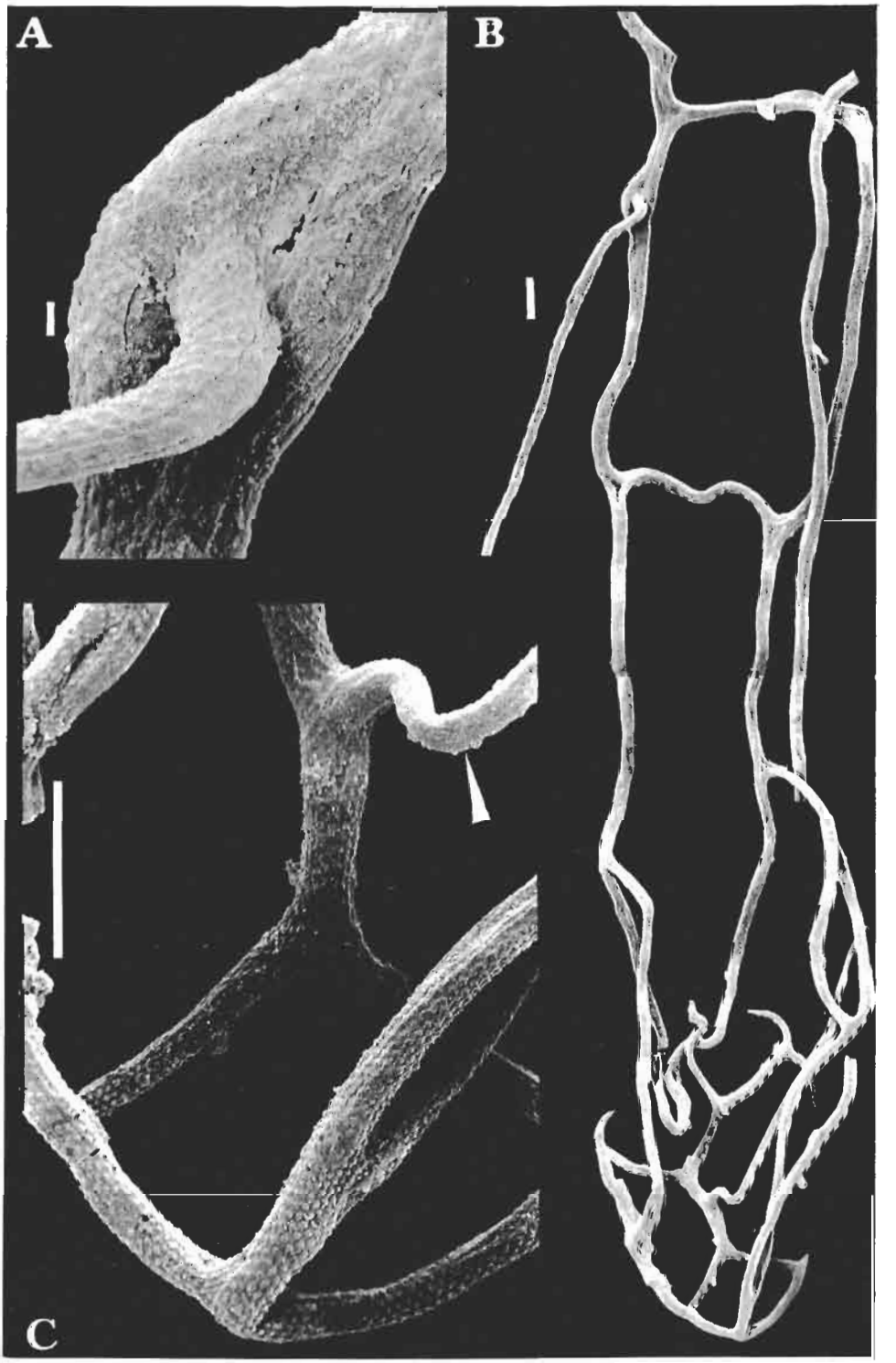
Fig. 25. *Sokolovograptus telleri* sp. n. Fragment of mature rhabdosome seen on lateral wall, ZPAL G. XVI/1876, Zawada 1603.1–1609.1 m. A. Subapertural list arrowed, bar scale 100 μm, B. Bar scale 1 mm.

Material. — 12 slightly flattened fragments of rhabdosomes, ZPAL G. XVI/1870–1881. Borehole Zawada 1, depth 1607.1–1604.1 m.

Description. — Maximum rhabdosome length 9.0 mm, with 7 thecal pairs (Fig. 20H). Width (measured between pleural lists) 0.6–0.9 mm proximally, medially 1.1–1.6 m, distally to 1.7 mm, exceptionally 2.6 mm. The fragment having maximum length is damaged proximally, but is wider than other rhabdosome: 1.1 mm proximally and 2.1 mm distally. Distance between subapertural lists is about 1.2 mm. Reticulo-clathrial complex proximally is dense, meshes increasing in width distally.

Variability. — *Sokolovograptus telleri* can be divided into two forms. The form A (Fig. 20H) with a wider rhabdosome (to 2,6 mm), has strongly curving pleural lists, occasional reticulo-clathrial elements in the lateral walls, and thicker pleural and subapertural lists. The curvature of pleural →

Fig. 26. *Sokolovograptus polonicus* sp. n. proximal part of immature rhabdosome ZPAL G. XVI/1903, Zawada 1621.7–1628.0 m. A. Abnormal connection of parietal with pleural list, bar scale 10 μm, B. Inside view of ventral wall with ancora, bar scale 100 μm, C. Ancora seen on inside, virgula arrowed, bar scale 100 μm.


A
B
C

lists is probably due of postsedimentary deformation. The second form B (Fig. 25) possesses almost straight pleural lists, a narrower rhabdosome distally, and a better formed reticulo-clathria in the lateral wall.

Remarks. — *S. telleri* differs from *S. polonicus* in having a reticulo-clathrial complex in the lateral wall.

Sokolovograptus polonicus sp. n.

Figs 24A; 25.

Holotype: ZPAL G. XVI/1882.

Type horizon and locality: Wenlock, *C. murchisoni/M. riccartonensis*? Zone, borehole Zawada 1, depth 1621.7 m.

Derivation of the name: From Latin *polonicus* meaning Polish.

Diagnosis. — Ventral walls formed of subapertural and pleural lists, reticulum absent. Lateral walls with parietal lists occasionally present, reticulum absent.

Material. — 8 slightly flattened fragments of rhabdosome with 3–7 thecal pairs and 15 immature specimens, ZPAL G. XVI/1882–1903. Borehole Zawada 1, depth 1621.7 m.

Description. — Specimens damaged. The length of the best preserved specimen, with 3 thecal pairs consist 4.4 mm. Ancora umbrella is rounded (Fig. 26B–C), width of ancora is about 0.9 mm. Width between pleural lists is difficult to establish. Lists of ancora form 5 meshes, sometimes not closed (Fig. 26B). Distance between apertural lists is about 0.9 to 1.1 mm, distance from ancora to first theca about 1.4 to 1.9 mm. Parietal lists occasionally present (Fig. 26B). Three specimens have a list forming a loop on the supraapertural list of 1st thecae. Ventral wall with subapertural and pleural lists, reticulum absent. Rest of apertural lists without additional elements.

Remarks. — *S. polonicus* is most closely related to *S. telleri*, but differs by lacking a reticulo-clathria in the lateral walls, and also in having a clearly rounded ancora umbrella.

Genus *Gothograptus* Frech 1897

Type species: *Retiolites nassa* Holm 1890.

Emended diagnosis. — Ventral wall formed of apertural, medial and pleural lists. Virgulolateral wall formed of horizontal parietal lists linked to virgula, which is incorporated into this wall distal of the aperture of theca 1^1; parietolateral wall formed by slightly oblique parietal lists. Reticulum well-developed. Apertural apparatuses variably developed.

Species included. — *G. nassa* (Holm 1890); *G. pseudospinosus* Eisenack 1951; *G. kozlowskii* Kozłowska-Dawidziuk 1990; *G. obtectus* Kozłowska-Dawidziuk 1990.

Genus *Neogothograptus* gen. n.

Type species: *Neogothograptus purus* sp. n.

Diagnosis. — Finite rhabdosome, narrowing distally and ending with appendix. Virgula free throughout rhabdosome. Lateral walls formed by almost horizontal parietal lists. Pleural lists present. Reticulum and apertural apparatuses present or absent.

Remarks. — Eisenack (1951: p. 159), in summarizing his study, assigned *Retiolites mancki*, *R. balticus* and *R. erraticus* to the new informal genus *Holoretiolites*, characterized by an appendix and a central virgula. Bouček and Münch (1952) divided this genus into two subgenera *Holoretiolites (H.)* and *Holoretiolites (Balticograptus)*. Two of the species *R. balticus* and *R. erraticus*, were assigned to *H. (B.)* having as a diagnostic character zigzag lists in the lateral wall. Specimens of *R. balticus* from Mielnik borehole do not show this character, but the lateral wall is formed by parietal lists arranged almost horizontally and linked with pleural lists. *R. erraticus* is built differently (without pleural lists) than *R. balticus* and is here regarded as a *Holoretiolites*.

Species included. — *N. balticus* (Eisenack 1951), *N. purus* sp. n., *N. romani* sp. n.

Neogothograptus purus sp. n.

Fig. 27F–G.

Holoretiolites (*Holoretiolites*) *mancki* (Münch); Lenz 1993: pl. 12: 1–12.

Holotype: ZPAL G. XVI/1341.

Type horizon and locality: Ludlow, *L. scanicus*/*L. invertus* Zone, erratic boulder 149 from Jaroslawiec, Poland.

Derivation of name: From Latin *purus* means pure, clear, not ornamented.

Diagnosis. — Reticulum very rarely present, apertural apparatuses absent. Parietal lists almost horizontal.

Material. — Two well preserved finite rhabdosomes ZPAL G. XVI/1341 and 1353, from erratic boulders 22 and 149 from Jarosławiec and 15 immature rhabdosome ZPAL.XVI/1342 in the Mielnik borehole, depths 1036.0, 1019.0, and 1018.0 m.

Description. — Length of finite rhabdosome terminated by appendix is 7.0 mm, larger specimens bear 7 thecal pair (Fig. 27F). Maximum width of lateral wall of large specimen (measured between pleural lists) is proximally 0.45 mm, about 0.9 mm at level of first thecal aperture of th 1^1, in medial 0.38 mm and at base of appendix 0.32 mm. Width of lateral walls in small specimen 0.64 mm in proximal part, 0.7 mm at level of first thecal aperture, and 0.38 mm in distal part. Distances between supraapertural lists in proximal part of rhabdosome about 1.06 mm, in medial 0.9 mm, and in distal 0.7 mm. Medial lists above aperture in medial and distal parts of rhabdosome broken or not fully grown (Fig. 27). Pleural lists in holotype and specimen ZPAL G. XVI/1342 bent in a curve at half their length to include an angle of 130–145 degree in proximal part of rhabdosome; and distally become vertical, as in specimen ZPAL G. XVI/1342. Virgula preserved only in holotype in proximal and distal parts, due to non-dissolved sediment. This rhabdosome terminated by short, broken appendix

with fine meshes. Specimen possessing 4 pairs of thecae with only single lists in place of appendix (Fig. 27G).

Variability. — The two finite rhabdosomes show that theca can vary at least from 5 (Fig. 27G) to 14 thecae (Fig. 27F). The shape of the rhabdosome is conical, but the longer specimen tapers more gradually towards the distal end.

Remarks. — *N. purus* is similar to *N. romani*, but differs in lacking a reticulum, and having more thecae in finite rhabdosomes. The longer form resembles *N. balticus* in the shape of the rhabdosome.

Neogothograptus balticus (Eisenack 1951)

Retiolites balticus Eisenack; Eisenack 1951: pp. 134–136; pl. 22: 4–8, pl. 24: 5.
Holoretiolites (Balticograptus) balticus Eisenack; Bouček & Münch 1952: pp. 17–19; fig. 5b.
Holoretiolites (Holoretiolites) mancki (Münch 1931); Lenz 1993: pl. 12: 1–12.

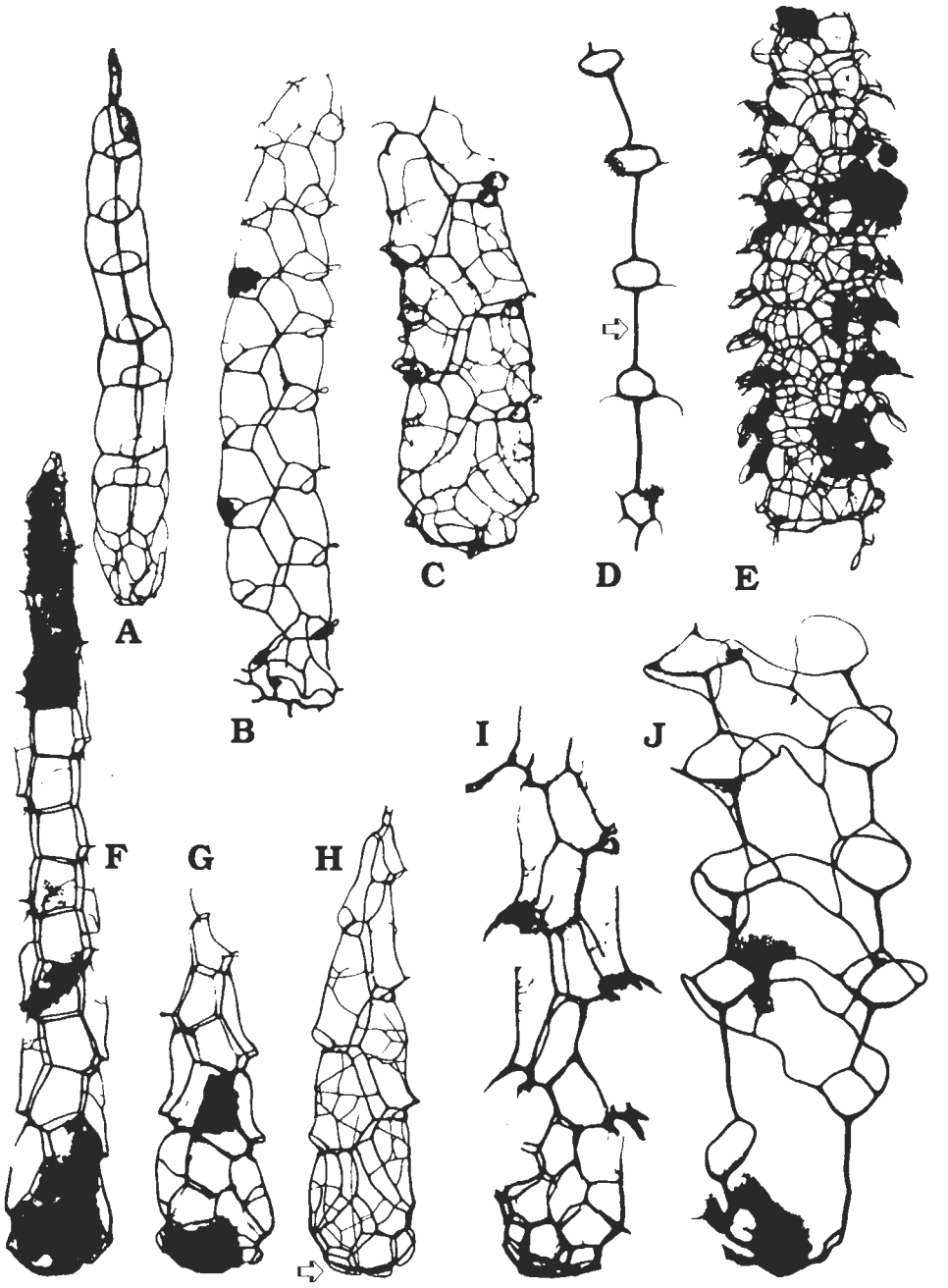
Emended diagnosis. — Single apertural processess composed of reticular loops, situated on the supraapertural lists. Few lists of reticulum in ventral walls.

Material. — 1 finite rhabdosome and a fragmentary medial part ZPAL G. XVI/1345, 1346, slightly flattened, from the Mielnik borehole, depth 1026.0 m.

Description. — Length of finite rhabdosome ranges up to 6.3 mm. Maximum width across corona is 0.73 mm, in medial part 0.70 mm and distally narrowing to 0.45 mm. Final rhabdosome consist 6 thecal pairs. Clathria are formed of rather thick lists. In medial and distal parts of rhabdosome medial lists below apertures are fine. Reticulum of thick, sparse lists, is present only in lateral walls. Apertural processes are formed of single loop-shaped lists, enclosing a reticulum, situated on supraapertural lists and partly covering aperture. Apertural processes are lacking in first and distal thecae. In one of the two avaiable finite rhabdosomesappendix is damaged and virgula not preserved, but in second is visible only in proximal parts filled with sediment. In finite rhabdosome.

Remarks. — *N. balticus* was assigned to the genus *Agastograptus* by Obut & Zaslavskaya (1983), based on an incorrect interpretation of the structure (see Kozłowska-Dawidziuk 1991: p. 146). This species does not possess such diagnostic for *Agastograptus* characters as paired supraapertural processes and zigzag pattern of clathria on the lateral wall.

Fig. 27. ❑A. *Holoretiolites mancki* (Münch 1931) finite rhabdosome with apendix, ZPAL G. XVI/1421, Mielnik 978.0 m; × 14. ❑B. *Holoretiolites manckoides* sp. n. finite rhabdosome, dorso-lateral view, ZPAL G. XVI/1350, Mielnik 954–960.0 m; × 10. ❑C. *Holoretiolies erraticus* Eisenack 1951 fragment of mature rhabdosome (dorso-lateral view), ZPAL G. XVI/1408, Mielnik 978.0 m; × 20, ❑D. *Plectodinemagraptus gracilis* gen. et sp. n. ventral part, fragment of mature rhabdosome, medial list is marked, ZPAL G. XVI/1409, Mielnik 946.0 m; × 20. ❑E. *Plectograptus wimani* (Eisenack 1951) mature rhabdosome, damaged in proximal part, ZPAL G. XVI/1607, Mielnik 1044.0 m; × 10. ❑F–G. *Neogothograptus purus* gen. et sp. n. F. Lateral view of finite rhabdosome, holotype ZPAL G. XVI/1341, erratic boulder 149 from Jarosławiec;



× 15. G. Finite rhabdosome, ZPAL G. XVI/1353, erratic boulder 22 from Jarosławiec; × 16. ❑H. *Holoretiolites erraticus* Eisenack 1951 finte rhabdosome with outer ancora arrowed, ZPAL G. XVI/1373, Mielnik 978.0 m, × 20. ❑I. *Neogothograptus* cf. *balticus* (Eisenack, 1951) fragment of rhabdosome (view on lateral wall), ZPAL G. XVI/1344, Mielnik 1031.0 m; × 20. ❑J. *Semiplectograptus urbaneki* gen et sp. n. mature rhabdosome (ventro-lateral view), medial list is marked, ZPAL G. XVI/1394, Mielnik 972.0 m; × 31.

Neogothograptus balticus differs from *N. purus* in having a reticulum and apertural processes. The development of the reticulum is similar to that of *N. romani*, which lacks apertural processes.

Neogothograptus cf. *balticus* (Eisenack 1951)

Fig. 27I.

Material. — One specimen ZPAL G. XVI/1344 consisting of 4 pairs of thecae, damaged in the medial part and without distal end; Mielnik borehole, depth 1031.0 m.

Description. — Length of the rhabdosome is 3.67 mm, width of its corona 0.7 mm, width of lateral wall in medial part (measured between medial lists) 0.64 mm. Pleural lists curve dorsally to make contact with oblique parietal lists. Medial lists are well developed. Ventral walls have very fine reticular lists, perpendicular to medial lists. Supraapertural lists of thecae 1^1 and 1^2 bear paired reticulofusellar processes, but successive thecae are simple or paired. Apertural processes of th 3^2 etc. paired, except for theca 2^1, which forms a simple lobe. Apertural processess of thecae 2^1 and 3^1 are forked distally. The processes of a single pair are not symmetrical, in theca 1^2 the left is smaller, in theca 2^2 the right is smaller (Fig. 27I)

Remarks. — This fragmentary rhabdosome is similar to *N. balticus* in shape and dimensions but differs in size, position and number of apertural processes. In typical specimens of the species these are uniform in shape and always single, not branching. The lack of order in position and structure of apertural processes suggests that this rhabdosome may be aberrant.

Neogothograptus romani sp. n.

Fig. 6.

Holotype: ZPAL G. XVI/1355.

Type horizon and locality: Ludlow, *L. parascanicus* Zone, erratic boulder 45 from Jaroslawiec, Poland.

Derivation of the name: from the first name of the late Roman Kozłowski.

Diagnosis. — Reticulum in proximal and medial parts, apertural processes absent.

Material. — 14 finite rhabdosomes and fragments of well preserved specimens, ZPAL G. XVI/1353 and 1355–1362. Erratic boulder 45 from Jarosławiec and Mielnik borehole, depth 1014 m.

Description. — Rhabdosomes are small, of up to 4 pairs of thecae. Length of finite rhabdosomes is about 2.5–2.8 mm.

Width of corona 0.8 mm, proximally 0.7 mm, medially 0.6 mm and distally 0.4–0.2 mm. Reticulum in medial part of rhabdosome reduced and absent in distal region; finer on ventral wall than on lateral. Length of medial lists 0.4–0.5 mm. Medial lists situated under subapertural list of first thecae undulate in and out, S-shaped. Parietal lists are oblique in proximal part of rhabdosome, becoming almost horizontal distally. Some specimens have fine virgella preserved. Appendices of finite rhabdosomes

are ot well developed, formed of only one or two distally directed lists. Apertural processes are absent.

Variability. — The density of the reticulum depends on astogenetic stages. In immature rhabdosomes the reticular lists are finer.

Remarks. — *N. romani* sp. n. differs from other representatives of the genus in having less than 4 thecal pairs in the finite rhabdosome. The reticulum is denser than in *N. purus*, especially in the lateral wall, in contrast to *N. balticus*, which has a similarly developed reticulum in ventral walls. Both *N. purus* and *N. balticus* have elongate rhabdosomes, slightly undulating distaly and consisting of about 7 pairs of thecae, in contrast to *N. romani*, which most often possess 3 or 4 pairs of thecae and is short and narrowing considerably distally (Fig. 6). Only short form of *N. purus*. is similar in shape to *N. romani* but without reticulum.

Genus *Holoretiolites* Eisenack 1951

Type species: *Holoretiolites mancki* (Münch 1931).

Emended diagnosis. — Finite rhabdosome, narrowing distally and ending with appendix. Virgula free throughout rhabdosome. Parietal lists formed zigzag pattern, pleural lists present. Reticular meshwork poorly developed or absent, apertural processes not present.

Species included — *H. mancki* (Münch 1931); *H. erraticus* Eisenack 1951, *H. manckoides* sp. n., and *H. atrabecularis* sp. n.

Holoretiolites mancki (Münch 1931)

Figs 27A; 29D.

Retiolites mancki Münch; Münch 1931: pp. 35–42; pl. 1: 1–13.

Holoretiolites mancki Münch; Eisenack 1951: pp. 135–138, 148–153, 156; pl. 24: 6.

Holoretiolites simplex sp. n.; Eisenack 1951: pp. 84–86, pl. 4: 16, pl. 7: 1.

Holoretiolites simplex Eisenack; Reichtein 1962: pp. 539–543, pl. 1: 5–12, pl. 2: 1–12.

Emended diagnosis. — Finite rhabdosome of 3 to 12 thecae. Reticulum absent. Length of subapertural lists about 0.25–0.32 mm.

Material. — 17 finite rhabdosomes and 98 incomplete specimens ZPAL G. XVI/1411–1510. Mielnik borehole (29 specimens), depth 996.0, 980.9 m, 978.9 m, 963.9 m, 962.9 m, 960.0–954.0 m, and 954.0 m and erratic boulders from Jarosławiec 145, Władysławowo 128, and Ustka 137.

Description. — Length of finite rhabdosomes measured to base of appendix is about 1.9–2.3 mm in forms of 3 or 4 thecae; and 4.25–4.70 mm in longest forms. Length of appendix is up to 1.47 mm (Fig. 29D). Finite rhabdosomes contain usually 6 pairs of thecae. Width of corona measured between pleural lists is 0.4–0.6 mm, but measured on dorsolateral side 0.77–0.9 mm. Maximum width of rhabdosome across second pair of thecae about 0.6–0.7 mm. Rhabdosomes narrow to 0.19 mm at base of appendix. Ancoral lists are clearly thicker than the remaining ones. Length of subapertural lists is 0.25–0.32 mm, length of medial lists about 0.52–0.77 mm.

Variability. — The finite rhabdosomes of *H. mancki* most often contain 12 thecae, but about 10% of the specimens have only 3 to 5 thecae. Several

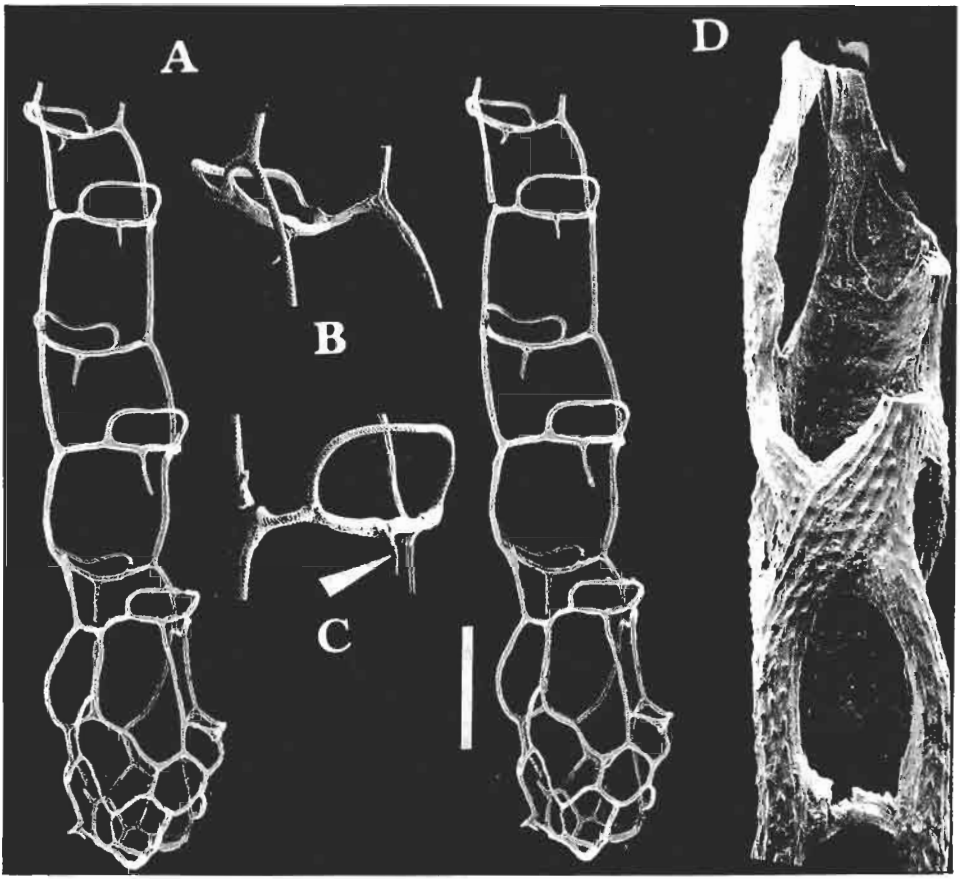


Fig. 28. ❑A–C. *Holoretiolites atrabecularis* sp. n. A. Stereopair of finite rhabdosome, ZPAL G. XVI/1531, Mielnik 972.0 m, bar scale 500 μm. B. Inside view of of 3/2 theca, C. Outside view of aperture 3/1 theca, reduced medial list is arrowed. ❑D. *Holoretiolites mancki* (Münch 1931) fragment appendix, ZPAL G. XVI/1421, Mielnik 996.0 m; × 90. B, C × 55.

specimens possess abnormally curved rhabdosomes, flattened at different levels, apparently because of diagenetic deformation. One specimen from the Mielnik borehole and one from an erratic boulder from Jarosławiec have disorders in the development of medial lists; these rhabdosomes are also shorter than typical, possessing 9 thecae. The distortions appear as interruptions or thickened medial list, below the subapertural list. In 4 of the incomplete rhabdosomes from Mielnik, depth 954.0–960.0 m, the medial lists are considerably thicker than the rest.

Remarks. — *H. simplex* is here included in *H. mancki* because of a very similar arrangement of the lists. The two forms differ in the numbers of thecae in finite rhabdosomes, 3–4 thecae in *H. simplex*, and 12 thecae in *H. mancki*. This is prpobably an intraspecies variation: for example in *Eisenackograptus eisenacki* the number of thecae ranges from 3 to 19, in *Neogothograptus purus* from 4 to 14. In the Mielnik borehole forms

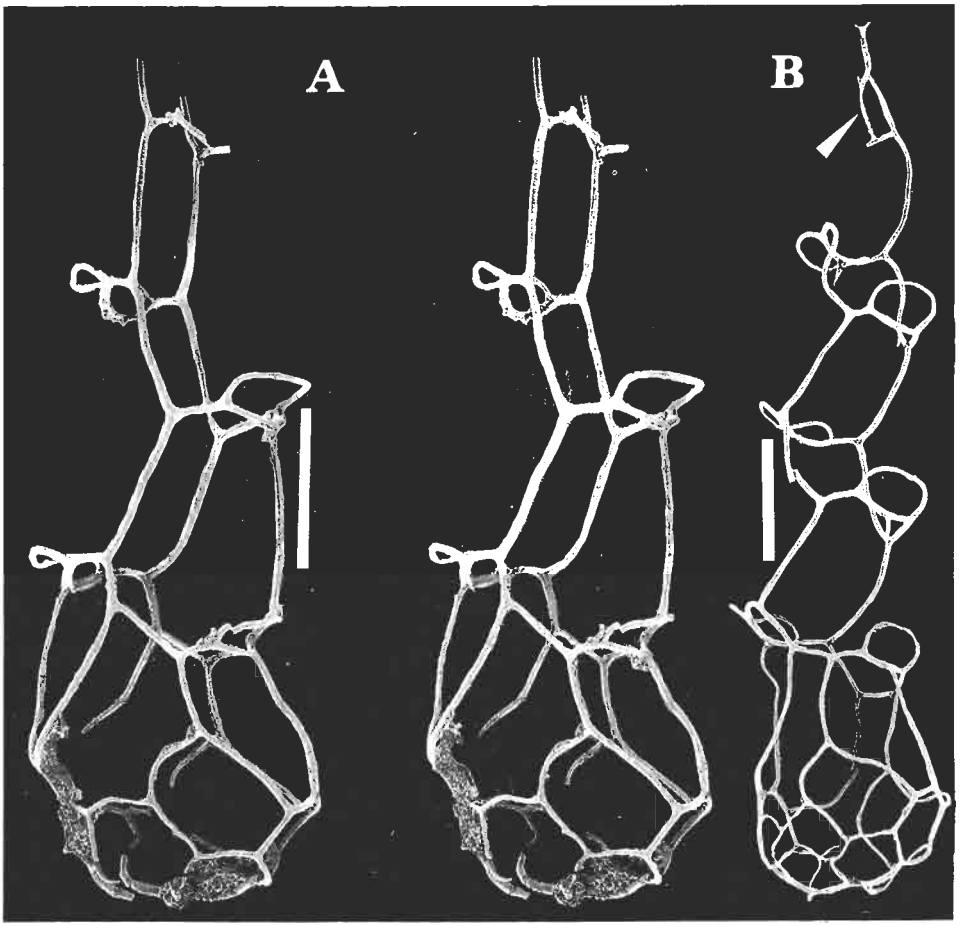


Fig. 29. *Holoretiolites atrabecularis* sp. n. A. Steropair of finite rhabdosome damaged in distal part, ZPAL G. XVI/1530, Mielnik 972.0 m, bar scale 100 μm. B. Finite rhabdosome ZPAL G. XVI/1532, Mielnik 972.0 m, with structure similar to appendix (arrowed), bar scale 100 μm.

corresponding to *H. simplex* occur at depths of 996.0 m and 990.0 m, whereas the range of *H. mancki* is wider, from 998.0 m to 954.0 m. Dimensions of *H. mancki* given by Münch (1931) and Eisenack (1951) correspond to the longest form found in this study.

Holoretiolites manckoides sp. n.

Fig. 27B.

Holotype: ZPAL G. XVI/1347.

Type horizon and locality: Ludlow, *C. hemiaversus/C. aversus* Zone, Mielnik borehole, depth 954.0–960.0 m, Poland.

Derivation of the name: *manckoides*, similar to *Holoretiolites mancki*.

Diagnosis. — *Holoretiolites* similar to *H. mancki*, but more than twice as long and wider. Length of subapertural lists about 0.7 mm.

Material. — Three well preserved specimens, including 2 almost finite, ZPAL G. XVI/1347–1354, Mielnik borehole, depth 954.0–960.0 m, and four fragments of rhabdosomes from erratic boulders 134 from Gdynia Orłowo.

Description. — Maximum length of almost finite rhabdosom, with 9 pairs of thecae is 7.5 mm, maximum width 1.29 mm. Rhabdosome narrows slightly distally. Clathria are formed of rather thick lists. Subapertural lists and parietal lists are thicker then other lists. Reticulum is absent. Corona forms several rounded hexagonal meshes. Lateral walls are formed of almost horizontal, rather short parietal lists and elongated dorsal lists forming a zigzag pattern. Length of medial lists increases distally from 0.6 mm to 0.9 mm. Length of subapertural lists is about 0.7 mm. Appendix not identified.

Remarks. — *H. manckoides* is very close to *H. mancki*, but differs in size, number of thecae, and proportions. It is more than twice as long and wide and has 9 thecal pairs in the finite rhabdosome, rather than the 6 in *H. mancki*. The medial lists are shorter than in *H. mancki*, and over twice as long as the subapertural lists. The new species narrows rapidly in the distal part, whereas in *H. mancki* narrows gradually from the medial part to the appendix.

Holoretiolites atrabecularis sp. n.

Figs 28A, C; 29.

Holotype: ZPAL G. XVI/1529.

Type horizon and locality: lower Ludlow, *L. parascanicus* Zone, Mielnik borehole, depth 972.0 m, Poland.

Derivation of the name: From Latin *a* — without, *trabecula* — list.

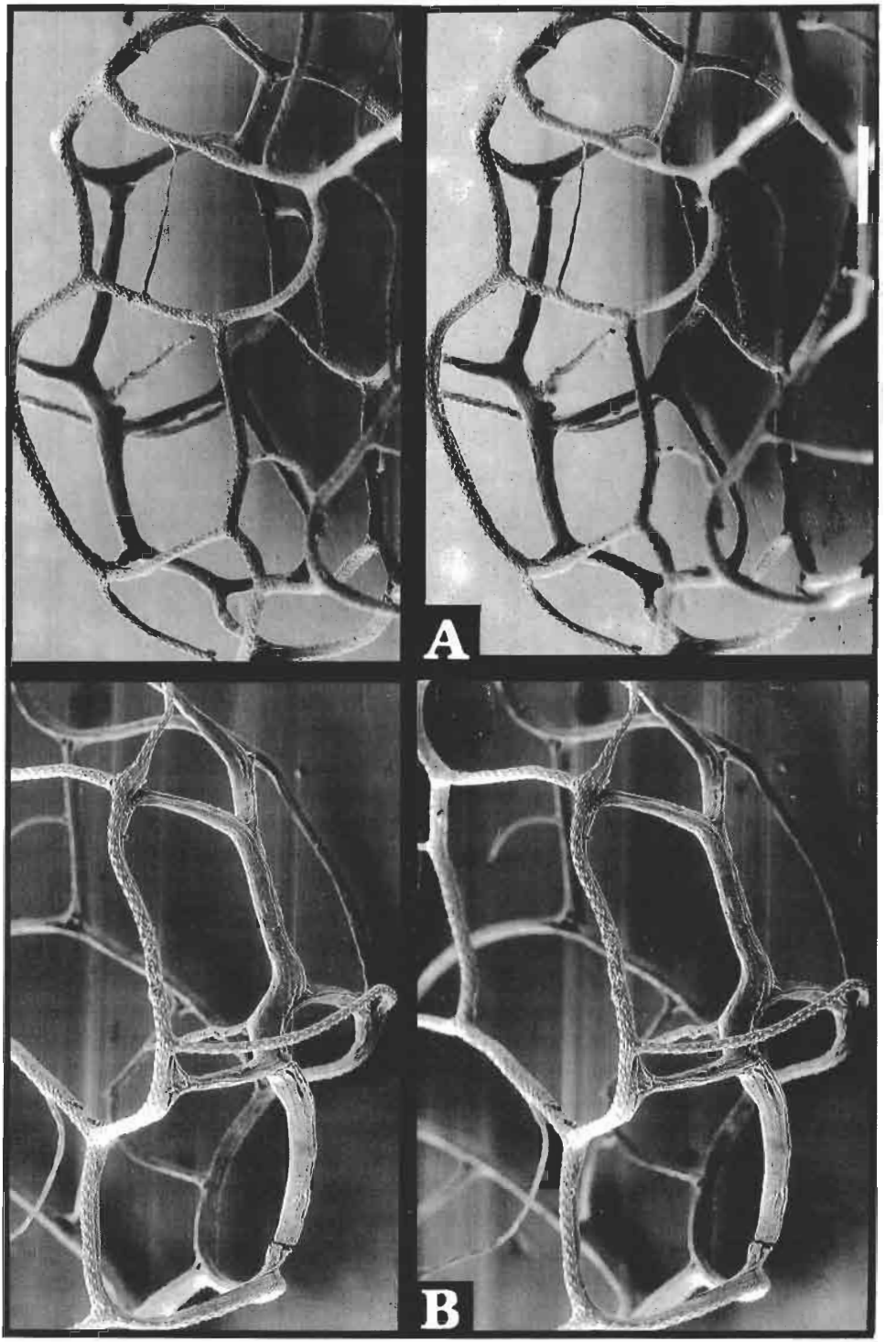
Diagnosis. — *Holoretiolites* with normally developed medial lists on two or three first thecae, but in later thecae medial lists reduced to short spines on supraapertural lists.

Material. — Four finite rhabdosomes and 18 fragments of rhabdosomes, well preserved, ZPAL G. XVI/1529–1551, Mielnik borehole depth 972.9 m.

Description. — Finite rhabdosome bears 4 pairs of thecae, length without appendix is 3.54–3.61 mm. Length of appendix is 0.5 mm (Fig. 29B). Ancoral lists are evidently thicker then the rest. Corona rounded, about 0.64–0.74 mm wide. Rhabdosome is 0.58 mm wide across 2nd thecal pair, then narrowing to 0.38 mm under aperture of last theca. Length of subapertural lists is about 0.25–0.32 mm. Thecae of first pair and sometimes of thecae 2^1 mostly have fully developed medial lists (Fig. 29A). Rest of thecae with short spine-like vestigial medial lists up to 0.19 mm long.

Remarks. — The rhabdosome of *H. atrabecularis* is closest to *H. mancki* in shape and dimensions, but is about 1 mm shorter and has fewer thecae in the finite rhabdosome.It also differs in the pronounced reduction of the

Fig. 30. *Holoretiolites erraticus* Eisenack 1951, stereopairs of proximal part of mature rhabdosome with outer ancora, bar line 100 μm. A. ZPAL G. XVI/1370, Mielnik 978.0 m. B. ZPAL G. XVI/1373 photograph by D.B. Bates.


A
B

medial lists in the middle and distal parts of the rhabdosome. *H. atrabecularis* occurs in Mielnik borehole only at a depth of 972.0 m, while *H. mancki* occurs between 978.0 m and 954.0 m.

Holoretiolites erraticus Eisenack 1951

Figs 27C, H; 30.

Holoretiolites erraticus sp. n.; Eisenack 1951: pp. 136–137, pl. 24: 7, fig. 3.

Holoretiolites (Balticograptus) erraticus (Eisenack 1951); Bouček & Münch 1952: pp. 17–19, fig. 5a.

Emended diagnosis. — *Holoretiolites* with reticulum, apertural processes absent.

Material. — 26 rhabdosomes and fragments ZPAL G. XVI/1408–1410 and ZPAL G. XVI/1368–1391, Mielnik borehole, depths 978.0 m and 1000.0 m and erratic boulder 228 from Jarosławiec.

Description. — Length of finite rhabdosomes is about 3.29–4.77 mm. Width of corona is 0.6–0.7 mm, sometimes 0.9 mm, decreasing to about 0.4–0.6 mm across medial part of 3th pair of thecae. Rhabdosome is proximally cylindrical, strongly narrowing beyond 3rd pair of thecae to about 1/3 width; ends in short appendix (Fig. 27H). In most long rhabdosomes additional lists form an outer ancora (Figs 27H, 30). These lists connect with ancora and have their course similar to ancoral lists. Supraapertural lists are slightly bent towards aperture. Medial lists, about 0.6–0.9 mm long, S-shaped. Reticulum developed proximally and reduced distally. Single reticular lists occur occasionally beginning from 3rd pair of theca. In borehole specimens appendix very often damaged; the longest fragment present is in length 1.9 mm. Two finite rhabdosomes from erratic boulders have appendices 0.8 mm and 1.3 mm long, and possess 3 or 4 pairs of thecae. These are probably aberrant rhabdosomes, curving dorsally and rapidly narrowing.

Variability. — In immature rhabdosomes the outer ancora is only partly developed, and is present in only one-third of specimens from the erratic boulder from Jarosławiec. Presumably the outer ancora grows during mature stages of growth.

Remarks. — The material from the Mielnik borehole has a similar shape to that described by Eisenack (1951). However the reticulum at the distal end of rhabdosome shows a marked reduction.

Genus *Spinograptus* Bouček & Münch 1952

Type species: *Retiolites spinosus* Wood 1900.

Emended diagnosis. — Rhabdosome may indicate tendency to finite growth. Virgula free throughout. Ventral wall formed of apertural, pleural and variably developed, sometimes incomplete medial lists. Lateral walls formed of parietal lists arranged in zigzag pattern. Pronounced lateral orifices above ancora umbrella. Reticulum well developed or absent. Apertural processes paired, reticulofusellar.

Remarks to emended diagnosis. — The genus was established for *S. spinosus* by Bouček and Münch (1952) and for a long time remained monospecific. Lenz & Melchin (1991) assigned *Retiolites nevadensis* Berry & Murphy 1975 to this genus, a species which had been included in *Agastograptus* by Obut & Zaslavskaya (1983). Probably also their *Agastograptus clathrospinosus* and *A. munchi* should be placed in *Spinograptus*. Similarities between *Agastograptus* and *Spinograptus* include: central position of virgula, arrangement of lateral wall with a zigzag forming by parietal lists, a tendency to reduction of the medial lists in ventral wall, and similarly shaped lateral orifices. The differences between species are: different dimensions, variation in the density of the reticulum, and different types of apertural processes. *S. nevadensis* and *S. apoxys* seem to form a generically separate, but closely related to to *Spinograptus*, group because of the presence of single lists inside the thecae in *S. nevadensis* (Lenz 1993: pl. 19: 1, 3), and sigmoidal processes and inner connecting lists in *S. apoxys* (Lenz 1993: pl. 18: 4–7).

Species included. — *S. spinosus* (Wood 1900), *S. clathrospinosus* (Eisenack 1951), *S. munchi* (Eisenack 1951), *S. lawsoni* (Holland, Rickards, & Warren 1969), *S. quadratus* (Lenz 1993).

Spinograptus spinosus (Wood 1900)

Fig. 15B.

Retiolites spinosus; Wood 1900: pp. 485, pl. 29A–B, fig. 26A–N.

Spinograptus spinosus (Wood): Obut & Zaslavskaya 1983: pp. 111–112, pl. 27: 1–6.

Emended diagnosis. — Clathrial lists forming lateral wall fine, poorly visible against finemesh of reticulum. Medial lists partly incomplete. Supraapertural list long and curved toward subapertural list. Apertural processes forming long paired spines with reticulofusellar structures visible only in their distal parts (see Obut & Zaslavskaya 1983).

Material. — Two well preserved rhabdosomes with up to 11 pairs of thecae, ZPAL G. XVI/1904–1905, Mielnik borehole, depth 1038.9 m.

Description. — Maximum length of rhabdosomes is 9.6 mm. Width of ancora is about 0.6 mm. Width increases distally: in proximal part reaches 0.9 mm, in medial up to 1.2 mm, and in the distal part slightly less. Pleural lists are prominent and flexed at half their length towards the middle of lateral wall and towards the centre of rhabdosome; they join to horizontally situated subapertural lists at the point of undulation. Supraapertural lists are longer and curved towards subapertural lists. From the junction of supraapertural and pleural lists, paired apertural processes run laterally, diverging slightly, and narrowing towards distal reticulofusellar parts, and form the thickest elements of this rhabdosome. Medial lists are quite reduced, occasionally developing as very thin lists. Virgula free, placed in the middle of the rhabdosome, extending beyond it (Fig. 15B).

Variability. — The studied specimens differ slightly in the thickness of the reticulum lists and clathria in the total length of rhabdosome. Apertural

processes have almost the same length but throughout, the lengths of the distal reticulofusellar parts are different.

Remarks. — *Spinograptus spinosus* is closest to *S. clathrospinosus* because both possess a reticulum in the lateral walls. However, the reticulum is better developed in *S. spinosus*, whereas clathrial lists are poorly visible. A characteristict feature of *S. spinosus* is the presence of long, curved supraapertural lists (Fig. 15B). In *S. clathrospinosus* these lists are shorter and their curvature is poorly visible. Apertural processes in *S. spinosus* are much thinner and the reticulofusellar structure is visible only in their distal part, whereas in *S. clathrospinosus* it forms throughout their length. The range of *S. spinosus* in the Mielnik borehole is similar to those of *S. clathrospinosus* and *S. munchi*: in the upper part of *L. nilssoni* Zone.

Spinograptus clathrospinosus (Eisenack 1951)

Figs 31B; 32C.

Retiolites clathrospinosus; Eisenack 1951: p. 139, pl. 23: 1–2.

Spinograptus cf. *spinosus* (Wood); Lenz 1978: p. 636, pl. 7: 1, 2, 6.

Agastograptus clathrospinosus (Eisenack); Obut & Zaslavskaya 1983: pp. 108–109, pl. 25: 1–3.

Agastograptus? clathrospinosus (Eisenack); Lenz & Melchin 1991: p. 216, fig. 15E–F, H.

Agastograptus clathrospinosus (Eisenack); Lenz 1993: pp. 15–16, pl. 3: 1, 2, 4, 7, pl. 4: 6, 8.

non *Agastograptus clathrospinosus* (Eisenack); Lenz 1993: pp. 15–16, pl. 3: 3, 5, 6, pl. 4: 1–5, 7.

Emended diagnosis. — Reticulum well developed, ecpecially in lateral walls. Medial lists may be developed only as short processes or denticles or may be absent. Apertural processes long, reticulofusellar spines in all thecae.

Remarks on emended diagnosis. — This revised diagnosis of *S. clathrospinosus* is based on comparison with well preserved, isolated material, noting particularly development of medial lists as small spine or denticles. In Eisenack's (1951) material it is impossible to establish clearly the presence of these lists.

Material. — Five fragments of rhabdosome, well preserved, ZPAL G. XVI/1908–1912, Mielnik borehole, depth 1046.9 m.

Description. — Length of fragment of rhabdosome with 6 thecal pairs is 8.7 mm. Width of lateral walls is 1.8 mm proximally, 2.25 mm distally. Reticulum is usually developed only in lateral walls, occasionally in ventral walls. Medial lists develope either as small denticles on subapertural list, or short spines. Processes are shorter proximally and distally, but medially reach 1.55 mm in length. Apertural processes of proximal thecae are shortest: 0.19–0.45 mm. Basal 0.4 mm of apertural processes is often filled with periderm, but distal part reticulofusellar (Fig. 32C). Subapertural lists project horizontally, but supraapertural lists are curved and a little longer.

Variability. — The material studied varies in the thickness of the clathrial lists. Virgulae are damaged, making it impossible to measure their length. Apertural processes vary very little in length in medial part of rhabdosome.

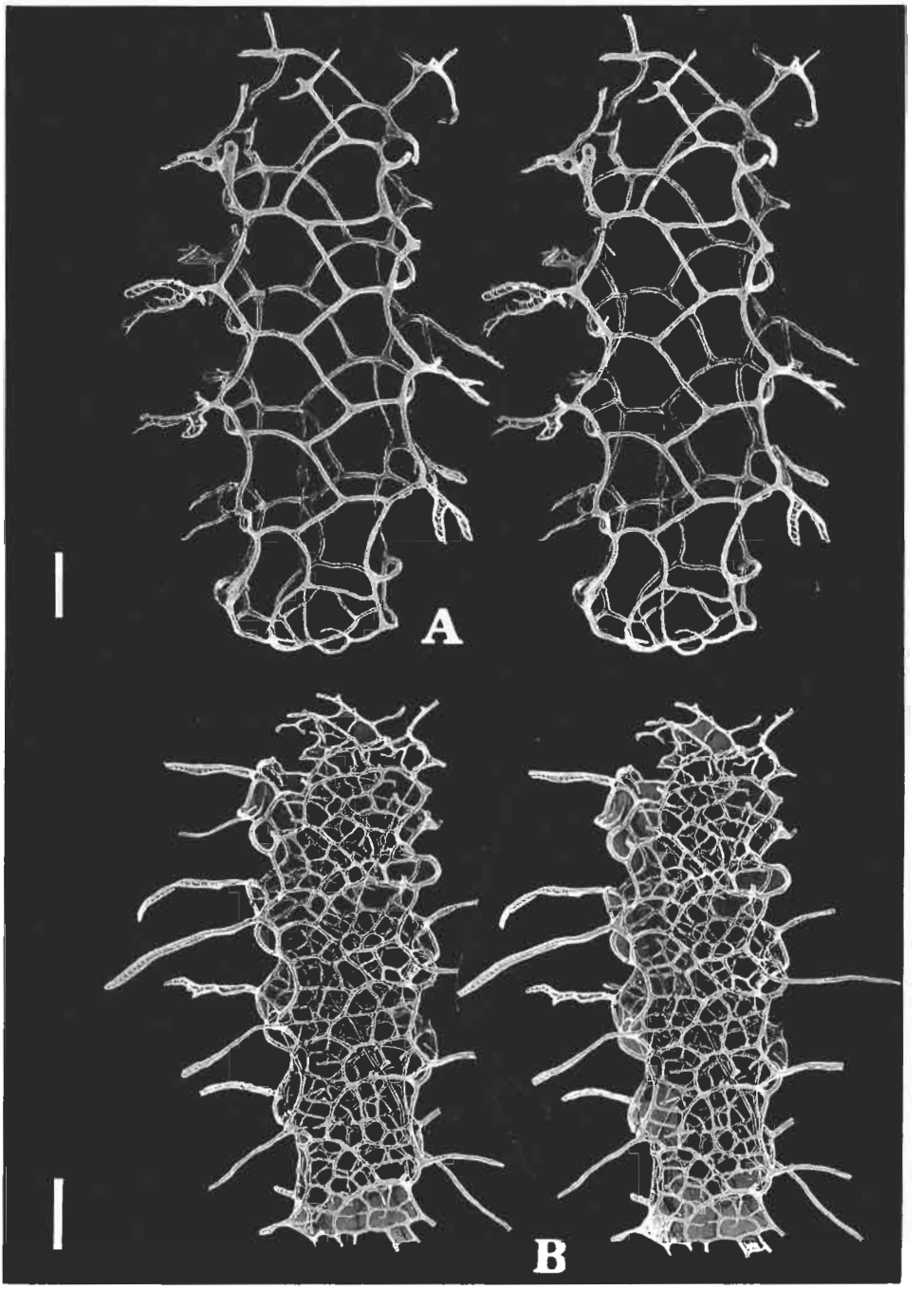


Fig. 31. ❑A. Stereopair of mature rhabdosome *Spinograptus munchi* (Eisenack 1951), ZPAL G. XVI/1922; Mielnik 1044.0 m. ❑B. *Spinograptus clathrospinosus* (Eisenack 1951), ZPAL G. XVI/1910, Mielnik 1044.0 m, bar scale 500 μm.

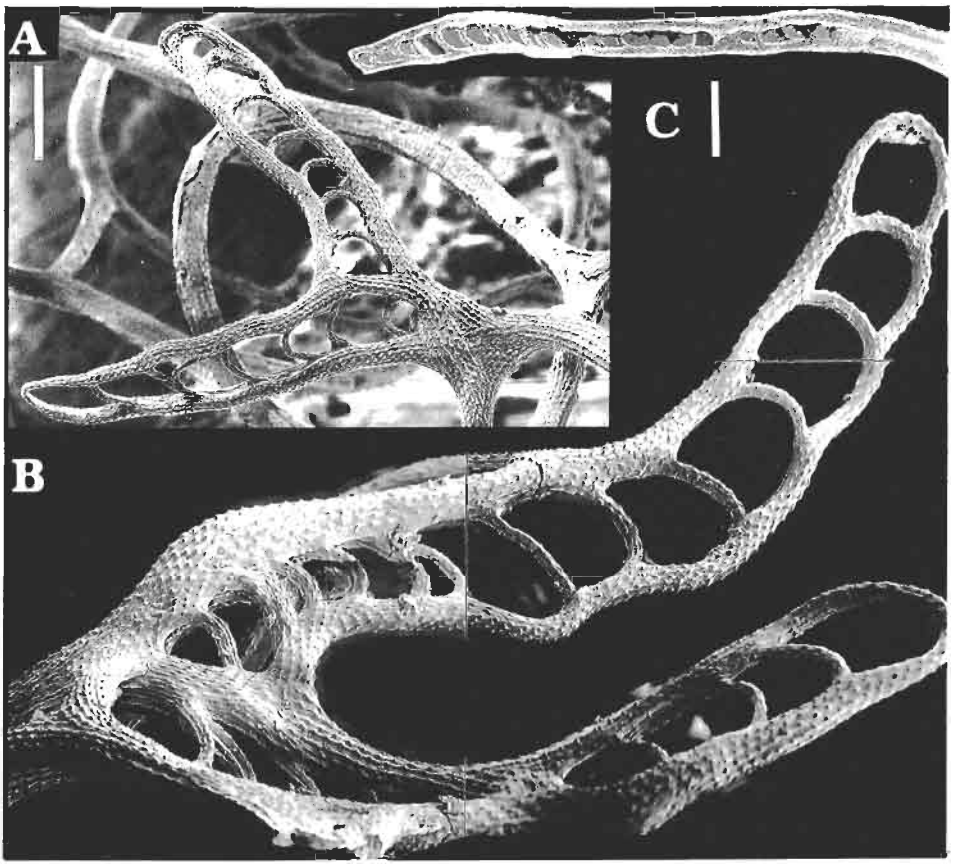


Fig. 32. ❑A–B. *Spinograptus munchi* (Eisenack 1951), ZPAL G. XVI/1922, Mielnik 1044.0 m, branching apertural processes. ❑C. Apertural process of *Spinograptus clathrospinosus* (Eisenack 1951), ZPAL G. XVI/1910, Mielnik 1044.0 m. Bar scale 100 μm.

Remarks. — *S. clathrospinosus* is most closely related to *S. spinosus*. However, the reticulum of this species is less dense in the lateral walls, and the apertural processes are reticular-fusellar in construction throughout their length.

Spinograptus munchi (Eisenack 1951)

Figs 31A; 32A–B.

Retiolites munchi; Eisenack 1951: p. 136, pl. 22: 9–12, pl. 23: 3–5, pl. 24: 1.

Agastograptus munchi (Eisenack); Obut & Zaslavskaya 1983: pp. 111–112, pl. 22: 4, pl. 26: 1–4.

Diagnosis. — Reticulum absent. Medial lists only developed as denticles on subapertural lists. Reticulofusellar apertural processes branching dichotomously in the basal part, sometimes also in the distal part.

Material. — Six well preserved fragments of rhabdosome ZPAL G. XVI/1920–1925, Mielnik borehole, depth 1044.9 m.

Description. — Length of rhabdosome ranges up to 9.2 mm. Width of corona is about 1.1–1.3 mm, width of lateral wall is similar to that of

corona and in distal part narrows to 0.6 mm. Rhabdosome bears with 8–10 thecal pairs. Clathrial lists are finer distally, except in longer rhabdosomes where they are thick throughout. Proximal apertural processes are up to 0.6 mm long, dichotomously branching in their basal parts, near subapertural list (Fig. 31A). Apertural processes branching dichotomously in their middle and distal parts, occur in the medial part of rhabdosome. Virgula of 1.4 mm length is preserved in only one rhabdosome.

Variability. — The apertural processes vary in the length at which they branch, and in the size of thickened basal parts. Variations in virgular length are probably due to damage.

Remarks. — *S. munchi* is characterised by a total lack of reticulum, thick clathrial lists, and shorter and branching apertural processes.

Genus *Plectograptus* Moberg & Törnquist 1909

Type species: *Retiolites macilentus* Törnquist 1887.

Diagnosis. — Ancora umbrella reduced. Lateral wall in coronal part of rhabdosome is absent. Ventral wall created by sub- and supraapertural, medial and pleural lists. Parietal lists of lateral wall with pronounced zigzag pattern. Aperture rectangular.

Remarks. — The lack of lists in the coronal part of rhabdosome was not mentioned as a diagnostic character by Bouček & Münch (1952). *Semiplectograptus* gen. n. and *Plectodinemagraptus* gen. n. also with reduced ancora umbrella, as well as total lack of a lateral wall in case of *P.* gen. n., shows these features are of great importance in distinguishing *Plectograptus*.

Species included. — *P. macilentus* (Törnquist 1887); *P. wimani* (Eisenack 1951).

Plectograptus macilentus (Törnquist 1887)

Fig. 33.

Retiolites macilentus sp. n.; Törnquist 1887: p. 91, fig. 3.

Plectograptus tetracanthus sp. n.; Eisenack 1951: pp. 140–142, pl. 23: 6–8, pl. 20: 9, fig. 4, 5.

Retiolites sp. indet.(?); Eisenack 1951: p. 147, pl. 23: 9, fig. 6–7.

non: *Retiolites (Plegmatograptus) obesus* var. cf. *macilentus*; Elles & Wood 1908: p. 343, pl. 34: 13a–b, fig. 224.

Diagnosis. — Reticulum and apertural processes absent.

Material. — 24 incomplete specimens, most slightly flattened, ZPAL G. XVI/2928–2950, Mielnik borehole, depth: 1008.9 m, 1004.9 m, 1001.9 m 999.9 m, and 991.9 m and immature rhabdosomes (ancora stage and first thecae) come from an erratic boulders 22 and 25 from Jarosławiec.

Description. — Maximum length of rhabdosome, containing 12 pairs of thecae is 10.1 mm. Ancora width ranges from 1.2 mm to 1.8 mm. Rhabdosome in lateral view is almost parallel-sided or gently tapering towards distal end from 2.5 to 2 mm. Parietal lists appear near subapertural lists of first pair of thecae (Fig. 33B). Aperture of first thecae forms on opposite side of ancora, about 0.64 mm from virgella. Ventral orifices possess very thin lists situated laterally (Fig. 33C). Length of medial lists

ranges from 0.25 to 0.52 mm. Central virgula is preserved only in proximal part of rhabdosome (Fig. 33B).

Variability. — All immature specimens are formed of fine lists, and possess very fine bifurcations on the end of the ancoral lists, which disappear in mature rhabdosomes formed of thickened periderm. The medial lists vary in length from 0.25 to 0.52 mm. Thus the differences depend on the degree of thickening of the apertural lists which, similarly to the remains of the clathrial lists (except of medial lists) are also considerably thickened during astogenetic growth. Therefore, the medial lists in juvenile rhabdosomes are longer than in older ones, where with the increase in thickness of the subapertural and supraapertural lists, the length of the medial lists is decreased. The medial lists are shorter in the distal parts of rhabdosome in specimens of 12 pairs of thecae. In fragments of rhabdosome with equal thickness of lists, the medial lists are usually not preserved or are damaged.

Remarks. — The investigated material is of similar dimensions and morphology to the specimens described by Eisenack (1951) as *Retiolites tetracanthus*. The Eisenack's specimen (1951: Fig. 5) is the fragment of the proximal part of a mature rhabdosome, as shown by the thickness of the lists.

The investigated specimens do not possess a virgula throughout the length of the rhabdosome, but only the virgella in the proximal parts. Specimens from the Holy Cross Mountains described by Tomczyk (1956: pl. 1: 2b), and Czech material described by Bouček & Münch (1952: fig. 7, pl. 1: 2–4) possess quite thick virgulae running throughout the length of rhabdosome, and in astogenetic younger specimens running even beyond the rhabdosome. Hence the virgulae in this isolated material are probably damaged. *Plectograptus macilentus* is related to *P. wimani*, but differs in the lack of a reticulum, and apertural processes, and in having a wider rhabdosome.

Plectograptus wimani (Eisenack 1951)

Fig. 27E.

Retiolites wimani sp. n.; Eisenack 1951: pp. 145–147, pl. 25: 8.

Material. — Three mature specimens, partly damaged, ZPAL G. XVI/1607, 1609, 2951, and one at ancora stage of growth ZPAL G. XVI/2952, Mielnik borehole, depth 1044.9 m.

Description. — The longest rhabdosome ZPAL G. XVI/1607 with 11 pairs of thecae, reach 11.7 mm long. Width of corona is about 1.4 mm. Width of proximal part of rhabdosome (measured between pleural lists) is about 2.1 mm, and 3.5 mm over apertural processes. Width at medial part of rhabdosome is 3.5 mm, distally decreasing to 1.4 mm (measured between pleural lists), but 3.2 mm over apertural lists. Immature specimen at ancora stage show fine lists and fragments of ventral orifice. Distance between pleural lists is 1.7 mm, from ancora to first parietal list 1.3 mm. In mature rhabdosome 1607 the coronal part is not preserved (Fig. 27E). Specimen ZPAL G. XVI/1609 has reticulum preserved proximally.

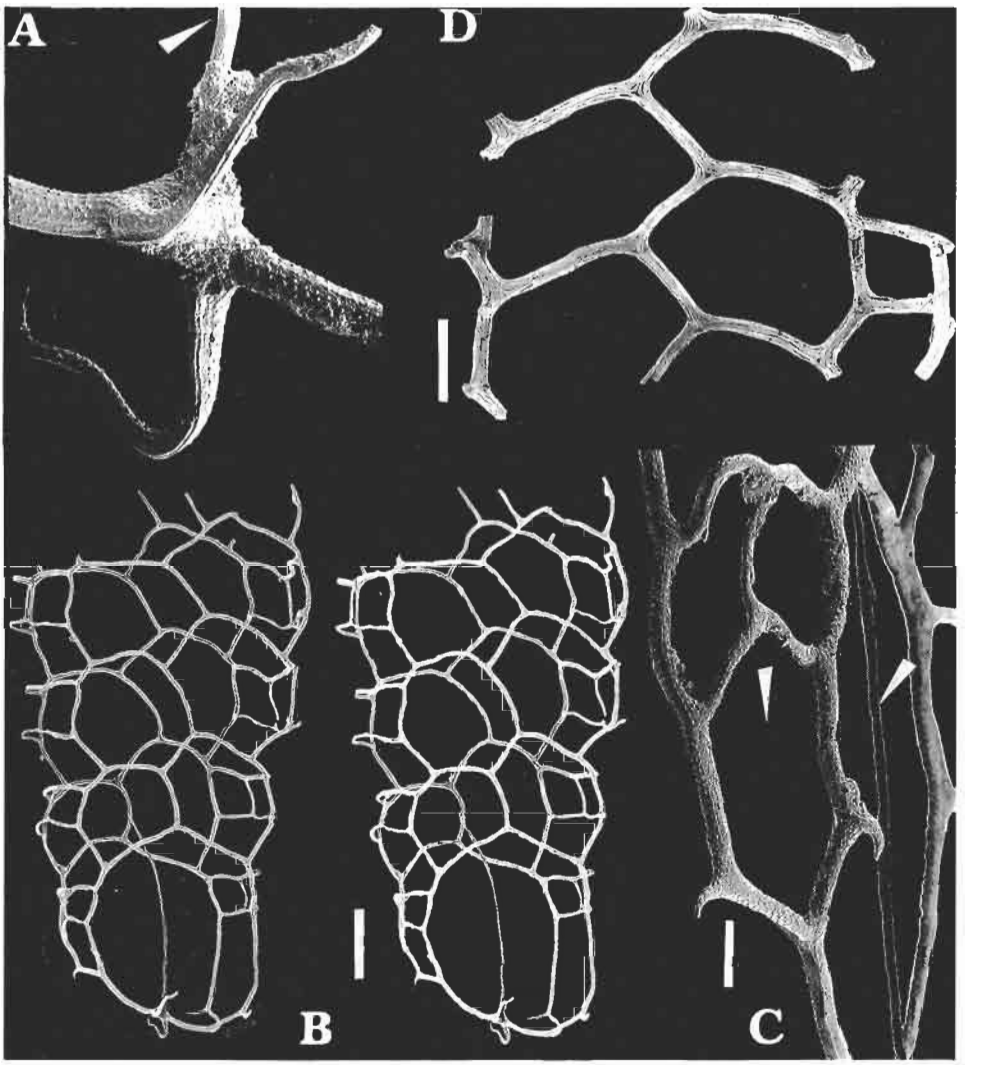


Fig. 33. *Plectograptus macilentus* (Tornquist 1887). A–C. ZPAL G. XVI/2931, erratic boulder 22 from Jaroslawiec. A. Reduced ancora umbrella with virgella arrowed; × 175. B. Stereopair of fragment of mature rhabdosome, bar scale 100 μm. C. Fragment of proximal part with ventral orifice (arrowed) and virgula (arrowed), bar scale 100 μm. D. Fragment of lateral wall of mature rhabdosome of strong thickened lists (inside view), ZPAL G. XVI/2930, erratic boulder 22 from Jaroslawiec; bar scale 500 μm.

Supraapertural lists bear apertural processes of irregular multifold loops of variably thickened lists. Distance between subapertural lists is up to 0.7–0.9 mm. In specimen ZPAL G. XVI/1609 middle part of ventral wall is damaged, so medial lists are not fully preserved and are present only in 3 first thecae. Those lists are fine in the middle part of rhabdosome.

In specimen 2951, medial lists are preserved. The subapertural lists are damaged and fragmentary. Pleural lists are flattened, zigzag in shape.

Reticular lists are rarely developed in ventral walls, especially near the pleural lists. Lateral wall is formed of thick clathrial and reticular lists. Parietal and dorsal lists are developed in the middle part of lateral wall, forming of hexagonal meshes with zigzag pattern. Aperture is rectangular in shape, with rounded corners. Virgula is not preserved.

Remarks. — *P. wimani* differs from *P. macilentus* by the presence of a well developed reticulum and apertural processes. In *P. wimani* they are multifold loops built of fine lists. The pleural lists are similar to *P. macilentus*, making a rather slight zigzag pattern. The mature rhabdosome of *P. wimani* from the Mielnik borehole narrows distally, perhaps indicating finite growth.

Genus *Semiplectograptus* gen. n.

Type species: *Semiplectograptus urbaneki* sp. n.

Diagnosis. — Ventral walls formed by hexagonal orifices, apertural lists of rhomboid shape and by medial lists; lateral walls formed by parietal lists creating zigzag pattern. Medial lists of the first thecal pair about twice as long as the rest.

Remarks. — The rhabdosome of *Semiplectograptus* gen. n. differs from that of *Plectograptus* in the shape of the apertural lists, which in *Semiplectograptus* are rhomboid, and without pleural lists, whereas in *Plectograptus* the apertural lists are approximately rectangular. Some species of *Gothograptus* possess a rectangular aperture, with pleural lists. *Holoretiolites* has pleural lists and an aperture of approximately rhomboid shape with rounded angles.

Semiplectograptus urbaneki sp. n.

Figs 27J; 34A.

Holotype: ZPAL G. XVI/1392.

Type horizon and locality: Ludlow, *C. hemiaversus*/*C. aversus* Zone, Mielnik borehole, depth 973 m.

Derivation of name: honouring Adam Urbanek, Polish graptolite specialist.

Diagnosis. — Length of medial lists of first pair of thecae about 0.7–0.8 mm, the rest about 0.27–0.4 mm. Width of rhabdosome constant to fifth pair of thecae.

Material. — 12 incomplete rhabdosome, with 4 to 5 thecal pairs; well preserved, ZPAL G. XVI/392–1403, Mielnik borehole, depth 973.0 m.

Description. — Length of rhabdosome with 5 thecal pairs of thecae ranges up to 4.2 mm. Width of rhabdosome changes slightly, from 1.4 to 2.0 mm across corona, and to 1.7 mm across the 5 pairs of thecae. Apertural lists of ventral hexagonal orifices are attached to ancora at about 0.4–0.5 mm from proximal end (Fig. 34A). Length of medial lists of first pair of thecae is about 0.7–0.8 mm, the next are about half as long. Medial lists are thicker than the rest, dorsal lists (about 0.4 mm in length) and parietal lists of lateral walls curved. Young rhabdosomes show virgulae up to 0.9 mm long, developed to second thecal pair; in two specimens to 4th thecal

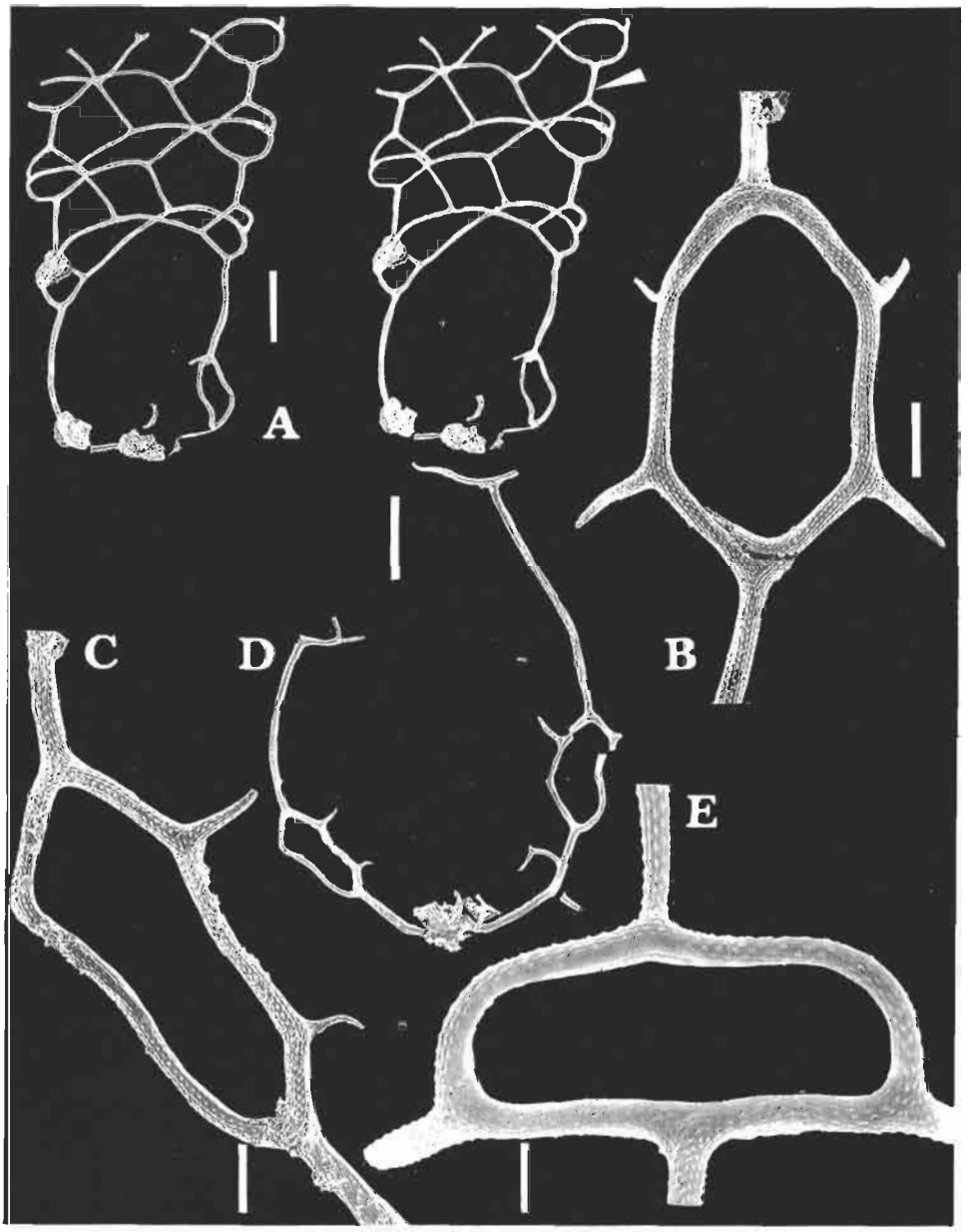


Fig. 34. ❑A. *Semiplectograptus urbaneki* gen. et sp. n., steropair of mature rhabdosome, damaged in distal part with marked medial list (arrowed), holotype ZPAL G. XVI/1392, Mielnik 972.0 m; bar scale 500 µm. ❑B–E. *Plectodinemagraptus gracilis* gen. et sp. n. B–C. Proximal ventral orifices, bar scale 50 µm, ZPAL G. XVI/1408, Mielnik 946.0 m. D. Proximal part of demaged young rhabdosome, bar scale 250 µm. E. Aperture of medial theca, ZPAL G. XVI/1409, Mielnik 972.0 m, bar scale 50 µm.

pair. Clathrial lists of immature rhabdosomes are clearly thinner than in mature ones. Thecal apertures of rhomboid shape, are formed by curved

supraapertural and subapertural lists. One specimen has two very thin lists running from the ancora.

Remarks. — *S. urbaneki* possesses medial lists which are thicker than the other clathrial lists, in contrast to the genus *Plectograptus* in which the medial lists are thinner in mature specimens.

Genus *Plectodinemagraptus* gen. n

Type species: *Plectodinemagraptus gracilis* sp. n.

Derivation of name: Latin *plecto* — from related genus *Plectograptus* Moberg & Törnquist 1909 and from *Dinemagraptus* Kozlowski 1951 — an Ordovician genus which bears some resemblance to the new Silurian species.

Diagnosis. — Ventral wall formed by hexagonal orifices, medial and sub- and supraapertural lists; lateral walls only represented by separate very short parietal lists.

Remarks. — *P. gracilis* represents the simplest rhabdosome so far found not only among plectograptids, but also among all retiolitids. This new species does not possess lateral lists; these appear to be reduced to very short lists on apertural lists (Fig. 34E). The rhabdosome of *P. gracilis* is therefore made of only two chains formed of apertural and medial lists, linked together by the ancora. Stratigraphicaly it occurs in the upper part of *C. hemiaversus/C. aversus* Zone, and is the youngest retiolitid known.

Plectodinemagraptus gracilis sp. n.

Figs 27D; 34B–E.

Holotype: ZPAL G. XVI/1406.

Type horizon and locality: Ludlow, *C. hemiaversus/C. aversus* Zone, Mielnik borehole, depth 946.0 m.

Diagnosis. — Width of ancora up to 0.7 mm, the length of medial lists narrow towards distal part and up to 0.4–0.6 mm long.

Material. — Three fragments of rhabdosome with proximal ends and four with medial parts ZPAL G. XVI/1406–1412, Mielnik borehole, depths 946.9 and 940.5 m — C. *hemiaversus/C. aversus* Zone.

Description. — The holotype is composed of corona and two pairs of thecae and fragments of five further thecae. Width of proximal part across first pair of thecae is about 0.7 mm. The lists of the first ventral orifice are located 0.25 mm from the proximal end. Apertures of ventral orifices are approximately hexagonal in shape, with short processes developed on the angles (Fig. 34B–C). Processes of successive thecae sometimes bifurcate towards their ends. Below orifices two short bifurcate lists are developed. Length of medial lists of theca 1/1 is 0.45–0.6 mm, of theca 1/2 0.7 mm. Length of medial lists of successive thecae less than 0.4–0.5 mm. Apertural widths range from 0.25 to 0.32 mm, apertural lists are thicker then other lists.

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Streszczenie

Obfita fauna retiolitidowa została wyizolowana z rdzeni wiertniczych wenloku i ludlowu NE Polski oraz z bałtyckich głazów narzutowych. Analiza materiału w mikroskopie świetlnym i skaningowym pozwoliła prześledzić proces postępującego uproszczenia retikulowanego szkieletu. Polega on na redukcji retikuli i katrium, redukcji szkieletu tekalnego (transverse rods)

oraz na zmianie położenia wirguli z bocznego na centralny. Obserwuje się zmniejszenie liczby tek w rabdozomach. Dowodem daleko posuniętej redukcji jest najmłodszy, napotkany, w zonie *C. hemiaversus*, najbardziej uproszczony rabdozom bez ścian lateralnych *Pl. gracilis* gen. et sp. n.

Od górnego wenloku ma miejsce proces finalizacji wzrostu kolonii, połączony ze zmniejszaniem liczby tek. W skrajnym przypadku forma *H. simplex* o zakończonym wzroście liczy cztery teki. Położenie wirguli, obecność elementów szkieletu tekalnego, budowa klatrium oraz tendencja do finalizacji wzrostu rabdozomu, stanowią kryteria do podziału rodziny Retiolitidae na linie rozwojowe: *Retiolites*, *Paraplectograptus*, *Sokolovograptus*, *Gothograptus* i *Plectograptus*.

Wysunięto hipotezę, iż przodkiem *Paraplectograptus eiseli* i *Pseudoplectograptus praemacilentus* był *R. geinitzianus*, o czym świadczy obecność beleczek szkieletu tekalnego. U najstarszego przedstawiciela linii *Gothograptus*, wenlockiego *Eisenackograptus eisenacki*, pochodzącego prawdopodobnie od linii *Paraplectograptus*, beleczki tekalne mają postać szczątkową, zaś zanikają u pochodzących od niego gatunków rodzaju *G.* z górnego wenloku, u których wirgula włączona jest jeszcze do ściany wentralnej. Wirgula ma położenie centralne u ludlowkich gatunków zaliczonych do rodzaju *Neogothograptus* i *Holoretiolites*, a wywodzących się od *G.* Linia *Sokolovograptus*, jako jedyna wenlocka, charakteryzuje się centralnym położeniem wirguli. O jej pochodzeniu trudno przy obecnym stanie wiedzy spekulować. Być może od *S.* pochodzi linia *Plectograptus* znana z ludlowu. Formy pośrednie, nieobecne w badanym materiale, przypuszczalnie występowały w najwyższym wenloku. W linii *Pl.* prześledzić można kolejne etapy redukcji rabdozomu od *Pl. wimani*, *Pl. macilentus* przez *Semiplectograptus urbaneki* gen. et sp. n. aż do *Plectodinemagraptus gracilis* gen. et sp. n.