

GRAPTOLITES AND STRATIGRAPHY OF THE WENLOCK AND LUDLOW SERIES IN THE EAST EUROPEAN PLATFORM

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The sequence of graptolite faunas in the Wenlock and Ludlow Series in the East European Platform is presented. The morphology of the graptolites discussed is based on the material isolated from the cores and from Baltic erratic boulders. Main trends of morphological evolution have been recognized and characterized. Along with the updating of the earlier record on biostratigraphy, new data including those on retiolitids are provided. A modified zonal graptolite subdivision, comprising the Late Ludfordian is presented.

Key words: Graptolites, Biostratigraphy, Silurian, Wenlock, Ludlow, East European Platform.

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GRAPTOLITE FAUNAS OF THE WENLOCK SERIES

This series, recognized over a vast area of the Polish part of the East European Platform (EEP), represents a fairly uniform, horizontally lying complex of claystones (LANGIER-KUŹNIAROWA 1976) with carbonate intercalations. It is only in the eastern extremity of the Peribaltic Syncline (Lake Okrągłe IG-1 borehole) and in the eastern Podlasie Depression (boreholes: Kaplonosy IG-1, Mielnik IG-1, Parczew IG-1, and others) that marly-dolomitic-carbonate sediments prevail (JAWOROWSKI 1965; JAWOROWSKI and MODLIŃSKI 1968; TELLER 1967, 1976, 1986; TOMCZYK 1968, 1976; TOMCZYKOWA 1983).

The description of the series is almost completely based on the rich graptolite fauna encountered in several boreholes (TELLER 1969). The SW Peribaltic Syncline features, in sedimentary continuity above the late Llandovery, grey limy claystones in which the proportion of carbonate material increases towards the top. This is especially marked by intercalations of grey muddy limestones up to 20 cm thick. The thickness of the series attains 148 m (the Łębork IG-1 borehole TOMCZYK 1968). There is no sedimentary hiatus between these deposits and those of the overlying Gorstian stage of the Ludlow Series. The more shallow parts of the epicontinental basin are dominated by marly-carbonate facies (boreholes: Lake Okrągłe IG-1 and Goldap IG-1, TOMCZYK 1964; MODLIŃSKI 1974) whilst in the eastern Podlasie Depression (boreholes: Mielnik IG-1, Bielsk Podlaski IG-1, Widowo IG-1, Terespol IG-1, and others TOMCZYKOWA and TOMCZYK 1979) marly claystones, limestones, and dolomites containing benthic fauna are more characteristic. Their thickness varies between 40 and 60 m. They overlie the early Ashgillian with a hiatus in sedimentation (MODLIŃSKI 1973), attributable to the Taconian phase (MODLIŃSKI 1967; BEDNARCZYK 1968).

The neritic facies were connected via Belarus with Lithuania and Estonia in the north, and via Volhynia with Podolia in the south (KALJO and JURGENSON 1977; KLAAMAN and EINASTO 1982). It is believed that in the Wenlock, the transgression on the EEP attained a peak, reaching far to the east and even joining the Moscow Basin (KALJO 1971).

Prevailing in the western part of the Podlasie Depression and also in the Lublin Region are argillaceous facies similar to those recognized in the western Peribaltic Syncline. Their thickness attains 100 m, and they grade vertically into Ludlow deposits, apparently without a hiatus in sedimentation or any changes in lithology.

Wenlock deposits are also known from the marginal zone of the EEP. They have been recorded in the Wierzchocina-1 and 4 boreholes within Koszalin–Chojnice belt. Dark grey claystones with an apparent thickness of 50 m, and dipping 20–50° there, were probably associated with the Caledonian Geosyncline (TELLER 1974).

Development of graptoloid fauna. — Among the rich graptolite fauna of Wenlock deposits, the genus *Cyrtograptus* plays a special role. However, in addition to the Cyrtograptids, represented by such species as *C. centrifugus* BOUČEK, *C. insectus* BOUČEK, *C. munchisoni* CARRUTHERS, *C. radians* TÖRNQUIST, *C. ramosus* BOUČEK, *C. mancki* BOUČEK, *C. lapworthi* TULLBERG, *C. rigidus* TULLBERG, *C. perneri* BOUČEK,

C. hamatus (BAILY), *C. lundgreni* TULLBERG, and *C. urbaneki* TELLER (TELLER 1969, 1976), there are also representatives of other groups.

Predominant among the species of the genus *Monograptus* are those having thecae of the *priodon* type, e.g. *M. priodon* BRONNGIART, a holdover from the Llandovery which becomes extinct in the Wenlock; short-lived *M. riccartonensis* LAPWORTH, a marker of the zone of the same name; and *M. flemingi* (SALTER), present throughout the Wenlock. *M. flexuosus* (TULLBERG) and *M. antennularius* (MENEHINI) are also present, and represent slender forms with a unique thecal character, the second being the marker of a separate zone. Another numerous species is *M. belophorus* MENEHINI, easily recognizable thanks to a very long virgella and unusual thecae of the *flemingi* type. *M. testis* (BARRANDE) (URBANEK and TELLER 1974; JAWOROWSKI 1965) a distinctive form, co-occurs in the late Wenlock, with *C. lundgreni* TULLBERG, just as it does in other sequences throughout the world, with *C. lundgreni* TULLBERG, occasionally forming mass accumulations (TELLER 1986; LENZ and MELCHIN 1990).

The genus *Monoclimacis* is represented by numerous specimens of *M. griestoniensis* (NICHOLSON), *M. crenulata* TÖRNQUIST, *M. hemipristis* (MENEHINI), *M. flumendosae* (GORTANI), *M. zawadensis* TELLER, and *M. vomerina* (NICHOLSON). These species have a great vertical range and co-occur with other index species (TELLER 1986).

Representatives of the *dubius* group, abundant in the section discussed, are highly conservative. In successive mass reappearances of new populations, and as compared to the preceding forms, it displays only slight morphological changes, mainly in the thecal apertures.

Retiolitids are characterized by great abundance and diversity as has recently been shown in KOZŁOWSKA'S-DAWIDZIUŁ studies (1995). The *R. geinitzianus* (BARRANDE) and few *Pseudoretiolites* sp. pass from the Llandovery into the Lower Wenlock Series. The Sokolovograptids like *S. textor* (BOUČEK *et* MÜNCH), *S. parens* (OBUT *et* SOBOLEVSKAJA) are very common in the Middle Wenlock and only *S. telleri* KOZŁOWSKA-DAWIDZIUŁ is present in the lower part of this series. *Paraplectograptus eiseli* (MANCK) is known from the entire Wenlock, while in its middle part occur a few *Pa. sagenus* LENZ, a species related to the genus *Pseudoplectograptus*. In the Middle Wenlock *Eisenackograptus eisenacki* (OBUT *et* SOBOLEVSKAJA) is abundant, while in the Upper part of the series appear seldom *Gothograptus pseudospinosus* (EISENACK) and *G. obiectus* (KOZŁOWSKA-DAWIDZIUŁ). The last three species belong to gothograptids, which in the upper part of the Wenlock Series are represented only by *G. nassa* (HOLM) (KOZŁOWSKA-DAWIDZIUŁ 1995).

With the exception of the *dubius* group and retiolitids, the graptolite fauna extending to the top of the *C. lundgreni* Zone becomes extinct. Its extinction is part of a world-wide crisis. The two surviving species undergo a sudden radiation in the uppermost Wenlock (JAEGER 1991; KOREN' 1979; KOREN' and URBANEK 1994), producing a number of new lineages which, in turn, initiated the development of the Ludlow fauna.

Trends in cyrtograptids (Fig. 1). — Although *Cyrtograptus* was the leading Wenlock graptolite, the knowledge of its phylogeny is inadequate, the prevailing view being that it had a polyphyletic origin. Thanks to their cosmopolitan nature and a characteristic architecture of the colonies, representatives of this genus are highly suitable for interregional correlations. However, the Polish sections have not, so far, yielded any of the uppermost Llandovery species which, most probably, are the oldest representatives of this group. These are *C. laqueus* JACKSON *et* ETHERINGTON known from Arctic Canada and Greenland (JACKSON and ETHERINGTON 1969; BJERRESKOV 1992), *C. sakmaricus* KOREN' reported from the Northern Urals (KOREN' 1968), and *C. polyrameus* FU *et* SONG recorded in China (FU LI-PU 1985, 1994).

One should not rule out the possibility that the presence of these species in the above mentioned regions is attributable to provincialism, an idea emphasized by MELCHIN (1989) and LENZ and MELCHIN (1990, 1991), as well as by RICKARDS *et al.* (1990). The concept of Silurian faunal provinces, however, seems to be arguable, being still an open question (see BJERRESKOV 1992). What is important, however, is the fact that those oldest multiramous colonies gave start in the Wenlock to a burst of development of *Cyrtograptus* whose multidirectional evolution went on till the genus became completely extinct before the end of the Wenlock.

The Polish material made it possible to distinguish all the zones based on this genus, from *C. centrifugus* BOUČEK to *C. lundgreni* TULLBERG. LENZ and MELCHIN (1989) derive *Cyrtograptus* from the *Monograptus turriculatus* or closely related line on the one hand, and from *M. tullbergi* — on the other. From a very general analysis offered by RICKARDS *et al.* (1977) it follows that there exist at least four lines of development, and perhaps even more. DENG BAO (1986), however, derives this genus directly from the *Oktavites spiralis* (GEINITZ) line or the *M. planus* (BARRANDE) line, a suggestion discounted by LENZ and MELCHIN (1989) on the base of distinct morphological differences.

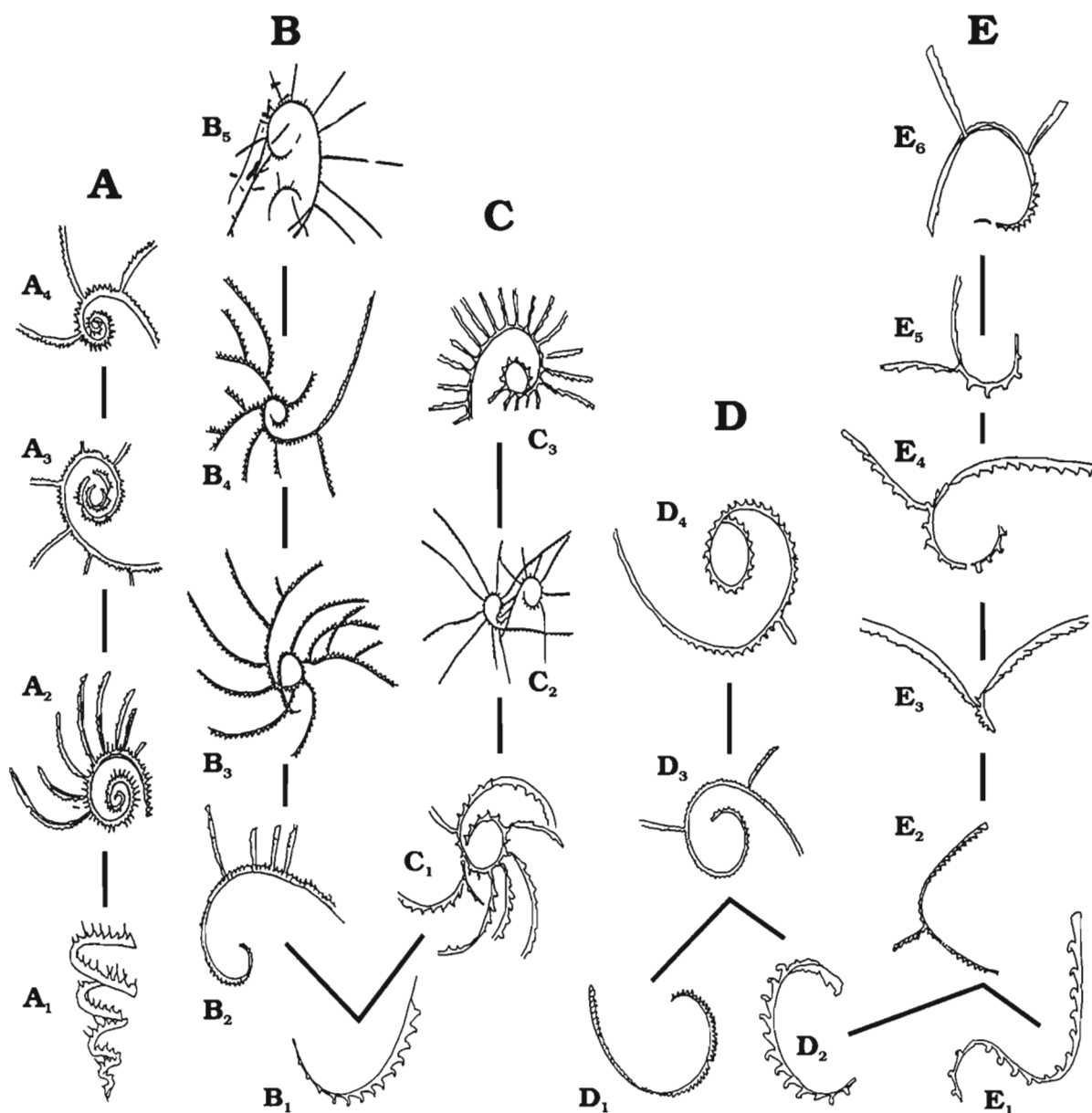


Fig. 1

Tentative phylogeny of cyrtograptids; A–E main trends in morphological evolution, further explanations in text.

Among the elements of the colony common to all representatives of the genus and showing a tendency to change, the degree of coiling of the proximal part of the procladium should be mentioned. This feature is most strongly pronounced in the earlier forms coming from the uppermost Llandovery, their trochospiral procladium involving 3–2.5 coils (*C. sakmaricus*, *C. solaris*).

In Lower Wenlock forms, the number of coils decreases to 1.5 in *C. centrifugus* and 1.25, in *C. murchisoni* (FU LI-PU 1985; HUO SHI-CHENG *et al.* 1986; HUO SHI-CHENG and FU LI-PU 1981; HUO SHI-CHENG and SHU DE-GAN 1981). Full helices in the proximal part, but planispiral or low trochospiral shapes in the horizontal plane are displayed by *C. laqueus*, *C. multiramis*, *C. radians*, and *C. ramosus*.

Many species, beginning with *M. polyrameus* in the late Llandovery, and on to *C. falcatus*, *C. lapworthi*, *C. mancki*, *C. rigidus*, *C. perneri*, and *C. hamatus* to as late as *C. lundgreni* in the uppermost Wenlock, show a stable tendency towards straightening and gracilization of the proximal part.

Thecal cladia constitute another element illustrating the colony development. Variation is expressed in their number and rate of appearance. For many species this is an important diagnostic feature (TELLER 1994).

Of great importance also are changes in thecal characters. These include the shape of the thecae (hooked or straight), their being isolated or overlapping one another, the shape and morphology of the aperture, e.g. the presence or absence of apertural processes, and also a distinct bimorphism or even trimorphism (TELLER 1994).

One more important character is the 180° torsion of the procladium accompanied by a shift of the thecae from their primary position so that the ventral side becomes inwardly oriented.

On the basis of the above characters one can assign the species recognized so far to several groups which could be regarded as separate stocks.

The first group (A) would include the late Llandovery forms, *C. sakmaricus* (A₂) and *C. solaris* (A₃), together with early Wenlock *C. centrifugus* (A₄). They share the following characters: trochospiral coiling of the proximal part, a similar type of thecae, and progressive reduction of thecal cladia. This group might have derived from *M. turriculatus* (A₁) (MELCHIN and LENZ 1986; LENZ and MELCHIN 1989).

The second group (B) which, according to the present author, comprises *C. polyrameus* (B₂), *C. laqueus* (B₃), *C. munchisoni* (B₄), and *C. ramosus* (B₅), displays an incomplete or closed planispiral coiling of the proximal part, a fairly simple thecal morphology, and thecal cladia budding at varying distances from one another (BJERRESKOV 1975, 1992; LENZ and MELCHIN 1989, 1991; LENZ 1978). The presence of the cladia of the second [*C. laqueus* (B₃), *C. munchisoni* (B₄)], or third [*C. munchisoni* (BOUČEK 1933)] order is another important character of this group. In *C. laqueus* this feature is expressed in the second cladium alone (LENZ 1978), while in *C. munchisoni* it is much more common (BOUČEK 1933).

It cannot be excluded that the earliest representatives of the second group constitute a continuation of the Llandovery monograptids from the *Oktavites planus* lineage (DENG BAO 1986).

The third (C) group, represented by multiramous forms typical of the late Wenlock, are *C. multiramis* (C₁), *C. mancki* (C₂), and *C. radians* (C₃). Their distinguishing feature is planispiral coiling of the proximal part with an insignificant shift in the horizontal plane; they also have a similar though morphologically more simplified type of thecae and a larger number of cladia. In an extreme case, as e.g. in *C. radians*, cladia bud from each successive theca. The forms composing this stock may be a continuation of the early Wenlock representatives assigned to the second group (BOUČEK 1933).

The fourth group (D) represented by *C. lapworthi* (D₃) and *C. insectus* (D₄) comprises those forms whose proximal part is coiled planispirally, whose thecal morphology resembles that of the first group and whose cladia are considerably reduced. No more than two or three cladia are present as a rule (BOUČEK 1933). Both forms may have derived from the same stem, i.e. from *Monograptus decipiens* as suggested by MELCHIN 1989 (D₁), but they could also be a continuation of two independent lineages, *M. decipiens* (D₁) and *M. flagellaris* TÖRNQUIST (D₂).

The fifth group (E) is meant to contain all the forms with a straightened or only slightly coiled proximal part, triform thecae, and no more than one thecal cladium (with the exception of *C. lundgreni* (E₆) that may have up to three). Thecal cladia bud at an early stage of the astogeny following the appearance of 5–10 thecae on the procladium which undergoes torsion immediately afterward. The group may include *C. falcatus* (E₂) from the late Llandovery (LENZ and MELCHIN 1991), *C. rigidus* (E₃), *C. perneri* (E₄), *C. hamatus* (E₅), and *C. lundgreni* (E₆). The ancestry may be seen in Llandovery monograptids from the *tullbergi* (E₁) (LENZ and MELCHIN 1989) or *flagellaris* (D₂) lineages.

A 180° torsion of the procladium axis, so typical of the genus *Cyrtograptus*, accompanied by a shift of the thecae from the external position to the internal side seems to be a regularity in all the species, the differences being in the stage of the astogeny at which these changes might occur.

In many cyrtograptids thecal cladia appear in a rapid succession, budding from every second, every third or every fourth theca. They may also be irregularly spaced at fairly large intervals. In such forms the torsion of the axis is delayed until after the appearance of the last cladium, that is until the colony attains the stage of maturity. In all those forms which have either only one thecal cladium or two or three cladia spaced wide apart, however, the procladium torsion comes after the appearance of the first cladium, involving 3–7 thecae (BOUČEK 1933; LENZ 1978, 1988; LENZ and MELCHIN 1989; TELLER 1994).

Rhabdosome torsion is also known in several species of the Llandovery monograptids. This phenomenon has been recorded in *M. decipiens volens* PŘIBYL *et* MÜNCH, and *M. minutus* from the *minor* Zone, and also in *M. flagellaris* TÖRNQUIST, *M. proteus* (BARRANDE), *M. tullbergi* BOUČEK from the *crispus* and *griestoniensis* Zones, and *M. spiralis excentricus* BJERRESKOV from the *griestoniensis* and *sakmaricus* Zones (BJERRESKOV 1975 1992; LENZ 1978, 1988; LENZ and MELCHIN 1989; TELLER 1994).

The torsion of the procladium is hard to understand and interpret. Since this feature is present in a number of Llandovery monograptids, it seems reasonable to assume that it was a genetically determined

trait. The preservation of torsion in cyrtograptid colonies with their extremely complex architecture as well as in some monograptids, may point to a connection with the colony hydrodynamics, especially in the forms with only a few thecal cladia.

In the last-mentioned forms, the torsion of the axis might have contributed to the buoyancy of the colony in the water column; it could also have increased the depletion zone of individual specimens within the colony. In multiramous colonies branching of thecal cladia takes place in a rapid succession. This explains why these rhabdosome fragments might have been too short to provide enough space for both torsion and corresponding changes of thecal characters.

A multiramous colony occupied a large space in the water column and was well balanced, and the feeding depletion zone of its individuals was great. Therefore it would be difficult to find objective prerequisites for such an overall colony shape except for its adaptive significance.

The assignment of the cyrtograptid species recognized so far to hypothetical groups represents no more than a tentative picture of the genus development. However, it can be assumed with a high degree of probability that the genus had a polyphyletic origin. Its possible ancestors may be seen amongst Llandovery monograptids. A better understanding of the adaptive radiation of this group at the close of the Llandovery requires further studies.

GRAPTOLITE FAUNAS OF THE LUDLOW SERIES

Studies on the subsurface Silurian of the East European Platform have contributed to a better knowledge of the graptolite faunas of what was known as the Lower Ludlow in classical literature (WOOD 1900). TOMCZYK (1962, 1968) introduced the name Mielnik Beds for a series of strata roughly equivalent in their stratigraphic position to the former Lower Ludlow of British stratigraphers. This informal unit, which was subject to a number of re-definitions (as Formation or regional stage – the Mielnikian), represents a convenient subdivision for the local study of graptolite faunas (URBANEK 1966). One of the reasons is its close correspondence to the natural intervals in the development of monograptid faunas, a feature not shared by the internationally recognized subdivision of the Ludlow Series into the Gorstian and Ludfordian Stages (see HOLLAND 1989). By delegating the Leintwardine (an equivalent of *leintwardinensis* Biozone) to the latter Stage, this subdivision sets the stratigraphic boundary across the continuous lines of graptoloid evolution. For this reason, we follow a compromise when discussing the development of graptolite faunas in the EEP; we present first the problem of Wenlock–Ludlow boundary in the light of the studies made on the Polish part of EEP, then we discuss the recent interpretation of the *nilssonii* Zone as the base of the Gorstian stage as presently understood (LAWSON and WHITE 1989), and finally we discuss the Gorstian to *leintwardinensis* Biozone interval and the post-*leintwardinensis* interval.

The problem of Wenlock–Ludlow boundary in the EEP. — The interval in question is inadequately recognized in the Polish part of the EEP, but the best insight can be found in JAWOROWSKI's (1965) study based on Bartoszyce IG-1 and Goldap IG-1 deep borings, situated in NE Poland (the Lithuanian depression). He established a detailed succession within the critical interval of the *C. perneri*–*G. nassa* Zones, focusing on the faunal changes in the last representatives of the diversified *lundgreni*–*testis* fauna. While locally, *C. lundgreni* appears considerably earlier than *Monograptus (Testograptus) testis*, their extinction is coeval. Therefore one can distinguish the *lundgreni/testis* cenozone, although, there is no basis for distinguishing a separate *testis* Zone, at least in the region under study. As the top of the *lundgreni* Zone coincides with the extinction of cyrtograptids and hooked monograptids of the *priodon*–*flemingi* group, JAWOROWSKI (1965) proposed drawing the Wenlock/Ludlow boundary at this horizon. He followed at the same time, the classical approach introduced by WOOD (1900).

Beds overlying the *lundgreni* Zone abound in *Gothograptus nassa* accompanied by *Pristiograptus dubius* and related pristiograptids. *Plectograptus* sp. is known to appear in the *lundgreni* Zone and continues into the *nassa* horizon.

The idea that the *lundgreni* faunal turnover, in one way or other defines, the Wenlock–Ludlow boundary has always been widely accepted by Polish stratigraphers (TOMCZYK 1962, 1970; TELLER 1969; TOMCZYKOWA 1988; TOMCZYK and TOMCZYKOWA 1980). The boundary in question was usually placed between the *lundgreni* Zone and the *nassa* Zone, the latter being considered the earliest unit of the Ludlow Series.

Further studies resulted in a revision of WOOD's (1900) classical standpoint. The Wenlock–Ludlow boundary in the type area was shifted upwards. The *nassa* and *ludensis* biozones were included in the Wenlock as its Homeric Stage, *M. ludensis* being now considered the senior synonym of *M. vulgaris* (HOLLAND, RICKARDS, and WARREN 1969). Correspondingly, the Ludlow Series began with the *nilssoni* Zone. These stratigraphic conclusions were accepted by Silurian Subcommittee (HOLLAND 1989).

These stratigraphic and nomenclatorial decisions were met with a sharp criticism of JAEGER (1991: pp. 311–313), supported by URBANEK (this volume, p. 102). As the role of the *lundgreni* Event is now generally recognized (JAEGER 1991; KOREN' 1994; KOREN' and URBANEK 1994; KOREN' and SUYARKOVA 1994; LENZ 1993a, 1994a) and the principles of event stratigraphy are gaining wider understanding, a return to the earlier definition of the Wenlock–Ludlow boundary, seems fully justified. In our opinion this problem deserves to be reconsidered by the Silurian Stratigraphic Subcommittee.

The borehole sections with complete coring (such as Żarnowiec IG-1, Prabuty IG-1, Pasłęk IG-1, Łębork IG-1, Bartoszyce IG-1, Gołdap IG-1 and some others) feature unbroken sequences across the *lundgreni*–*nassa* turnover interval. Unfortunately, the faunal assemblages above the *lundgreni* Zone are inadequately known and have not been properly studied. The horizon yielding *nassa* is distinct and usually thick, and can be easily traced over wide areas within otherwise monotonous clayey-muddy sediments. TOMCZYKOWA (1988: p. 26; see also JAEGER 1991) reported, however, that the appearance of *G. nassa* is systematically associated with a change of lithofacies (an abrupt increase in carbonate content). According to TOMCZYKS' (personal communication) this carbonate-rich bed provides a marker horizon which may easily be traced over the distance of hundreds of km by geophysical sounding. The details of this most intriguing observation have not been published yet. Moreover, one of us (L.T.) has analysed geophysical data on some boreholes, and could find no distinct anomaly, which could be related to the above described marker horizon. This matter evidently needs further consideration.

Progress in the ongoing studies on the critical interval (KOZŁOWSKA-DAWIDZIUK), based on isolated material from Bartoszyce IG-1 and some other borings, might soon supply crucial data concerning the graptolite sequence between the *nassa* Zone and the *ludensis* Zone in the Polish part of the EEP. As yet no index fossils of this interval have been recognized yet (see Table 1).

A new interpretation of the *nilssoni* Zone and the significance of the linograptid trend. — The studies on three-dimensionally preserved graptolite remains from Baltic erratic boulders and Mielnik IG-1 core-samples (EEP) have revealed a number of new details concerning *Neodiversograptus nilssoni* (BARRANDE) (URBANEK 1954, 1958; JAEGER 1959). *Monograptus nilssoni* was known as an important index species of a graptolite zone, defining the basal horizon of the Gorstian in the recent stratigraphic classification. More detailed studies of the morphology and stratigraphic occurrence of early Ludlow graptolites have revealed, however, that this name enveloped two different, albeit superficially similar species, distinguished primarily as "*nilssoni* A" (true *nilssoni*) and "*nilssoni* B" (URBANEK 1963). While the true *nilssoni*, representing an early linograptid specialization, should be assigned to the genus *Neodiversograptus*, "*nilssoni* B", later recognized as an independent species *Lobograptus progenitor* URBANEK, may be placed in the cucullograptid lineage. An unusual overall similarity between *N. nilssoni* and *L. progenitor* could be explained as the result of an incipient divergence from a common ancestral species. This ancestral species was later identified as "*Monograptus*" *sherrardae* SHERWIN, 1974, from the *praedeubeli* Zone of the Homeric (KOREN' 1992b; KOREN' and URBANEK 1994). Although representing quite different trends, both species were closely related sharing a number of common (synapomorphic) traits, inherited from the common ancestor, in turn closely related to *Pristiograptus dubius*. That is why many previous records of *N. nilssoni* were incorrect as the specimens actually belonged to *L. progenitor*.

The redefinition of *N. nilssoni* and of the eponymous zone was confirmed by PALMER (1971) for the British Isles and later applied to more remote territories (e.g., Central Nevada, BERRY and MURPHY 1975).

The material from the EEP and from the Baltic erratic boulders provides evidence for an early origin of the linograptid trend and enables one to understand the early phases of the linograptid phylogeny, namely the gradual transformation of *N. nilssoni* into a more advanced *Neodiversograptus beklemishevi* (URBANEK 1963) which occurred in the *parascanicuss*–*scanicus* Zones. *N. beklemishevi* displayed an ability to generate more than one sicular cladium which foreshadowed the multiramous conditions characteristic of *Linograptus posthumus*. The last named species appeared at the top of the *leintwardinensis* Zone representing a long-lasting taxon which attained its species-specific features during the Ludfordian time (cf. URBANEK, in this volume). *L. posthumus* as traced during the Přidolian was subject to only minor

The Gorstian to *leintwardinensis* Zone interval. —

Material etched from core samples of the Mielnik IG-1 deep boring (URBANEK 1966) threw a new light on the composition of the faunal assemblage and the morphology of the species represented within this interval. The picture of the diversification of the monograptid subfamily Cucullograptinae (Fig. 2), the leading element of the fauna, surpasses all that could be expected from the data earlier provided by both *in situ* sequences (described e.g. by WOOD 1990; BOUČEK 1936 and others) and Baltic erratic material (especially KÜHNE 1955; URBANEK 1958).

The most general feature of the cucullograptid evolution is determined by the fact that the group represents a distinct morphological type which can be termed "operculate". The key feature of the group is the presence of an apertural apparatus made of paired, laterally situated lobes that, in ancestral forms, are symmetrical and opercular in shape (as in *Lobograptus simplex* URBANEK 1966).

Further evolution within the group involved enlargement, shape modification and development of asymmetry in the apertural apparatus, which in all cucullograptids, is made up of standard fusellar tissue.

The overall shape of the cucullograptid rhabdosome is fairly stable, except for the replacement of the gentle dorsal curvature of its proximal part (observed in *L. progenitor* and *L. simplex* and inherited from their Homeric ancestors) by a practically straight or slightly ventrally curved rhabdosome. The habitus is very slender and the entire subapertural portion of the rhabdosome is very much alike in all Cucullograptinae.

In contrast, the apertural segments of the thecae display great diversification expressed as species-specific elaborations responsible for the morphological within-group diversity. However, all these modifications may be seen as certain variations of a given "Grundplan" evident in early lobograptids (stem lobograptids, Fig. 3) and manifested in juvenile growth stages of more advanced species. This basic structure is composed of paired, symmetrical apertural lobes produced on either side of the aperture by arcuate fuselli. In *L. progenitor* these lobes represent incipient elevations while in *L. simplex* they are transformed into genuine lobate projections of the aperture (Fig. 3). Morphological and stratigraphic

data suggest that *L. simplex* represents a central species of the entire group – a probable common ancestor to all the five lineages and one side line distinguished within the Cucullograptinae (URBANEK 1966). The pattern of differentiation of the ancestral type of the apertural apparatus (as seen in *L. simplex*) was not the same in each lineage. There is only one lineage where a progressive elaboration of paired apertural lobes is combined with the preservation of primary bilateral symmetry (the *expectatus* lineage, Fig. 3). Together with its forerunners, it constitutes the S-cucullograptid morphological group ("S" in the name stands for "symmetric"). In the majority of the species the enlargement of the apertural lobes was inevitably connected with the development of some kind of asymmetry. The bulk of species is characterized by enlargement of both apertural lobes combined with the hypertrophy of the right-hand one (R-cucullograptids in URBANEK 1966). In a minor group of species, however, an increase in the size of the lobes is usually associated with a strong hypertrophy of the left lobe (L-cucullograptids, *ibidem*).

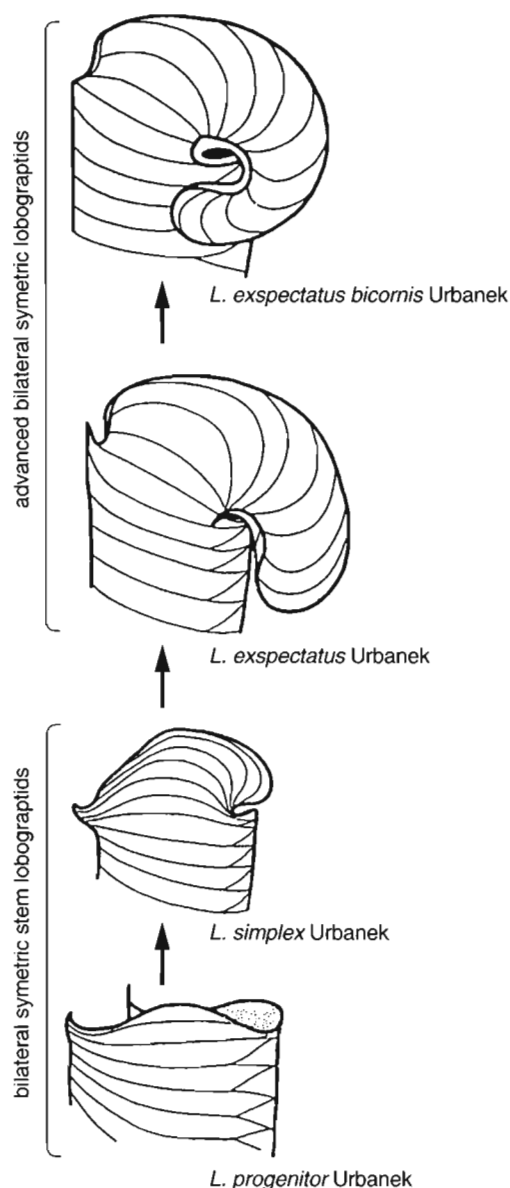


Fig. 3

Diagram revealing the origin and evolution of apertural apparatus in bilaterally symmetric lobograptids (S-cucullograptids). Note the gradual increase in the size of apertural lobe until the beak-like termination is formed (after URBANEK 1966).

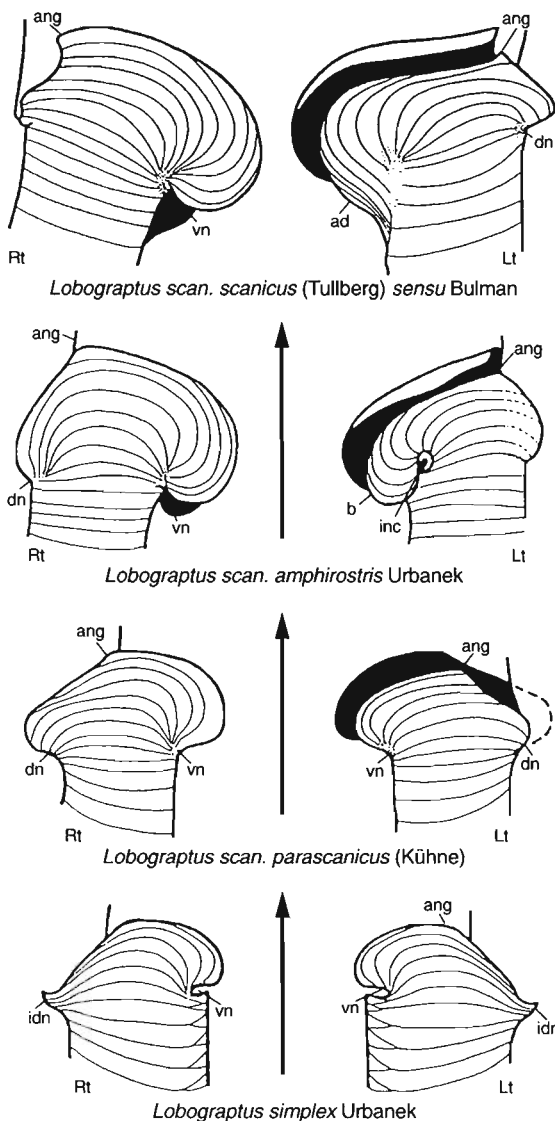


Fig. 4

Diagram showing the changes in size and shape of apertural lobes within the *Lobograptus scanicus* lineage. Note the development of the hypertrophy of the right lobe (R-cucullograptids, after URBANEK 1966). Abbreviations: Rt – right (reverse) view, Lt – left (obverse) view, ad – adapertural plate, ang – angular bending of the upper margin of apertural lobe, b – beak-like ventral termination of the lobe, dn – dorsal node, idn – incipient dorsal node, vn – ventral node.

have derived from the former, subject to quite a radical restructuring of the growth pattern and arrangement of the fuselli (growth bands). As yet, no transients are known to fill the morphological gap between the stem lobograptids and the highly specialized *C. pazdroi*.

The Cucullograptinae sequence, as recognized in the Mielnik bore core, was used by URBANEK (1966) to improve the zonal subdivision (see Table 1). According to that scheme five zones should be distinguished above the *nilssoni* Zone instead of the three in the classical British subdivision. To achieve this higher resolution it is necessary to identify cucullograptid species – an uneasy task in the case of flattened specimens. URBANEK (1966) considered it advisable to use, for this purpose a rather general term “cucullograptid band” instead of the less accurate but still commonly used designation, the *scanicus* Zone.

The development of asymmetry in the apertural apparatus of the Cucullograptinae is a remarkable feature of their evolution because the vast majority of the Graptoloidea remain symmetrical, and except for a few cases, the principle of bilateral symmetry is deeply rooted in their entire organization.

The R-trend is represented by two main lineages: the *scanicus* lineage and the *invertus*–*cirrifer* lineage. The evolution of the apertural apparatus in the former (Pl. 3: 1, 2, Fig. 4) represents a directional change within a single line of descent. As to the latter lineage, the initial species *L. imitator* produced two daughter species, *L. invertus* and *L. cirrifer*. Fig. 5 summarizes the morphological results of the splitting. However, one can generalize that the morphological evolution of the apertural apparatus in R-cucullograptids generated not only enlarged lobes but also some secondary structures (“superstructures”) such as beaks and adapertural or apertural plates. Perhaps the most advanced superstructures produced in this group are elongated paired apertural spines superimposed on the apertural lobes in *L. cirrifer* and giving it a bizarre appearance (Fig. 5).

L-cucullograptids, displaying a hypertrophic left apertural lobe, comprise the *hemiaversus*–*rostratus* lineage and the *pazdroi* side-line (Fig. 6). The derivation of the *hemiaversus*–*rostratus* lineage from *L. simplex* does not present any difficulties thanks to the presence of a transient link represented by *Cucullograptus hemiaversus* with slightly asymmetric thecae and whose asymmetry increases distalwards. *Cucullograptus aversus aversus* exhibits a rudimentary right lobe and a strong hypertrophy of the left one (Fig. 6). *C. aversus rostratus* has some new structures added to the hypertrophic left lobe, e.g. rostral process, gular plate, etc. (Pl. 3: 3–10, Fig. 6). Hence in this lineage evolution may be described as gradual oriented change within a single line of descent (phyletic evolution).

The origin of the *pazdroi* side-line (Figs 2, 6, broken lines and ?mark), however, poses some problems. Its strongly convex apertural lobes with a fairly complex internal structure are strikingly different from those in *L. simplex* (cf. URBANEK 1966). There is a distinct morphological discontinuity between *L. simplex* and *Cucullograptus pazdroi*. The latter might

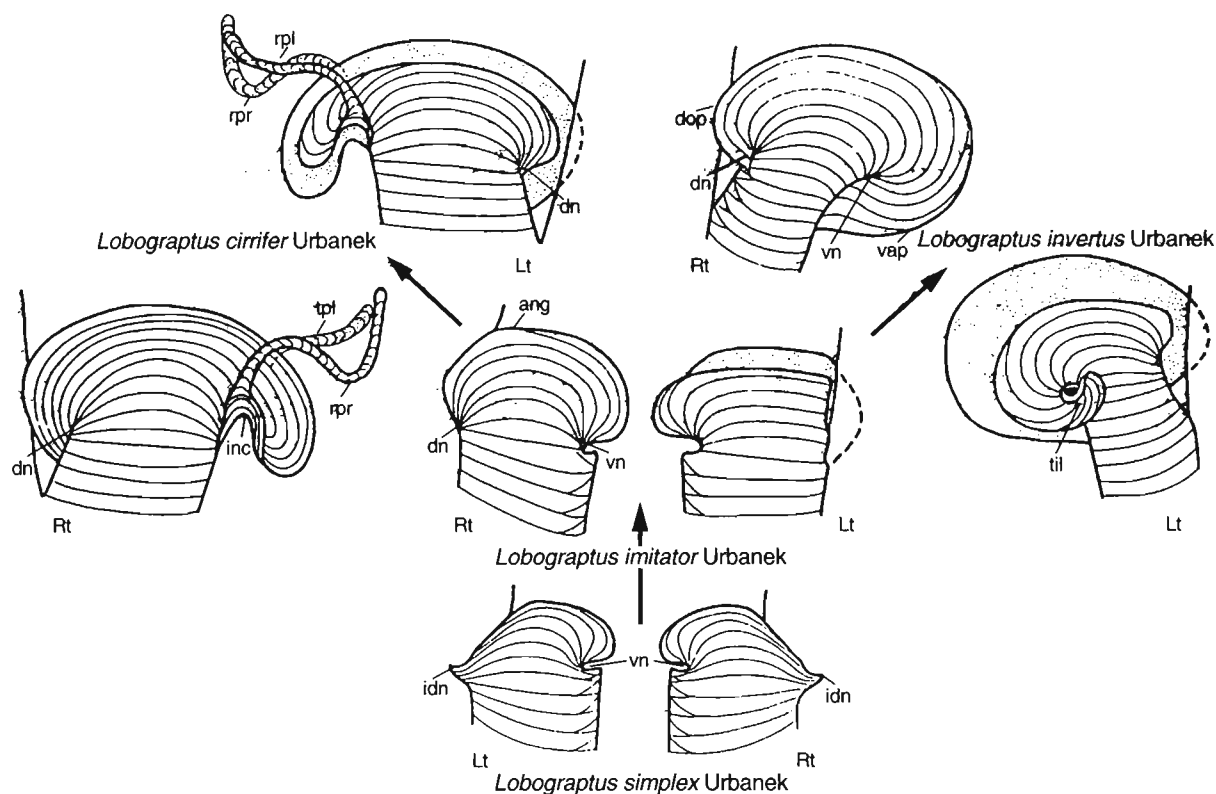


Fig. 5

Diagram showing the morphological change in the size and structure of apertural lobes in an alternative trend of evolution within the R-cucullograptids, namely in the *Lobograptus imitator*–*L. cirrifer* and *L. imitator*–*L. invertus* lineages (after URBANEK 1966). Abbreviations: dap – dorsal apertural plate, inc – incision of ventral apertural notch, lpl – rostral process of the left lobe, rpl – rostral process of the right lobe, tll – termination of the left lobe, vap – ventral apertural plate. Further explanations as in Fig. 4.

Besides cucullograptids displaying the operculate adaptive type, the monograptid fauna of the Gorstian comprises representatives of the Saetograptinae (*Colonograptus* and *Saetograptus*). They also exhibit a distinct morphological type which may be called “spinose”. The presence of paired symmetric lappets or apertural spines combined with a fairly robust appearance of the rhabdosome, is a highly characteristic feature of the group.

The earlier representatives from the *nilssoni* Zone are usually assigned to *Colonograptus* PŘIBYL. This genus includes species with rather broad ear-like paired and symmetric apertural lappets (e.g. in *C. roemeri*). Such species may be derived directly from the conservative *dubius* stock though some transient links represented by *praedeubeli* and *ludensis* (= *vulgaris*). Convincing evidence for this phylogeny was presented by JAEGER (1978a, 1991) and KOREN' (1992b).

The proposed evolutionary series features a gradual development of the lobes from incipient elevations observed in *C.?* *praedeubeli* to large lappets seen in *C. roemeri* (increased expressivity) as well as a growing number of thecae equipped with lobes (increased penetrance from *C.?* *praedeubeli* to *C. roemeri*).

URBANEK (1960) suggested that broad apertural lappets of *Colonograptus* were subject to partial reduction and transformation into narrow spines characteristic of *Saetograptus* PŘIBYL. Such structures prevail in the middle and upper parts of the Gorstian (the *scanicus* to the *leintwardinensis* Zone) and morphological transients between these two extreme structural types can be observed. Hence, *Saetograptus* may be derived from *Colonograptus* assuming the modification and distal spreading of the apertural lobes.

This view was criticized by JAEGER (1978a: pp. 43–48) mainly because of the structural differences between the apertural spines in *C. colonus* and *S. chimaera* as well as because in the latter these spines are spread along the entire length of the rhabdosome. Thus the transformation of *colonus* into *chimaera* would require not only the distal spreading of the ancestral type of apertural spines (as postulated by

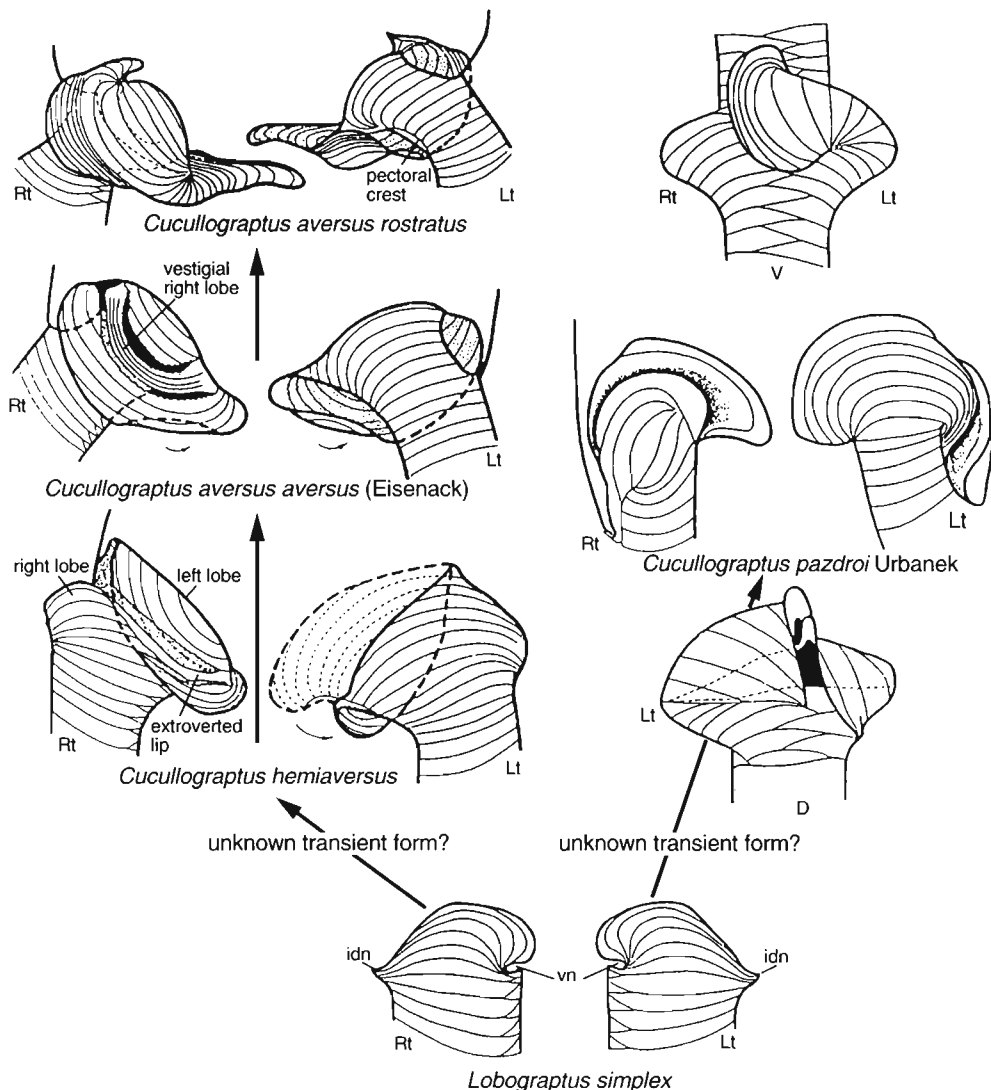


Fig. 6



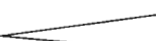
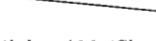


Evolutionary changes in size and shape of apertural apparatus within *Cucullograptus*, representing the L-cucullograptid trend (after URBANEK 1966). While the phyletic evolution in *C. hemiaversus*–*C. aversus* lineage involved gradual changes, the origin of *C. pazdroi* implies a rapid transformation. Abbreviations: D – dorsal view, V – ventral view. Further explanations as in Figs 4 and 5.

URBANEK's theory of the introduction of phyletic novelties to monograptid colonies), but also a substantial modification of the spines themselves, classified by JAEGER as a qualitative change. Structural differences between lobate and spinose apertural appendices were, however, recognized and carefully studied earlier (URBANEK 1958, 1960). They may be explained as a result of reduction (rudimentation) leading to the narrowing of the surface of the primary lobe and to a semitubular folding of its anterior border. In the face of the existing evidence one can hardly have serious doubts as to the close affinity between *Colonograptus* and *Saetograptus*. JAEGER's (1978a) scepticism concerning the derivation of *Colonograptus* and *Saetograptus* has also lost ground in the light of his own studies (JAEGER 1991) and recent papers by KOREN' and SUYARKOVA (1994) and KOREN' and URBANEK (1994).

The phylogeny of the Saetograptinae has not been established in full detail – the forms from the Mielnik bore core have not been published yet. A preliminary study of the material indicates that the lower zones are dominated by less robust morphotypes with spines situated at the proximal end of the aperture and frequently provided with lobate outgrowths. They correspond to *Saetograptus chimaera cervicornis* URBANEK characteristic of the *parascanicus* Zone. The extremely robust type corresponding to BARRANDE's (1850: pl. IV: 34) original specimens and therefore classified as *S. chimaera chimaera* BARRANDE

Table 1

Graptolite zonation for the Wenlock, Ludlow and Přidoli Series in the East European Platform: 1–5 main bioevents.
Further explanations in text.

SERIES	STAGE		GRAPTOLITES ZONES
PŘIDOLI			<i>Istrograptus t. transgrediens</i> <i>Monograptus perneri</i> <i>Monograptus bouceki</i> <i>Istrograptus t. samsonowiczi</i> <i>Istrograptus t. chelmiensis</i> <i>Neocolonograptus lochkovens</i>  <i>N. l. lochkovens</i> Subzone <i>Neocolonograptus ultimus</i>  <i>N. l. branikensis</i> Subzone <i>Neocolonograptus parultimus</i>
LUDLOW	LUDFORDIAN	UPPER	<i>Monograptus (U.) spineus</i> <i>Monograptus (U.) protospineus</i> <i>Monograptus (U.) acer</i>  <i>M. (U.) acer aculeatus</i> Subzone  <i>M. (U.) acer acer</i> Subzone <i>Pseudomonoclimacis latilobus</i> / <i>M. (Slovinograptus) balticus</i>
		LOWER	<i>Neocucullograptus kozłowski</i> <i>Neocucullograptus inexpectatus</i> <i>Neolobograptus auriculatus</i> <i>Bohemograptus cornutus</i> <i>Bohemograptus praecornutus</i>
	GORSTIAN		<i>Cucullograptus aversus</i>  <i>C. aversus rostratus</i> Subzone (= <i>S. leintwardinensis</i>)  <i>C. aversus aversus</i> Subzone
			<i>Cucullograptus hemiaversus</i> <i>Lobograptus invertus</i> <i>Lobograptus scanicus parascanicus</i> <i>Lobograptus progenitor</i> <i>Neodiversograptus nilssoni</i>
WENLOCK	HOMER		<i>Colonograptus ludensis</i> XX zones between <i>nassa</i> and <i>ludensis</i> on Polish part of the EEP not yet recognized <i>Gothograptus nassa</i>
	SHEINWOOD		<i>Cyrtograptus lundgreni</i> <i>Cyrtograptus ellesae</i> <i>Cyrtograptus rigidus</i> <i>Monograptus belophorus</i> (= <i>M. flexilis</i>) <i>Monograptus antennularius</i> <i>Monograptus riccartonensis</i> <i>Cyrtograptus murchisoni</i> <i>Cyrtograptus centrifugus</i>

appears somewhat later (in the *invertus* Zone) and occurs within the upper portion of the *S. chimaera cervicornis* range (cf. URBANEK 1966: p. 310).

The proximal thecae of late saetograptids such as *S. fritschi* or *S. leintwardinensis* have long and rather straight spines displaced distalwards. As observed by URBANEK (1966: p. 311) this displacement was a novel character as compared to the proximal introduction of apertural lobes/spines. The morphotype with distal displacement of spines is therefore the terminal evolutionary pattern in spinose monograptids, preceding their final extinction caused by the *leintwardinensis* Event.

Saetograptids provide grounds for a zonal subdivision which may serve as an alternative to that based on the vertical distribution of cucullograptids (see Table 2). JAEGER (1962: p. 39) pointed out that the use of the saetograptid zonation might be a more practical equivalent to the *scanicus* Zone *s.l.* The saetograptid subdivision can be easily identified while the *scanicus* Zone appears to consist of a number of separate taxa whose identification in the flattened state of preservation is rather difficult. JAEGER's statement is partially true, and the application of either subdivision depends very much on the quality of the material available and the methods used.

Table 2

<i>Cucullograptus aversus</i> (EISENACK)	1) <i>Cuc. aversus rostratus</i>	<i>S. leintwardinensis</i> (HOPKINSON)
	2) <i>Cuc. aversus aversus</i>	
<i>Cucullograptus hemiaversus</i> URBANEK		<i>Saetograptus fritschi</i> (PERNER)
<i>Lobograptus invertus</i> URBANEK		
<i>L. scanicus parascanicus</i> (KÜHNE)		<i>S. chimaera chimaera</i> (BARRANDE)
<i>Lobograptus progenitor</i> URBANEK		<i>S. chimaera cervicornis</i> URBANEK
<i>Neodiversograptus nilssoni</i> (BARRANDE)		<i>Colonograptus colonus</i> (BARRANDE) <i>sensu</i> PERNER

A comparison of the zonal subdivision based on cucullograptids and saetograptids encountered in the East European Platform can be seen on the Table 2. JAEGER's (1991) most recent suggestion does not recognize the *fritschi* Zone (below the *leintwardinensis* Zone). What he proposes instead is to distinguish the *fritschi linearis* Zone immediately above the *leintwardinensis* Zone. Both these suggestions might be biased as based primarily on specific regions (the East European Platform *versus* Saxo-Thuringicum), and a real standard zonation for the purposes of correlation is still a task to be addressed.

Retiolitids of the Plectograptinae subfamily constitute the third important element of the Gorstian graptolite fauna. The progress in their understanding was much delayed. It is only the last few decades that have seen a change towards a better understanding of their morphology (EISENACK's study on the Baltic erratic material, 1951) and stratigraphic distribution (BOUČEK and MÜNCH 1952; URBANEK 1966; OBUT and ZASLAVSKAYA 1976). Quite recently papers by LENZ (1993b, 1994b), KOZŁOWSKA-DAWIDZIUK (1990, 1991), and KOREN' (1991, 1992a) have provided new evidence of a growing interest in the plectograptine retiolitids of the Upper Silurian.

It can be assumed that this group of graptoloids suffered the least from the environmental changes during the *lundgreni* Event and soon became predominant in the graptolite fauna. *Gothograptus nassa* appears in the *lundgreni* Zone, but immediately above that zone exhibits a mass occurrence frequently associated with an unusually large size of rhabdosomes. The Late Homeric saw an extensive diversification of retiolitids represented by numerous species which had a rapid turnover (KOREN' 1991, 1992a). This interval of retiolitid evolution is still inadequately known from the EEP. Retiolitid diversity in the Early Gorstian is, as can be seen from the studies of the Mielnik IG-1 borehole material (URBANEK 1966) still considerable. This study identified, for the first time the stratigraphic position of several species described by EISENACK (1951) from Baltic drift material. However, the recent detailed study by KOZŁOWSKA-DAWIDZIUK (1995) throws considerable new light on the morphology, phylogeny and stratigraphic distribution of retiolitids within the Gorstian to *leintwardinensis* Zone interval. All belong to the Plectograptinae BOUČEK *et* MÜNCH, 1952 subfamily. In general a rather modest frequency is combined with a high species diversity. A trend towards the reduction of the size of the rhabdosome and of apertural apparatus as well as trend to reduce the reticulum and simplify the clathria are observed in all lineages within the interval in question.

Two main evolutionary lines among the Gorstian plectograptines were distinguished by KOZŁOWSKA-DAWIDZIUK, namely the (1) gothograptid line (*Eisenackograptus*, *Gothograptus*, *Neogothograptus*, *Holoretiolites*) with finite rhabdosomes (and known since late Wenlock) and (2) the newly appeared plectograptid line (*Spinograptus*, *Plectograptus*, *Semiplectograptus*, *Plectodinemagraptus*), with reduced corona, probably related either to Wenlock *Sokolovograptus* OBUT *et* ZASLAVSKAYA, 1976 or to *Paraplectograptus* BOUČEK *et* MÜNCH, 1948.

First representatives of Gorstian plectograptines appear in the *nilssoni* Zone and include *Plectograptus wimani* (EISENACK, 1951) and *Spinograptus muenchi* (EISENACK, 1951). Somewhat later appear *Sp. clathrospinosus* (EISENACK, 1951) and *Sp. spinosus* (WOOD, 1900). *Sp. clathrospinosus* appear, however, well down in the upper Homerian in the Arctic Canada (LENZ 1993b). All these forms are characterized by the presence of well developed reticulum and spinose apertural processes.

In the *progenitor* Zone retiolitids in the Mielnik IG-1 boring are represented solely by the gothograptid line, namely by the *Neogothograptus* KOZŁOWSKA-DAWIDZIUK, 1995. The plectograptid line is temporarily absent, most probably because of the local incompleteness of the record. *Neogothograptus* is provided with a central virgula in which it differs from Wenlock members of the line, where virgula is incorporated in lateral wall. *N. purus* KOZŁOWSKA-DAWIDZIUK with reduced reticulum and reduced apertural apparatus as well as with varying number of thecae in its finite rhabdosome is the first species of this line encountered in the Mielnik IG-1 borecore. Later species still preserves primitive features: the presence of reticulum and reticulate apertural shields in *N. balticus* (EISENACK, 1951) and reticulum in *N. romani* KOZŁOWSKA-DAWIDZIUK, 1995.

The plectograptid evolutionary line reappears in the upper part of the *parascanicus* Zone, being represented by *Plectograptus macilentus* (TÖRNQUIST, 1887). It differs from presumably related *Pl. wimani*, by the absence of reticulum and apertural processes. Still younger is *Semiplectograptus urbaneki* KOZŁOWSKA-DAWIDZIUK, 1995, a representative of a newly erected genus, with smaller size, without the pleural lists and, in general, displaying a further step in the reduction of the rhabdosome.

The retiolitids in the *parascanicus* Zone are chiefly members of the gothograptid line, namely species of the genus *Holoretiolites* BOUČEK *et* MÜNCH, 1952. As compared with its possible ancestor, *Neogothograptus*, the latter genus exhibits simplified rhabdosomes (e.g. absence of pleural lists). *H. erraticus* (EISENACK, 1951) is commonly associated with *H. mancki* (MÜNCH, 1930), which survives into higher *hemiaversus*–*aversus* Zone. *H. mancki* is devoid of reticulum while its finite rhabdosome is composed of varying number of thecae. KOZŁOWSKA-DAWIDZIUK considers *H. simplex* as conspecific with *H. mancki*, as a four thecal morph, characteristic of the populations of the lower part of the vertical distribution range of the latter species. *H. atrabecularis* KOZŁOWSKA-DAWIDZIUK, 1995, occurs in the uppermost part of the *parascanicus* Zone, has small number of thecae in rhabdosome with reduced pleural lists. In the upper part of the vertical range of *H. mancki* she discovered a form twice as big – *H. manckoides* KOZŁOWSKA-DAWIDZIUK, 1995.

H. mancki is not the latest retiolitid as was believed. The youngest retiolitid recorded so far is a representative of the plectograptid line, *Plectodinemagraptus gracilis* KOZŁOWSKA-DAWIDZIUK, 1995 (*hemiaversus*–*aversus* Zone, around the *leitwardinensis* Zone as currently defined). Its strongly reduced rhabdosome bears a superficial resemblance to Ordovician *Dinemagraptus* KOZŁOWSKI, 1952. Its diminutive rhabdosome is composed solely of an ancora and medial and apertural lists. This latest representative of Retiolitidae is also most advanced in the reduction of the colony, representing a terminal link in this process which may be traced through Gorstian up to the *leintwardinensis* Zone.

The overall features of the succession of retiolitids encountered in Mielnik-1 boring are, thus, the following: *nilssoni* Zone exhibits abundant *Spinograptus* and temporarily no *Gothograptus*, whilst the overlying *progenitor*–*scanicus* Zone is marked by the reappearance of a modified *Gothograptus* accompanied by derivatives of *Plectograptus*. The top of the *scanicus* and the *invertus* Zones yields a profusion of *Holoretiolites*.

The abundance and diversity of retiolitids decrease progressively at higher stratigraphic levels until they finally disappear from the known successions around the *leintwardinensis* Zone. The latest among the retiolids observed are specialized derivatives of *Plectograptus*.

The EEP sequence reveals the important role plectograptine retiolitids played throughout the entire Gorstian. Moreover, it demonstrates their unexpectedly late disappearance. In her recent papers, KOREN' (1991, 1992b) supports this view and provides more evidence of the evolutionary dynamics of this group. The monograptids and the plectograptine retiolitids appear to have responded to the same environmental pressures in opposite ways; that is a decrease in the diversity of the former was commonly compensated by an increased diversification of the latter.

The extinction of retiolitids caused by the *leintwardinensis* Event had a profound effect on further evolution of graptoloids for a distinct adaptive type was eliminated and never replaced by a similar one. As a result, the morphological diversity of Upper Silurian graptoloids was irreversibly reduced. What is more, a gradual decrease in the abundance and diversity of retiolitids prior to their extinction may indicate that they suffered from competition with two other co-eval groups, namely cucullograptids and saetograptids. The documentation of the pattern of extinction across the *leintwardinensis* Zone provided by the Mielnik IG-1 borecore (URBANEK 1966) suggests that this time retiolitids showed greater vulnerability than saetograptids or especially cucullograptids and were the first to suffer from environmental disturbances. Thus retiolitid behaviour during this particular crisis was quite different from the way in which retiolitids responded to the previous *lundgreni* Event, in which they smoothly survived across the extinction horizon.

The final issue, however, was the extinction of both saetograptids and cucullograptids. Among the survivors, including such pristograptid-like species as *Pristiograptus dubius* s.l. or *Pseudomonoclimacis dalejensis* and also linograptids and *Bohemograptus*, it was the latter alone that were destined to play a crucial role in subsequent recovery. *Pristiograptus* preserved its splendid conservative behaviour – another specific feature by which the post-*leintwardinensis* recovery differs from post-*lundgreni* developments.

The post-*leintwardinensis* Ludfordian fauna. — The next natural interval in the development of graptolite fauna begins with the *Bohemograptus* acme Zone and ends with *Neocucullograptus kozłowskii* Zone followed by a low diversity Interzone (URBANEK 1970). The *Bohemograptus* proliferation zone is the youngest graptolite occurrence recognized on the British Isles, and with the underlying *leintwardinensis* Zone, marks the base of the Ludfordian Stage (Table 1). On the Polish Lowland the equivalent beds are defined as the Siedlce Beds, an informal lithostratigraphic unit distinguished in the subsurface platform Silurian of Poland by TOMCZYK (1962, 1968). Its early part corresponds to the lower part of the Ludfordian Stage, minus *leintwardinensis* Zone (which is a component of the older link, called by TOMCZYK the Mielnik Beds (see also URBANEK 1966, 1970). The graptolite fauna of the upper part of the Siedlce Beds (= upper Ludfordian) is described in the present volume by URBANEK (see pp. 87–232), and summarized below.

The early Ludfordian as defined above, yield graptolites representing a distinct phase in the development of the monograptid fauna, analogous and equivalent on the one hand to the Lower Ludlow (Gorstian) and, on the other hand, to the late Ludfordian or the Přidoli. Following the extinction of the earlier elements, this phase features the emergence of new lineages, their development, diversification and subsequent decline coincident with the appearance of immigrant species. In other words, it tells us a complete evolutionary story of the “rise and fall” of a distinct faunal group. This monograptid fauna is also in many ways unique, its specificity being best demonstrated by the invention and wide application of a new peridermal fabric – the microfusellar tissue, a structural element extremely rare in other graptoloids (URBANEK 1958, 1970, 1976, Pl. 4: 11).

The *leintwardinensis* faunal turnover involves a number of events. The graptolite fauna of the former interval, the Mielnik Beds in the lithostratigraphic subdivision of the Polish Lowland, comprises a total of 36 species. The majority of them (saetograptids, cucullograptids and retiolitids, 19 species in all) died out close to the *leintwardinensis* Zone, leaving no descendants. Four species survived without changes, and eight new species arose from the indigenous survivors, during the early part of the second interval as defined above (the lower part of the Siedlce Beds in the regional lithostratigraphic subdivision). The total diversity attained in the second interval is thus reduced to twelve species, one third of the number recorded in the first interval, although they are unique in character.

The main extinction at the top of the *leintwardinensis* Zone may be regarded as a biotic crisis (C_2 in URBANEK's 1970 terminology, or the *leintwardinensis* Event in his 1993 paper) similar to “the big crisis” (C_1 , or the *lundgreni* Event) in the mid-Homerian, although less dramatic in the scale of disturbance or in the effects produced.

The uniqueness of the post-*leintwardinensis* assemblages is associated with the origin and gradual evolution of a single group classified as a monograptid subfamily, the Neocucullograptinae (URBANEK, 1970). In fact, it constitutes the most progressive faunal element in the interval between the *leintwardinensis* Zone and the *latilobus* Zone. The Neocucullograptinae comprise four genera: *Bohemograptus* PŘIBYL, 1967, *Neolobograptus* URBANEK, 1970, *Neocucullograptus* URBANEK, 1970, and *Polonograptus* TSEGELNJUK, 1976. The subfamily in question is limited in its stratigraphic distribution to the Gorstian and early Ludfordian, being represented in its lower interval by *Bohemograptus* alone and in the upper one by some

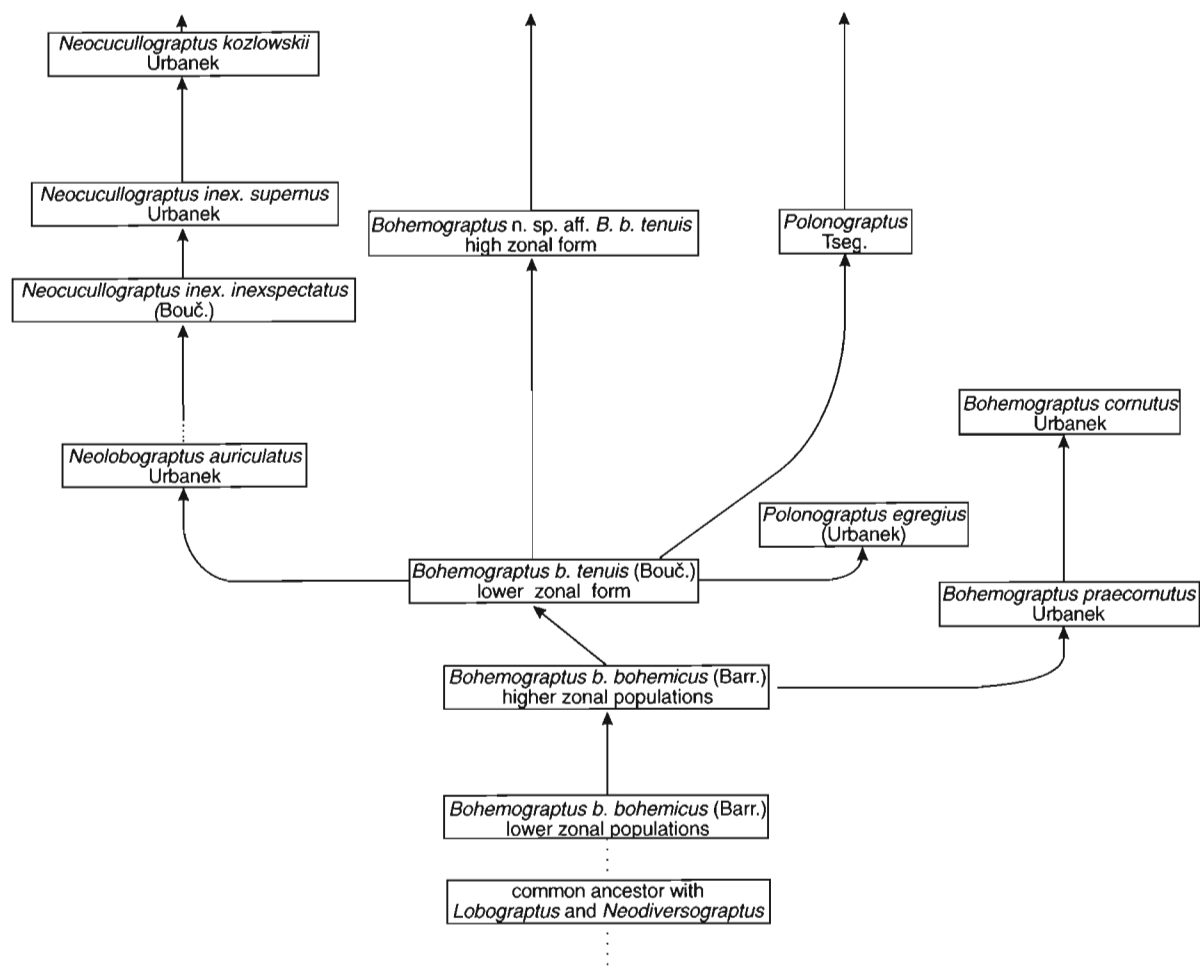


Fig. 7

Tentative phylogeny of Neocucullograptinae as revealed by the studies on isolated material from the Mielnik IG-1 borehole and subsequent studies in other areas (largely after URBANEK 1970, modified). Although close relation of *Polonograptus* to *Bohemograptus* stem species seems almost certain, its origination from *B. bohemicus tenuis* is conjectural.

new taxa of this genus as well as by *Neolobograptus* and *Neocucullograptus*. After the *leintwardinensis* Event, the bulk of neocucullograptids was produced from *Bohemograptus* ancestors as a result of reradiation. They reestablished the operculate adaptive type corresponding in the overall morphology to the earlier cucullograptids, but their apertural apparatus was made of a new skeletal fabric, the microfusellar tissue. It seems safe to conclude that neocucullograptids occupied an ecological niche close to that filled by cucullograptids in the Gorstian times. The Ludfordian adaptive radiation was, however, smaller in scale as compared with the Gorstian one. Hence, the taxonomic diversity dropped considerably although the level of morphological radiation remained fairly high.

On the basis of the neocucullograptid distribution (URBANEK 1970) one can suggest a subdivision of the post-*leintwardinensis* early Ludfordian into several graptolite zones (see Table 1).

The above scheme can only be regarded as provisional in character, as the ranges of the index species, based on a single bore hole, are represented only as topozones. A series of new discoveries in Europe, Asia and Arctic Canada have provided convincing evidence that these faunal elements are not endemic to the EEP, rather the reverse, they are rather widely distributed. Important studies by KOREN' (1989), (KOREN' and LYTOCHKIN 1992c) on the graptolite faunas of the Tokrau horizon in Kazakhstan as well as her research of the Kursala Formation in the Tien Shan (the Alai Range, Kirghizia) leave no doubts that the main faunal elements and graptolite biozones recognized long ago in the EEP can be reliably traced into Central Asia.

It is therefore hard to understand why, in his new proposal of a standard graptolite zonation, JAEGER (1991: p. 315) quite recently defined the entire interval between the *fritschii linearis* Zone and the

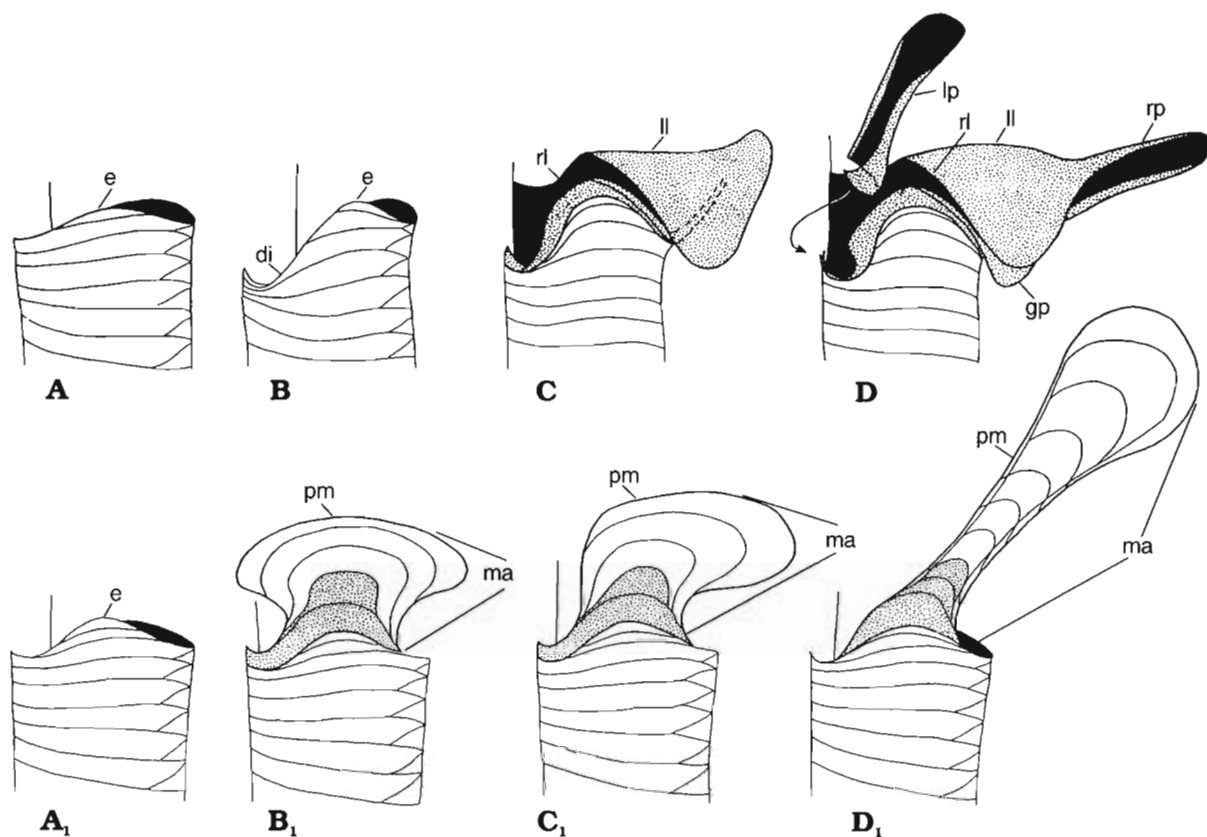


Fig. 8

Two major trends in the morphological evolution of thecal characters in neocucullograptids: *Bohemograptus bohemicus tenuis*–*Neocucullograptus kozlowskii* lineage (A–D) and *B. b. tenuis*–*Bohemograptus cornutus* lineage (A₁–D₁). Evolution in the first trend involved appearance of gentle elevation (e) on the apertural border (A, *B. b. tenuis*), origin of dorsolateral incision (di) in *Neolobograptus auriculatus* (B), formation of apertural apparatus made of microfusellar tissue and composed of right and left apertural lobe (C, *Neocucullograptus inexpectatus*, rl, ll), and finally addition of apertural superstructures in form of rostral process (rp) and lateral process (lp) as well as a gular plate (gp) as seen in *Neocucullograptus kozlowskii* (D). The second trend passed through a similar starting phase represented by *Bohemograptus* (A₁) followed by *Bohemograptus praecornutus* (B₁–C₁) provided with additions made of microfusellar (dotted) and pseudomicrofusellar (pm) tissue. These fairly irregular and variable structures were later transformed into regular rod-like processes terminating with fan-like, rapidly widening membranes in *Bohemograptus cornutus* (D₁). True microfusellar tissue shown dotted; ma – microfusellar additions.

fragmentalis Zone as “Standardzonen nicht etabliert”. Since the index species are well known and have wide geographic distributions, such a conservative stand was, however hardly justifiable. Moreover, the Ludfordian graptolite sequence recognized recently by ŠTORCH (1995) in the Barrandian area, corresponds so well with that reported from Mielnik IG-1 borehole, that no doubts are left as for the significance of the zonal scheme suggested by URBANEK (1970).

Phylogeny of neocucullograptids. — The lowermost part of the post-*leitwardinensis* interval is distinguished by a remarkable impoverishment of its graptolite fauna due to the extinction of a number of lineages during the *Saetograptus leintwardinensis* zonal interval. This radical decrease in diversity was compensated by the mass occurrence of *Bohemograptus bohemicus* (BARRANDE) thus producing a convenient marker. In his contribution presented at the Third International Symposium on the Silurian/Devonian boundary, Leningrad, URBANEK (1968, published 1971) recognized, immediately above the *leintwardinensis* Zone, a peak zone which he called “the *bohemicus* proliferation Zone”. A similar peak or acme zone (epibole) can be distinguished in the Baltic erratic boulders, where abundant *Bohemograptus bohemicus tenuis* (BOUČEK) is accompanied by a scanty graptolite association or occurs monospecifically (the “0” association or the “0” class of boulders as defined by URBANEK 1970: p. 260). Another horizon yielding abundant *Bohemograptus* in an analogous stratigraphic setting has been recognized in Britain (HOLLAND and PALMER 1974).

Specialized neocucullograptids may have derived from generalized representatives of *Bohemograptus*. The stem taxon of the entire stock was probably *Bohemograptus bohemicus tenuis*. Within the underlying Gorstian, the *Bohemograptus* lineage displayed the zonal evolution expressed as a gradual disappearance of robust morphotypes, concomitant with a progressive increase of the gracile variety. The only noteworthy change was the acquisition of a novelty, the appearance of the microfusellar tissue, a special peridermal material made of narrow and densely crowded growth bands (microfuselli). The late populations of *B. bohemicus bohemicus* are characterized by the appearance of a new morphotype capable of producing peculiar apertural structures composed of this new tissue and called microfusellar additions (Pl. 4, compare 8, 9a, m, 10 and 11).

The presence of this tissue is rare although not unique among the Graptoloidea, but its wide utilization in the further evolution of neocucullograptids presents an exceptional phenomenon unparalleled in other groups. Therefore it would be impossible to explain this evolutionary event without introducing a number of notions which might be considered rather un-conventional in routine graptolite research. It has been suggested that the late *Bohemograptus* populations and also some of the derived species were polymorphic; namely they were composed of a *veliger* morph (able to produce microfusellar additions) and a standard morph devoid of this capability (URBANEK 1970: pp. 208–209). One could assume that a balanced polymorphism was responsible for the steady presence of two, clear-cut morphs in the populations. At the same time the microfusellar structures around the sicular aperture and thecae were capriciously variable, without producing species specific features. As outlined by URBANEK (1970), the further evolution of neocucullograptids probably involved a change from balanced to transient polymorphism, which resulted in secondarily monomorphic populations with microfusellar additions stabilized in a species – specific form.

At the same time the *Bohemograptus* split to form two lines of descent. In the *hemiaversus*–*aversus* Zones one could trace the presence of two lineages – one represented by relatively gracile *Bohemograptus bohemicus tenuis* and the other, by a robust type, namely *Bohemograptus praecornutus*. The last named species resembles lower zonal morphotypes of *Bohemograptus* and may be considered as an essentially plesiomorphic species, while *B. bohemicus tenuis* is in this case an apomorphic species (Fig. 7).

This slight divergence in morphological trends defined at the same time quite different directions of future specialization. *Bohemograptus praecornutus* led to a much more advanced *Bohemograptus cornutus*, with the microfusellar additions modified into apertural projections forming long ribbons (Fig. 7A₁–D₁). In etched specimens the distal parts of these projections are usually broken off, but well preserved flattened specimens found by KOREN' in Tien Shan (unpublished) have a bizarre "hairy" appearance. The other line initiated a trend which soon split into *Neolobograptus auriculatus* and the higher zonal populations of *Bohemograptus bohemicus tenuis*, characterized by minor but distinct morphological traits (URBANEK 1970). This morph should probably be recognized as a separate temporal species or subspecies, characteristic of *inexpectatus*–*kozłowskii* Zones. It matches *Bohemograptus garratti* described from the *kozłowskii* Zone of NE Tasmania (RICKARDS, DAVIDSON, and BANKS 1993) and from the same Zone in the Barrandian area (ŠTORCH 1995).

The occurrence of other *Bohemograptus* species, as indicated by some faunas (e.g. from Yukon, JACKSON and LENZ 1972), is possible. However, TSEGELNJUK's attempt (1976b: pp. 126–131) to discriminate as many as 7 species and subspecies (plus one new genus) within *Bohemograptus* group in Lesnian-skaya suite of Belarus is hardly acceptable, especially as this splitting practice is based mostly on scanty and imperfectly preserved material.

Neolobograptus auriculatus (Fig. 8B), a form resembling to some extent the earlier *scanicus* Group, (= *Lobograptus*) may be considered a probable forerunner of a trend which led to most advanced neocucullograptids. They are represented by *Neocucullograptus inexpectatus* and *N. kozłowskii* – both homeomorphic with *Cucullograptus aversus* (Figs 8C–D, 9, Pl. 4: 1–7), but representing (neo)operculate monograptids with a bohemograptid foundation and complex apertural apparatus made of microfusellar tissue!

This picture of the adaptive radiation of *Bohemograptus* and its derivatives in Ludfordian time, should be completed by including the line of "comet"-like monograptids, represented by *Polonograptus* TSEGELNJUK, 1976. They represent forms displaying a strongly attenuated proximal part but a rapid distal increase in the width and in thecal overlap, and a strong ventral curvature of the rhabdosome (Fig. 10). They have been described from the Barrandian, Volhynia, the Carnic Alps and Central Asia (PŘIBYL 1983; TSEGELNJUK 1976b; JAEGER 1975; KOREN', personal information). *Polonograptus* most probably represents a strongly modified *Bohemograptus*, with a steep gradient in the allometric control of growth and size as

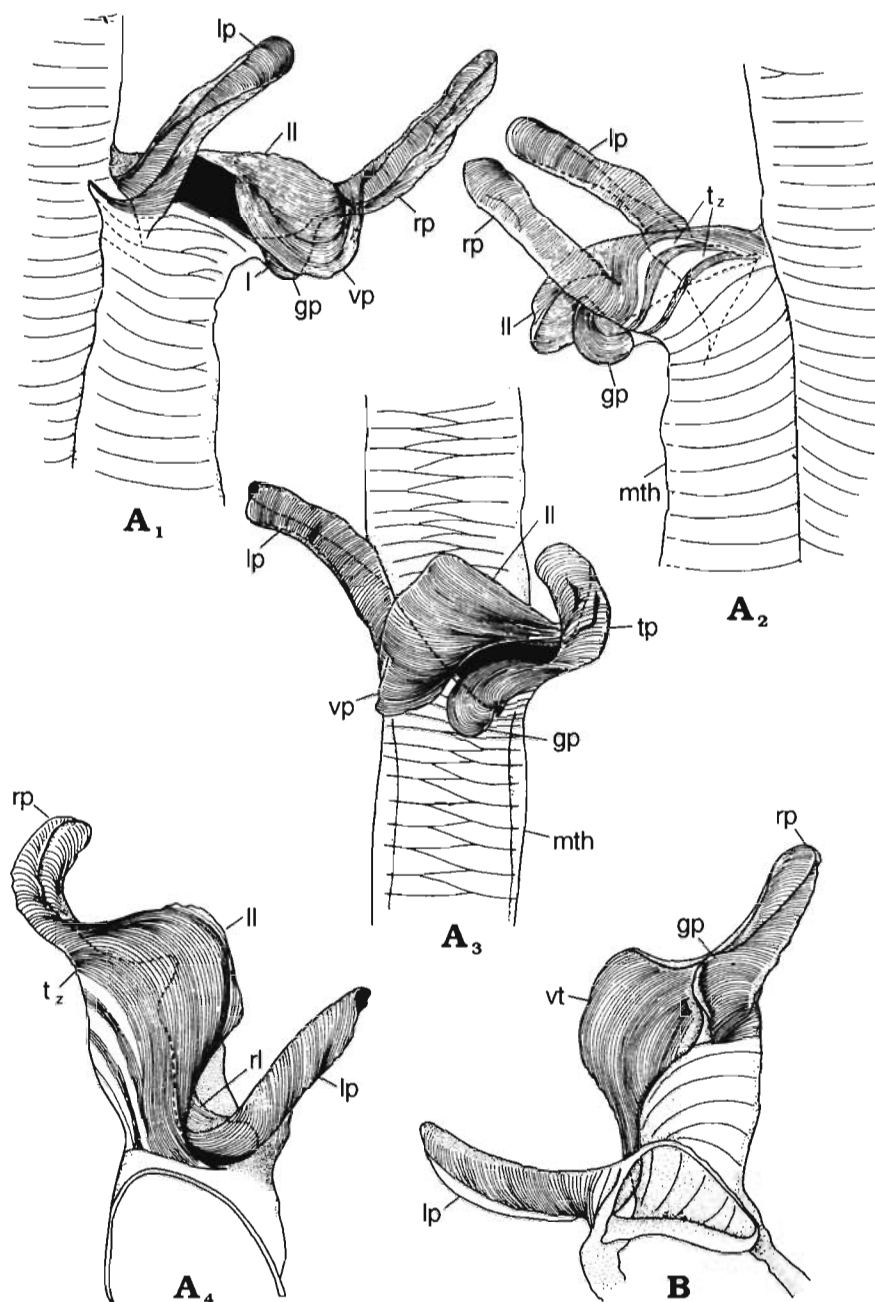


Fig. 9

Advanced apertural apparatus in *Neocucullograptus kozlowskii* seen in different aspects (A₁–A₄. B) illustrates the development of asymmetry and the full use of microfusellar tissue as the main fabric in neocucullograptid evolution (from URBANEK 1970). Note superstructures built over the lobes proper (ll, rp) such as rostral (rp), lateral (lp) and ventral (vp) process, as well as the gular plate (gp) situated on otherwise strongly reduced right lobe. While the morphology clearly suggests highly specialized trophic function of the apertural apparatus, significance of particular details remains obscure. Mielnik IG-1 borehole, E Poland, *kozlowskii* Zone. Abbreviations: l – apertural lip, mth – distal part of metatheca, tz – transient zone between fusellar and microfusellar tissue with intercalary wide bands.

well as of the overlap of the thecae. It is a monograptid analogue to biserial *Cephalograptus* or *Petalograptus*. Although the transient forms bridging the gap between *Bohemograptus* and *Polonograptus*, are not yet known, the morphology of the latter is indicative of a bohemograptid ancestry. Moreover, “*Monograptus*” *egregius*, described by URBANEK (1970) from the early Ludfordian of EEP, and considered by him as an aberrant form of a cryptogenetic origin, may in fact, be referred to as an early representative of *Polonograptus* (URBANEK 1993; ŠTORCH 1995).

Along with *neocucullograptids*, *Polonograptus* belongs to highly characteristic faunal elements of the early Ludfordian. *Polonograptus* should, however, be redefined since its type species *Monograptus butovicensis* BOUČEK (1936: pl. I: 6, 7) is a *nomen dubium*. Two original specimens of *M. butovicensis* (including the holotype), housed in the Narodni Muzeum in Prague (N.M.L. 17753, 199968), represent slightly curved distal fragments of the rhabdosome, displaying a strong thecal overlap, but otherwise lacking any specific characters which could justify their assignment to *Polonograptus*. Dr Radvan HORNY, an authority in the Barrandian Silurian, maintains that the lithology of the sample with original specimens of *butovicensis* is highly characteristic of the nodules with *Orthoceras* and *Cardiola* from the *nilssoni* Zone in the Butovice locality, the *locus typicus* as stated by BOUČEK (1936: p. 4). However, all the remaining *Polonograptus* material was recorded from much higher strata and there is no other evidence for its presence within Gorstian. JAEGER's *M. butovicensis* (1975: pl. 1: 1, 2 and 6 therein), most probably cannot be referred to *M. butovicensis* BOUČEK as it occurs within distinctly higher Zone, (*Cardiola*-Niveau, Bank 24 of the Cellon section of Carnic Alps, situated within *latialatus* conodont Zone, well above the *leitwardinensis* Zone in the graptolite sequence), and is probably conspecific with *Polonograptus podoliensis* PŘIBYL, 1983. Therefore *Polonograptus podoliensis* is the first reliably defined and described representative of *Polonograptus* and as such should be designated as its type species. ŠTORCH (1995) has recently described from the *inexpectatus-kozlowskii* Zone of the Kosov Quarry, a well-known locality near Beroun (Kopanina Formation, Barrandian), an assemblage of polonograptids (*P. egregius*, *P. podoliensis*, *P. podoliensis* cf. *australis*, and *P. sp.*). He has supplied new data concerning their morphology and presumed phylogeny, however, he retains as the type species of *Polonograptus*—*Monograptus butovicensis* BOUČEK.

In our opinion *Monograptus butovicensis* BOUČEK, 1936 might be a “preservational species” representing merely distal fragments of *Colonograptus roemeri* (BARRANDE, 1850), common in its association in Butovice and one of monograptids with an extensive thecal overlap in the distal part of the rhabdosome. PERNER's (1899) originals of *C. roemeri* from Butovice, housed at Narodni Muzeum (Prague, Nr 36675) and made available to us, show a remarkable similarity to BOUČEK's *M. butovicensis*.

A measure of confusion is the fact that the two specimens of *Polonograptus*, collected by Professor Ivo CHLUPAČ in the Velký vrch (Koneprusy) section, at the same level and within the bed of the same lithology (dark grey bituminous limestone), were identified first as *M. butovicensis* (by JAEGER 1975: pl. 1: 6), and second as *P. podoliensis* (by PŘIBYL 1983: pl. II: 4; pl. IV: 4). These specimens are housed at the Narodni Muzeum in Prague (but not numbered, while PŘIBYL's specimens bear also numbers of Czech State Geological Survey, UUG 6072). In the light of the present knowledge, JAEGER's and PŘIBYL's specimens are doubtlessly conspecific (see PŘIBYL 1983: pp. 158–159), and their stratigraphic position within the Kopanina Formation may be assigned to *N. inexpectatus*–*N. kozlowskii* Zone.

Late Ludfordian graptolite fauna and stratigraphic subdivision. — The late Ludfordian graptolite sequence has, for a long time, been sort of lost interval, since knowledge of it was delayed as compared with most other Silurian graptolite faunas. Except for a few findings of poorly preserved graptolite remains in the Kopanina Formation of Prague basin (Barrandian), its systematic study was initiated only by TSEGELNJUK (1976a, b), who described a diversified monograptid fauna of this age from the deep borings of Volhynia and adjacent territory of Belarus. Equivalents of these assemblages were soon found in Central Asia (KOREN' 1989; KOREN' and LYTOCHKIN 1992) and the stratigraphic ranges and utility of some taxa were better defined. Meanwhile, PŘIBYL's (1983) paper offered a new evaluation of findings within the Kopanina Formation as compared with progress in their knowledge on EEP (URBANEK 1970; TSEGELNJUK 1976b).

Initially all the late Ludfordian graptolite sequences of the Polish part of EEP were seen to be a series of sediments characterized by common or mass occurrences of graptolites from the “*formosus* Group”, under which some species displaying superficial resemblance were lumped together (TOMCZYK 1962, 1968; TELLER 1966, 1969).

In light of recent studies (URBANEK, this volume, p. 104) it is evident that the late Ludfordian fauna appears in the East European Platform after the *kozlowskii* Event (URBANEK 1993). Due to this event and following faunal turnover, the graptolite sequence of the Ludfordian is distinctly bipartite, being composed of an early and late faunal assemblage, with only a few elements in common. The event resulted in the extinction of specialized early Ludfordian representatives of *Neocucullograptus* and *Polonograptus*, as well as of the last survivors of *Bohemograptus*, above which there appeared a low diversity assemblage composed only of relatively common *Linograptus posthumus* and *Pristiograptus dubius* s.l. This, in turn, they gave way to a true late Ludfordian fauna represented by *Pseudomonoclimacis latilobus* (TSEGELNJUK,

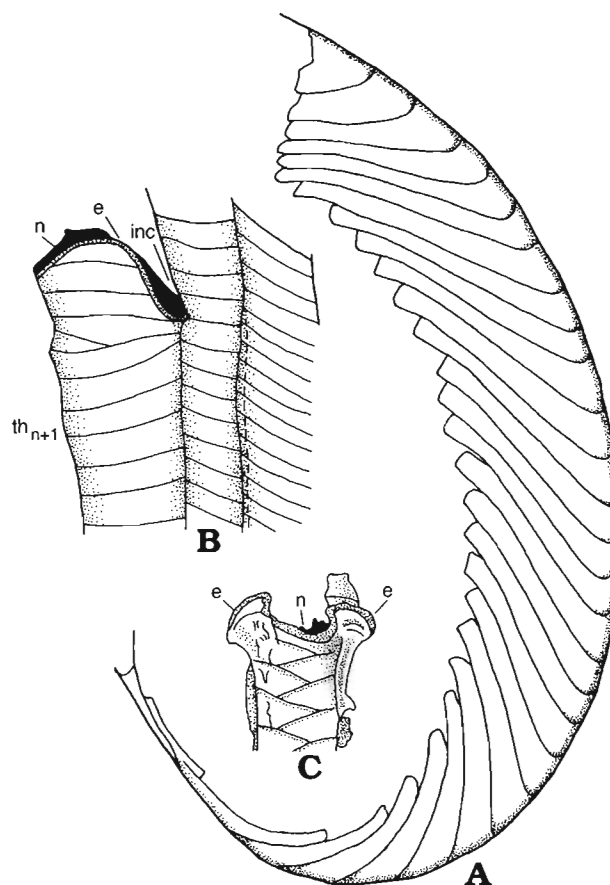


Fig. 10

Third major trend of morphological evolution amongst early Ludfordian monograptids is represented by *Polonograptus*. It displays a rapid increase in the length and overlap of thecae as seen in *P. podoliensis* PŘIBYL, 1983 (A) combined with only limited modifications of thecae, producing gentle elevations of apertural border (B, C, e, n). Slightly diagrammatical drawings made from a photograph of a specimen from Kosov Quarry near Beroun, Central Bohemia, *Acantholomina minuta* Beds (= *kozłowskii* Zone), Kopanina Formation (photograph obtained by courtesy of Dr P. ŠTORCH, Prague). Abbreviations: e – elevations of the apertural border, inc – dorso-lateral incisions, n – ventral apertural notch.

1976b), *Pristiograptus dubius fragmentalis* (BOUČEK, 1936), *Monograptus* (*Slovinograptus*) *hamulosus* TSEGELNJUK, 1976, and *M. (Formosograptus) formosus* BOUČEK, 1931. They appeared in a rapid succession, that is almost simultaneously, marking a single graptolite assemblage zone, namely the *latilobus/balticus* Zone. The real novelty in this assemblage is the reappearance of hooded monograptids, after a long gap in the record, most probably due to Lazarus effect (for more extended discussion see URBANEK 1993, 1995 and this volume, p. 105). TSEGELNJUK (1976b, 1981) has found a number of other monograptid species within this assemblage, and Volhynian faunas appear to be even more differentiated than recorded in the Mielnik IG-1 borecore. On the other hand KOREN' (personal communication) has found that the first hooded monograptids reappear as early as the *leintwardinensis* Zone (base of the early Ludfordian) in the Alai Range of Tien Shan (Kyrgystan). Also LENZ (1988) has found *Monograptus ceratus*, a hooded monograptid in the last named zone of the N Yukon (Canada). The migration of new faunal elements due to Lazarus effect was thus a diachronous process, albeit taking place entirely within the Ludfordian.

The higher strata of the late Ludfordian are subdivided on the basis of a single lineage, namely the *acer-spineus* lineage (URBANEK 1995). The first representative of this lineage, *Monograptus (Uncinograptus) acer* (TSEGELNJUK, 1976), appears above the *latilobus/balticus* Zone defining in this way the lower boundary of the eponymous zone. This zone is subdivided into a lower and an upper Subzone, based on the lower occurrence of the index subspecies *M. (U.) acer acer* (TSEGELNJUK, 1976), and upper occurrence of *M. (U.) acer aculeatus* (TSEGELNJUK, 1976) respectively. Their taxonomic position was redefined recently by URBANEK (1995). They differ mainly in the degree of the dorsal curvature of the the proximal part, a trait that while increasing gradually upwards, permits the recognition of two sub-

species and, therefore of two discrete subzones. The next horizon is marked by the occurrence of *Monograptus (Uncinograptus) protospineus* URBANEK, 1995, which in the Mielnik IG-1 borehole, is represented by a thin bed (some 40 cm). This species represents a transient link between hooded and spinose (lobate-spinose) monograptids. Since the Gushcha-4015 borehole (Volhynia) as well as Łeba-3 boring (W Pomerania, Poland) reveal conspecific forms, the *protospineus* Zone was recognized (URBANEK 1995) as a separate unit. It is followed stratigraphically by the occurrence of *M. (U.) spineus* (TSEGELNJUK, 1976), defining an eponymous zone, and recognized as a biostratigraphic unit by KOREN' and LYTOCHKIN (1992c) in Tien Shan sections (Kyrgystan). The species, doubtlessly the most remarkable monograptid of late Ludfordian, was described from Volhynia, but is also present in E Poland and in Central Asia. It is a good candidate for a standard index fossil of the late Ludfordian (KOREN' 1992a; URBANEK 1995).

The upper part of the late Ludfordian sequence encountered in the Mielnik IG-1 borehole thus reveals a clear temporal replacement in the vertical distribution of the members of the *acer-spineus* plexus. Consequently they are interpreted as chronospecies (or subspecies) within a single line of descent. In other areas, the sequence within this lineage is less clearly established. TSEGELNJUK (1976a, 1981) maintains that all species of the *acer-spineus* lineage co-occur within a single assemblage and are associated with species from the *latilobus/balticus* Zone. Hence, he distinguishes only one graptolite zone for the entire late Ludfordian. This difference in opinion may probably be explained by different resolution used in the study of borecore material rather than by real differences in the vertical distribution over small distances in question. KOREN' and LYTOCHKIN (1992c) mentions the co-occurrence of *M. (U.) acer aculeatus* and *M. (U.) spineus* in her sections from the Kursala Formation of Tien Shan (Kyrgystan). Moreover, all these species are referred by her to a broadly understood *formosus/spineus* Zone of the late Ludfordian (see URBANEK, this volume, p. 96 for comment).

The tentative graptolite zonation of the late Ludfordian of the EEP is given on Table 1 (p. 35).

The extinction of *M. (U.) spineus* may be related to the next faunal turnover named the *spineus* Event by KOREN' (1992a). The filtering effect of this event was less severe than that of *leintwardinensis* Event and even less drastic as compared with *kozłowskii* Event; nevertheless, lobate-spinose monograptids became extinct while hooded monograptids display a distinct Lazarus effect and re-appear only in the *lochkovensis* Zone of the Přidoli. Among relatively specialized forms an exception is *Monograptus (Formosograptus) formosus* which, while common throughout the entire late Ludfordian, crosses the Ludlow/Přidoli boundary. It is accompanied by the notorious hold-overs such as *Linograptus posthumus* and *Pristiograptus dubius* s.l. Otherwise, the late Ludfordian assemblage cannot be expected to provide direct forerunners of the early Přidoli fauna, because of the *spineus* Event. The Přidoli fauna originated *de novo* from nonspecialized pristiograptids, from which we can search for the ancestry of *parultimus-ultimus* lineage. This indigeneous faunal assemblage was later enriched by Lazarus taxa, namely reappearing hooded monograptids. In the Mielnik IG-1 borecore *spineus* Event is marked by a 70 m thick series of strata with characteristically impoverished fauna.

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GRAPTOLITES AND STRATIGRAPHY OF THE WENLOCK AND LUDLOW SERIES
IN THE EAST EUROPEAN PLATFORM

PLATE 1

Representative thecal morphologies in monograptids of the Wenlock age. All samples from the Zawada-1 well.
Abbreviations: Si — sícula, Vi — virgella, pV — pseudovirgula, Th — theca, l — lapet, a — aperturae, sp — spine.

Cyrtograptus radians (TÖRNQUIST)

1. Sícula with two proximal hooked thecae, *lundgreni* Zone; $\times 30$.
3. Thecal cladium with two thecae, *lundgreni* Zone; $\times 32$.
6. First theca of the thecal cladium incompletely developed, *lundgreni* Zone; $\times 42$.

Cyrtograptus perneri BOUČEK

2. Two proximal thecae with long spines, *ellesae* Zone; $\times 50$.

Cyrtograptus hamatus (BAILY)

4. Thecal cladium with three thecae, *lundgreni* Zone; $\times 30$.

Cyrtograptus lundgreni TULLBERG

- 5, 8. Thecae of the procladium, *lundgreni* Zone; 5×25 , 8×125 .

Monograptus belophorus MENECHINI

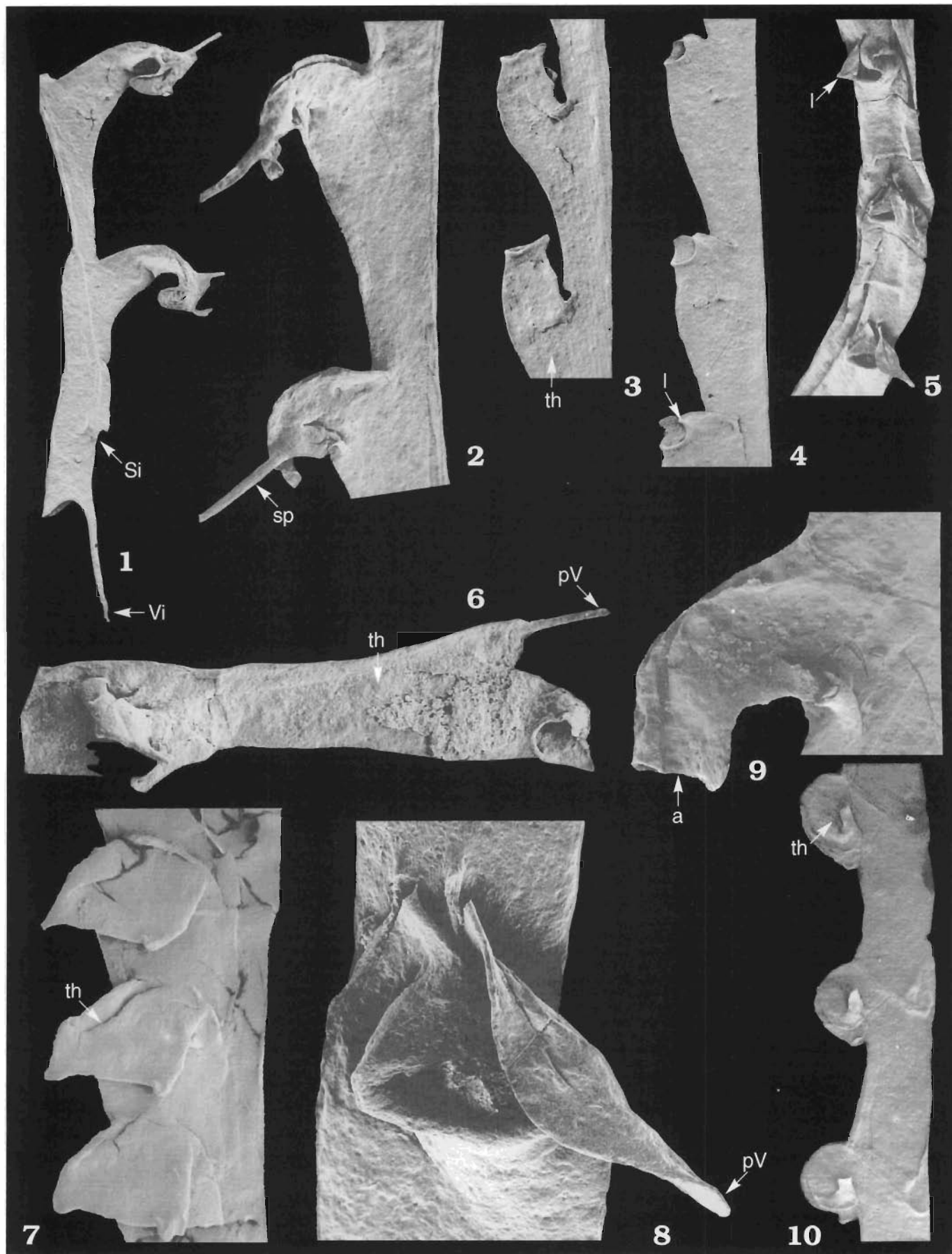
7. Medial thecae, *belophorus* Zone; $\times 30$.

Monograptus antennularius (MENECHINI)

9. Lateral view of a hooked theca, *antennularius* Zone; $\times 200$.

Monograptus flexuosus (TULLBERG)

10. Medial three thecae, *antennularius* Zone; $\times 30$.



GRAPTOLITES AND STRATIGRAPHY OF THE WENLOCK AND LUDLOW SERIES
IN THE EAST EUROPEAN PLATFORM

PLATE 2

Representative thecal morphologies in monograptids of the Wenlock Age. All samples from the Zawada-1 well.

Abbreviations: Vi – virgella, Si – sícula, Th – theca, Sp – spine, l – lapet, e – ear, h – hood.

Cyrtograptus lundgreni TULLBERG

1. Three thecae of the procladium, *lundgreni* Zone; $\times 25$.
2. Three thecae of the thecal cladium, *lundgreni* Zone; $\times 25$.

Monograptus flemingi (SALTER)

3. Proximal thecae and sícula, *antennularius* Zone; $\times 30$.

Cyrtograptus rigidus TULLBERG

4. Distal thecae of the procladium, *rigidus* Zone; $\times 30$.
6. Proximal thecae of the procladium, *rigidus* Zone; $\times 25$.

Monograptus (Testograptus) testis (BARRANDE)

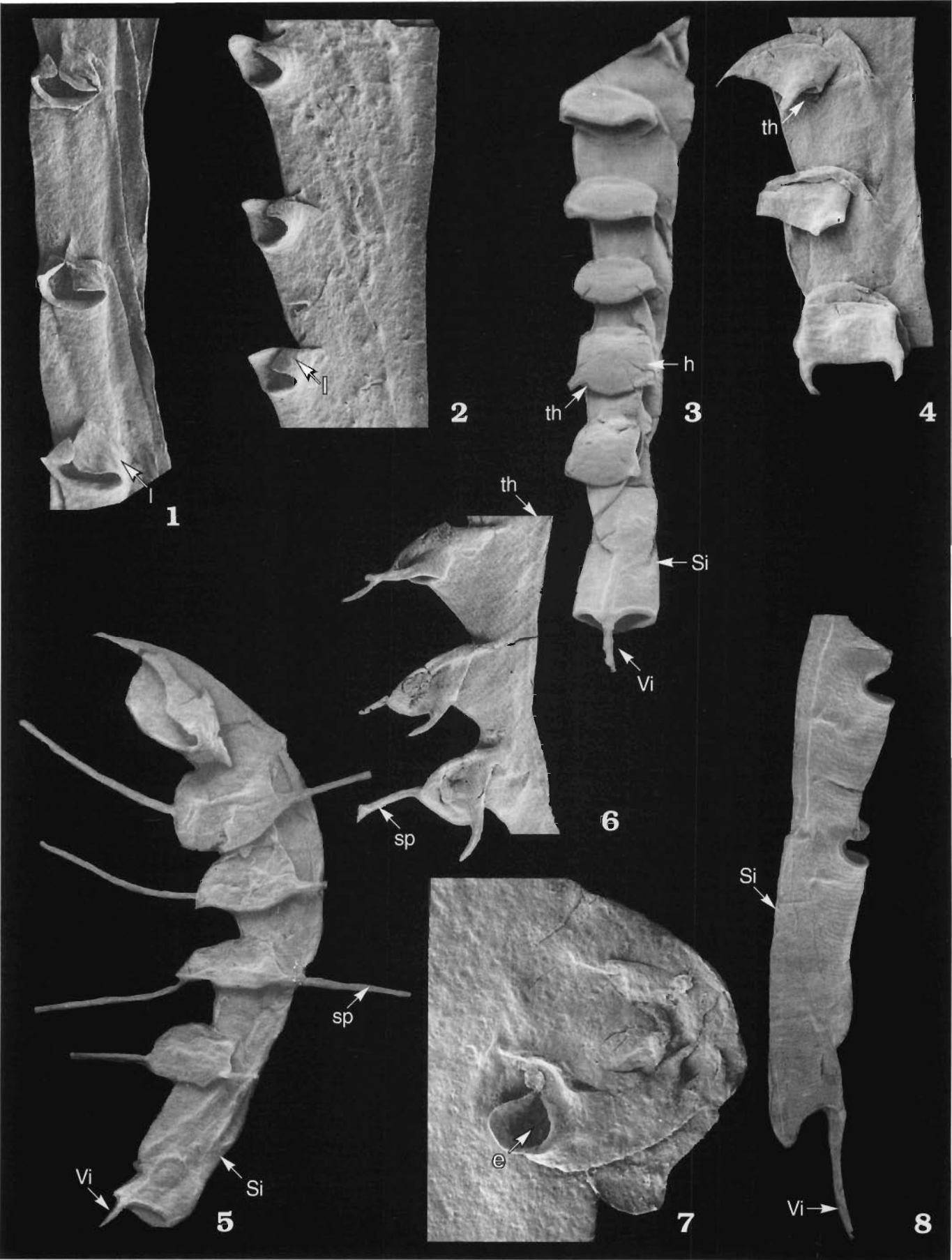
5. Juvenile rhabdosome, *lundgreni* Zone; $\times 30$.

Monograptus flexuosus (TULLBERG)

7. Apertural hood with open ears, *antennularius* Zone; $\times 125$.

Monoclimacis zawadensis TELLER

8. Proximal thecae and sícula, *lundgreni* Zone; $\times 40$.



GRAPTOLITES AND STRATIGRAPHY OF THE WENLOCK AND LUDLOW SERIES
IN THE EAST EUROPEAN PLATFORM

PLATE 3

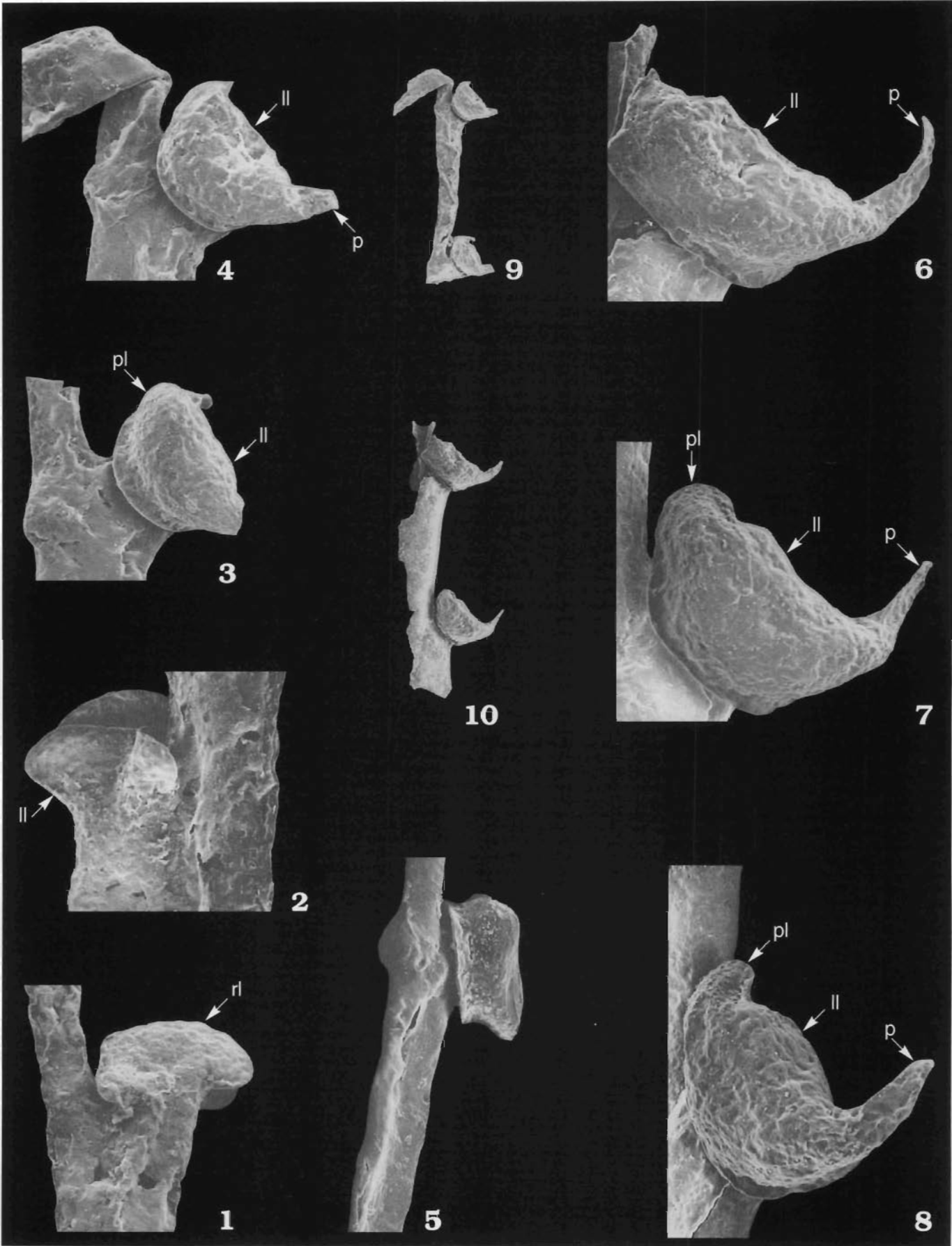
Representative thecal morphologies in monograptids of the Gorstian and early Ludfordian Age. Abbreviations: ll – left apertural lobe, rl – right apertural lobe, p – rostral process, pl – gular plate and dorsal eaves of the lobe.

Lobograptus scanicus parascanicus (KÜHNE)

1–2. Aperture of a R-cucullograptid, Baltic erratic boulders, S.181, W Pomerania, *parascanicus* Zone; $\times 110$.

Cucullograptus aversus rostratus URBANEK

3–10. Different aspects of apertural apparatus (3–8) as well as proximal (9) and distal (10) thecae in, Mielnik IG-1 boring, depth 924.40–921.70 m, *aversus* Zone; 3–8 $\times 110$; 9, 10 $\times 25$.



GRAPTOLITES AND STRATIGRAPHY OF THE WENLOCK AND LUDLOW SERIES
IN THE EAST EUROPEAN PLATFORM

PLATE 4

Representative thecal types of early Ludfordian Age.

Abbreviations: a – aperture, m – microfusellar additions, ll – lateral apertural lobe, p – rostral process, pl gular plate.

Neocucullograptus inexpectatus (BOUČEK)

1–2. Apertural apparatus, Mielnik IG-1 boring, depth 887.70 m, *inexpectatus* Zone; $\times 110$.

Neocucullograptus kozłowski URBANEK

3–7. Apertural apparatus, seen laterally (3–4), ventro-laterally (7) and in ventral (5) and dorsal (6) aspects.
Mielnik IG-1 boring, depth 873.40 m, *kozłowski* Zone; 3, 5 $\times 55$; 4, 6, 7 $\times 110$.

Bohemograptus bohemicus aff. *tenuis* (BOUČEK)

8. Simple thecal aperture (a), Mielnik IG-1 boring, depth 889.50 m, *inexpectatus* Zone; 8 $\times 180$.

Bohemograptus praecornutus URBANEK

9. Thecal aperture with microfusellar additions (m), Mielnik IG-1 boring, depth 911.60 m, *praecornutus* Zone; 9 $\times 110$.

Pseudomonoclimacis micropoma (JAEKEL)

10. Standard fusellar tissue with characteristic ventral zig zag suture as seen with LM on bleached thecal wall.
Mielnik IG-1 wellcore, depth 1019.40 m, *progenitor* Zone; $\times 130$.

Neocucullograptus kozłowski URBANEK

11. Typical example of microfusellar tissue (m) with a structural transient zone (t) as seen with LM on bleached apertural lobe. Mielnik IG-1 wellcore, depth 873.40 m, *kozłowski* Zone; $\times 130$.

