THE SUBSURFACE SILURIAN IN THE EAST EUROPEAN PLATFORM

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A state of art overview of the Silurian System within the deep substratum of the East European Platform (EEP) is presented. Structural Regions are characterized in terms of biostratigraphy, tectonics and palaeogeography. The most instructive sections based on keywells have been briefly described with an emphasis on the western margin of the platform. The Silurian basin displays a typical platform development and may be traced from the neritic to the deep basinal facies. While the neritic belt is recognized from Gotland through Estonia, Volhynia to Podolia, the deep basinal facies has been documented NE of the Törnquist-Teisseyre lineament. The results presented are based on some 700 deep borings. They offer a summary of Silurian history of NE Poland and the adjacent areas, as well as a setting for graptolite biostratigraphy.

Key words: Silurian, East European Platform, Biostratigraphy, Tectonics, Palaeogeography.

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HISTORY OF RESEARCH

An especially great contribution to the knowledge of the Palaeozoic sedimentary cover above the crystalline basement in the EEP was made between 1957–1970. It was the time when a wide-scale study of subsurface geological structures in the Polish Lowland was conducted in association with mineral resources prospecting. This project involved drilling of hundreds of deep boreholes, 100 per cent of which, in the early period, were completely cored. As a result, new research material became available, so plentiful that its detailed analytical study was beyond the capacity of the Polish Geological Institute. Silurian deposits were revealed or pierced in more than 320 boreholes. Their preliminary faunal documentation, especially that concerning graptolites, considerably enriched the general knowledge of the Silurian System not only in Poland (Fig. 1).

Until the mid-1950s, sediments of this age had only been known from the outcrops in the Holy Cross Mountains and in the Sudeten. Their stratigraphy was chiefly described by CZARNOCKI (1919, 1942), SAMSONOWICZ (1916, 1934) as well as by DAHLGRÜN and FINCKH (1934) and FINCKH (1932), FINCKH *et al.* (1942).

The materials analyzed mainly by the Polish Geological Institute and by the oil prospecters provided a deep insight in the stratigraphy and tectonic structure of the Paleozoic cover of the Platform area. A rich and varied fauna contained in the drilled sedimentary series was the source of fascinating and frequently unique palaeontological material.

The most interesting among Silurian deposits were the unfolded series encountered in the Polish part of the south-western EEP over a large area of 100 thousand km^2. The Törnquist-Teisseyre (T.T.) lineament forms the SW boundary of the Silurian sediments not folded in Caledonian time (Fig. 1).

The Silurian sediments deposited in this part of the Platform are fairly thick. Their thickness increases as the Platform slope plunges south-westwardly, reaching a maximum of 3340 m (TOMCZYK 1976) in the borehole near Słupsk.

Unfolded platform Silurian deposits were recorded for the first time in 1936 in the Łeba borehole below Zechstein. The borehole was drilled on the elevation of the same name by the former German Reichsamt für Bodenforschung in 1935/1936. The section obtained was 609 m thick (664.5–1273.4 m) and represented only the Upper Silurian. Its preliminary description was made by DAHLGRÜN and SEITZ (1944) and TELLER (1962). Over one hundred further boreholes drilled close to one another in 1960–1975 confirmed the conclusions of both of these earlier studies (TOMCZYK 1968, 1976) (Fig. 1).

Chełm IG-1 (Fig. 1), a borehole drilled by the Polish Geological Institute in 1954/1955, was another well within the SE-most edge of the Polish part of the marginal EEP, where Silurian fossil-bearing strata were demonstrated palaeontologically. Here, at a depth of 1207.4–1607.4 m, an almost 400 m thick Přidoli Series was penetrated in sedimentary continuity below the lower Lochkovian (TOMCZYK and TELLER 1956; TELLER 1960). It contained a rich graptolite (TELLER 1964) and benthic (KOREJWO and TELLER 1964) fauna similar to the one known from the present Přidoli Series of the Prague Basin (HAVLIČEK and ŠTORCH 1990;

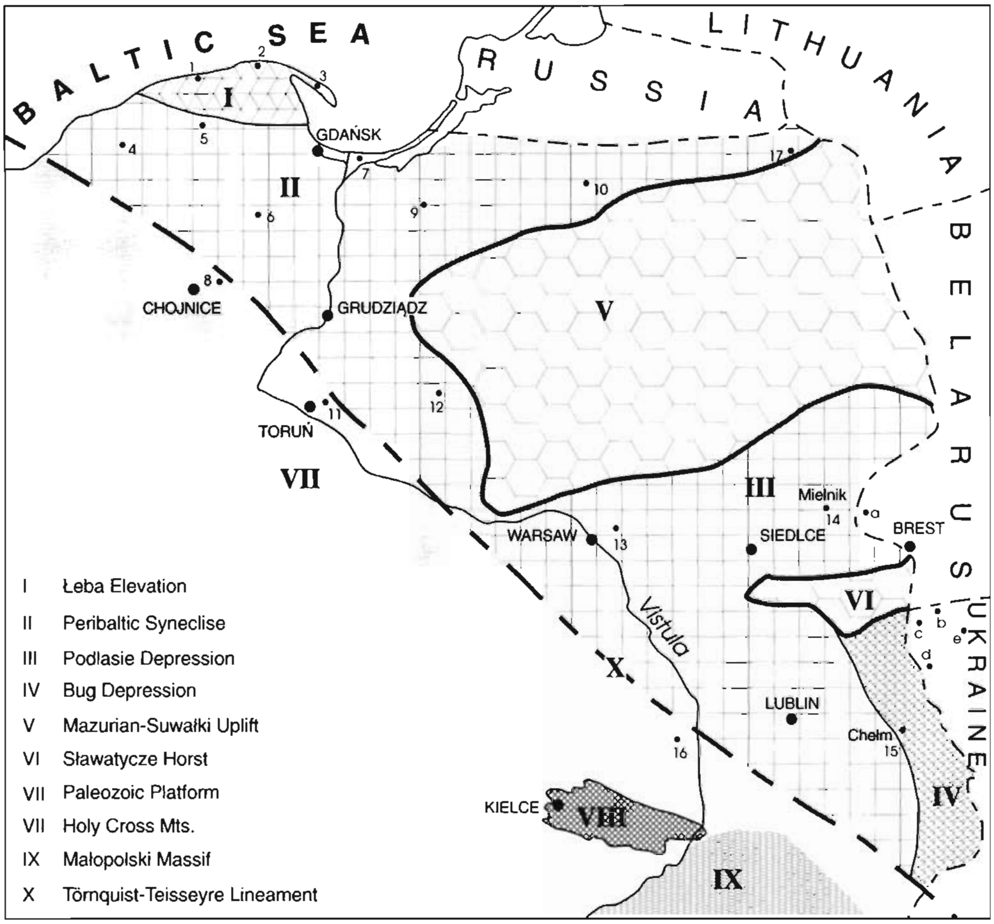

Fig. 1
A structural map of the marginal part of the EEP (Poland).
Selected Polish boreholes: 1 – Łeba, 2 – Żarnowiec, 3 – Hel, 4 – Słupsk, 5 – Lębork, 6 – Kościerzyna, 7 – Gdańsk, 8 – Lutom, 9 – Pasłęk, 10 – Bartoszyce, 11 – Toruń, 12 – Szczawno, 13 – Okuniew, 14 – Mielnik, 15 – Chełm, 16 – Ciepielów, 17 – Okrągłe Lake. Selected boreholes outside Poland: a – Brest-1, b – Pishcha-16, c – Tomashovka-406, d – Gushcha-4015, e – Yegorany-409.

Přibyl 1940, 1981, 1983; Horny 1955; Kříž *et al.* 1986). At that time this was the second locality in the world with this kind of fauna. Its stratigraphic position and correlation, especially in relation to the British sequence which at that time was generally accepted and regarded as classical, posed an uneasy task for geologists and palaeontologists.

A number of boreholes drilled in SE Poland and the Bug Depression (Tomczyk 1974a–d, 1975a–d, 1977) in later years have confirmed the results obtained for Chełm IG-1 section.

The next well of importance drilled during the second half of the 1950s was the prospecting well Mielnik IG-1 (Fig. 1) located in the eastern part of the Podlasie Depression. It yielded an interesting and rich Lower Ludlow (Gorstian) graptolite fauna and also, above the *leintwardinensis* Zone, a new Early Ludfordian fauna subsequently studied by Urbanek (1963, 1966, 1971). His studies shed light on the evolution of this graptolite fauna, revealing a new, heretofore unknown stage in the development of monograptids whose mass occurrence was recorded for the first time in the Polish subsurface Silurian. The study of the Late Ludfordian graptolite fauna, based on the Mielnik IG-1 material (Urbanek this volume p. 89) supplements the preliminary results presented by Tsegelnjuk (1976a, b) for Volhynia and Podolia.

The information concerning this fauna which began appearing as early as the beginning of the 1960s (Teller 1966, 1971; Urbanek 1963, 1966, 1971) did not bring a ready response from specialists in the field. It was not until some time later that similar fossil assemblages although less numerous (with the exception of, probably, Volhynia and Asia, were encountered in various sequences around the world: Canada – Jackson and Lenz (1963, 1972), Jackson *et al.* (1978), Lenz and Jackson (1971); Volhynia

– TSEGELNJUK (1976a, b); Central Asia – MIKHAILOVA (1971, 1976), KOREN' (1983, 1986, 1989); Australia – JENKINS (1982); Morocco – WILLEFERT (1962); Prague Basin – PŘIBYL (1981 1983); ŠTORCH (1995).

Silurian deposits associated with the late Caledonian movements in the SE branch of the Caledonian geosyncline running through Poland have also been recorded in several points along the T.T. lineament marginal zone. They have been penetrated by deep borings within the narrow Koszalin–Chojnice belt (TELLER and KOREJWO 1968a, b, c; TELLER 1969; DADLEZ 1967) and also in SE Poland (TOMCZYK 1962; DADLEZ 1974a, b, c). It is not impossible that these deposits (mainly Ordovician and Silurian) have been partially overthrust onto the EEP (DADLEZ 1967, 1974c) (Fig. 1).

New material supplied by the boreholes since 1956 was studied from the point of view of stratigraphy by TELLER (1960–1990), TELLER and KOREJWO (1968a, b, c) and TOMCZYK together with TOMCZYKOWA (1958–1990). Palaeontological research of the graptolite fauna has been conducted since 1954 by TELLER (1962, 1964, 1966, 1975, 1976, 1988) and URBANEK (1954, 1958, 1960, 1963, 1966, 1970, 1976).

Other faunas have been described by KOREJWO and TELLER (1964), TOMCZYKOWA (1971, 1975), TOMCZYKOWA and WITWICKA (1972, 1974), NEHRING (1973), NEHRING-LEFELD (1985, 1987), WOLSKA (1969), WRONA (1980), and ŻBIKOWSKA (1973a, b, 1974). LANGIER-KUŹNIAROWA (1967, 1971, 1976) carried out penetrating petrographic studies. JAWOROWSKI (1965, 1966, 1971) and JAWOROWSKI and MODLIŃSKI (1968) conducted sedimentological and some stratigraphic research.

The results thus obtained provided a complete picture of the development of the Silurian deposits and faunas in the Polish part of the EEP. This places the Polish Silurian among the best recognized in Central Europe, a fact, which for reasons unknown, has been overlooked by many researchers (COCKS *et al.* 1992).

The problem that requires further work is the lithostratigraphic subdivision of the sediments. The subdivision suggested by TOMCZYK (1962: pp. 10–23, 110) was highly useful at the early stages of investigations, but is now inadequate for the present state of knowledge on the subject.

Having distinguished the Pasłęk, Mielnik, Siedlce and Podlasie Beds, TOMCZYK (1962: p. 119, tables 2 and 10) did not specify either the litho- or the chronostratigraphic criteria necessary for their discrimination, nor did he define the nature of the units recognized. In later years he never reconsidered his original scheme, but instead, only offered numerous interpretations and correlations of it.

In some of his papers the above author maintains that the units recognized by him correspond to beds (TOMCZYK 1970), in others, to regional stages (TOMCZYKOWA 1983) or even to formations (TOMCZYK and TOMCZYKOWA 1983). The same discrepancies are evident when analyzing the various correlation tables compiled by these authors (TOMCZYKOWA 1988: table 1; TOMCZYK 1990: table 16).

The entire Silurian in Poland fits well in the existing international chronostratigraphic subdivision, the regional names introduced by TOMCZYK (1962) having a purely local significance. They are the equivalents of the names of formations, groups, members, and beds in an informal lithostratigraphic subdivision; it is not until they have been redefined in conformity with the Polish stratigraphical code that some of them may acquire a formal status.

The unfolded platform Silurian deposits of Poland and the fauna they contain are fully comparable from the point of view of both their chrono- and biostratigraphy with coeval sediments of other regions in and outside Europe. Furthermore, the youngest Series of the System (Ludlow and Přidoli) are much more complete in Poland than are their counterparts in the regions of classical development (e.g., Britain, Bohemia).

THE WESTERN MARGINAL ZONE OF THE EAST EUROPEAN PLATFORM

What is understood by the western marginal zone (Fig. 1) is the region NE of the T.T. lineament that cuts Poland diagonally and extends from Koszalin in the NW to Dobruja and the mouth of the Dnester River to the Black Sea in the SE. Bathymetrically differentiated, this area was, during the Silurian, covered by an epicontinental sea (POŻARYSKI 1974a, b; TYSKI 1974). As such, it displayed a varied carbonate-dolomitic-marly sedimentation and is richly fossiliferous. The epicontinental sedimentation embraced the present-day eastern part of the Baltic Sea with Silurian deposits cropping out on several islands, e.g. Gotland (BASSETT *et al.* 1989), Saaremaa or Hiiumaa, and also Western Estonia (EINASTO *et al.* 1980; KALJO *et al.* 1970, 1977, 1991; KALJO 1971; NESTOR and EINASTO 1977, 1982), Lithuania (PAŠKEVIČIUS 1979, 1986), Latvia (ULST 1968), NE Poland, Belarus, and Volhynia and Podolia (KRANDIEWSKI *et al.*

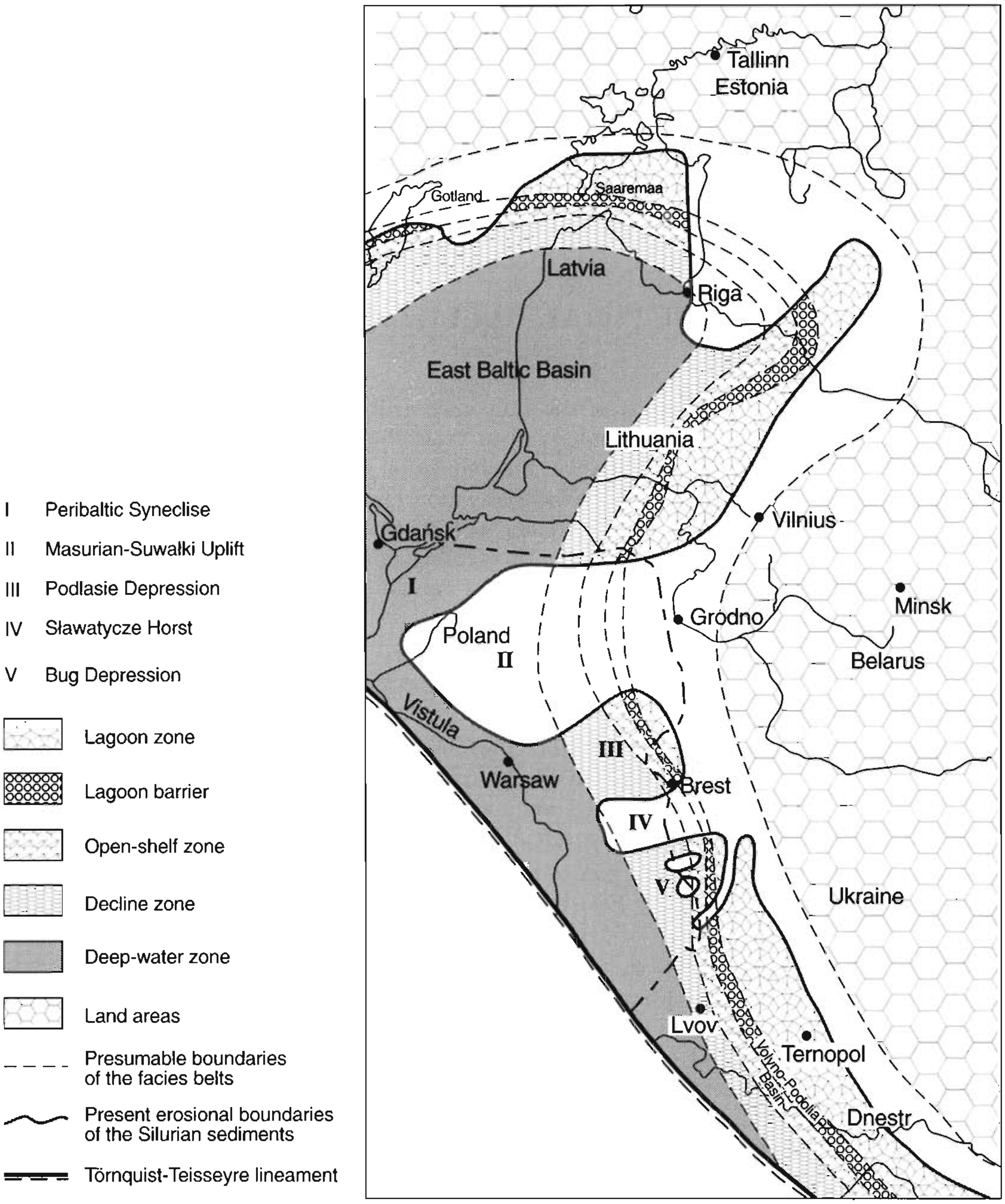

Fig. 2
The facies belts of the western margin of the EEP (Upper Wenlock time).
After EINASTO *et al.* (1986), modified.

1968; TSEGELNJUK 1983a, b) where the presence of Silurian rocks has been recorded in numerous boreholes (Fig. 2).

One of the world's most beautifully exposed Silurian rocks of the same epicontinental basin can be found along the north bank of the Dnester River and its tributaries in Podolia (NIKIFOROVA *et al.* 1972) (Fig. 3).

Towards the SW, the East European Platform marginal zone features an abrupt overdeepening, forming a slope. The epicontinental basin becomes a deep-water one connected to the NW with the SE branch of the Caledonian geosyncline. The entire basin displays a predominantly continuous argillaceous-marly sedimentation. The planktonic graptolite faunas amassed in these sediments are abundant and continuous as to allow a study of their phylogeny and astogeny (TELLER 1969).

The deep-water zone forms a fairly narrow belt parallel to the T.T. lineament. Throughout the epicontinental area and the deep-water basin situated on the Platform slope, Silurian deposits did not undergo folding at the Caledonian time, the only folded structures having been encountered in the elevated foreland of the EEP in the Koszalin–Chojnice belt (TELLER and KOREJWO 1968b; MODLIŃSKI 1968, 1982; DADLEZ 1974a, c) and also encountered in several boreholes in the SE (TELLER 1964; TOMCZYK 1968) (Fig. 1).

STRUCTURAL FACIAL REGIONS

In the Palaeozoic, the marginal zone of the Epigothic EEP was fairly labile, which accounted for a considerable differentiation of the morphology of its crystalline basement and also of the sedimentary cover (POŻARYSKI 1974b). The Silurian Sea was a continuation of the Cambrian basin, limited on the N and NE by the crystalline Baltic Shield and on the SE by the Ukrainian Shield. The bathymetric conditions prevailing in the extensive and calm basin together with a moderately warm climate contributed to the development of a rich and varied organic world. This facilitated a detailed stratification of the sediments, permitting a reconstruction of the basin's history and compilation of litho- and biostratigraphic schemes instrumental in interregional correlation.

NE of the T.T. lineament, one can distinguish several negative and positive structures that had a strong impact on the development of the sediments and fauna in that region (TYSKI 1974; POŻARYSKI 1974b) (Fig. 1).

The largest is the well-recognized Peribaltic Syneclise. It includes Latvia, Lithuania, part of SW Estonia, a small section of N and NW Poland which stretches from Koszalin to the Okrągłe Lake in the east, via the Łeba Elevation, the Gdańsk Bay, and a narrow belt running from Elbląg. That narrow strip forms the southern limb of the Peribaltic Syneclise in that area.

The Silurian sediments of the eastern part of the Syneclise (Estonia, Latvia, Lithuania) are described, especially by Estonian geologists, as the East-Baltic Silurian forming part of the East-Baltic Sedimentary Basin recognized there (EINASTO *et al.* 1986; KALJO 1971; KALJO *et al.* 1970; KALJO and JURGENSON 1977).

Within the Polish part of the EEP slope, as well as in the more shallow parts of the Peribaltic Syneclise, it is possible to distinguish larger and smaller structures of the second order. Some authors (ZNOSKO 1962, 1963, 1964, 1965, 1970; ZNOSKO and PAJCHLOWA 1968; TYSKI 1974; POŻARYSKI 1974a, b) associate the structures with the Caledonian movements, whilst others (VASILIAUSKAS 1965; SUVEJZDIS 1968) ascribe them to the Variscan movements. Among the most important structures are the Łeba elevation, the Masurian–Belarussian Anteclise, the Podlasie Depression, and also a number of smaller uplifts and depressions in the SE Lublin Region and in Southern Podlasie (Fig. 1).

The epicontinental Silurian of the marginal zone of the EEP also features two main sedimentary basins, each having a different configuration. These are the East Baltic and Podolian Basins (EINASTO *et al.* 1980) (Fig. 2).

The East Baltic Basin cut deeply into the Fennosarmatian continent forming an open bay whose N and NW shores marked the S slope of the Baltic Shield and the NW slope of the Ukrainian Shield, respectively. This basin was an extension of the Central European Caledonian geosyncline tapering out towards the East.

On the contrary, the fairly narrow Podolian Basin extended almost meridionally, running parallel to the SW margin of the crystalline Ukrainian Shield. It descended rapidly south-westerly to become an open sea (EINASTO *et al.* 1980).

Connected with the same marginal epicontinental sea, both the basins basically developed along the same lines. There was a considerable difference, however, in that the Early Silurian transgression began in the East Baltic Basin as early as the Middle Llandovery, whilst in the Podolian Basin it did not start until the onset of the Wenlock. Similarly, the Late Silurian regression, which in the East Baltic Basin was recorded as early as the Late Silurian (Přidoli), does not appear in Podolia until the Early Devonian (the Dniester Formation) (EINASTO *et al.* 1980). A transition zone between the two basins has also been confirmed by boreholes in eastern Poland (TOMCZYKOWA and TOMCZYK 1979).

The East Baltic Basin (Latvia, Lithuania and the SW part of Estonia) (Fig. 2). — Thanks to natural exposures in W Estonia and on Saaremaa and Hiiumaa islands, as well as to numerous boreholes drilled in Estonia, Lithuania and Latvia, the basin has been well described (EINASTO 1986; EINASTO *et al.* 1980; KALJO *et al.* 1970; NESTOR 1994; PAŠKEVIČIUS 1979, 1986; PAŠKEVIČIUS *et al.* 1994; ULST 1968; GAJILIITE *et al.* 1967). Throughout the entire Silurian, highly favourable living conditions existed for the continuous development of fauna. This made possible the execute a graptolite-based orthostratigraphic subdivision that could be further correlated with the areas featuring the predominance of argillaceous facies (PAŠKEVIČIUS 1986). Orthostratigraphic subdivisions based on conodonts, ostracods and ichthyofauna allowed, in turn, the more shallow facies of the basin to be connected and correlated with the regions farther West and South (the Podolian Basin).

Bathymetric analysis permitted three regions to be distinguished in the basin (KALJO *et al.* 1983). They are:

1) The shelf showing a predominance of various carbonates and distinctly subdivided into three macrofacial zones with a specific rock and faunal composition.

2) The gentle slope of the crystalline basement with prevailing muddy-carbonate-terrigenous rocks; the top part is dominated by calcareous marls containing numerous concretions and intercalations of detrital-muddy limestone, whilst in the lower portions, marls are fairly uniform.

3) A depression area featuring basically muddy-terrigenous facies and occupying the deepest central part of the basin. The rock is predominantly dark grey bituminous laminated horizontal claystones interbedded with marls (NESTOR and EINASTO 1977; KALJO *et al.* 1970; EINASTO, *et al.* 1980; KALJO and JURGENSON 1977).

According to KALJO *et al.* (1983), there were three basic stages of sedimentation each strongly influenced by transgressions and regressions, changes in climatic and alimentation conditions, extent of terrigenous material transport, tectonic development, and finally through the rate of sedimentation. The first stage was of a limited duration, namely from the Early to the Middle Llandovery. It was characterized by a limited supply of terrigenous material and a rapid deepening of the basin. The second stage, which began in the Late Llandovery and lasted until about the end of the Ludlow, displayed a fairly intensive muddy-carbonate sedimentation in the open shelf area, a marly-muddy type on the slope, and a muddy one in the deeper parts of the basin. The third stage is associated with the latest Silurian — the Přidoli, and extends into the Early Devonian. During that time the sedimentation of terrigenous material was quite intensive due to the Caledonian orogenic movements to the North.

The Podolian Basin (Fig. 2). — The Basin belonged to the same epicontinental area which, in the Silurian, stretched along the marginal zone of the EEP. Connected with the East Baltic Basin via E Poland, Belarus, Lithuania, and Latvia, the Podolian Basin can be easily distinguished as a separate one (EINASTO *et al.* 1986) by its position on the platform, its facial zonation and also by the timing of the Early Silurian transgression and the Late Silurian regression.

On the western slope of the Ukrainian Shield, the Podolian Basin displays a predominance of carbonate-marly deposits interbedded with dolomites. They contain rich, diverse and adequately studied benthic fauna. Where the slope of the EEP plunged and the sea became deeper, clayey-marly and clayey-muddy sedimentation prevailed, yielding abundant faunas (TSEGELNJUK *et al.* 1983b; KOREN' *et al.* 1989).

Silurian deposits are conspicuously exposed along high escarpments (100–200 m) of the north bank of the River Dnester flowing in a deeply cut valley and along its north tributaries. Stretching for about 100 km, between the villages Naddnestrovka in the East and Dnestrovoe in the West, the outcrops reveal Cretaceous and Tortonian deposits 30 to 50 m thick.

Due to the monoclinal aspect of the layers and their gentle 1–2° dip, towards WSW, the oldest deposits are exposed in the East, and the youngest, in the West (NIKIFOROVA *et al.* 1972; TSEGELNJUK *et al.* 1974).

The Silurian deposits disconformably overlying the Ordovician rocks, are in turn, overlain by a conformable and continuous sequence of marine Early Devonian terrigenous-carbonate sediments. According to some estimates (NIKIFOROVA *et al.* 1972), their thickness attains 370 m, whilst other authors (TSEGELNJUK *et al.* 1983b) suggest a thickness as high as 471 m.

The Podolian section (Fig. 3) features a complete sedimentation cycle starting with a marine transgression in the Early Silurian (Late Llandovery) and ending in a regression and replacement of the marine conditions by the continental ones in the Early Devonian (NIKIFOROVA *et al.* 1972; PREDTECHENSKY *et al.* 1983). Carbonate deposits prevail throughout the cycle, with dolomites, some barren or Red Beds also

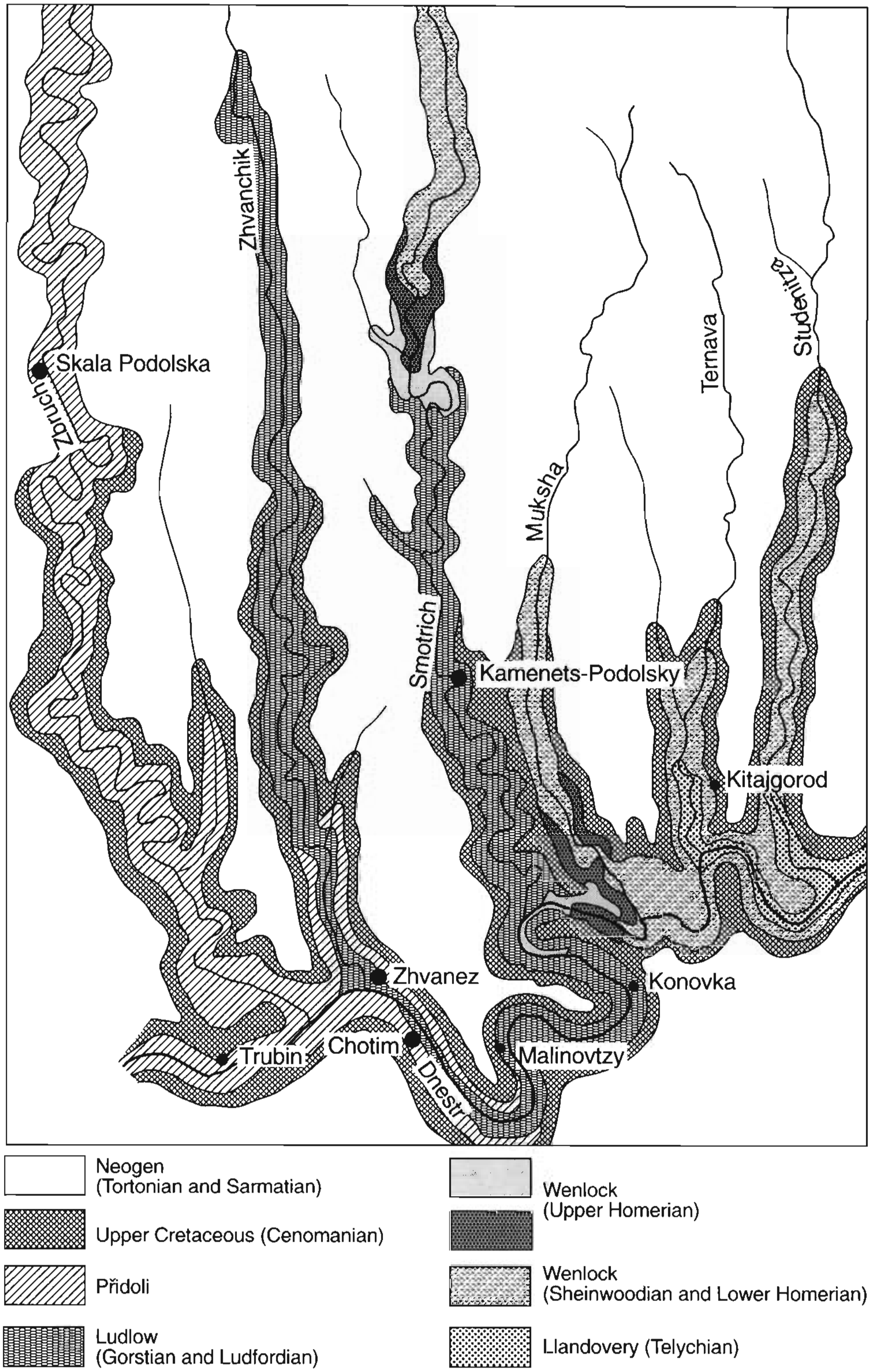

Fig. 3
Silurian key section of Podolia outcroping along the Dniester tributaries.
After O.I. NIKIFOROVA *et al.* (1972) and T.N. KOREN' *et al.* (1989), modified.

occurring at different stratigraphic levels. All this is suggestive of a considerable mobility of the sea bottom, including the possibility of breaks in deposition. However, on the basis of the continuity of the fauna (NIKIFOROVA *et al.* 1972), a break in sedimentation seems unlikely.

The western part of the Peribaltic Syneclise (Fig. 1). — Numerous structural boreholes and those for oil and gas prospecting drilled between 1960 and 1980 revealed, under the Permian cover, an erosional surface of Silurian deposits varying in age. They were either partly penetrated or bored through. The thickness of the Silurian rocks ranges from about 300 m in the East, in the southern limb of the Peribaltic Syneclise (the Gołdap IG-1 borehole), to about 3300 m in the western part (the Słupsk IG-1 borehole) (TELLER 1969; TOMCZYK 1968).

The extreme west of the Syneclise featuring a fairly sudden overdeepening of the Silurian Basin that developed in the marginal zone of the EEP, is dominated by clayey-muddy facies with subordinate carbonate interbeds. Silurian deposits rest on an uneven Late Ordovician surface of the epeirogenic Taconian phase. The chief faunal elements are graptolites which serve as the basis for biostratigraphic subdivision (TELLER 1964, 1969; URBANEK 1966, 1970), although Late Silurian (Ludlow, Early Přidoli) deposits in the region of the epicontinental facies development (the Łeba Elevation and further East) also yield an abundant benthic fauna instrumental in achieving a more accurate biostratigraphy (MARTINSSON 1964; TOMCZYKOWA and WITWICKA 1972, 1974; ŻBIKOWSKA 1973a, b).

The onset of the Llandovery Series is marked by the deposition of graptolite-bearing black claystone interbedded with a barren grey-green variety and having thin intercalations of dolomitic limestone with scarce brachiopods. In some parts of the basin, interbeds of unfossiliferous red-brown claystone are found. The thickness of the series varies, ranging from 25 m near the Pasłęk IG-1 and Prabuty IG-1 boreholes to almost 70 m in the Kościerzyna IG-1 deep boring. This is indicative of a fairly varied relief on the Ordovician surface. The abundant and well-preserved graptolite faunas provide a complete record of the Llandovery Series from the *acuminatus* Zone up to the *crenulata–spiralis* Zone (TELLER 1969).

The Wenlock Series is characterized by a uniform and fairly monotonous clayey sedimentation with a growing local proportion of carbonates. The deposits contain a rich and well-preserved graptolite fauna permitting the recognition of a complete section (TELLER 1976, 1986). The thickness of the series ranges between 80–100 m, although in places (the Lębork IG-1 borehole) it may reach 150 m. The Wenlock seems to be a time when the Late Silurian transgression in this area reached its peak, whereas the later Silurian tends to have a regressive character.

The Early Ludlow (Gorstian) Series is a continuation of the Wenlock clayey sedimentation, but there is a distinct interval between the two marked by a crisis in the graptolite fauna when almost all Wenlock representatives become extinct and new lines appear. This event has a global range and is recorded in every better known section the world over (JAEGER 1991; KOREN' and URBANEK 1994). The postcrisis dynamic development of the Gorstian fauna was studied by URBANEK (1966, 1970) using etched material from the Mielnik IG-1 borehole, the Podlasie Depression. URBANEK established several new graptolite zones which were subsequently confirmed not only in other Polish sections but also in a number of coeval sections throughout the world. The thickness of the Ludlow (Gorstian) Series varies between 270 m on the Łeba Elevation to 350 m in the Lębork IG-1 borehole (TOMCZYK 1968).

The Late Ludlow (Ludfordian) Series displays a considerable increase in the thickness of the deposits, 800 m at the most, starting from the *aversus* Zone and embracing vast areas of the western part of the Peribaltic Syneclise. The muddy fraction becomes more prominent. The graptolite faunas present in clayey interbeds allow zonal subdivisions from the *aversus* Zone to the *spineus* Zone (URBANEK and TELLER, this volume, p. 35).

The latest unit of the Silurian, the Přidoli Series is distinctly regressive, the basin showing signs of gradual shallowing and general disappearing as a result of the final stage of the Caledonian orogeny. The clayey-muddy facies gives way to a marly-carbonate one with abundant benthic faunas in frequent carbonate intercalations, whilst graptolite plankton becomes eliminated.

The western Peribaltic Syneclise, as demonostrated by trilobites and ostracodes (TOMCZYKOWA and WITWICKA 1972, 1974), contains only the Lower Přidoli, the absence of its upper part and of Devonian deposits being probably due to the pre-Permian erosion.

The southern slope of the western part of the Peribaltic Syneclise can be traced in Poland to the Lithuanian and Russian borders as a narrow belt extending from the Gołdap IG-1 borehole in the East as far as the Żarnowiec IG-1 borehole in the West. The Silurian deposits recorded here show a greater carbonate content and reduced thickness. That sedimentation occurred in much more shallow conditions is evidenced by the presence, in the Early Llandovery, of nodular limestone overlying Ordovician deposits with only a small break in sedimentation. The complex of younger Silurian sediments contains a much greater proportion of carbonates yielding a rich graptolite fauna. Here again various units of the latest

Silurian are sometimes missing; where they do occur, marls bear abundant benthic faunas, especially trilobites, which make careful biozonation possible (TOMCZYKOWA 1988).

In this region, the development of the Silurian sedimentation is closely associated with facial zones typical of the East Baltic Basin. As a result of the recent Masurian–Suwałki Elevation, whose Silurian deposits have been eroded, these zones (Fig. 1) were connected with the eastern part of the Podlasie Depression and the Bug Depression, extending further through Volhynia and what is known today as Podolia and as far as the Black Sea in the south east.

The Podlasie Depression (Fig. 1). — The western Epigothic EEP was strongly restructured during the Caledonian and Variscan times. The megastructures that appeared then had a great impact on the development of the Palaeozoic sedimentation cover (POŻARYSKI 1968). The Podlasie Depression was formed due to the elevation of the Masurian–Belarus Anteclise as late as the Variscan time (SUVEJZDIS 1968). The Baltic Syneclise was split into the Peribaltic Syneclise which developed in the North and the Podlasie Depression situated to the South of it. The Bug Depression and the Łuków–Wisznica horst (POŻARYSKI 1968) also appeared at the same time.

Silurian deposits recognized in the Podlasie Depression show a considerable facial diversity, as well as the lack of some stratigraphic units at the base and the top of the series. In the western part of the Depression (boreholes: Okuniew IG-1, Dobre IG-1, Terebin IG-1, Żebrak IG-1, Siedliska IG-1, and others, TOMCZYK 1975a, c, d, TOMCZYKOWA and TOMCZYK 1979), various parts of the Early Llandovery are represented by argillaceous-muddy deposits that overlie Late Ordovician deposits with a Taconian hiatus. Their age is well-established due to graptolites occurring in all sections.

The Ludlow and Přidoli Series continue the argillaceous-muddy sedimentation, although some parts have been removed by post-Silurian erosion. The erosion surface of the Silurian is overlain by Carboniferous, Permian, or Jurassic deposits. The thickness of the Silurian deposits, ranging within 300–1300 m, increases considerably towards SW, especially those of the Ludfordian.

The eastern part of the Depression (boreholes: Wrotnów IG-1, Biała Podlaska IG-1, Terespol IG-1, Mielnik IG-1, Stadniki IG-1, Bielsk Podlaski IG-1, and Widowo IG-1, TOMCZYKOWA 1988) displays a chiefly carbonate-marly facies, with the base of the section being made up of the most completely developed Wenlock and partly Llandovery Series overlying the Ordovician strata with a sedimentation hiatus (PUSHKIN *et al.* 1991). Abundant graptolites (URBANEK 1966, 1970) and trilobites (TOMCZYKOWA 1988) allow the age to be confidently defined.

The Ludlow is dominated by marly deposits yielding a rich graptolite fauna which served as the basis for not only a new zonal subdivision scheme of the series (TELLER 1971; URBANEK 1963, 1970, 1971), but also for establishing the presence of a new, heretofore unknown developmental stage of this fauna.

The Přidolian Series is complete only in the lower part, its upper member having been removed by erosion. The thickness of the Silurian succession varies between 9 and 225 m and is incomplete.

Towards SW, the belt containing Silurian deposits tapers out, and, on the Łuków–Wisznica horst, they are completely absent.

The Bug Depression (Fig. 1). — In the Bug Depression, Silurian deposits are shown to be present in deep boreholes: Kaplonosy IG-1, Krowie Bagno IG-1, Busówno IG-1, Chełm IG-1, Białopole IG-1, Narol IG-1, Terebin IG-1, and Strzelce IG-1) (TELLER 1964; TOMCZYKOWA 1988). Some of the sections repeatedly display the transition from the marine Silurian to the marine facies of the Early Gedinnian (Early Lochkovian). Argillaceous-muddy sediments prevail, their carbonate-content increasing towards the top. This is evidenced by fine intercalations of argillaceous limestone and carbonate nodules. Complete Silurian sections as well as the Early Devonian developed in the Rhine facies (Gedinnian) can be traced on the basis of abundant graptolites (TELLER 1964; TOMCZYKOWA and TOMCZYK 1979). Apart from graptolites, there are abundant and diverse benthic fauna (trilobites, bivalves, crinoids, brachiopods, and others) (KOREJWO and TELLER 1964; TOMCZYKOWA 1975), revealing strong ties with the Mediterranean (Palaeotethys). The unfolded Silurian of the Bug Depression extends south-westwardly as far as the T.T. lineament, whilst coeval strongly folded sequences have been discovered on the foreland of the area elevated by the EEP in the Ruda Lubycka and Rawa Russkaya boreholes and also in the boreholes near the city of Lvov. The thickness of the undeformed Silurian deposits of the Bug Depression can attain 1100 m.

The East European Foreland (Fig. 1). — Penetrated in only a few wells, Silurian deposits of the T.T. lineament zone are associated with the Caledonian structural complex. Their folding and, probably, partial overthrust onto the rigid platform occured during the fading phases of the Caledonian orogeny (Dadlez 1967, 1974a, b; Znosko 1962, 1963, 1964, 1965, 1970; Modliński 1968, 1982; Teller 1969, 1974; Teller and Korejwo 1968a, b, c; Tomczyk 1980).

In NW Poland, various fairly thick members of Llandovery, Wenlock and Ludlow deposits have been documented as lying below the Devonian, Carboniferous or the Permian deposits of the Koszalin–Chojnice zone (Modliński 1968; Teller and Korejwo 1968a, b, c; Czermiński 1967; Dadlez 1967; Hajłasz 1967).

In the boreholes of nearby Rugia, however, Franke (1967, 1978) and Jaeger (1967) have encountered a very thick complex of variably dipping Ordovician graptolitic shales.

In Central Poland (the Warsaw Synclinorium), the Caledonian structural complex is rather poorly known (Dadlez 1974a, b). Silurian sediments penetrated in several borings attain a considerable thickness and must have been deposited in a geosynclinal basin. However, volcanism and intrusive magmatism are lacking, and there are no signs of Caledonian movements. The presence of Upper Silurian folded deposits has also been recorded in the extreme SE Polish part of the T.T. lineament, in the Ruda Lubycka borehole (Tomczyk 1962; Teller 1964), and also not far away, but already beyond the Polish border, in the Rava Russkaya well.

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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 Syneclise (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 Syneclise 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 Lębork 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 Gołdap 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 conected 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).

Prevaling 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 Syneclize. Their thickness attains 100 m, and they grade vertically into Ludlow deposits, appearantly 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. murchisoni* 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* (MENEGHINI) 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* MENEGHINI, 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* (MENEGHINI), *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-DAWIDZIUK 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-DAWIDZIUK 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. obtectus* (KOZŁOWSKA-DAWIDZIUK). The last three species belong to gothograptids, which in the upper part of the Wenlock Series are represented only by *G. nassa* (HOLM) (KOZŁOWSKA-DAWIDZIUK 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.

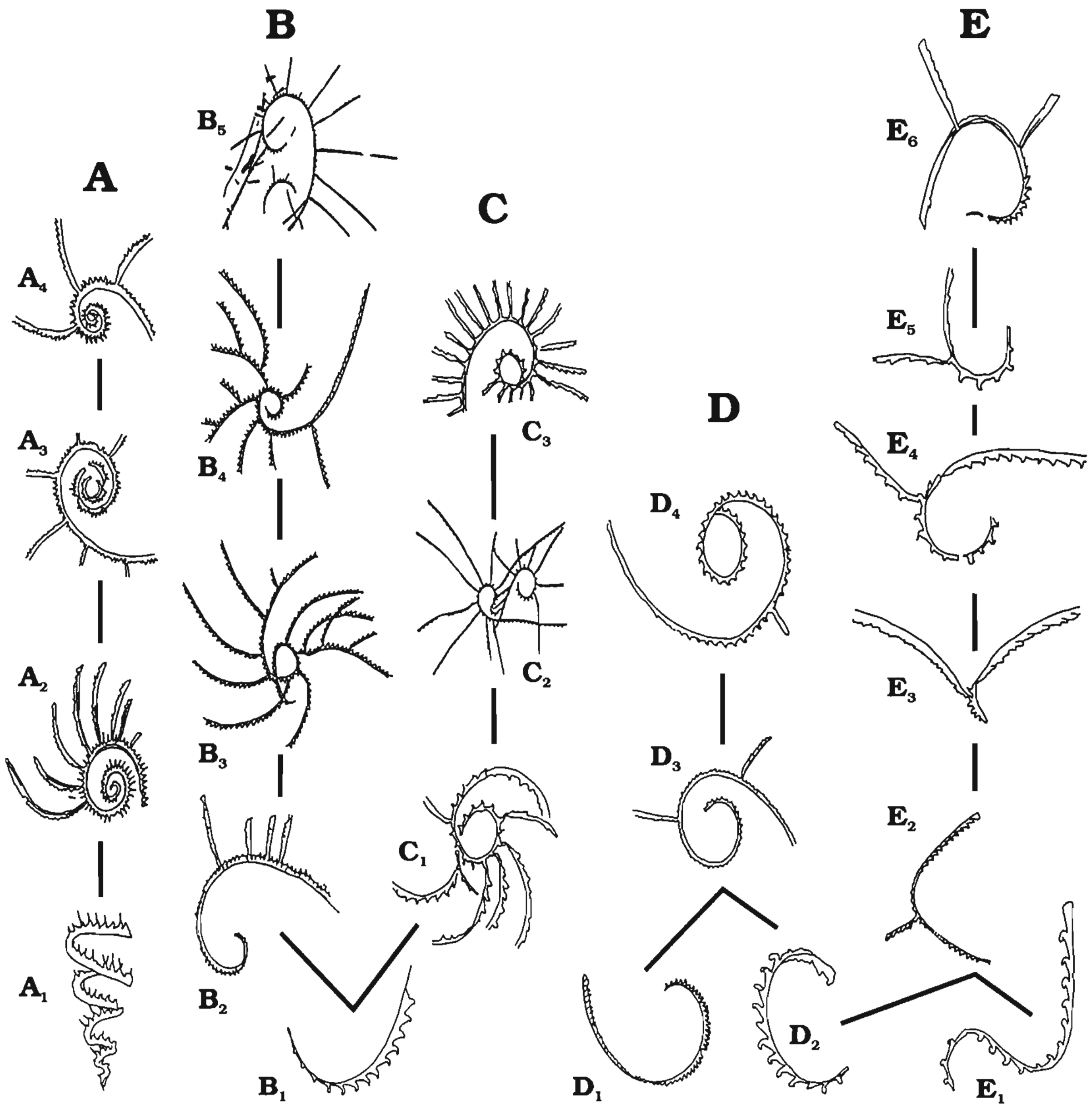

Fig. 1
Tentative phylogeny of cyrtograptids; A–E main trends in morphological evolution, further explanations in text.

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* (A_2) and *C. solaris* (A_3), together with early Wenlock *C. centrifugus* (A_4). They share the folowing 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* (A_1) (MELCHIN and LENZ 1986; LENZ and MELCHIN 1989).

The second group (B) which, according to the present author, comprises *C. polyrameus* (B_2), *C. laqueus* (B_3), *C. murchisoni* (B_4), and *C. ramosus* (B_5), displays an incomplete or closed planispiral coiling of the proximal part, a fairly simple thecal morphology, and thecal cladia budding at varying distanses from one another (BJERRESKOV 1975, 1992; LENZ and MELCHIN 1989, 1991; LENZ 1978). The presence of the cladia of the second [*C. laqueus* (B_3), *C. murchisoni* (B_4)], or third [*C. murchisoni* (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. murchisoni* 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* (C_1), *C. mancki* (C_2), and *C. radians* (C_3). 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* (D_3) and *C. insectus* (D_4) 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 (D_1), but they could also be a continuation of two independent lineages, *M. decipiens* (D_1) and *M. flagellaris* TÖRNQUIST (D_2).

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* (E_6) 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* (E_2) from the late Llandovery (LENZ and MELCHIN 1991), *C. rigidus* (E_3), *C. perneri* (E_4), *C. hamatus* (E_5), and *C. lundgreni* (E_6). The ancestry may be seen in Llandovery monograptids from the *tullbergi* (E_1) (LENZ and MELCHIN 1989) or *flagellaris* (D_2) 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 presevation 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 to 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 interpretration of the *nilssoni* Zone as the base of the Gorstian stage as presently understood (LAWSON and WHITE 1989), and finally we discuss the Gorstian to *leintwardinesis* 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 Gołdap 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 Homerian 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 Subcommission (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 *ludgreni* 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 Subcommision.

The borehole sections with complete coring (such as Żarnowiec IG-1, Prabuty IG-1, Pasłęk IG-1, Lębork IG-1, Bartoszyce IG-1, Gołdap IG-1 and some others) feature unbroken sequences across the *lundgreni–nassa* turnover interval. Unfortunatelly, 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 Homerian (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 eponyomous 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 changes in a number of cladia (JAEGER 1969). Its characteristic organ, the virgellarium, was observed for the first time by TELLER (1964) in Přidolian linograptids from the Chełm IG-1 boring (EEP), although this structure must have been acquired earlier (well before the *latilobus* Zone, that is by the end of the early Ludfordian. This assumption was recently confirmed by ŠTORCH (1995), who found *L. posthumus posthumus* provided with virgellarium in the *kozlowskii* Zone of Barrandian.

After having emerged in the *N. nilssoni* Zone, the linograptid trend continued its directional evolution to become extinct as late as the *M. praehecynicus–hercynicus* Zone. During this considerable time-span it underwent remarkable changes which, evaluated taxonomically, led to the origin of three genera (*Neodiversograptus, Linograptus*, and *Abiesgraptus*). Except for the late (terminal) diversification of *Abiesgraptus* into a number of co-occurring species (unknown from the EEP), the bulk of the lineage was represented by sequential species (chronospecies), replacing each other in time. In this sense linograptids are unique, as they constitute a single line of descent in which large macroevolutionary effects were attained due to phyletic evolution (see URBANEK, this volume, p. 235).

Apart from *N. nilssoni*, linograptids have a minor stratigraphic significance, being represented by either rather rare (*N. beklemeshevi*) or long-lasting (*L. posthumus*) species. They, however, represent a unique group of truly pelagic monograptids with a sophisticated colony pattern and several striking contrivances, e.g. virgellarium, and multiple budding from the sicula.

The above picture of faunal diversity in the *nilssoni* Zone has been recently completed by the study of RICKARDS *et al.* (1994) on graptolite fauna of the Quarry Creek district in New South Wales (Australia). Along with the cosmopolitan elements, which enabled the recognition of *nilssoni* and *progenitor* Zone, a number of endemic elements were found. In the former zone they are represented foremost by early multiramous forms, assigned by RICKARDS *et al.* (1994) to *Linograptus* (*L. orangensis*), as well as by transients between lobograptids and true bohemograptids (*Bohemograptus urbaneki*), providing new evidence for a close relationship between these lineages (see also URBANEK, this volume, p. 237). Unusual, however is an earlier-than-expected occurrence of advanced lobograptids such as *L. simplex* and *L. exspectatus*. As observed by RICKARDS, these species have not been seen in *nilssoni* assemblages elsewhere. In my opinion these strata may represent a younger horizon, namely the *scanicus* band. Moreover, their co-occurrence with *N. nilssoni* disagrees with the earlier suggested morphological order of their evolution. While certain differences might be expected when comparing sequences from remote areas, Australian *nilssoni* fauna represents a sort of anomaly which needs more comparative studies in order to be properly evaluated.

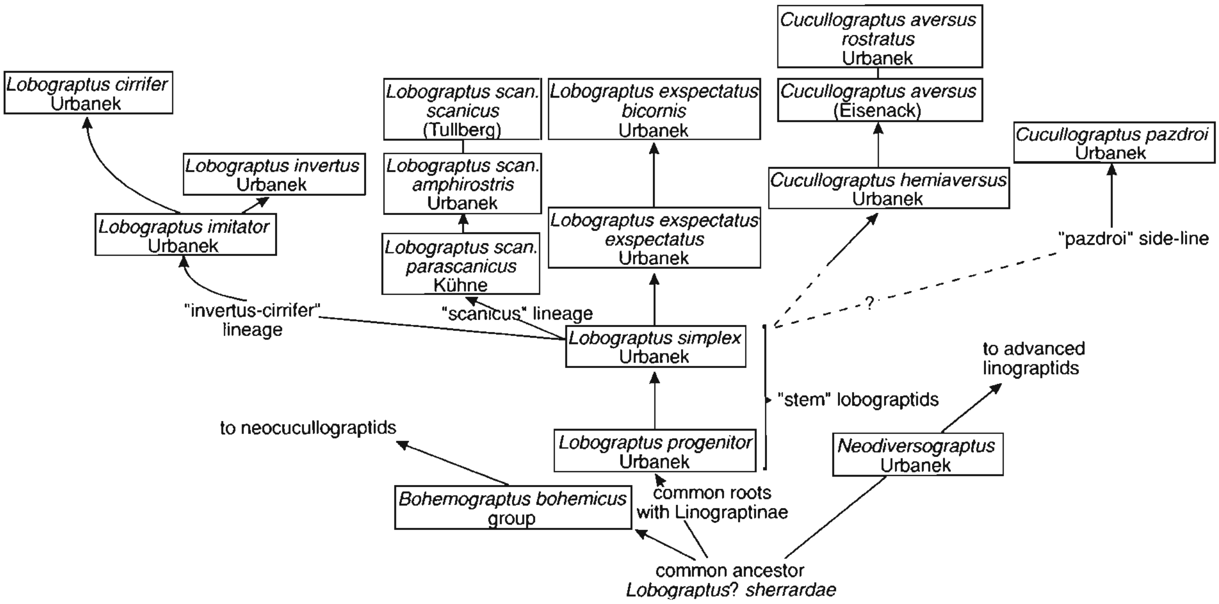

Fig. 2

Tentative phylogeny of Cucullograptinae as illustrated by material isolated from the Mielnik IG-1 borehole (after URBANEK 1966, modified). Diagram shows also the adaptive radiation which occurred in relatively short interval of time from nonspecialized "stem" lobograptids.

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 Homerian 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-the 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 *exspectatus* 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*).

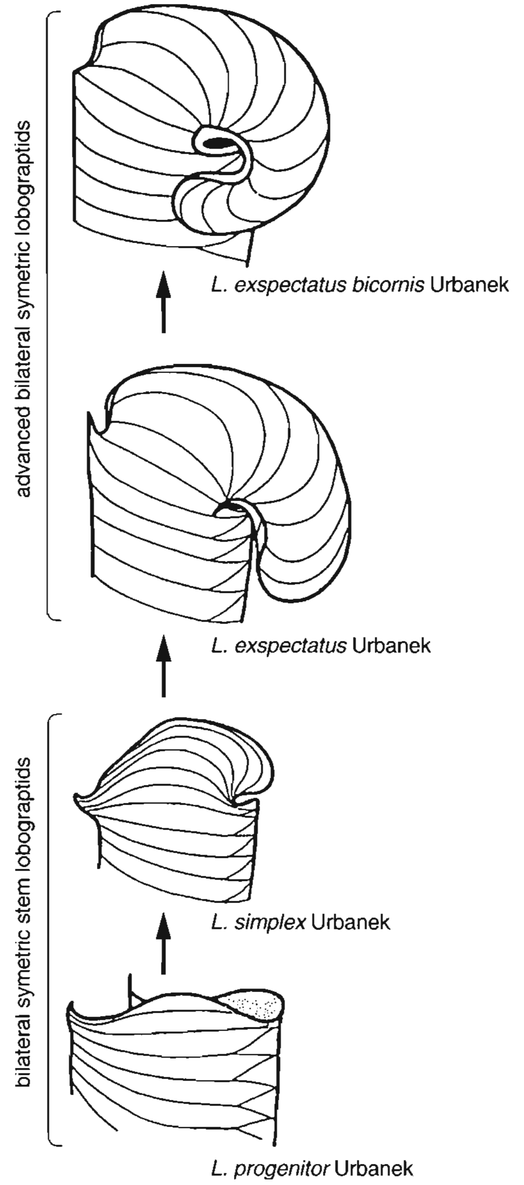

Fig. 3
Diagram revealing the origin and evolution of apertural apparatus in bilaterally symmetric lobograptids (S-cucullograptids). Note the gradual increase in the size of apertural lobe until the beak-like termination is formed (after URBANEK 1966).

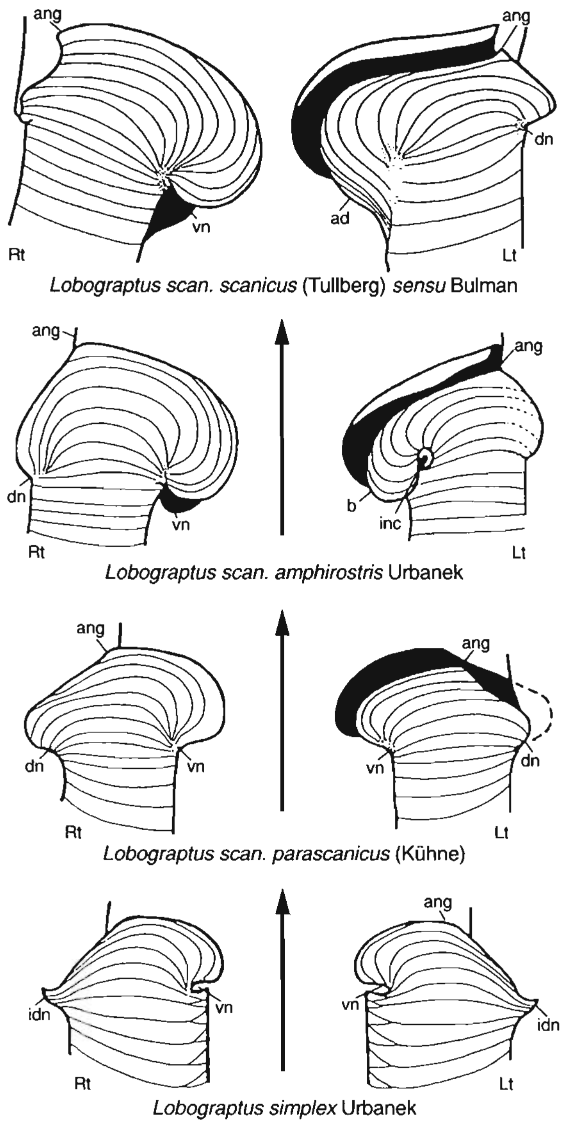

Fig. 4

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 aperural lobe, b – beak-like ventral termination of the lobe, dn – dorsal node, idn – incipient dorsal node, vn – ventral node.

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 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.

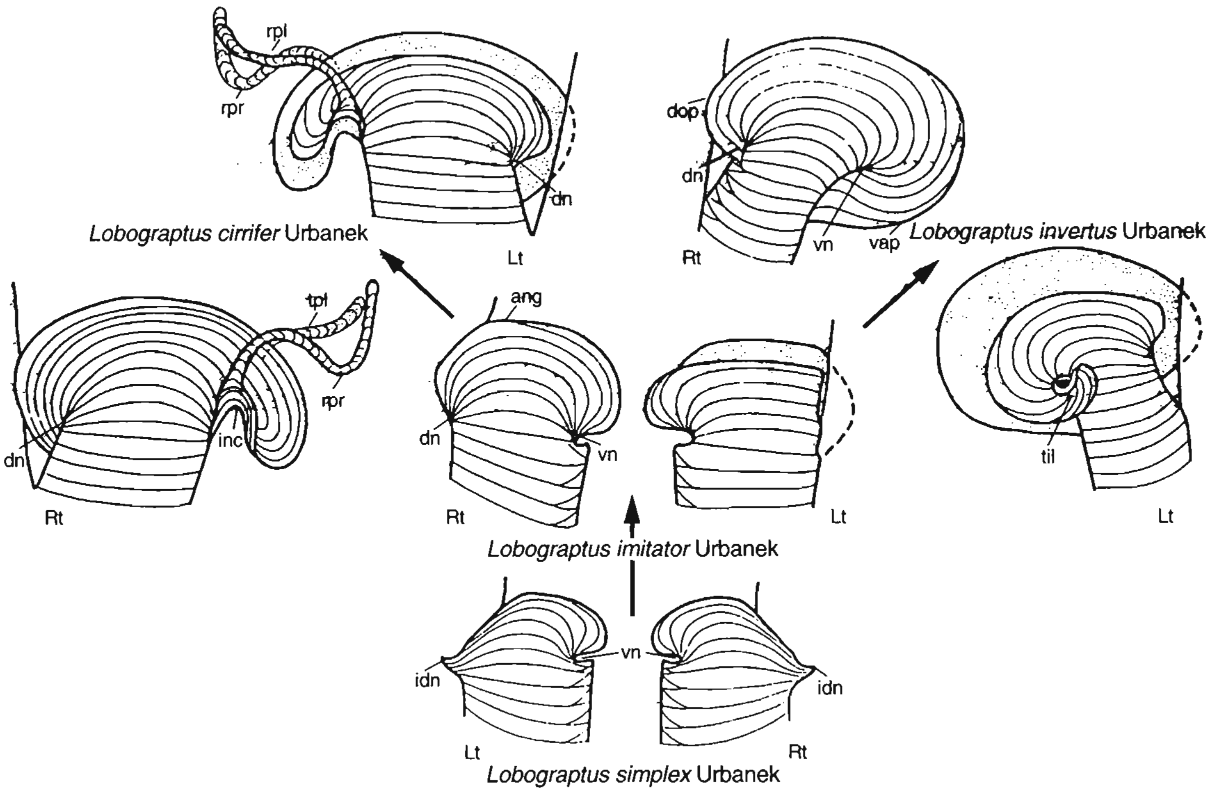

Fig. 5

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 charateristic 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

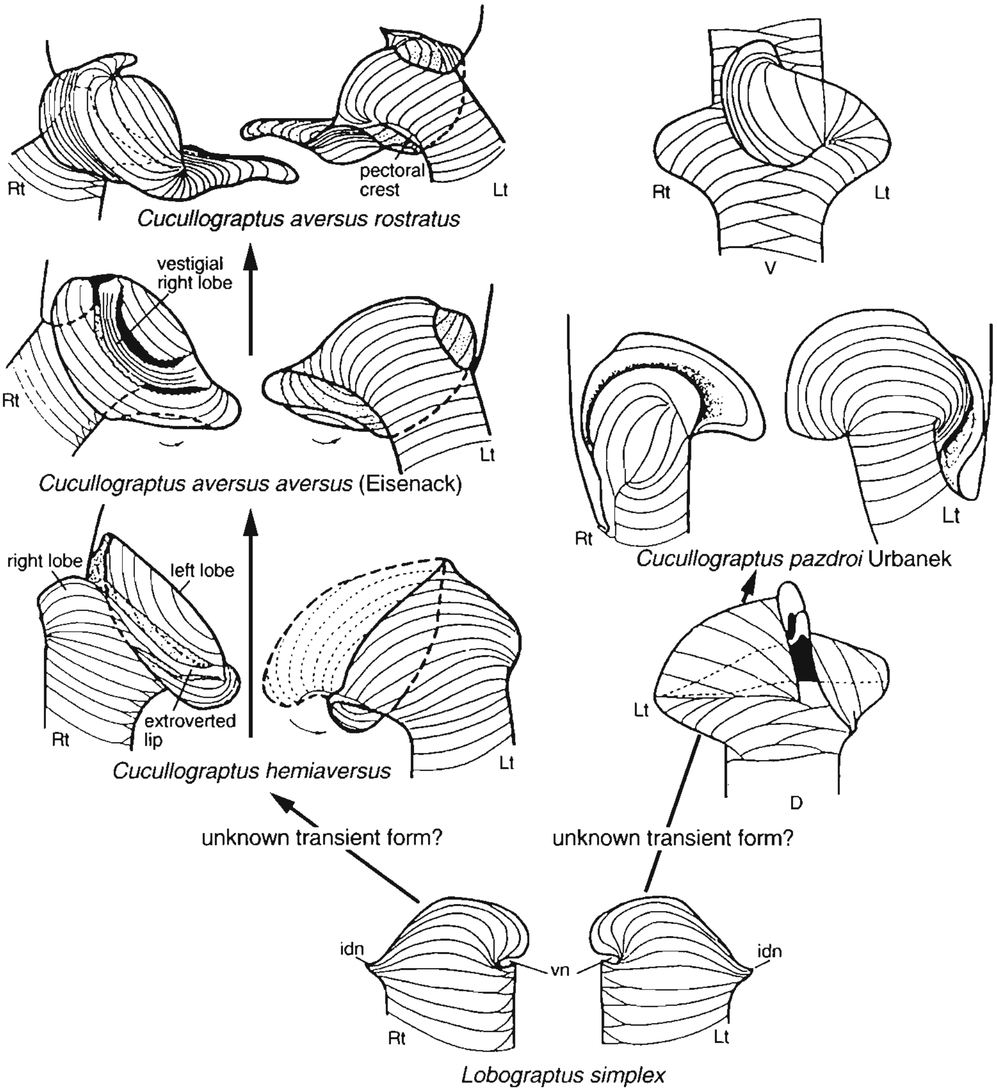

Fig. 6

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			*Istrograptus t. transgrediens*		5
			Monograptus perneri		
			Monograptus bouceki		
			Istrograptus t. samsonowiczi		
			Istrograptus t. chelmiensis		
			Neocolonograptus lochkovensis	*N. l. lochkovensis* Subzone *N. l. branikensis* Subzone	
			Neocolonograptus ultimus		
			Neocolonograptus parultimus		
LUDLOW	LUDFORDIAN	UPPER	*Monograptus (U.) spineus*		4
			Monograptus (U.) protospineus		
			Monograptus (U.) acer	*M. (U.) acer aculeatus* Subzone *M. (U.) acer acer* Subzone	
			Pseudomonoclimacis latilobus / M. (Slovinograptus) balticus		
		LOWER	*Neocucullograptus kozlowskii*		3
			Neocucullograptus inexspectatus		
			Neolobograptus auriculatus		
			Bohemograptus cornutus		
			Bohemograptus praecornutus		
			Cucullograptus aversus (= S. leintwardinensis)	*C. aversus rostratus* Subzone *C. aversus aversus* Subzone	2
	GORSTIAN		*Cucullograptus hemiaversus*		
			Lobograptus invertus		
			Lobograptus scanicus parascanicus		
			Lobograptus progenitor		
			Neodiversograptus nilssoni		
WENLOCK	HOMER		*Colonograptus ludensis*		
			XX zones between *nassa* and *ludensis* on Polish part of the EEP not yet recognized		
			Gothograptus nassa		
			Cyrtograptus lundgreni		1
	SHEINWOOD		*Cyrtograptus ellesae*		
			Cyrtograptus rigidus		
			Monograptus belophorus (= M. flexilis)		
			Monograptus antennularius		
			Monograptus riccartonensis		
			Cyrtograptus murchisoni		
			Cyrtograptus centrifugus		

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

Cucullograptus aversus (EISENACK)	1) *Cuc. aversus rostratus*	*S. leintwardinensis* (HOPKINSON)
	2) *Cuc. aversus aversus*	*Saetograptus fritschi* (PERNER)
Cucullograptus hemiaversus URBANEK		
Lobograptus invertus URBANEK		
L. scanicus parascanicus (KÜHNE)		*S. chimaera chimaera* (BARRANDE)
Lobograptus progenitor URBANEK		*S. chimaera cervicornis* URBANEK
Neodiversograptus nilssoni (BARRANDE)		*Colonograptus colonus* (BARRANDE) *sensu* 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 bettter understanding of their morphology (EISENACK's study on the Baltic erratic material, 1951) and stratigraphic distributiuon (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 Homerian 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 incompletness 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 reappeares 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 kozlowskii* 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 apprearance 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

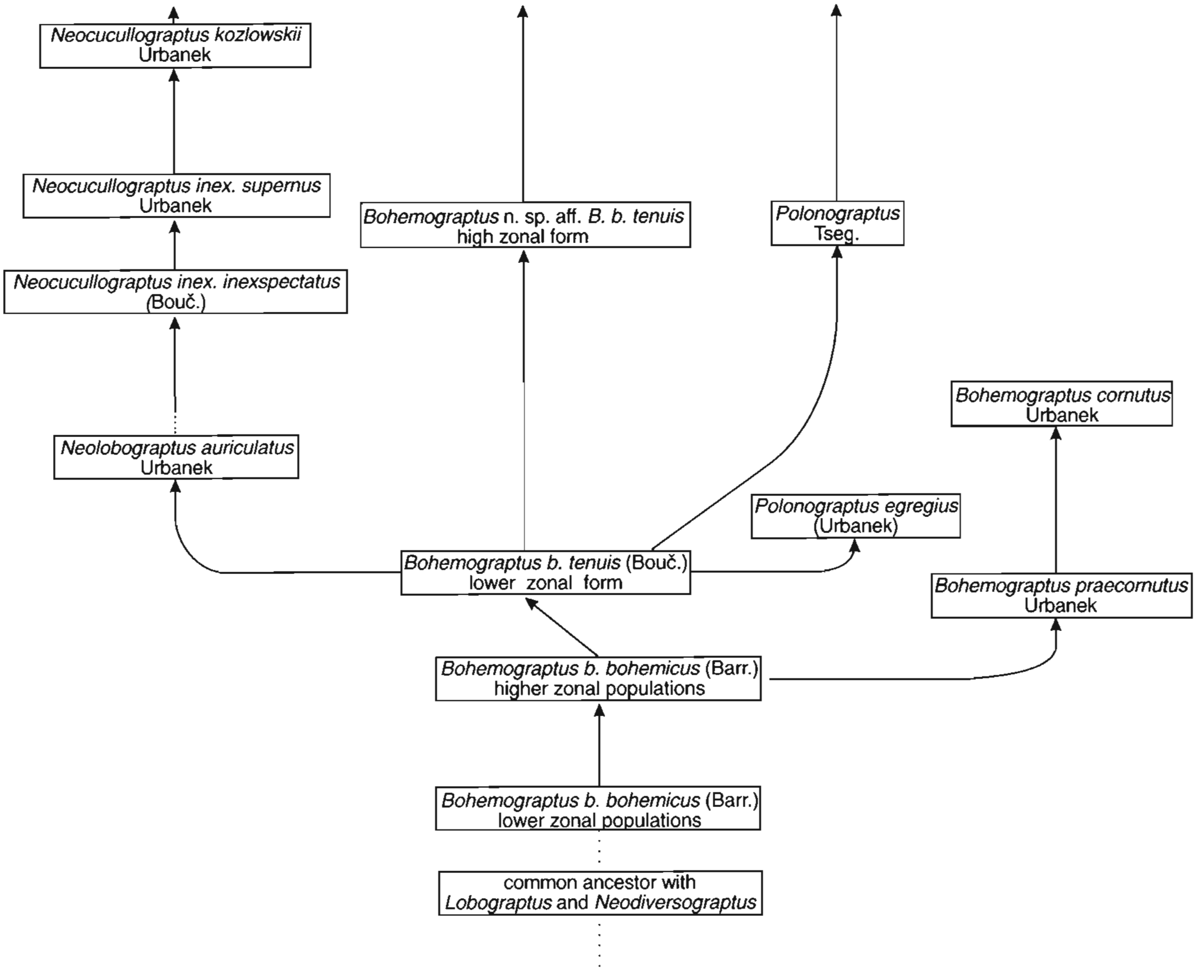

Fig. 7

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 suggests 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 *fritschi linearis* Zone and the

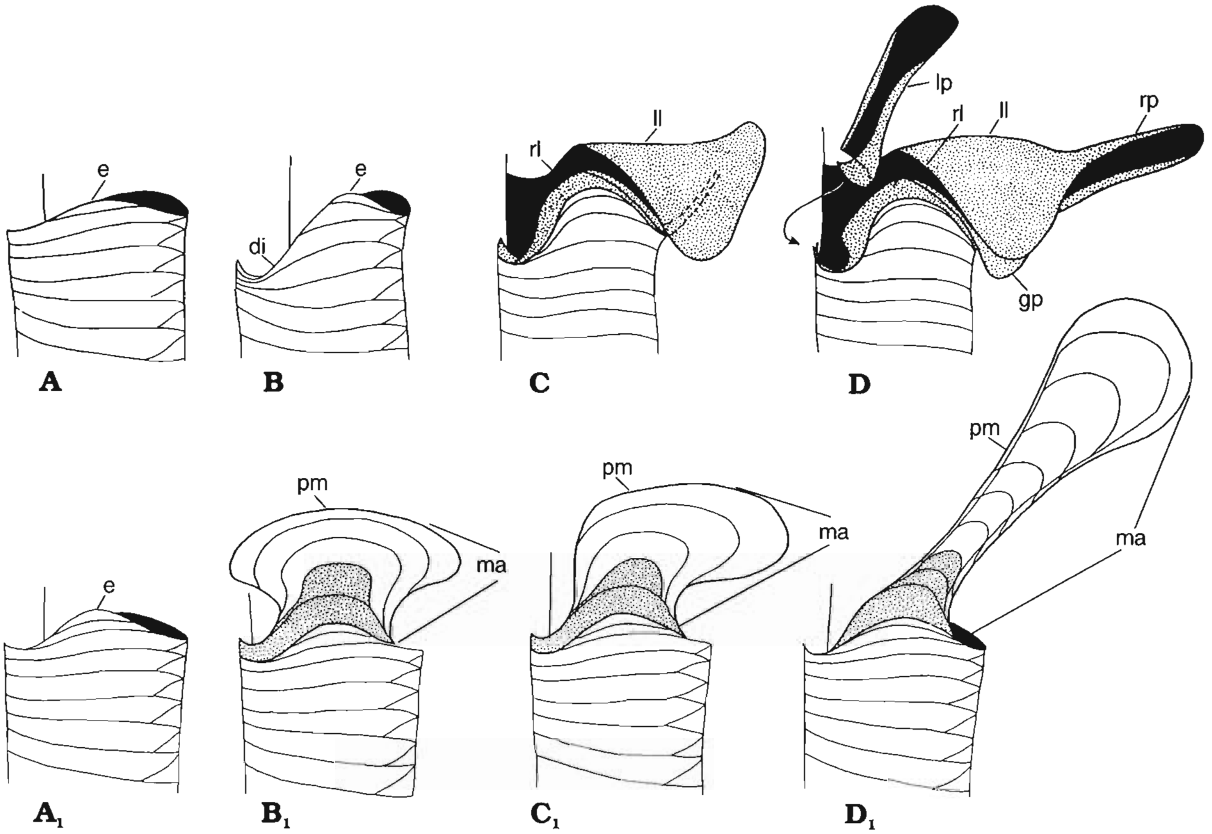

Fig. 8

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 (**A**$_1$–**D**$_1$). 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 inexspectatus,* 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* (**A**$_1$) followed by *Bohemograptus praecornutus* (**B**$_1$–**C**$_1$) 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* (**D**$_1$). 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 relativelly 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. 7A$_1$–D$_1$). 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" appearence. The other line initiated a trend which soon split into *Neolobograptuxs auriculatus* and the higher zonal populations of *Bohemicus 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 *inexspectatus–kozlowskii* Zones. It matches *Bohemograptus garratti* described from the *kozlowskii* 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 Lesnianskaya 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 inexspectatus* and *N. kozlowskii* – 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

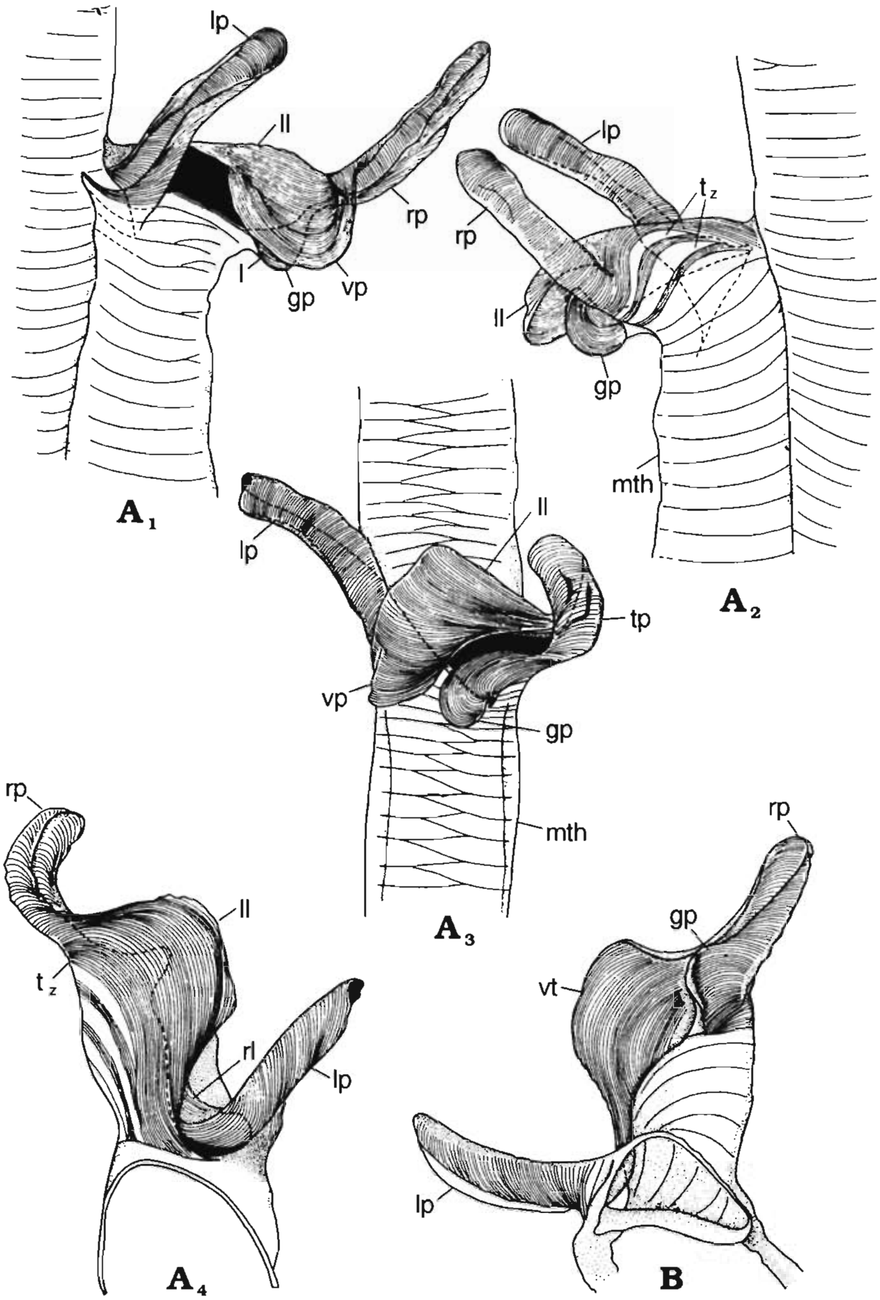

Fig. 9

Advanced apertural apparatus in *Neocucullograptus kozlowskii* seen in different aspects (**A**$_1$–**A**$_4$. **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 assignement 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 *inexspectatus–kozlowskii* Zone of the Kosov Quarry, a well-known locality near Beroun (Kopanina Formation, Barrandian), an assemblage of polonograptids (*P. egregius, P. podoliensis 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 CHLUPAĆ in the Velky vrch (Koneprusy) section, at the same level and within the bed of the same lithology (dark grey bituminuous 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. inexspectatus–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 asemblages 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,

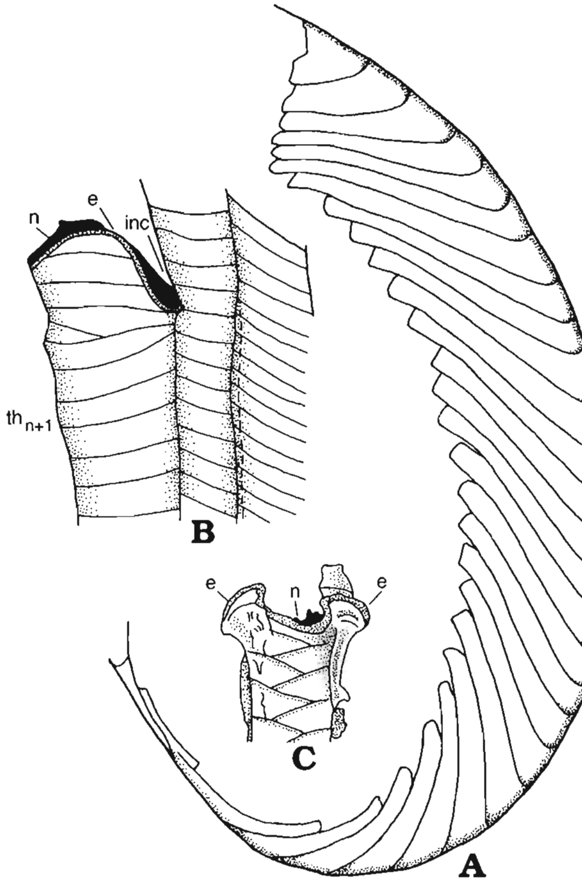

Fig. 10
Third major trend of morphological evolutiom amongst early Ludfordian monograptids is represented by *Polonograptus*. It displays a rapid increase in the length and overlap of thecae as seen in *P. podoliensis* PŘIBYL, 1983 (**A**) combined with only limited modifications of thecae, producing 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 (= *kozlowskii* 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 (Uncinatograptus) 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 subspecies and, therefore of two discrete subzones. The next horizon is marked by the occurrence of *Monograptus (Uncinatograptus) 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-occurence 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 *kozlowskii* 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 — sicula, Vi – virgella, pV – pseudovirgula, Th – theca, l – lapet, a – aperturae, sp – spine.

Cyrtograptus radians (TÖRNQUIST)

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

Cyrtograptus perneri BOUČEK

2. Two proximal thecae with long spines, *ellesae* Zone; × 50.

Cyrtograptus hamatus (BAILY)

4. Thecal cladium with three thecae, *lundgreni* Zone; × 30.

Cyrtograptus lundgreni TULLBERG

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

Monograptus belophorus MENEGHINI

7. Medial thecae, *belophorus* Zone; × 30.

Monograptus antennularius (MENEGHINI)

9. Lateral view of a hooked theca, *antennularius* Zone; × 200.

Monograptus flexuosus (TULLBERG)

10. Medial three thecae, *antennularius* Zone; × 30.

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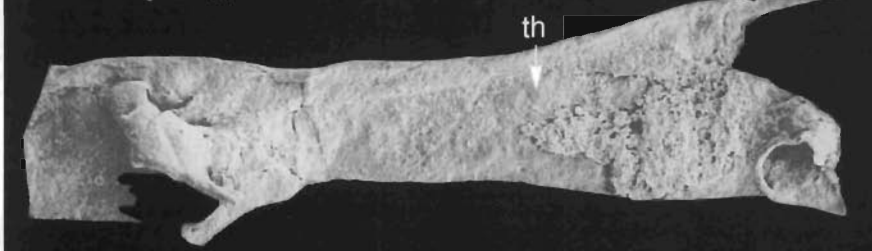

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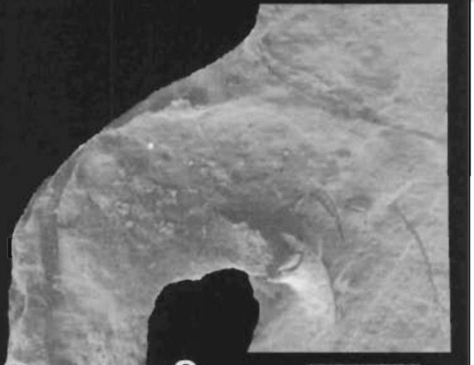

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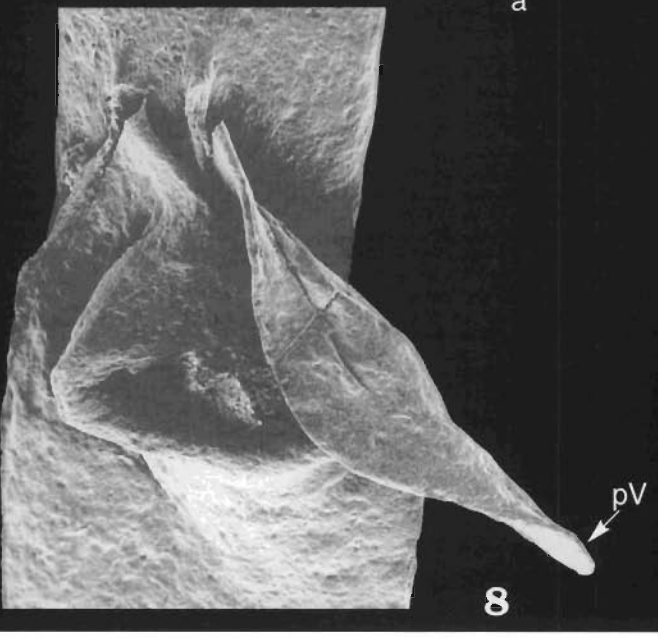

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GRAPTOLITES AND STRATIGRAPHY OF THE WENLOCK AND LUDLOW SERIES
IN THE EAST EUROPEAN PLATFORM

PLATE 2

Representative thecal morphologies in monograptids of the Wenlock Age. All samples from the Zawada-1 well. Abbreviations: Vi – virgella, Si – sicula, Th – theca, Sp – spine, l – lapet, e – ear, h – hood.

Cyrtograptus lundgreni TULLBERG

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

Monograptus flemingi (SALTER)

3. Proximal thecae and sicula, *antennularius* Zone; × 30.

Cyrtograptus rigidus TULLBERG

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

Monograptus (Testograptus) testis (BARRANDE)

5. Juvenile rhabdosome, *lundgreni* Zone; × 30.

Monograptus flexuosus (TULLBERG)

7. Apertural hood with open ears, *antennularius* Zone; × 125.

Monoclimacis zawadensis TELLER

8. Proximal thecae and sicula, *lundgreni* Zone; × 40.

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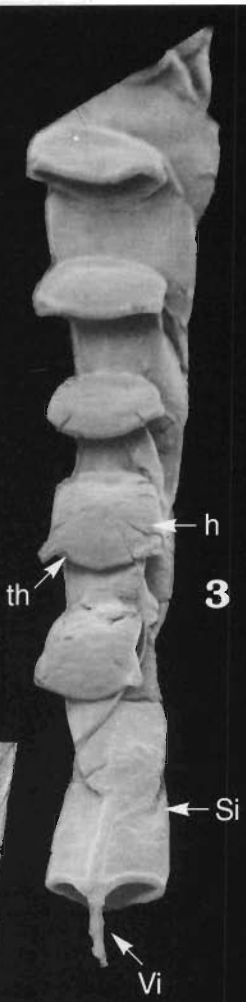

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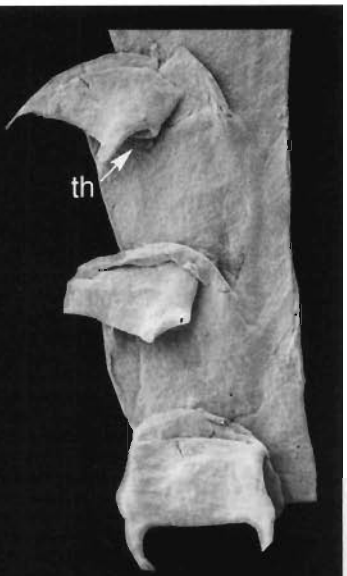

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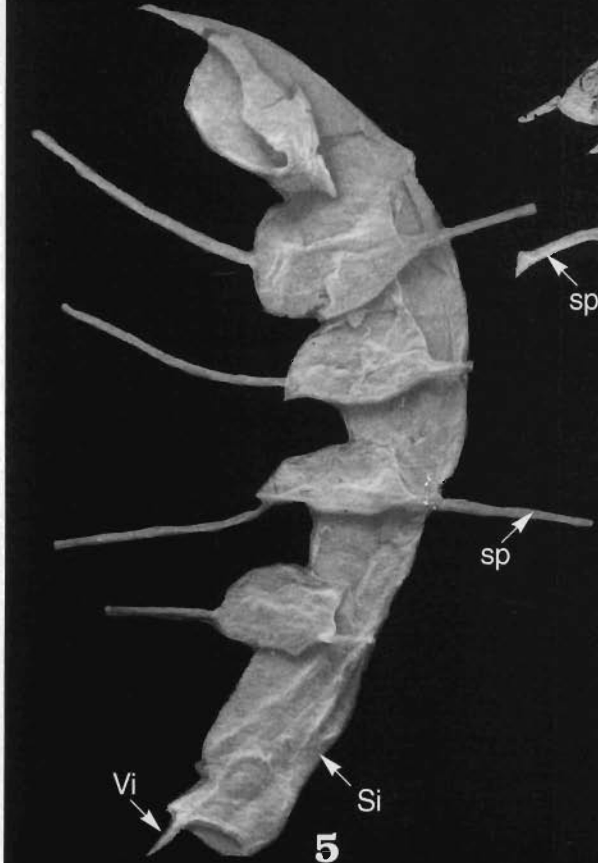

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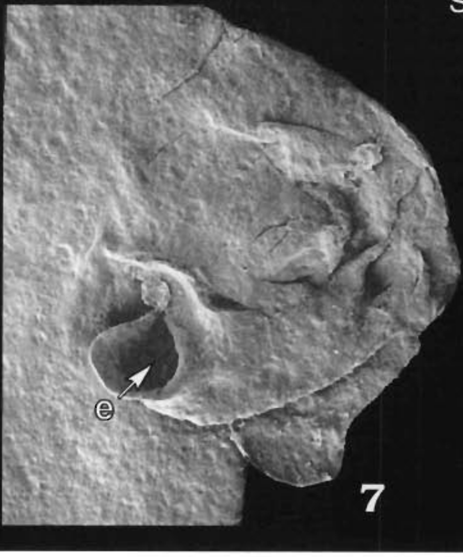

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GRAPTOLITES AND STRATIGRAPHY OF THE WENLOCK AND LUDLOW SERIES
IN THE EAST EUROPEAN PLATFORM

PLATE 3

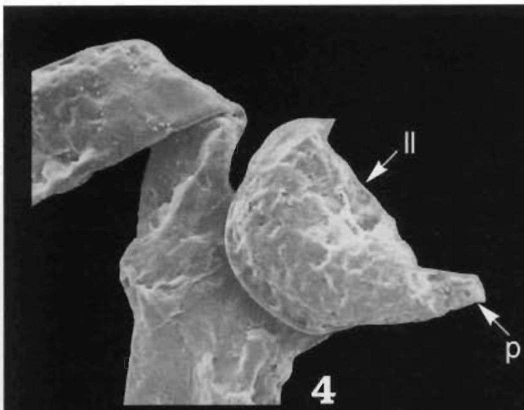
Representative thecal morphologies in monograptids of the Gorstian and early Ludfordian Age. Abbreviations: ll – left apertural lobe, rl – right apertural lobe, p – rostral process, pl – gular plate and dorsal eaves of the lobe.

Lobograptus scanicus parascanicus (KÜHNE)

1–2. Aperture of a R-cucullograptid, Baltic erratic boulders, S.181, W Pomerania, *parascanicus* Zone; × 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 × 110; 9, 10 × 25.



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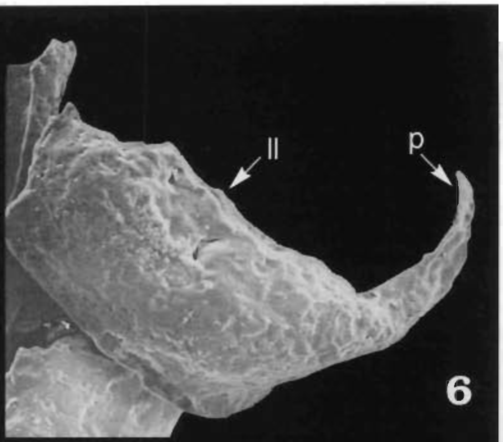

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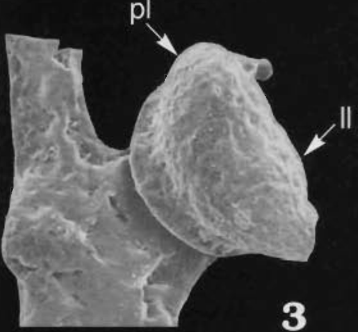

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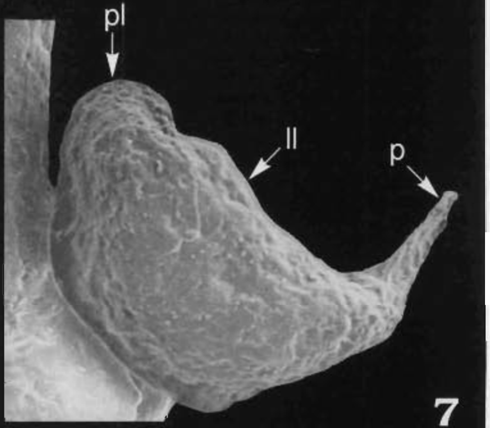

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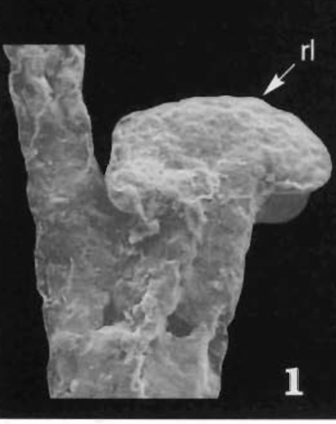

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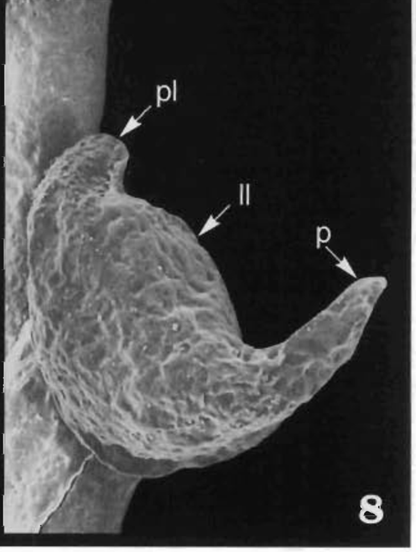

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PLATE 4

Representative thecal types of early Ludfordian Age.
Abbreviations: a – aperture, m – microfusellar additions, ll – lateral apertural lobe, p – rostral process, pl gular plate.

Neocucullograptus inexspectatus (BOUČEK)

1–2. Apertural apparatus, Mielnik IG-1 boring, depth 887.70 m, *inexspectatus* Zone; × 110.

Neocucullograptus kozlowskii 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, *kozlowskii* Zone; 3, 5 × 55; 4, 6, 7 × 110.

Bohemograptus bohemicus aff. *tenuis* (BOUČEK)

8. Simple thecal aperture (a), Mielnik IG-1 boring, depth 889.50 m, *inexspectatus* Zone; 8 × 180.

Bohemograptus praecornutus URBANEK

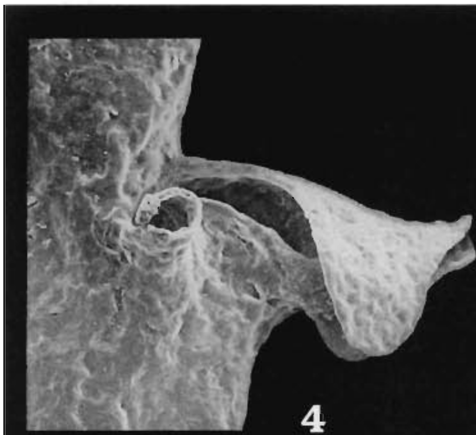
9. Thecal aperture with microfusellar additions (m), Mielnik IG-1 boring, depth 911.60 m, *praecornutus* Zone; 9 × 110.

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; × 130.

Neocucullograptus kozlowskii 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, *kozlowskii* Zone; × 130.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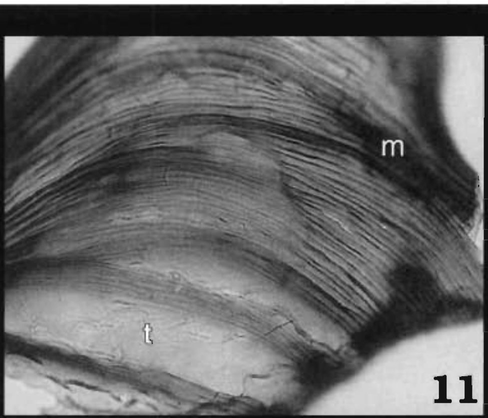

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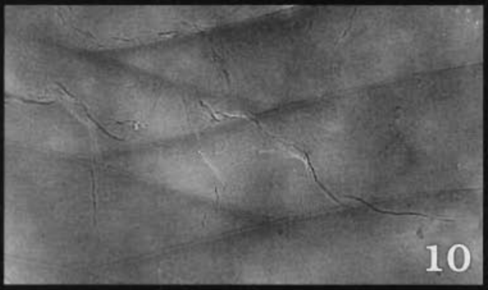
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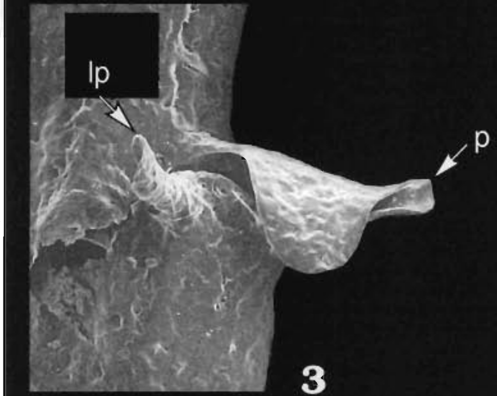

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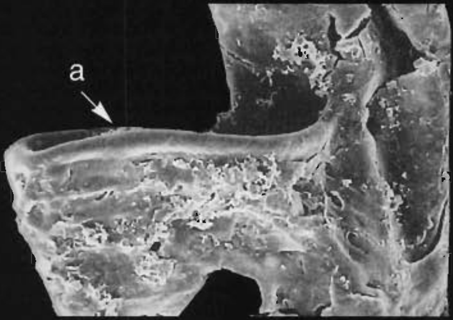

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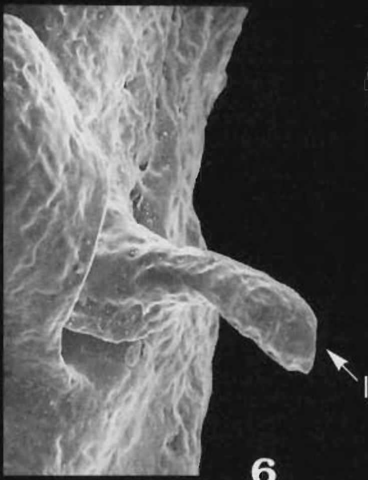

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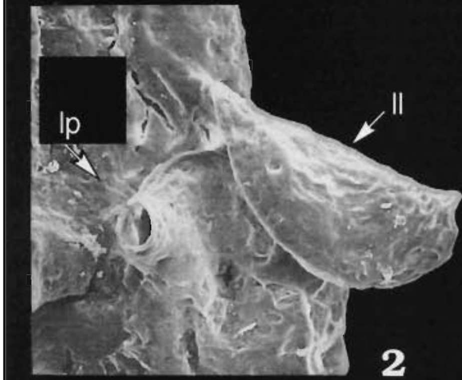

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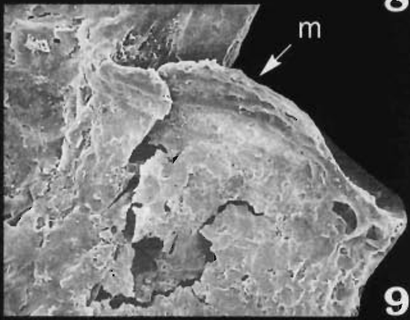

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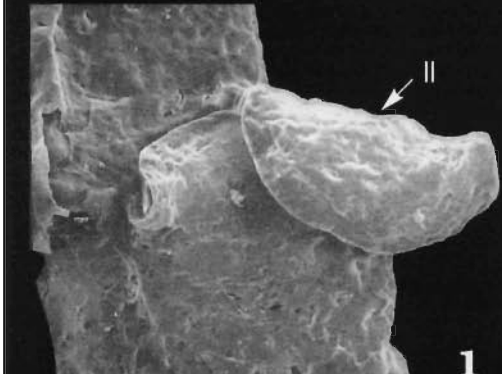

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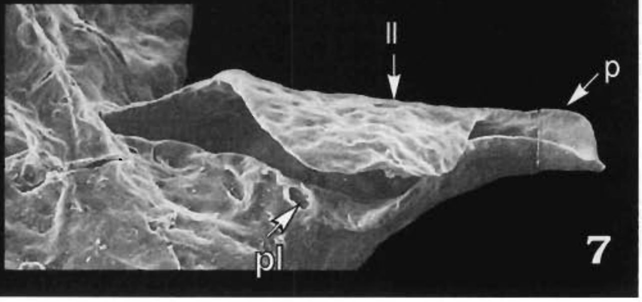

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GRAPTOLITES AND STRATIGRAPHY OF THE PŘIDOLI SERIES IN THE EAST EUROPEAN PLATFORM

LECH TELLER

Teller, L. 1997. Graptolites and Stratigraphy of the Přidoli Series in the East European Platform. *In:* A. URBANEK and L. Teller (eds), Silurian Graptolite Faunas in the East European Platform: Stratigraphy and Evolution. — *Palaeontologia Polonica* **56**, 59–70.

The paper revises the earlier information and updates the Přidolian biostratigraphy in the East European Platform as well as compares it to other areas. An improved zonal subdivision of the Přidoli in Chełm keysection is proposed and compared to the graptolite sequence in the type area of Barrandian. The stratigraphic significance of the *transgrediens* stock is demonstrated and the position of numerous low-diversity assemblages, dominated by *Linograptus*, is specified.

Key words: Silurian, Přidoli, biostratigraphy, correlation.

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CONTENTS

INTRODUCTION

The Přidoli Series was encountered within the Polish part of the EEP in the Chełm IG-1 borehole, in 1954–1955. The borehole was drilled in the Bug Depression, on the Uherka River, 1 km North of the town of the same name. Uppermost Silurian deposits were documented by graptolites and a rich benthic fauna. The faunas appear at a depth of 1207.7 m and continue to the total depth of the well at a depth of 1611.7 m.

It was the first borehole among those drilled by the Polish Geological Institute that revealed Silurian deposits in the Palaeozoic sedimentary cover of the EEP, and the second one in the history of that system's investigation in the area (DAHLGRÜN and SEITZ 1944).

The horizontal sediments, not folded during either the Caledonian or any other orogenic phase, represent a claystone facies with minor carbonate intercalations. They were deposited in the bathyal zone of the EEP slope and pass, without interruption, into the marine Lower Devonian of the Rhine facies (Gedinian). Preliminary stratigraphic conclusions based on the graptolite fauna encountered there were published by TOMCZYK and TELLER (1956). They showed that the graptolite and benthic faunas present in the sediments were typical of the Přidoli Formation of the Prague Basin, suggesting a close palaeogeographic affinity between the two areas. The sediments penetrated by the borehole were assigned, following PŘIBYL (1940), to the Middle Ludlow. The mis-correlation can be explained by the fact that, at that time, most of the stratigraphers engaged in the study of the Silurian, chiefly representatives of the British school, rejected a possibility of the presence outside the British Isles of muddy and carbonate series yielding graptolites and a benthic fauna that could be younger than the British Ludlow.

A detailed lithological and stratigraphic study of the Silurian from the Chełm IG-1 borehole section was published in a later paper (TELLER 1960) whereas the faunas, both graptolite (TELLER 1964) and benthic (KOREJWO and TELLER 1964), became the subject of separate later monographs.

In the stratigraphic part of the graptolite monograph (TELLER 1964), the Chełm IG-1 borehole section was regarded as coeval with the Upper Ludlow, which was a compromise with the generally accepted British subdivision rather than a definition of the true stratigraphic position of the series. It was not until the new subdivision of the Silurian System was accepted in 1984, officially establishing the Přidoli Series as the uppermost Silurian series entirely younger than the British Ludlow, that the proper stratigraphic position of the Chełm IG-1 section, a key-section for the Polish part of the EEP, was recognized.

Later (1960s–1970s), several additional boreholes were drilled in the Bug Depression. Characteristically, they revealed, below the marine Lower Devonian, a claystone complex containing graptolites of the late horizons of the Přidoli (boreholes: Busówno IG-1 1947.0–2890.0 m, Białopole IG-1 1577.5–1830.0 m, Terebin IG-1 1358.0–2648.0 m, Krowie Bagno IG-1 1850.0–2724.0 m, Strzelce IG-1 1424.0–1545.0 m, Strzelce IG-2 1732.5–1890.0 m, and Bachus 2133.0–2438.0 m, see TOMCZYKOWA 1988).

Still further East, in the Lublin Region, some wells, drilled below the marine Lower Devonian of the Rhine facies (Gedinian), encountered in stratigraphic continuity Přidoli graptolite – bearing claystones.

Boreholes drilled more to the North, in the eastern Podlasie Depression, penetrated Přidoli deposits of a somewhat different lithology, that being a widespread marly-limestone facies associated with the more shallow parts of the vast epicontinental basin (see p. 16 herein).

Strongly folded Přidoli sediments have also been penetrated further South of the Chełm IG-1 borehole, in the T.T. lineament zone, by the Ruda Lubycka well (TELLER 1964; TOMCZYK 1962). Beyond, but close to, the Polish state border, their presence has been reported in the Rava Russkaya borehole (SANDLER and GLUSZKO 1955).

When discovered, the Přidoli section in the Bug Depression was, next to that in the Prague Basin, only the second in the world. But with the course of time, thanks to wide-scale investigations conducted in various regions first in order to draw the Silurian/Devonian boundary, and then to introduce a new subdivision of the Silurian and to select the stratotype for the Přidoli Series, more and more sections were recorded where the Přidoli and Devonian age of the sediments was established on the basis of graptolites.

Within a fairly short time the presence of the Přidoli was proved for Canada (JACKSON and LENZ 1969; JACKSON *et al.* 1978; LENZ and JACKSON 1971; LENZ 1988, 1990), Australia (JAEGER 1967; JENKINS 1982; RICKARDS *et al.* 1992) Austria (JAEGER 1975; SCHÖNLAUB 1979) Germany (JAEGER 1959), Kazakhstan (MIKHAJLOVA 1971, 1976; BANDALETOV 1971; BANDALETOV *et al.* 1983; KOREN' 1983, 1986, 1989) Kirgystan (OBUT *et al.* 1968; RINENBERG 1965, 1973, 1985; KOREN' 1994), Podolia and Volhynia (TSEGELNJUK 1976a, b 1980, 1981, 1983), Morocco (WILLEFERT 1962), North America (BERRY and MURPHY 1975), France, Normandy (JAEGER *et al.* 1965), the Ural Mountains (KOREN' 1973).

However, a revision of the Přidoli graptolite fauna conducted by JAEGER (in KRIŽ *et al.* 1986) in the stratotype area, together with the new data obtained from that region by PŘIBYL (1983), the founder of the Přidoli Series zonal subdivision, have stimulated the present author to once again revise the Chełm graptolite fauna and to present an updated biostratigraphic subdivision.

THE ZONAL SUBDIVISION OF THE PŘIDOLI IN THE CHEŁM KEYSECTION

Most of the existing zonal subdivisions established on the basis of the graptolite fauna (TELLER 1964) are still valid (Fig. 1). This chiefly concerns the *samsonowiczi*, *chelmensis*, *bouceki*, *perneri*, *transgrediens*, and *angustidens* Zones. The base of the Series, however, requires some modification because of the revised taxonomy of two species (*Pristiograptus bugensius* and *P. aduncus*), which the present author assigns both to *Neocolonograptus lochkovensis*. The Series lower boundary has also been shifted to run through the bottom of a new, *ultimus* Zone, that is within the early Přidoli, and not through that of the *bugensius* Zone as was earlier suggested (Fig. 1).

The critical part of the section embraces the interval between 1601.5 and 1611.7 m (10.2 m). It yields at various depths the following graptolite species (Fig. 1):

1611.7–1608.5 m *Pristiograptus* ex.gr. *dubius* SUESS
1611.7–1607.4 m *Istrograptus transgrediens rarus* (TELLER)
1606.4–1601.5 m *Neocolonograptus ultimus* (PERNER)
1608.5–1607.4 m *Linograptus posthumus* (Reinhard RICHTER).

The highest form belongs to *P. dubius* s.l., a conservative lineage which persisted since the Wenlock. Its representatives appear abruptly at varying time intervals and in large numbers marking each time a population burst. Morphological differences between successive populations are, however, fairly small, and as such can be regarded as intraspecific variation. Therefore, in spite of the fact that the populations are distinctly separated from one another by representatives of other species, it would be hardly reasonable to classify each population as a separate species. Thus *P.* ex.gr. *dubius* has no stratigraphic significance and its presence can merely be recorded.

The next in line, *Istrograptus transgrediens rarus* (TELLER), is represented by a dozen or so clearly distinctive specimens. Their diagnostic feature is a beak-like first theca made up of two elaborated lateral lobes whilst the remaining thecae are all straight, of the *dubius* type. The ancestors of this subspecies can probably be found among Přidolian pristographids. With a high degree of probability we can posit that

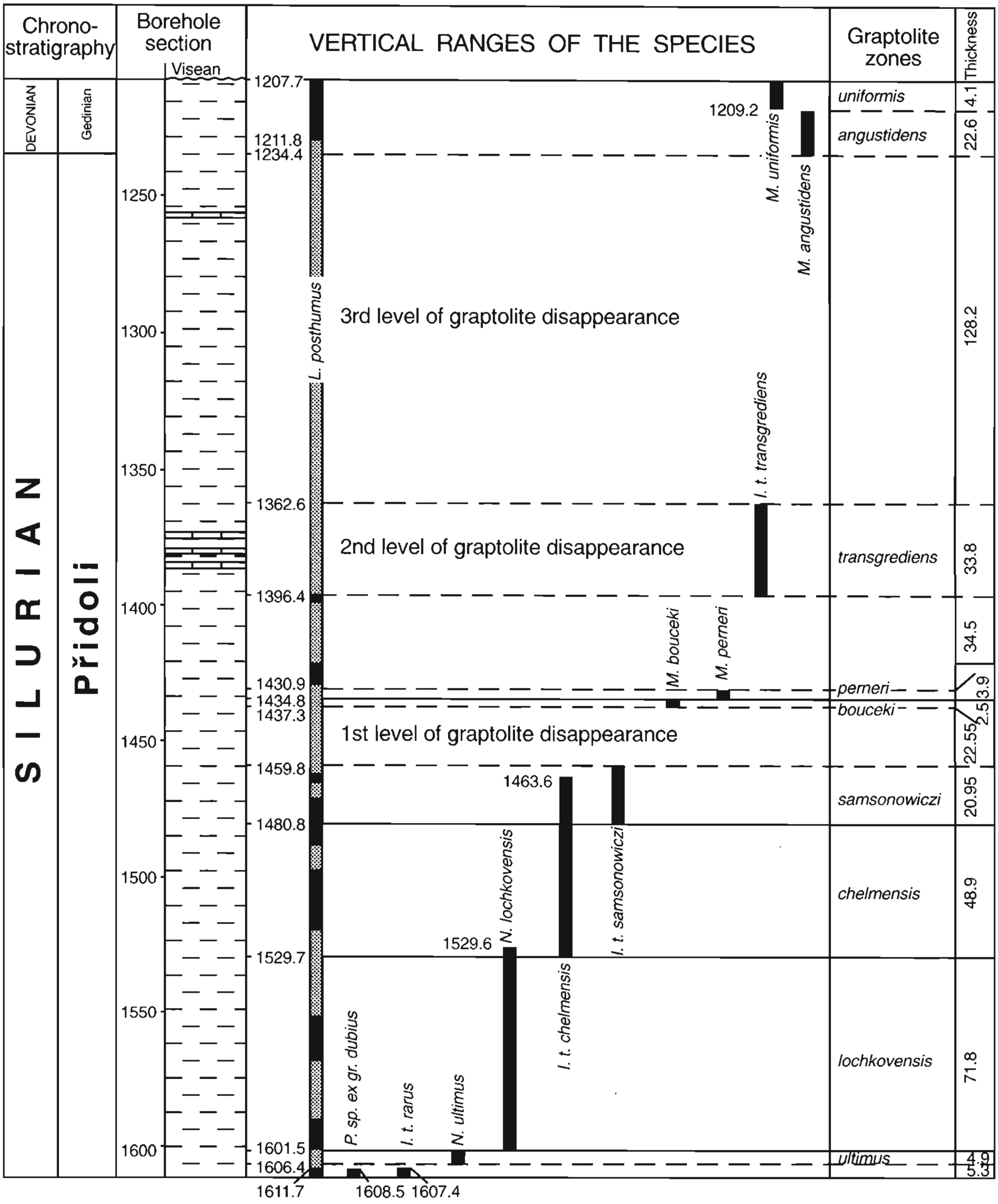

Fig. 1
Vertical ranges of the Pridoli monograptids within the Chełm IG-1 wellcore and suggested zonal subdivision.

I. t. rarus gives rise to the *transgrediens* phylogenetic stock, which, in the Chełm IG-1 section, is represented by at least three further distinct populations (cf. p. 73).

Neocolonograptus ultimus (PERNER) is the most important form encountered at a depth of 1606.4–1601.5 m (Fig. 1). It marks the *ultimus* Zone which is here no more than 4.9 m thick, a small zonal thickness not dissimilar to that found in the Mielnik IG-1 section – 3.4 m (URBANEK this volume p. 168). It should, however, be noted that the Chełm IG-1 *ultimus* Zone may be even thicker given the section's location on the EEP slope and, moreover, it may also embrace some of the uncored interval at a depth between 1601.5 and 1599.9 m.

Putting aside all the uncertainties, it is clear that the *ultimus* Zone of the Chełm IG-1 section is at least 4.9 m thick and that it is the oldest Přidoli zone established there on a faunal basis. Whether the part of the section between 1611.7 and 1606.4 m (4.3 m) is also part of the *ultimus* Zone or whether it already belongs to the *parultimus* Zone, remains an open question.

The above interval of the section also contains *Linograptus posthumus* (Reinhard RICHTER) (1608.5–1607.4 m) (1.1 m). This species occurs discontinuously throughout the entire section of the series drilled (Fig. 1), displaying short periods of mass occurrence discussed below.

The interval of 1599.9–1529.6 m (70.3 m) (Fig. 1) features a mass occurrence of *Neocolonograptus lochkovensis* (PŘIBYL) showing different astogenetic stages. This form, highly characteristic and typical of that part of the Přidoli Series, shows great intraspecific variation, a fact which originally led to its division into two separate species, *P. bugensius* and *P. aduncus*, included in the *bugensius* Zone (TELLER 1964). The *lochkovensis* Zone was proposed as early as 1960 (TELLER 1960), but, as now recognized, both its stratigraphic position and species identification were erroneous.

Having revised the identifications, the author has assigned all the forms of *bugensius* (1599.9–1529.6 m) and *aduncus* (1573.5–1530.5 m) to *Neocolonograptus lochkovensis* PŘIBYL. In this way, the *lochkovensis* Zone, whose boundaries are marked by the first appearance of the index species at a depth of 1599.9 m and by its disappearance at a depth of 1529.6 m, has been recognized in the Chełm IG-1 section as having a thickness of 70.3 m.

Within the vertical range of the index species there are two intervals with mass occurrences of *L. posthumus* (Reinhard RICHTER), at a depth of 1599.0–1589.0 m (10 m) and 1573.3–1549.4 m (23.9 m), respectively (Fig. 1).

In the Mielnik IG-1 boring, URBANEK (this volume) subdivides the *lochkovensis* Zone into the lower, *branikensis* Subzone and the upper, *lochkovensis* Subzone. The two are separated by *Monograptus (Dulebograptus) trimorphus* TSEGELNJUK. This subdivision is not recognizable in the Chełm IG-1 section (see the discussion following the description of the *lochkovensis* Zone).

At the top of the *lochkovensis* Zone, at a depth of 1529.7 m, appears a highly distinctive elongated and slim form whose first two thecae are beak-like and the rest represent the *dubius* s.l. type. That form, described (TELLER 1964) as a *P. chelmensis*, marks a separate zone at depths 1529.7–1480.8 m (48.9 m). At the top, it is replaced by a much broader and more robust form with at least the first three thecae beak-like, identified (TELLER 1964) as *P. samsonowiczi* and marking another independent zone at depths 1480.8–1459.85 m (20.95 m) (Fig. 1).

In the course of a recent revision, the author now recognizes that both of these species belong to the *transgrediens* morpho-type and has instead formed two sequential subspecies of *I. t. transgrediens* out of them, namely *I. t. chelmensis* and *I. t. samsonowiczi* (Fig. 1).

The above two zones also contain three intervals featuring a mass occurrence of *L. posthumus* (Reinhard RICHTER). They lie at depths 1518.2–1497.1 m (21.1 m), 1486.1–1471.0 m (15.1 m), and 1466.8–1465.4 m (1.4 m).

At depths of 1459.8–1437.3 m (22.5 m), only benthic faunas were encountered. It is the first of the three barren, nongraptollitiferous intervals in the section.

The interval between 1437.3 and 1434.8 m (2.5 m) contains a well-defined species, *Monograptus bouceki*, constituting the eponymous zone. Towards the top, *M. bouceki* gives way to *M. perneri* which occupies the interval between 1434.8–1430.9 m. (3.9 m) and marks a distinct and well-defined eponymous zone (Fig. 1). Both zones were originally established in the Prague Basin (PŘIBYL 1940) and have subsequently been recognized in other sections of the world. They constitute reliable correlation markers for this part of the Přidoli Series.

Above the *perneri* Zone, two intervals with *L. posthumus* (Reinhard RICHTER) have been recorded, lying at a depths of 1427.5–1420.8 m (6.7 m) and 1398.5–1396.4 m (2.1 m), respectively. The narrow interval, 1418.9–1419.5 m (0.6 m), yields a proximal fragment of a *Monograptus* rhabdosome showing a preserved sicula and three thecae. In their morphology, the thecae closely resemble those of *M. hornyi* JAEGER, a species described by JAEGER in KRIŽ *et al.* (1986) from the Prague Basin and having about the same stratigraphic position there.

The interval between 1396.4 and 1362.6 m (33.8 m) (Fig. 1) contains an abundant graptolite complex representing various astogenetic forms belonging to the *transgrediens* morphotype. The present author (TELLER 1964) earlier described, within this complex, three new species, *P. separabils, P. admirabilis*, and

P. perbrevis, and also typical forms of *P. transgrediens* (s.s.). Two of the species, *P. admirabilis* and *P. perbrevis*, not unlike the type form, were then considered index species. Following the present revision, those new species distinguished at the time are now all re-assigned to *Istrograptus transgrediens transgrediens* (PERNER) because they represent only different developmental stages of the type form. Thus the *transgrediens* Zone has become increased to include the above interval, its total thickness now being 33.8 m.

Above the *transgrediens* Zone, up to a depth of 1234.4 m (128.2 m), the section yields no graptolites. Benthic faunas, however, are rather abundant (KOREJWO and TELLER 1964), while at a depth of 1257.8–1257.0 m (0.8 m) there is a limestone layer containing orthocones, bivalves, and conodonts indicative of the uppermost Přidoli – the *eosteinhornensis* conodont Zone (WOLSKA 1969).

Still higher up, between the depth of 1234.4 m and the erosional boundary with the Visean at 1207.7 m (26.7 m), graptolites were again encountered, together with a highly abundant benthic fauna (KOREJWO and TELLER 1964). Among the graptolites are several specimens belonging to *Monograptus angustidens* PŘIBYL (1234.4–1211.8 m) (22.6 m) and one of *M. uniformis* PŘIBYL (1209.2–1209.0 m) (0.2 m) in association with *Acastella* cf. *tiro* R.E. RICHTER, pointing to an early Gedinian age for this part of the section. The Silurian (Přidoli)/ Lower Devonian (Lochkovian) boundary can be tentatively drawn in the Chełm IG-1 section at a depth of 1234.4 m, that is at the first appearance of *M. angustidens*. This species also marks the eponymous zone, which is here about 22.6 m thick (1234.4–1211.8 m) (Fig. 1), while the youngest *uniformis* Zone is represented only by 4.1 m of sediments (1211.8–1207.7 m).

The *angustidens* Zone features mass occurence of linograptids, for the ninth time in this section. Their accumulations occur between the depths of 1227.8–1212.0 m (15.8 m).

There are three nongraptolitiferous intervals in the Chełm IG-1 section, at depths 1459.85–1437.3 m (22.55 m), 1430.9–1396.4 m (34.5 m), and 1362.6–1234.4 m (128.2 m).

The first interval, 1459.85–1437.3 m (Fig. 1) has yielded some representatives of benthos and not a single graptolite fragment (KOREJWO and TELLER 1964). The second, 1430.9–1396.4 m, features only two population bursts of *L. posthumus* (Reinhard RICHTER) assemblages, and a fairly abundant benthic fauna. What we observe here is a distinct diversity decrease leading to the domination by a single species. This becomes even more conspicuous due to the fact that at a depth of 1437.3–1430.9 m (6.4 m) the first two nongraptolitiferous intervals are separated by a sudden appearance of cryptic elements (URBANEK 1993), namely *M. bouceki* and *M. perneri*. Being markers of separate graptolite zones, both of them occupy the same stratigraphic position in many sections all over the world, which confirms the global nature of this phenomenon.

The third nongraptolitiferous interval, 1362.6–1234.4 m (Fig. 1), contains benthic fauna alone, but the interval is preceded by 23.8 m of claystones displaying the presence of numerous *I. t. transgrediens* (1386.4–1362.6 m). This species belongs to a rather well-established phylogenetic line, confined to the Přidoli. It does not cut across the tentatively drawn Silurian/Devonian boundary, which in the Chełm IG-1 section is marked by the first appearance of *M. angustidens* superseded by *M. uniformis*. Both the species, associated with the *uncinatus* group appearing here after a fairly long break, can be described as typical immigrants. It is *L. posthumus*, which reappears in great numbers after a long absence, that alone can be regarded as a surviving species. In the final stage of its occurrence, *L. posthumus* undergoes a limited radiation giving rise to a new genus *Abiesgraptus*.

The distribution of *L. posthumus* (Reinhard RICHTER) should also be briefly summarized. It appears in the Chełm IG-1 vertical section as many as nine times (Fig. 1), each appearance being expressed as a population burst. Five from among the nine outbursts were short-lived (in terms of geological time): (1608.5–1607.4 m, 1599.0–1589.0 m, 1465.4–1466.8 m, 1427.5–1420.8 m, and 1398.5–1396.4 m), whereas the remaining four: 1573.4–1549.4 m, 1518.2–1497.1 m, 1486.1–14771.0 m, and 1227.8–1212.0 m lasted much longer. Not unlike *P. dubius, L. posthumus* belong to surviving species comprising a relic assemblage (URBANEK 1993). Limited radiation occurs not earlier than in the Lochkovian, although the Chełm IG-1 section has yielded, at a depth of 1553.95–1553.5 m one specimen which might have been a precursor of the above changes (TELLER 1964).

A comparison with other areas. — Graptolitiferous deposits of the Přidoli Series have been encountered in many sections throughout the world. But outside the Prague Basin, the series is most complete in Poland (TELLER 1964, 1966, 1969, 1987).

Prague Basin. — This region contains well-developed sequences of the Přidoli Series, and it is here that the stratotype (Požary section) was established (KRIŽ *et al.* 1986, 1989). The graptolite sequence as set up by PŘIBYL (1940, 1983) was only slightly altered by JAEGER in KRIŽ *et al.* (1986) but these changes made less clear the subdivision functioning for many years, especially in as far as the *lochkovensis* Zone and the *transgrediens* Interzone are concerned.

As the Chełm IG-1 section displays all the major graptolite zones, with the only exception of the *parultimus* Zone in the bottom, the correlation of its Přidoli Series with that of the Prague Basin is fairly easy. It was made for the first time as early as 1956 (TOMCZYK and TELLER 1956), while a detailed correlation dates from 1964 (TELLER 1964). The current revision of the material from the Chełm IG-1 section has revealed some differences as compared with JAEGER's subdivision (in KRIŽ *et al.* 1986).

The lack of the *parultimus* Zone in the Chełm IG-1 section is compensated for by its presence in the nearby Mielnik IG-1 section (URBANEK this volume, p. 166). The younger *ultimus* Zone is in the Chełm IG-1 section rather thin (4.9 m), although thicker than it is in the Mielnik IG-1 borehole – 3.4 m (URBANEK this volume, p. 168). Both of these values cannot, however, be compared with their equivalent in the Prague Basin because of the different palaeogeographic features of the two regions. The column or sections presented by JAEGER (in KRIŽ *et al.* 1986) show that, locally, the zone in question attains a thickness of as many as 4 m (Kosov Quarry) in the Prague Basin, although in most cases it does not exceed 1 m. According to PŘIBYL (1983), the thickness of this zone varies from 1.5 to 6.1 m. However, the latter author does not distinguish the *parultimus* Zone, as he does not recognize the validity of this species (personal information).

JAEGER's (in KRIŽ *et al* 1986) subdivision of the *lochkovensis* Zone into three subzones has not been corroborated by the data from the Chełm IG-1 section. What can be observed here is a fairly thick (70 m) interval of the *lochkovensis* Zone marked by the index species alone.

PŘIBYL (1940, 1983) recognizes the *lochkovensis* Zone in the Prague Basin, but unlike JAEGER he does not subdivide it into three subzones. PŘIBYL (1940, 1983) and JAEGER (in KRIŽ *et al.* 1986) agrees in establishing the *bouceki* Zone (with a thickness of 2.0–3.5 m) above the *lochkovensis* beds. Further up in the Prague Basin the former is replaced by the 2.0–3.0 m thick *perneri* Zone. This situation is similar to the Chełm IG-1 section not only from the point of view of the presence of both species but also of the thickness of the zones. JAEGER (in KRIŽ *et al.* 1986) introduces, between the two zones, the *M. beatus* Band. Such a sequence has not been observed in Chełm IG-1, but recorded at a depth of 1418.9–1419.5 m was a fragment which might be described as *M. hornyi*, a form originating from the Prague Basin.

No *M. pridoliensis* has been encountered either in the Chełm IG-1 section or in any other coeval sequence of the Polish part of the EEP. Hence no zone of this name can be distinguished there. Nevertheless PŘIBYL (1983) has established an independent *pridoliensis* Zone 1.5–6.3 m thick, recording in its top also the presence of *M. rectiformis*, a species unknown in Poland According to JAEGER (in KRIŽ *et al.* 1986), the Přidoli section of the Prague Basin is crowned by the *transgrediens* Interzone, which PŘIBYL (1940, 1983) defined as zone. This sequence has its analogues both in the Chełm IG-1 borehole and in other Polish sections. JAEGER's suggestion introducing an interzone seems to the present author unclear. In the Chełm IG-1 section, and not only there, the *transgrediens* morphotype features a distinct line of development: *I. t. rarus*, *I. t. chelmiensis*, and *I. t. samsonowiczi*, which makes it possible to distinguish at least three separate zones within the Přidoli. Both in the Chełm IG-1 section and in the Prague Basin, the *I. t. transgrediens* Zone terminates the Přidoli Series and with it, the Silurian.

The onset of the Devonian in both the Prague Basin and the Chełm IG-1 section is marked by the presence of two typical graptolites, *M. angustidens* and *M. uniformis.* According to JAEGER (1959), the first of them is a subspecies of the other, therefore not a zone but merely some basal beds should be recognized at the bottom of the sequence, and the only zone to be established there is the *uniformis* Zone. Within the Chełm IG-1 section these forms occur separately and function as index species of two independent zones The current analysis of the Chełm IG-1 graptolite sequence shows no considerable deviation from the results obtained by PŘIBYL (1983) and JAEGER (in KRIŽ *et al.* 1986) in their revisions of the Prague Basin. The small differences may have various causes and are of little significance for the biostratigraphic correlation of the two regions.

The predominance of carbonate sediments in the Prague Basin can be accounted for by its geographic position and chiefly shallow nerritic facies in the Přidoli time. The richness and abundance of the benthic fauna in the basin is not always matched by equal development of the graptoloid plankton whose diversity was controlled by a number of factors, e.g. tides, storms, water temperature, and wind direction. This explains why a continuous presence of graptolites was impossible in the Prague Basin. The possibility of breaks in sedimentation or periods with hard grounds cannot be eliminated either.

In the EEP, well-established graptolitiferous sections of Přidoli age are chiefly confined to the EEP slope region. The Palaeozoic sedimentary cover, overlying the Precambrian basement, was neither folded nor metamorphosed. The marine basin of a bathyal type had unrestricted open connections with the SW branch of the Caledonian geosyncline. Graptolitic plankton, thus, could easily drift, which resulted in a greater diversity of the graptoloid fauna making possible its more detailed analysis. The thickness of the sediments is also of importance.

One more proof of close Upper Silurian connections between the Prague Basin and the SE part of Poland is the presence of an extremely rich and diverse Přidoli benthic fauna in the Chełm IG-1 section (KOREJWO and TELLER 1964). Its composition is similar to that of the Prague Basin, revealing equally strong ties with the Mediterranean Palaeotethys.

Wolhynia and Podolia. — In the territory of Volhynia and Podolia sediments of Přidoli age have been recognized in many boreholes, but only some of them contain graptolite fauna, and that of the lower members of the series alone. One of the earliest descriptions of the graptolite fauna from this area [boreholes: Gushcha-4015, Tomashovka-4116, and Pishcha-1, KRANDIEVSKY *et al.* (1968)] lists a number of species typical of the Přidoli and used as a basis for the regional zonal subdivision. Two zones were established for the Přidoli, known then as the Tiver.

The fourth (IV) Volhynian zone with *M. ultimus* as the index species was recognised in the Gushcha-4015 borehole, at a depth of 677.2–626.8 m. It is supposed to be characterized by *Monoclimacis ultimus* (PERNER), *Monograptus similis* PŘIBYL (= *Monograptus pridoliensis* PŘIBYL), *Monograptus similis* PŘIBYL (= *Monograptus pridoliensis* PŘIBYL) var. *triangulatus* subsp. n. KRAND, and *Linograptus posthumus* (Reinhard RICHTER).

The fifth (V) Volhynian zone with *Pristiograptus spectatus* PŘIBYL as the index species was also established in the Gushcha-4015 section, at a depth of 826.8–563.5 m. The index species is presumably accompanied by *Monograptus similis* PŘIBYL (= *Monograptus pridoliensis* PŘIBYL) and *M. similis* (= *Monograptus pridoliensis P*ŘIBYL) var. *triangulatus* subsp. n. KRAND.

In the standard international biostratigraphic subdivision, these two regional Volhynian zones are believed to correspond to the *ultimus* and *lochkovensis* Zones of the Prague Basin (PŘIBYL 1940) and also to the *bugensius* and *samsonowiczi* Zones from the nearby Chełm IG-1 borehole (TELLER 1964).

In his description of the Gushcha-4015 section Krandievsky also records other graptolite species, including a mass occurrence of *M. formosus* at a depth of 821.7–677.2 m and *Monograptus lochkovensis* at a depth of 821.7–677.2 m (in the same interval), whilst the presence of *M. similis P*ŘIBYL (= *M. pridolensis* PŘIBYL), was reported from a depth of 778.5–563.6 m.

If all the above identifications were correct, it would be possible to accept that the Gushcha-4015 section contains the early Přidoli Zones of *parultimus*, *ultimus*, and *lochkovensis*. This would be in accord with the sequence recognized in not too remote sections in Mielnik IG-1 (URBANEK, this volume, p. 97) and Chełm IG-1 (TELLER, this volume, p. 62), lying west of the frontier River Bug.

KRANDIEVSKY's *et al.* (1968) identifications, however, are not quite reliable (cf. descriptions and the Tables), and his stratigraphic conclusions are also doubtful, and hard to accept.

The next approach to the graptolite fauna from the borings in the above-mentioned area was made by TSEGELNJUK (1976a, b). He etched the material from several boreholes, obtaining a rich graptolite fauna isolated from the rock matrix. The vast majority of the graptolites, coming chiefly from the Brest-1 and Gushcha-4015 borings, however, provide evidence of the presence of only the Ludfordian stage. Typical Přidoli species have been recorded in no more than four wells. The Yegorany-409 borecore has yielded at a depth of 277.1 m *I. t. rarus* TELLER, which in the Chełm IG-1 section was identified from the interval between 1611.7–1607.4 m. The Davideny-1 section contains *M. perneri* BOUČEK (2227.0–2232.0 m), and the Gushcha-4015 borehole features *M. ultimus* at a depth of 662.4–676.0 m, whereas in the Tomashovka-4116 well *I. transgrediens* has been encountered at a depth of 640 m.

Unfortunately, the stratigraphic methods applied by TSEGELNJUK to the study of the material in question were woefully inadequate, resulting in a high degree of confusion. This is especially true of the Ludfordian fauna, as is shown in detail by URBANEK (this volume, p. 43), and the present author fully shares his objections.

As far as species permitting the establishment of the Přidoli Series are concerned, the species listed by TSEGELNJUK are also present in the Chełm IG-1 section (TELLER 1964). The correlation of *I. t. rarus* TELLER and *M. perneri* creates no problems, provided the identifications are correct. However, the supposed 14-meter thick bed bearing *ultimus* in the Gushcha-4015 section seems to be an exagerration in comparison with that in the nearby Chełm IG-1 and Mielnik IG-1 borings. It seems likely that the 662.4–676.0 m interval embraces both the *parultimus* and *ultimus* Zones. *I. transgrediens*, recorded in the

Tomashovka-4116 boring is, however, an entirely different matter. According to JAEGER (in KRIŽ *et al.* 1986), the *transgrediens* morphotype can be encountered in different zones of the Přidoli Series, and, what is more, he introduces a subzone based on this species. In the Chełm IG-1 section, the *I. transgrediens* morphotype reappears at least four times, beginning with *I. rarus* in the bottom and ending in *I. t. transgrediens* at the top. From TSEGELNJUK's (1976b) considerations it is not at all clear which morph he is discussing, for it can be anything – a Lower, Middle or Upper Přidoli form. It also seems strange that TSEGELNJUK (1976b) skips over KRANDIEVSKY's *et al.* (1968) identifications and conclusions, although the material for analysis comes in both cases from the same source.

A close correlation between the Přidoli Series of the Bug Depression and that of the adjacent area lying E of the frontier river Bug is practically impossible. This is a great disappointment, for the graptolite fauna, obtained chiefly by TSEGELNJUK (1976b), is represented by a qualitatively and quantitatively rich association, which raises it, alongside the Polish assemblage (URBANEK 1970 and this volume; TELLER 1964 and this volume), to a very high rank of second in the world.

Central Asia. — In Kazakhstan the Přidoli Series was established as early as the 1960s but was then included in the Tokrau horizon (local stage?) recognized by BANDALETOV and MIKHAJLOVA (1971). The first graptolites suggestive of the Přidoli Series were identified by MIKHAJLOVA (1971, 1976) and revised by KOREN' (1983) who also described a number of new taxa. From the viewpoint of the present author, this more detailed study may raise some doubts, as the sequence features several new forms typical of the Ludlow (Ludfordian) rather than the Přidoli.

The same graptolite assemblage from the Tokrau horizon was described by KOREN' (1986) again, almost without changing its stratigraphic position. A further analysis of the fauna was presented in 1989 (KOREN' 1989). It was stressed in the conclusions (KOREN' 1989: p. 155) that the graptolite fauna in the Tokrau horizon did not provide full information about late Silurian graptolites (Ludfordian and Přidoli).

No matter how interesting, the Přidoli section of the Tokrau Regional Stage cannot at present be correlated with other coeval sections, including the Chełm IG-1 parastratotype in Poland. This may be a consequence of intense tectonic deformation of the beds, making impossible an accurate reconstruction of the graptolite sequence. Naturally, one cannot exclude the presence here of some fragments of the Přidoli Series, but the bulk of the graptolite fauna described up to now bears a Ludlow, especially Ludfordian, aspect. Any degree of provincialism of this fauna can hardly be taken into account because in the not too remote sections of South Tien Shan the Přidoli fauna appears in its typically cosmopolitan composition.

Tien Shan. — In Central Asia, the most complete Přidoli sections have been recognized in South Tien Shan. RINENBERG (in OBUT *et al.* 1968) describes a number of taxa indicative of the *bouceki*, *perneri*, *bugensius*, and *chelmiensis* Zones. ABDUAZIMOVA (1970) also reports the presence, in the section on the Isfara River, of a *bugensius* form, which in view of the revision presented herein is now assigned to *lochkovensis*.

Further data concerning the presence of the Přidoli Series in this region have been provided by SOLONCHENKO and RINENBERG (1984) who have recorded not only *Monograptus bouceki*, but also a number of other taxa characteristic of the Lower Devonian. RINENBERG (1985) also mentions some representatives of the Přidoli in the Isfara horizon Regional Stage of the Fergana Valley margin, suggesting that there, the morphotypes of the *transgrediens* stock co-occur with *M. formosus*, *M. bouceki*, and *M. perneri* – the taxa characteristic of the Přidoli Series.

These data are, however, too fragmentary to provide a complete picture of the Series and the graptolites it contains. Nevertheless, RINENBERG (1985) correlates the sections studied by her with the Prague Basin and the Chełm IG-1 section.

In their discussion of a biozonal scheme for the Upper Silurian of the Turkestan-Alai, KOREN', and LYTOCHKIN (1992) recognize, within the Přidoli Series, the following Zones: *parultimus*, *ultimus*, *branikensis*, *M.* aff. *lochkovensis*, *M. bouceki*, *M.* ex.gr. *transgrediens*, and *M. transgrediens.* They provide a correlation with the Prague Basin and with the zonal scheme established for it by JAEGER (in KRIŽ *et al.* 1986). This correlation seems to be perfectly correct in relation to the *parultimus*, *bouceki*, and *transgrediens* s.s. Zones, but it becomes dubious as regards *M. branikensis*, *M.* aff. *lochkovensis*, and *M.* ex. gr. *transgrediens.*

M. branikensis was distinguished by JAEGER (in KRIŽ *et al.* 1986) only once in the Branik section, in a one-meter band underlying the *pridoliensis* Zone. He also presumes its presence (JAEGER in KRIŽ *et al* 1986) in the Hviždalka section, but much higher up, at the boundary between the *pridolensis* Zone and the upper *lochkovensis* Subzone. In the present author's opinion the diagnosis of *M. branikensis* is generalised and unconvincing. JAEGER himself points to its similarity with *lochkovensis* and the difficulty in distinguishing one from the other, especially in the juvenile stages.

Having studied the holotype and the paratypes of the species in question in Prague, 1992, the present author is inclined to assign the taxon identified by JAEGER to *Neocolonograptus lochkovensis*, a form showing great intraspecific variation. The stratigraphic position of the taxon – above the *ultimus* and below the *pridolensis* Zone – is in conformity with that of the lower part of the *lochkovensis* Zone.

In Tien Shan, the stratigraphic position of *M. branikensis* seems to be similar to the interval occupied by the lower *lochkovensis* Zone (JAEGER in KRIŽ *et al.* 1986).

As to the form itself, the present author believes, after having examined the type material in St. Petersburg, that it should be identified as *lochkovensis*. KOREN' and SUYARKOVA (personal comunication) have also identified a new species *N. tumultuosus* KOREN' *et* SUYARKOVA. The taxon is very similar and most probably conspecific with *N. lochkovensis*. In the Tien Shan section, it occurs above *branikensis* and below *bouceki*, which confirms the author's conviction that it also represents the *lochkovensis* Zone. It is hard to find a reliable justification for the fundamental difference between the Přidoli graptolite faunas of Tien Shan, on the one hand, and those from the Prague Basin or the parastratotype Chełm IG-1 section, on the other. Why should only these two species, that are hardly distinquishable from *N. lochkovensis*, be an indication of provincialism, when all those recognized above and below are cosmopolitan?

Such species as *Monograptus bouceki*, *M. perneri*, and *Istrograptus transgrediens* provide another indicator of a close similarity between the sections, the Přidoli Series of Tien Shan being a sort of a replica of the zonal sequences in the Prague Basin and in Poland. In the EEP part of Poland with its unfolded sequence, the last of the three above species yields several distinct populations, constituting an evolutionary lineage. In Tien Shan, the *transgrediens* morphotype has been recorded in different intervals, being identified as s.l. and s.s. It is likely that each of the intervals contains a separate morph which would allow a correlation of the whole with the Polish sequence, resulting in a very similar picture.

The Tien Shan sections are tectonically highly deformed and isolated from one another, making studies of them susceptible to error. Nevertheless, it is highly probable that the Přidoli sequences of Tien Shan are very comparable to the sections known from the EEP (TELLER 1964) and the Prague Basin (PŘIBYL 1940; JAEGER in KRIŽ *et al.* 1986). It is its tectonic involvment and incomplete knowledge of the graptolite fauna that make an accurate correlation impossible.

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REVISION OF CERTAIN PŘIDOLI MONOGRAPTIDS FROM THE CHEŁM KEYSECTION (EEP)

LECH TELLER

Teller, L. 1997. Revision of certain Přidoli monograptids from the Chelm keysection (EEP). *In:* A. Urbanek and L. Teller (eds), Silurian Graptolite Faunas in the East European Platform: Stratigraphy and Evolution. — *Palaeontologia Polonica* **56**, 71–85.

A review and revision of important graptolite index species for the Přidoli Series (Silurian) are given. *P. rarus* Teller, *P. chelmiensis* Teller, and *P. samsonowiczi* Teller are herein regarded as chronosubspecies of the single *Istrograptus transgrediens* (Perner) lineage, while some other taxa described in the 1964 paper proved to be merely astogenetic variants of the latter species. *P. bugensius* Teller and *P. aduncus* Teller are now considered junior synonyms of *Colonograptus lochkovensis* Přibyl. The latter species is assigned to a new genus, *Neocolonograptus*, erected in this volume by Urbanek. A revised scheme of the Přidoli zonal subdivision based on graptolites is presented.

Key words: Graptolites, Silurian, Přidoli, biostratigraphy, taxonomy.

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CONTENTS

INTRODUCTION

The graptolite fauna from the Chełm IG-1 borehole was recognized in 1956, its description being published four years later (TELLER 1964). The study discussed all the taxa encountered in the core, providing a correlation with the Prague Basin. Evidence was presented of the presence of all Přidoli zones except for the lowest part of the Series which, according to much later findings (JAEGER in KRIŽ *et al.* 1986), corresponds to the *parultimus* Zone. In total, eight new species were described then, making the section of the Přidoli Series more complete.

With the course of time, as the presence of Přidoli graptolites was reported from various parts of the world, even if from fragmentary sections, it became necessary to revise the graptolite fauna from Chełm IG-1, a keyboring for the EEP.

A restudy of the original materials has revealed that such taxa as *Pristiograptus bugensius* TELLER, and *P. aduncus* TELLER are conspecific with *Neocolonograptus lochkovensis* (PŘIBYL). Both the species have been listed as synonyms of *N. lochkovensis* (PŘIBYL), which for the first time in Poland is described herein on the basis of non-isolated material. Its recognition in the Chełm IG-1 section also makes possible to establish the *lochkovensis* Zone, about 70 m thick.

Revision has embraced all the forms having a morphotype similar to that of *dubius*. Some, such as *Istrograptus t. rarus* (TELLER), *Istrograptus t. chelmiensis* (TELLER), *Istrograptus t. samsonowiczi* (TELLER), and *Istrograptus t. transgrediens* (PERNER) created no problems. This allowed the recognition of the *transgrediens* phylogenetic stock, probably initiated in the latest Ludfordian from an unknown ancestor of the *Pristiograptus dubius* group. It continues via chronosubspecies *rarus–chelmiensis–samsonowiczi* and ends up in *transgrediens.*

Moreover such taxa as *P. admirabilis* TELLER, *P. separabilis* TELLER, and *P. perbrevis* TELLER (TELLER 1964) have been redefined as juvenile stages in the astogeny of a typical *I. t. transgrediens* (PERNER) and listed as synonyms of that species.

The revision has resulted in establishing a somewhat modified zonal subdivision of the Přidoli Series for the keysectoin from the Chełm IG-1 borehole and the Polish part of the EEP. From top to bottom, the following Zones are recognized: *transgrediens, perneri, bouceki, samsonowiczi, chelmiensis, lochkovensis, ultimus* (see also the Table 1, p. 62).

The above sequence is almost identical with that in the Prague Basin (PŘIBYL 1940, 1983; JAEGER in KRIŽ *et al.* 1986) and very close to the one established by KOREN' *et al.* (1992) for the Tien Shan sections. Meanwhile individual zones can be correlated with the various sections around the world.

The material illustrated in the present paper is housed at the Institute of Palaeobiology of the Polish Academy of Sciences, Warszawa, Poland, and designated in the collection as ZPAL G.XXI.

THE *TRANSGREDIENS* STOCK

In spite of the recent more detailed knowledge of the morphology and astogeny of this species, disappearing ultimately in the uppermost Silurian, its phylogeny remains unclear. The *I. t. transgrediens* (PERNER) lineage is linked with the genus *Pristiograptus* which formed the stem group for the evolution of the Upper Silurian forms resembling it in basic morphology but differing in the structure of proximal thecae (KOREN' and URBANEK 1994; URBANEK 1997).

The ancestor of the true *I. t. transgrediens* (PERNER) form should be looked for among those Přidoli species which resemble the *transgrediens* morphotype. The Chełm IG-1 section features three intervals containing such morphotypes (Fig. 1).

The first of them, the *rarus* morphotype, occurs in the Lower Přidoli, in the *N. parultimus* and *N. ultimus* Zones. The form possesses a distinctly beak-like aperture of the first theca. The aperture is made up of two separate ear-like lobes. The successive thecae are tube-like, with straight apertures of the *dubius* type. It is at the very margin of the aperture that a slight roll-like thickening can be seen. The form is now classified as *I. t. rarus* (TELLER).

The subsequent younger form of the stock is *I. t. chelmiensis* (TELLER). It is characterized by possessing beak-like apertures in the first two thecae. Their structure is similar to that observed in *I. t. rarus* (TELLER). Subsequent thecae are of the *dubius* type with straight apertures while, on the whole, the taxon is slimmer than the type species. The occurrence *of I. t. chelmiensis* (TELLER), confined to a closely defined interval above *N. lochkovensis* (PŘIBYL, forms a separate zone about 50 m thick. In the top part of the zone it is

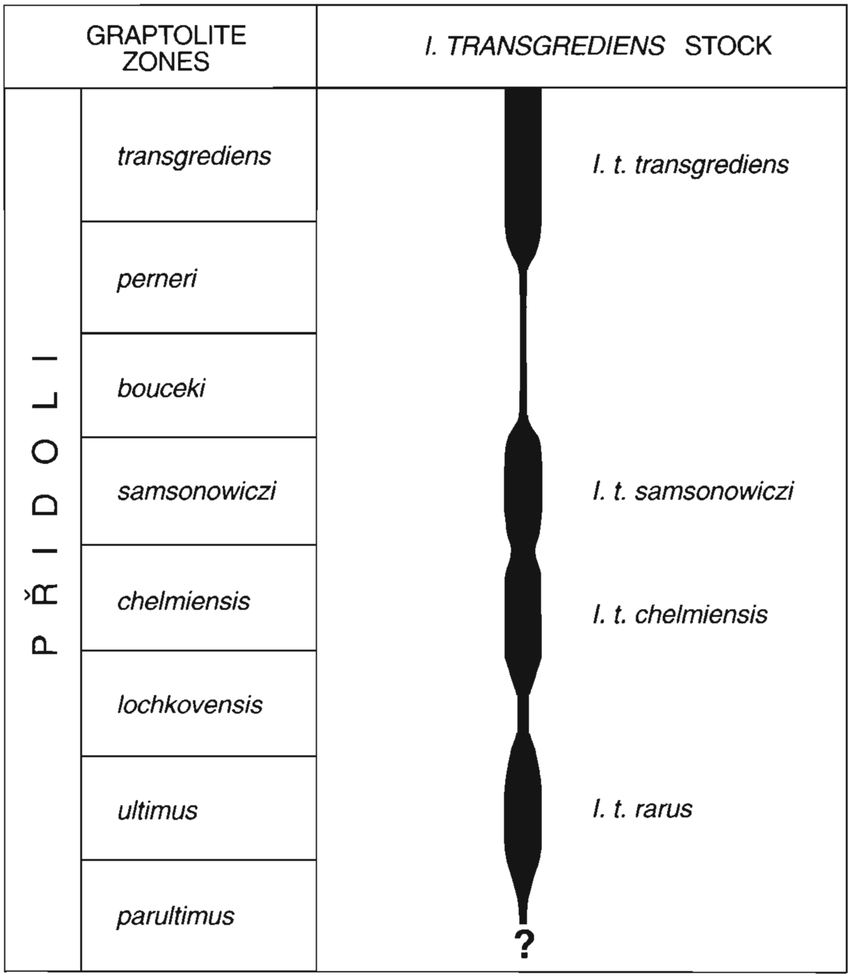

Fig. 1
Chronosubspecies of the *Istrograptus transgrediens* stock. Width visualizes abundance of the taxon within a given interval.

accompanied by *I. t. samsonowiczi* (TELLER) which constitutes the next link in the phylogenetic line. In this form, three subsequent proximal thecae show beak-like apertures resembling the ancestral *rarus*, the remaining thecae being straight, of the *dubius* type. In its general appearance the form is shorter than the preceding one but is more robust. In the Chełm IG-1 section, *I. t. samsonowiczi* (TELLER) marks an independent zone.

The *samsonowiczi* Zone is separated from the overlying *bouceki* Zone by a 23-meter nongraptolitic interval (cf. p. 63 herein). As to the *bouceki* Zone, it has yielded only one rhabdosome devoid of the proximal part but having thecae of the *dubius* type.

I. t. transgrediens (PERNER), the species terminating the *transgrediens* stock, is separated from *I. t. samsonowiczi* (TELLER) not only by the *perneri* Zone but also by one more nongraptolitic interval. The proximal part of this species features four or even five thecae with beak-like apertures. The successive two or three thecae may be in some cases slightly elaborated, but as a rule their apertures are almost straight, of the *dubius* type and rimmed by a roll-like thickening. The rhabdosome is long, wide and robust.

The order of appearance of the *transgrediens* morphotype, as seen in the Chełm IG-1 borehole, may shed light on the problems associated with the presence of this form in the Přidoli sections of the Prague Basin and Tien Shan, reported by JAEGER (in KRIŽ *et al.* 1986) and KOREN' (1992), respectively. In these sequences, the succession of the *transgrediens* morphotypes may well be very similar to that in the Chełm IG-1 section.

Above the *transgrediens* Zone, the Chełm IG-1 Silurian section yields no graptolites, linograptids being the only exception. Monograptids do not appear earlier than the Gedinnian (Lochkovian).

PALEONTOLOGICAL DESCRIPTIONS

Family **Monograptidae** LAPWORTH, 1873
Subfamily **Pristiograptinae** JAEKEL, 1889
Genus *Istrograptus* TSEGELNJUK, 1976
Istrograptus transgrediens rarus (TELLER, 1964)
(Pl. 1: 1)

1964. *Pristiograptus rarus* sp. n.; TELLER, p. 38, pl. 1: 1–3, pl. 9: 10–12, text-fig. 3a–c.
1976. *Skalograptus rarus* (TELLER); TSEGELNJUK, p. 102, pl. 32: 6–9.

Holotype: Form described by the present author in 1964 and illustrated there in Pl. 1: 1 and Pl. 9: 10 from the depth of 1610.5–1611.1 m.

Material. — Four well and several rather poorly preserved rhabdosomes from the Přidoli section of the Chełm IG-1 borehole, depth 1607.4 and 1611.1 m.

Remarks. — No considerable changes need to be introduced in the holotype description except for the part which concerns the first proximal theca. The beak-like appearance of its aperture is accounted for by the fact that two lateral lobes have been elaborated and separated by a ventral notch. They widen slightly towards the end forming ears. All this creates an illusion of a beak-like structure of the thecal aperture. The illusion is particularly strong in flattened specimens embedded in the matrix. The successive thecae have a regular *dubius* tube-like shape. Their apertures are slightly convex, with a roll-like thickening at the margin. The thecal structure and the rhabdosome shape manifest a close similarity between this taxon and *I. t. transgrediens*, although the former is much shorter and has only one beak-like theca, whereas the latter may feature three, four or even as many as five such thecae. The above great similarity supports for classifying the taxon as a subspecies of *I. t. transgrediens* and recognizing it as the initial form of the *transgrediens* stock. It leads via *chelmiensis* and *samsonowiczi* to the type taxon of the lineage (compare the description of *transgrediens*). TSEGELNJUK (1976) assigns the above taxon to his new genus *Skalograptus*. URBANEK (p. 156, this volume). questions the validity of his decision. What is important however, is the fact that TSEGELNJUK acknowledges the great similarity between *I. t. rarus, I. t. chelmiensis* and *I. t. samsonowiczi*, assigning the last two forms to the same species. His supposition has proved to be correct, but in respect to a different species.

Stratigraphic position. — The form has only been documented from the bottom part of the Chełm IG-1 section, the *ultimus* Zone, and maybe from the upper part of the *parultimus* Zone. Its stratigraphic position is similar in the nearby Gushcha-4015 boring (TSEGELNJUK 1976).

Geographic distribution. — Species recognized in the EEP. Its presence in Central Asia seems reasonable.

Assemblage. — *Neocolonograptus ultimus*, *Pristiograptus* ex gr. *dubius*, and *Linograptus posthumus posthumus* (Reinhard RICHTER).

Istrograptus transgrediens chelmiensis (TELLER, 1964)
(Pl. 1: 8–9)

1964. *Pristiograptus chelmiensis* sp. n.; TELLER, p. 45, pl. 3: 5–6, pl. 4: 1, 6–8, pl. 7: 1–7, pl. 13: 6, text-fig. 7a–c.
1978. *Pristiograptus chelmiensis* TELLER; JACKSON, LENZ, and PEDDER, p. 21, pl. 3: 10.

Holotype: Form described by the present author in 1964 and illustrated there in Pl. 3: 5; Pl. 7: 3 from the depth of 1514.1 m.

Material. — A dozen or so well-preserved rhabdosomes from the Přidoli section of the Chełm IG-1 borehole, depth 1463.65–1529.7 m.

Remarks. — The holotype was described by the present author (TELLER 1964) as *Pristiograptus chelmiensis*. To complete the initial description it should be added that the first two proximal thecae possess paired lateral ear-like lobes separated by a ventral notch. Slight widening of the lobes towards the end gives a deceptive beak-like impression, especially in flattened material or in the specimens embedded in the matrix.

Subsequent thecae lack lateral lobes, being similar to straight tube-like shapes typical of the *dubius* group. When seen laterally their apertures are slightly concave with the margin rimmed by a roll-like thickening.

I. t. chelmiensis (TELLER) strongly resembles *I. transgrediens transgrediens* (PERNER). The following characters distinguish it from the type species: (a) much lesser width of the rhabdosome and slower increase in width. This makes the subspecies discussed look distinctly slimmer; (b) the presence of elaborated lateral lobes in no more than the first two, rarely three, proximal thecae, whereas in *I. t. transgrediens* (PERNER) such lobes are a regular feature of the first three, commonly four and, rarely, five thecae; (c) *I. t. chelmiensis* (TELLER) is confined to a closely defined stratigraphic interval, always below *M. bouceki* (PŘIBYL), whereas the type *I. t. transgrediens*, has only been recorded above *M. perneri* (BOUČEK). The above distinguishing features are not sufficient to allow *I. t. chelmiensis* (TELLER) to be recognized as a separate species. It is, however, a link in the continuous line of the *transgrediens* morphological evolution and may be identified as a temporal subspecies.

Stratigraphic position. — A separate zone whose lower and upper boundaries are marked by the top of the *lochkovensis* Zone and the bottom of the *samsonowiczi* Zone, respectively. It lies at a depth of 1480.0–1530.0 m and is 50 m thick.

Geographic distribution. — A cosmopolitan species. In E Poland it has been recognized in the Chełm IG-1 section and in other boreholes penetrating the Přidoli Series. Its presence has also been reported from Arctic Canada, the Porcupine River,Yukon, and is not unlikely in Central Asia.

Assemblage. — The bottom of the interval contains *Neocolonograptus lochkovensis* (PŘIBYL), and the top, *I. t. samsonowiczi* (TELLER) and *Linograptus posthumus posthumus* (Reinhard RICHTER).

Istrograptus transgrediens samsonowiczi (TELLER, 1964)
(Pl. 1: 6–7)

1964. *Pristiograptus samsonowiczi* sp. n.; TELLER, p. 43, pl. 4: 2–5, 9, pl. 6: 9, pl. 8: 20, pl. 11: 9–10, text-fig. 6a–d.

Holotype: Form described by the present author (TELLER 1964) as *P. samsonowiczi* and illustrated there in Pl. 4: 3; Pl. 6: 7 from a depth between 1462.1–1462.2 m.

Material. — A dozen or so well-preserved rhabdosomes from the Přidoli of the Chełm IG-1 section at a depth of 1459.85–1480.80 m.

Remarks. — The 1964 description of the form requires a more detailed analysis in the part concerning the first three proximal thecae which, not unlike some proximal thecae in *I. t. chelmiensis* and *I. t. transgrediens*, are slightly beak-like. The apertures of these thecae have elaborated paired lateral ear-like rounded lobes separated by a ventral notch. The ear-like shape and roundness of the lobes give a deceptive beak-like impression, especially strong in the case of specimens embedded in the matrix.

Successive thecae, possessing no lateral lobes, are straight and tube-like as is typical of the *dubius* group. Their apertures are slightly concave, with the margin rimmed by a roll-like thickening.

Although *I. t. samsonowiczi* strongly resembles *I. t. transgrediens* and *I. t. chelmiensis*, it possesses several distinguishing features: (a) *I. t. samsonowiczi* widens much faster so that its mature form is never as long as that of the type species; (b) as a rule, *I. t. samsonowiczi* has three proximal thecae with elaborated lateral lobes, that is one more than the earliest subspecies *I. t. chelmiensis*, a generally longer and slimmer form. The type species possesses four, more rarely, three, and frequently even five thecae with lateral lobes; (c) the new subspecies always occurs below the *bouceki* Zone and above the *chelmiensis* Zone, in an interval between 1480.80–1459.85 m, marking the *samsonowiczi* Zone 21 m thick; (d) *I. t. samsonowiczi* is one more link in the final phase of the *I. t. transgrediens* phylogenetic stock initiated by *I. t. rarus*.

Stratigraphic position. — Separate zone whose upper and lower boundaries are marked by the top of the *chelmiensis* and the bottom of the *bouceki* Zone, respectively, depth 1459.0–1480.0 m (21 m thick).

Geographic distribution. — E Poland, Chełm GI-1 and other boreholes penetrating the Přidoli. The presence of this subspecies in Central Asia is not unlikely.

Assemblage. — *I. t. chelmiensis* (TELLER) in the lower part of the level.

Istrograptus transgrediens transgrediens (PERNER, 1899)
(Pl. 2: 1–11)

1899. *Monograptus transgrediens* sp. n.; PERNER, p. 13, pl. 17: 24.
1940. *Pristiograptus transgrediens* var. *proximus* var. n.; PŘIBYL, p. 69, text-fig. 1/6.
1940. *Pristiograptus transgrediens* var. n.; PŘIBYL, p. 69, text-fig. 1/5.
1964. *Pristiograptus transgrediens* (PERNER); TELLER, p. 52, pl. 2: 3, pl. 3: 1–4, pl. 7: 8–12, text-fig. 11a–c.
1964. *Pristiograptus admirabilis* sp. n.; TELLER, p. 47, pl. 5: 1–4, pl 8: 4–7, text-fig. 8a–c.
1964. *Pristiograptus separabilis* sp. n.; TELLER, p. 49, pl. 2: 2,10, pl. 7: 16–17, text-fig. 9a–c.
1964. *Pristiograptus perbrevis* sp. n.; TELLER; p. 50, pl. 1: 7–10, pl. 5: 6–9, pl. 8: 8–10, text-fig. 10a–c.
1986. *Monograptus transgrediens* PERNER; JAEGER, p. 326, pl. 1: 15, 17–18, pl. 2: 12, 16–17, 19, 22, 25, text-fig. 41a–c.

Material. — A few hundred well-preserved rhabdosomes, either in full relief or pyritized, showing different stages of astogeny.

Derivation. — Chełm IG-1 borehole, depth 1362.1–1396.4 m.

Stratigraphic position. — Upper Přidoli, *transgrediens* Zone.

Description. — Rhabdosome (Pl. 2: 1–3) straight,with a slight ventral curvature starting from th_{7-8}. Maximum length of the adult form attains 4.4 cm, but the majority of the rhabdosomes encountered are about 4 cm long. Rhabdosome width increases gradually from 0.9–1.0 (0.6–0.7) mm at th_1 to 1.8–2.0 (1.2–1.7) mm at th_{10} to as many as 2.2–2.25 (1.9–2.1) mm at th_{20}. Virgula robust.

Sicula. — Narrow (Pl. 2: 9–11), 2.3–2.4 mm long. Its apex usually reaches as far as the base of th_4, sometimes a little higher than the base or even not further than th_3. It widens gradually towards the aperture, attaining a width of 0.4–0.5 mm. Aperture can be: (a) wide, almost straight, having a hardly visible and slightly widened dorsal process, and a roll-like margin merging with the virgella (Pl. 2: 9, 11). The aperture of the sicula may be flared, although this is not a distinguishing feature, that feature being also present in *Bohemograptus bohemicus* and *Monograptus hercynicus*; (b) concave, showing a distinct wing-like dorsal process directed downwards (Pl. 2: 10) and a thick marginal roll merging with the virgella.

Dorsal process length is 0.2–0.3 mm. Rarely, one or two metasicular rings are present.

Thecae. — Biform. As a rule, the first three or, quite frequently, four and even five thecae (Pl. 2: 1, 2, 7) feature well-developed paired lateral lobes. At the first theca, lobes are elongated, forming a kind of tongue slightly curved downwards (Pl. 2: 5, 8). Ventral wall between the lobes is notched (Pl. 2: 7, 8). In successive th_2, th_3, and th_4, lateral lobes (Pl. 2: 7, 8) straighten up, with the notch gradually disappearing so that th_5 or th_6 acquires the shape of a tube looking almost the same as those in representatives of the *dubius* group. Subsequent distal thecae are uniform, differing only in length, which increases from 1.5–1.8 mm (th_{10}) to 1.9–2.3 mm (th_{15}) to 2.2–2.4 mm (th_{30}) (Pl. 2: 1, 2, 4). Thecal width is stable 0.5 mm. Th_1 buds as a rule at a distance of 0.2–0.3 mm from the sicular aperture. A line drawn across the rhabdosome in its distal part normally cuts through only one interthecal septum. All apertural margins are provided with a roll-like thickening that becomes thicker with the aging of the colony and is quite distinct in adult specimens (Pl. 2: 6). There are 9 thecae per 10 mm in the proximal part and 10–11 thecae in the distal part of rhabdosome.

Remarks. — *I. t. transgrediens* (PERNER) has always stimulated interest of the researchers, and recently a detailed description of its morphology has been presented (JAEGER in KRIŽ *et al.* 1986).

PŘIBYL (1940, 1943), following PERNER (1899), described this form from the Prague Basin. At that time he recognized three subspecies (*Pristiograptus t. praecipius* PŘIBYL, *P. t. proximus* PŘIBYL, and *P. t. concretus* PŘIBYL). According to JAEGER, all of them ought to be regarded as astogenetic varieties of the type species. JAEGER's criticism is fully justified in respect of the first two subspecies. In contrast, *P. t. concretus*, distinguished by PŘIBYL in 1943 (p. 32) as a subspecies, was based on misinterpretation. Having studied the holotype preserved in the Prague National Museum collection as sample No. L. 1965, the present author was able to conclude that the specimen consisted of two superimposed rhabdosomes. Separately, each of them could be an *I. transgrediens.*

By 1964, *I. t. transgrediens* (PERNER) were reported from Morocco (WATERLOT 1945) and Germany (MÜNCH 1962). In Poland this taxon was not known until 1956 when it was encountered in the Chełm IG-1 section (TOMCZYK and TELLER 1956); its detailed description was published later (TELLER 1964). Along with the true *I. t. transgrediens*, three new allied species were recognized (*P. admirabilis* TELLER, *P. separabilis* TELLER, and *P. perbrevis* TELLER). Two of them were used as index species for establishing respective graptolite zones (TELLER 1964).

In the current revision of the above species, the present author considers them to be juvenile stages of the type species *I. t. transgrediens* (PERNER), and as such they are listed in the present paper as synonyms.

Since 1964, the type species *I. t. transgrediens* has been recognized in many sections world over, except for the Antarctic and South America. A general review of its occurrences has been provided by JAEGER (in KRIŽ *et al.* 1986: p. 328).

Geographic distribution. — A cosmopolitan species recognized in all Upper Přidoli sections throughout the world.

Assemblage. — Form basically monospecific, although the vertical range of the Prague Basin displays occasional dendroids. Scarce *Linograptus posthumus posthumus* (Reinhard RICHTER) can also co-occur.

Genus *Neocolonograptus* (URBANEK, this volume)
Neocolonograptus lochkovensis (PŘIBYL, 1949)
(Pl. 3: 1–9)

1940. *Monograptus* (*Pristiograptus*) *lochkovensis* sp. n.; PŘIBYL, p. 69, pl. 1: 6.
1964. *Pristiograptus aduncus* sp. n.; TELLER, p. 42, pl. 1: 4–6, pl. 2: 1–6, pl. 7: 18–19, pl. 9: 4–9, text-fig. 5a–d.
1964. *Pristiograptus bugensius* sp. n.; TELLER, p. 40, pl. 2: 4, 5, 9, pl. 7 13–15, pl. 9: 1–3, text-fig. 4a–e.
1977. *Monograptus lochkovensis* PŘIBYL; JAEGER, p. 340, text-fig. 3a–c.
1983. *Saetograptus* (*Colonograptus*) *lochkovensis* (PŘIBYL); PŘIBYL, pl. 4: 10.
1986. *Monograptus lochkovensis* PŘIBYL; JAEGER, p. 324, pl. 1: 16, pl. 3: 16–17, text-fig. 30a–b.
1986. *Monograptus branikensis* sp. n.; JAEGER, p. 325, pl. 2: 10, 12, 14, text-fig. 40.
non 1986. *Monograptus lochkovensis* PŘIBYL; KOREN', p. 99, pl. 21: 1–6, text-fig. 17.

Material. — Several thousand well-preserved rhabdosomes either in half relief or pyritized, representing various stages of the astogeny.

Derivation. — E Poland, Chełm IG-1 borehole, depth 1530.5–1582.5 m.

Stratigraphic position. — Přidoli, *lochkovensis* Zone.

Description. — Rhabdosome (Pl. 3: 1–2, 4–5) fairly narrow, straight with a slight ventral curvature starting from th_{5-6} in the proximal part. The rest of the rhabdosome straight. Maximum recorded length of mature forms attains 3.3 cm, but most of the adult colonies are 2.3–2.7 cm long. The rhabdosome widens gently from 0.8–0.9 mm at th_1 to 1.3–1.4 mm at th_{10}, attaining maximum width of 1.5–1.6 mm at the level of th_{12-13}, and remaining constant thereafter.

Sicula. — Narrow (Pl. 3: 3, 6, 9), 2.1–2.2 mm long. Its apex, as a rule, reaches the base of th_3 or a little higher but never beyond th_3. Sicular aperture width is fairly stable ranging between 0.3–0.4 mm, the latter being a more common value. The apertural margin (Pl. 3: 8–9) is rimmed by a roll-like thickenning involving the apertural process and merging with the virgella. Apertural process is normally 0. 2 mm wide, but rarely attains 0.3 or 0.4 mm. The process is very prominent, resembling a broad shovel in shape ("wing-like" in URBANEK's terms) (Pl. 3: 7, 9). Virgella attains 0. 6–0.7 mm. One or two metasicular rings can be seen.

Thecae. — Biform. In mature colonies, the first 12 to 17, but more often, 15 proximal thecae possess elaborated paired lateral lobes. The lobes of the first 3–4 thecae are strongly convex and curved downwards producing, in flattened specimens, a beak-like appearance. However, etched specimens or those preserved in full relief show that the lobes are separated by a fairly conspicuously deep ventral notch. (Pl. 3: 2, 6) In some specimens the lateral lobes of th_1 are slightly curved inwards in their terminal portion and even overlap (Pl. 3: 7, 9). Younger thecae feature only the separating notch. With further growth of the colony, beginning from th_{12}–th_{14}, lateral lobes gradually disappear, the aperture being modified into a straight tube as is characteristic of the *dubius* type. Such straight thecae constitute the distal part of the rhabdosome, emphasizing its biformism.

The first theca buds at a distance of 0.2–0.3 mm from the sicular aperture, the successive ones overlapping, at first insignificantly and later, in the course of astogeny, more and more strongly, becoming especially conspicuous in the distal part of the rhabdosome. Here, thecae are 1.5 to 1.7 mm long, 0.4 to 0.5 mm wide, with the free ventral wall being 0.6–0.8 mm. A perpendicular cut across the distal part of the rhabdosome will generally reveal two interthecal septa (three in very mature forms).

Remarks. — A 52-meter thick claystone graptolitiferous series from the Chełm IG-1 section (depth 1530.5–1582.5 m) was described by TELLER (1964). Among the rich graptolite fauna of the interval, two species, *Pristiograptus aduncus* TELLER and *P. bugensius* TELLER, were identified.

These identifications were questioned, without sufficiently convincing arguments, by JAEGER (1977: p. 338) who assigned the above forms to *Monograptus ultimus*, an opinion he confirmed in 1986 (KŘÍŽ *et al.* 1986: p. 321).

The present revision reveals that the specimens earlier recognized as *P. bugensius* and *P. aduncus*, studied in both flattened and etched form, represent *Neocolonograptus lochkovensis*, a taxon not previously known in Poland.

The present description is based chiefly on the material embedded in matrix and, as such, differs in some details from that offered by URBANEK (see this volume, p. 169) who studied isolated material from the Mielnik IG-1 boring.

N. lochkovensis was described for the first time by PŘIBYL (PŘIBYL 1940) from the then recognized Přidoli beds of the Prague Basin. PŘIBYL assigned it the rank of an index species for the eponymous zone. For many years, however, *N. lochkovensis* had not been recognized in other parts of the world, until Spasov (1960) reported it from Bulgaria, although his identification seems doubtful.

JAEGER (1977: pp. 337 and 340) was next to mention *N. lochkovensis*. Two forms from the Lochkov section illustrated by him very well display the diagnostic characters of the species.

KOREN' (1986: pp. 99–101) provides the first description of it from Kazakhstan, although details of the proximal and medial thecal morphology are lacking, and some characteristic features and measurements obviously differ from those of the holotype. Furthermore, some of the drawings and photographs illustrated in that paper may also raise doubts. All this leads the present author to approach these forms with caution. They might rather be representatives of the *transgrediens* group, or it is quite possible that only some of them belong to *lochkovensis* (KOREN' 1986: fig. 17z, pl. 21: 4).

The first fairly comprehensive description accompanied by good photographs of the forms collected in the Prague Basin does not appear until several years later (JAEGER in KŘÍŽ *et al.* 1986: pp. 324–325). On the basis of their vertical distribution in that basin, JAEGER recognizes an upper and lower *lochkovensis* Subzones separated by the *pridoliensis* Subzone. This view seems to be rather controversial and difficult to corroborate outside the Prague Basin.

In the same paper, JAEGER (in KŘÍŽ *et al.* 1986: pp. 325–326) describes a new form, *Monograptus branikensis* JAEGER, which he believes to be "morphologically and temporally intermediate between *M. ultimus* and *M. lochkovensis* but morphologically much closer to *M. lochkovensis*". It is very difficult, however, to distinguish this new species from *N. lochkovensis*, a fact emphasized by JAEGER himself as he points to "one character only, namely the lack of overlap of the interthecal septa also in the distal part" (JAEGER in KŘÍŽ *et al.* 1986: p. 326). He adds that "it is easy to distinguish the large adult or half grown rhabdosomes of *M. lochkovensis* from the small *M. branikensis*, but it may be impossible to separate the juveniles of the two species". The doubts raised by JAEGER are sufficient to weaken the diagnostic force of the new species. It seems therefore more reasonable to regard the morphological differences, if any, in *M. branikensis* as intraspecific variation and not as a basis for distinguishing a new species (see also the opinion of URBANEK, this volume, p. 169).

KOREN' and SUYARKOVA (personal information) have distinguished a new species, *Monograptus tumultuosus* in the Tien Shan sections (Central Asia). According to the authors, this form occurs above *M. branikensis* and below *M. bouceki*, that is in the same stratigraphic position as does *N. lochkovensis* in many sections world over. Following my study of the type material in Sankt Petersburg (February 1994), I conclude that the overall shape of the rhabdosome and the structure of individual thecae in these forms are almost identical with those seen in the *lochkovensis* morphotype, the differences being so insignificant as to be considered intraspecific variation. Thus it seems justified to assign these forms to *lochkovensis*. In my opinion, qualifying them as a separate species is insufficiently substantiated. Among the huge population of the species *N. lochkovensis* from the Chełm IG-1 boring, forms can be encountered, both juvenile and adult, which show some slight deviations from the *lochkovensis* morphotype; e.g. the variable number of thecae with lateral lobes, their disappearance, the degree of elaboration, and also thecal overlapping in the distal part of the rhabdosome. I am convinced that such insignificant deviations within a population do not provide a sufficient ground for distinguishing new taxa.

Geographic distribution. — A cosmopolitan species recognized in many Early Přidoli sections throughout the world. Populations abundant.

Assemblage. — The form occurs monospecifically. *Linograptus posthumus posthumus* (Reinhard RICHTER) is the only co-occurring species.

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PLATE 1

Istrograptus transgrediens rarus (TELLER) 74

1. Flattened rhabdosome. The first theca provided with two lateral lapets. Successive thecae straight, of dubius type, depth 1610.5–1611.1 m; × 5.5

Neocolonograptus ultimus (PERNER)

2–5. Flattened rhabdosomes with well-developed first theca and notches on the successive ones, depth 2, 4, 5 – 1601.5–1601.6 m, 3 – 1606.2–1606.4 m; 2 × 9.5; 3 × 3.5; 4–5 × 4.5.

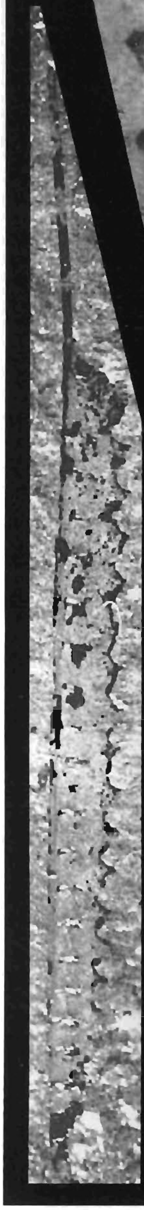
Istrograptus transgrediens samsonowiczi (TELLER) 75

6. Flattened and broken fragment of rhabdosome. Two proximal thecae provided with lateral paired lapets, depth 1461.3–1461.5 m; × 4.5.
7. Flattened complete rhabdosome. Two proximal thecae provided with paired lateral lapets, depth 1462.0–1462.1 m; × 4.5.

Istrograptus transgrediens chelmiensis (TELLER) 75

8–9. Flattened complete rhabdosomes. Three first thecae provided with paired lateral lapets, depth 8 — 1463.9–1464.8 m, depth 9 – 1514. 1 m; 8 × 4.5; 9 × 5.6.

All samples from the Chełm IG-1 borehole.



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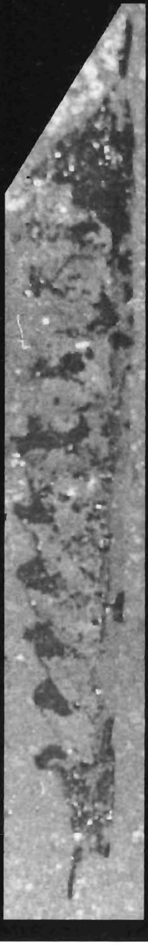

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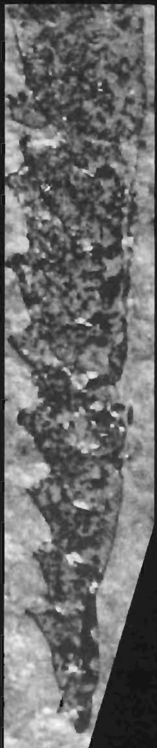

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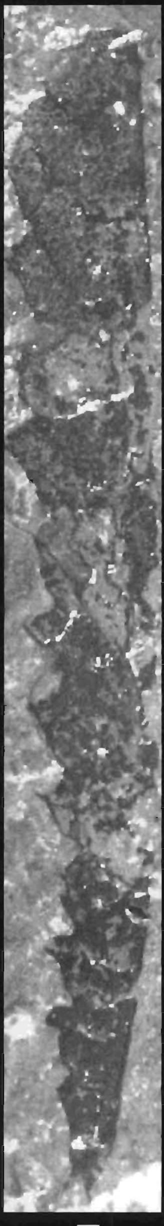

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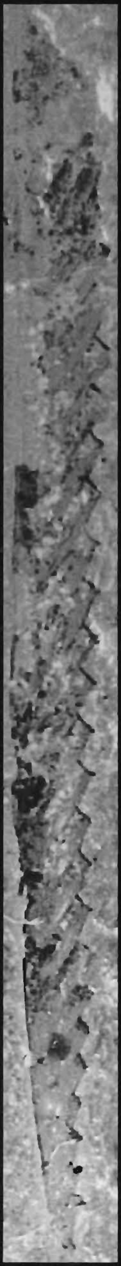

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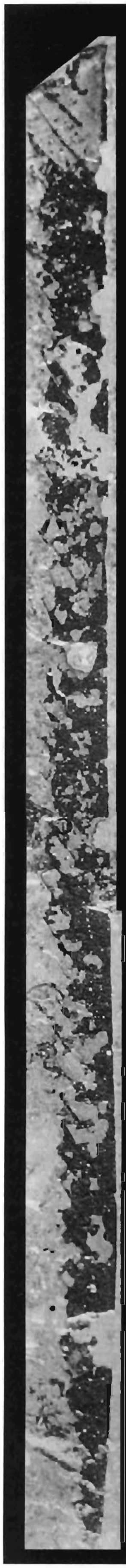
REVISION OF CERTAIN PŘIDOLI MONOGRAPTIDS FROM THE CHEŁM KEYSECTION (EEP)

PLATE 2

Istrograptus transgrediens transgrediens (PERNER) 76

1. Flattened complete rhabdosome, depth 1364.85–1365.1 m; × 5.3.
2. Medium size flattened rhabdosome. Five proximal thecae with well developed paired lateral lapets, depth 1383.5–1383.7 m; × 6.
3. Juvenile proximal part in half relief. Four thecae with developed paired lateral lapets, depth 1383.55–1383.7 m; × 6.
4. Juvenile broken proximal part. Five first of ten thecae with well-developed paired lateral lapets, depth 1383.9–1384.1 m; × 6.
5. Isolated first two thecae with well-developed lateral lapets and a notch, depth 1379.4–1379.5 m; × 43.
6. Isolated three distal thecae with a roll-like thickening surrounding the apertural margin, depth 1373.4–1375.8 m; × 30.
7. Isolated five proximal thecae and sicula. The thecae with well-developed lateral lapets and notches. Sicula simple with a slight wing-like process, depth 1382.5–1382.6 m; × 25.
8. Isolated broken proximal part with three thecae provided with well developed lateral lapets and notches. Sicula normal with a light dorsal process, depth 1379.7–1379.8 m; × 35.
9. Isolated sicula with a wide aperturae surrounded by a roll-like thickening. The first theca possesses a pair of well-developed lateral lapets, depth 1379.4-1379.5 m; × 40.
10. Isolated sicula with a big concave wing-like dorsal process and a thick roll – like margin with a virgella, depth 1382.5–1382.6 m; × 70.
11. Isolated sicula with a wide, almost straight, aperture and a slightly widened dorsal process. First theca provided with two lateral lapets, depth 1383.0–1383.2 m; × 53.

All samples from the Chełm IG-1 borehole.



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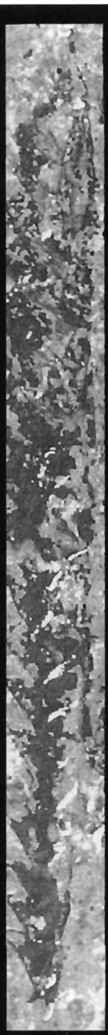

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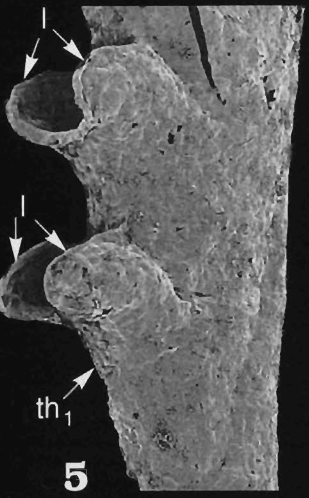

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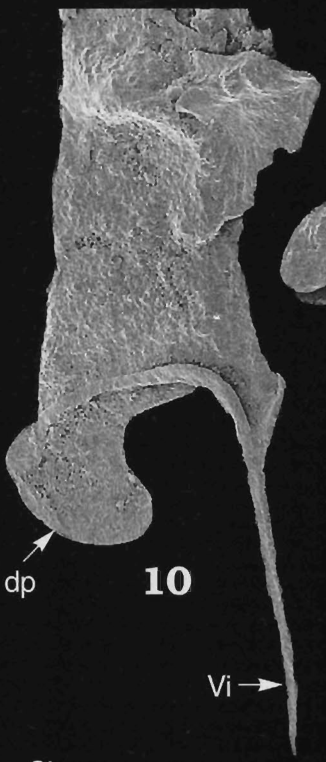

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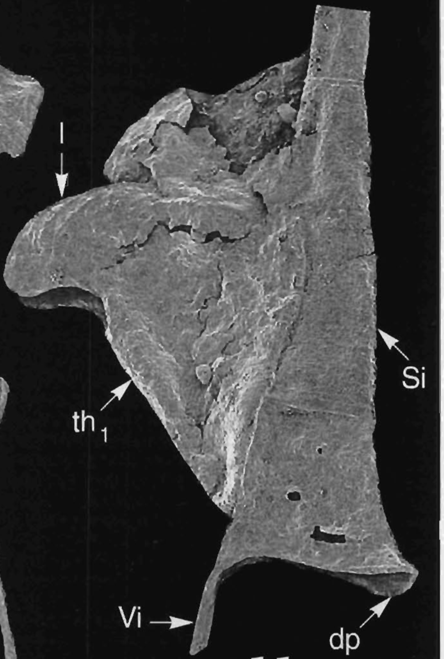

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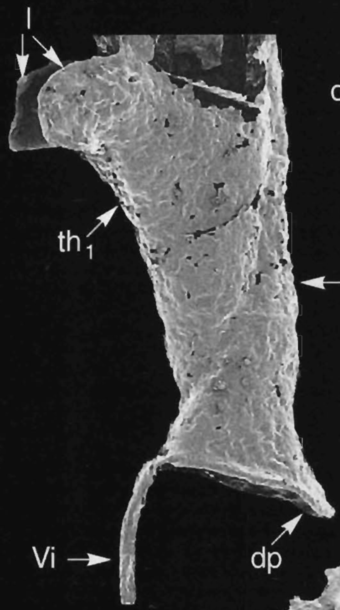

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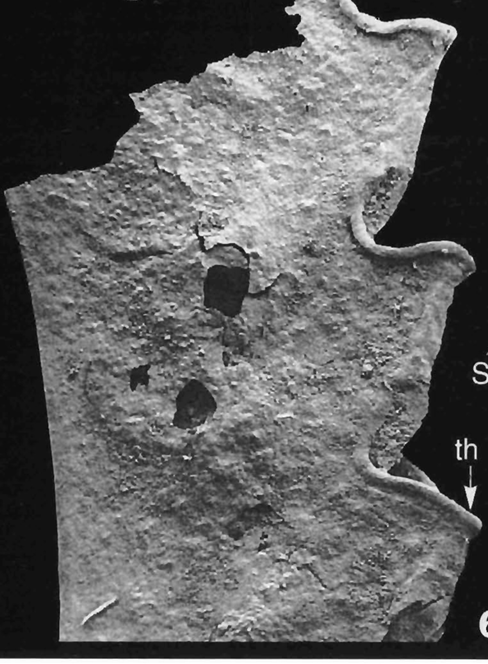

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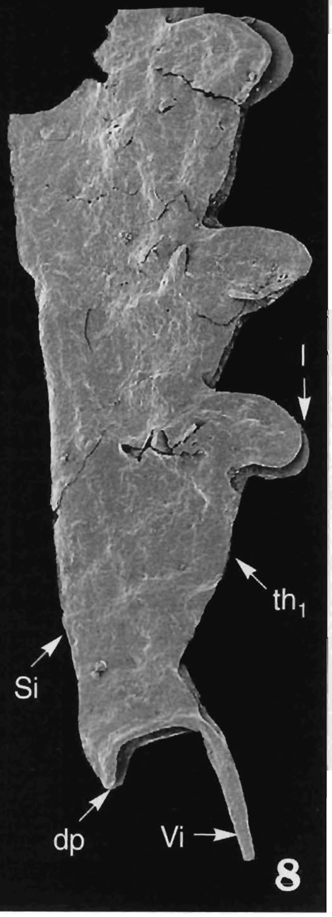

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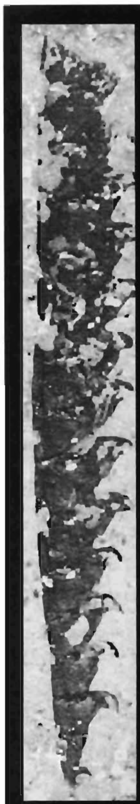
REVISION OF CERTAIN PŘIDOLI MONOGRAPTIDS FROM THE CHEŁM KEYSECTION (EEP)

PLATE 3

Neocolonograptus lochkovensis (PŘIBYL) 77

1. Flattened juvenile rhabdosome. Thecae provided with very distinct paired lateral lapets, depth 1547.6–1547.7 m; × 6.5.
2. Flattened juvenile rhabdosome. 8th thecae provided with distinct paired lateral lapets, depth 1542.5–1542.6 m; × 6.0.
3. Flattened two first thecae provided with paired lateral lapets, depth 1572.9–1573.1 m; × 8.0.
4. Adult flattened rhabdosome, 15 thecae provided with paired lateral lapets, depth 1547.6–1547.7 m; × 6.5.
5. Adult flattened rhabdosome, 25 thecae provided with paired lateral lapets, depth 1544.1 m; × 6.6.
6. Isolated broken fragment of rhabdosome with four thecae and a distinct sicula, depth 1514.5–1514.7 m; × 50.
7. Isolated sicula and first theca possessing two distinct lateral lapets. The dorsal process of the sicula wing-like and the apertural margin thickened, depth 1542.5–1542.6; × 46.
8. Isolated proximal thecae provided with two lateral lapets. The apertural margin of the sicula thickened, depth 1565.3–1565.5; × 50.
9. Isolated first theca with two lateral lapets. The sicula with a dorsal process and a thickening surrunding the aperturae, depth 1560.0 m; × 50.

All samples from the Chełm IG-1 borehole.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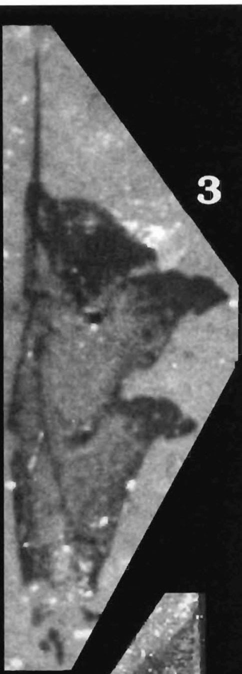
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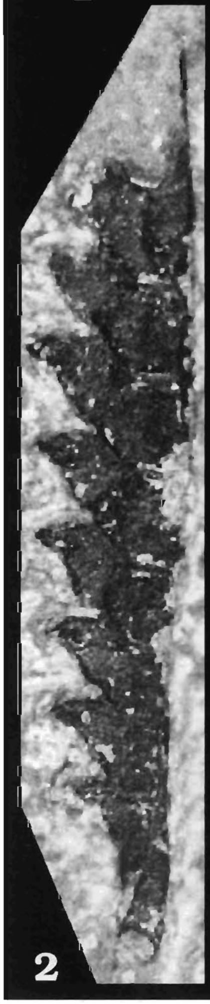
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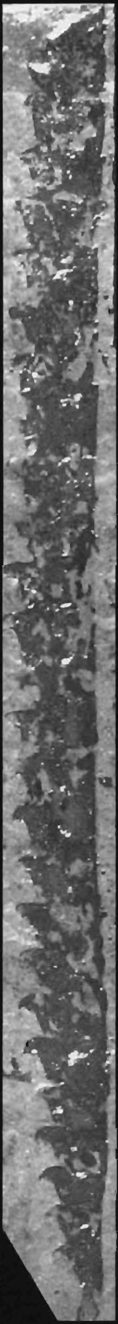
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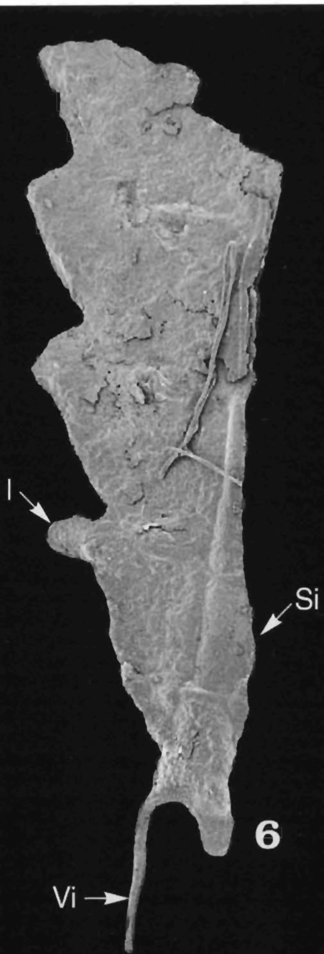
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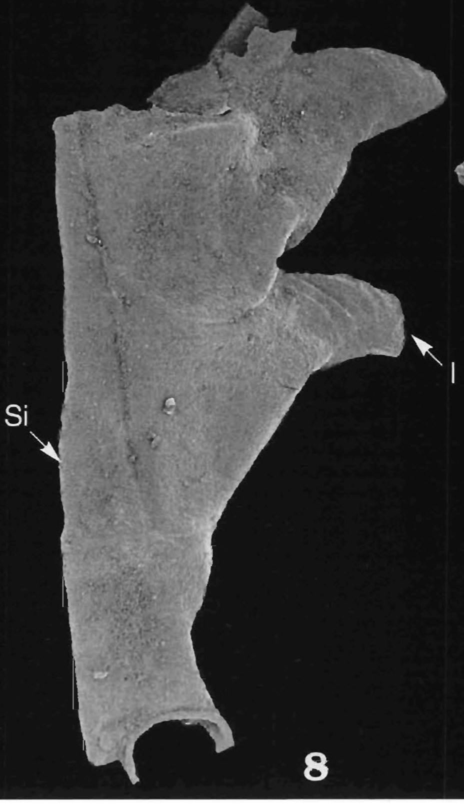
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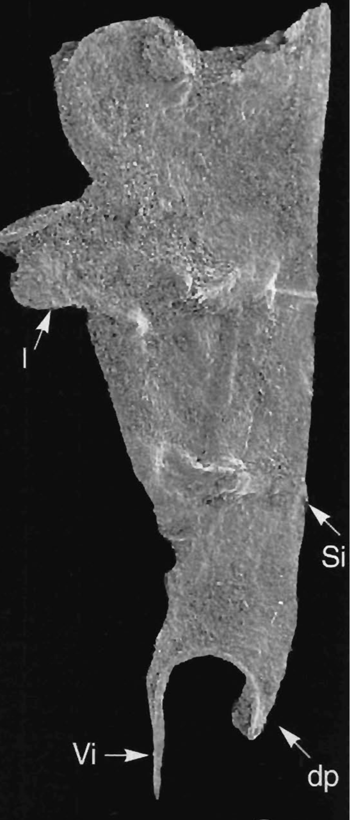
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LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

ADAM URBANEK

Urbanek, A. 1997. Late Ludfordian and early Přidoli monographtids from the Polish Lowland. *In:* A. Urbanek and L. Teller (eds), Silurian Graptolite Faunas in the East European Platform: Stratigraphy and Evolution. — *Palaeontologia Polonica* **56**, 87–231.

Graptolites etched from the Mielnik-1 wellcore (E Poland) reveal the main features of the development of monograptid faunas within the late Ludfordian–early Přidoli interval. Fifteen species and subspecies are described and *Monograptus (Slovinograptus)* subgen. n. as well as *Neocolonograptus* gen. n. are erected. Morphology of many species has been described adequately for the first time and their systematic position corrected. Four graptolite zones of the late Ludfordian are distinguished. The late Ludfordian fauna, which appears after the *kozlowskii* Event, is composed mainly of immigrants dominated by hooded monograptids. They reappear as a result of the Lazarus effect. Some of them initiated the lobate-spinose phyletic line terminating with *Monograptus (Uncinatograptus) spineus*, a highly characteristic index species. The lobate and the lobate-spinose types are accompanied by bilobate forms (*Pseudomonoclimacis latilobus*).
The graptolite sequence indicates that the appearance of the early Přidoli fauna was preceded by a biotic crisis, namely the *spineus* Event. Therefore this fauna is made up of a few holdovers and some new elements which developed from *Pristiograptus dubius* stem lineage (*Neocolonograptus* gen. n., *Istrograptus* Tsegelnjuk). This early assemblage, composed of bilobate forms, was later enriched by hooded monograptids, reappearing after the *spineus* Event. Both the late Ludfordian and early Přidoli assemblages abound in instances of homeomorphy and generic transitions. The latter occur due to independent acquisition by some forms of simple thecal characters which allows their assignement to a new genus. Another remarkable feature of Late Silurian monograptids is reduction in the number of sicular rings, and establishing of a steady relation between one of the rings and the virgella. This character state was independently achieved as a structural grade, by all, otherwise unrelated, phyletic lines of Late Silurian monograptids.

Key words: Late Silurian, graptolites, monograptids, stratigraphy, taxonomy, biotic crises, oligophyly, homeomorphy, adaptive repetitions, anagenesis.

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CONTENTS

To the memory of Bedřich BOUČEK and Alois PŘIBYL
whose life-long devoted activity has vastly increased
our knowledge of late graptolite faunas.

INTRODUCTION

The present paper deals with the graptoloid fauna of late Ludfordian and early Přidoli age, isolated from the borecore samples of the Mielnik IG-1 (Mielnik-1) key well (East Poland, Fig. 1), situated in the marginal zone of the East European Platform (EEP hereafter), within the Podlasie Depression. Recent studies on the Ludfordian in the graptolitic facies have shed an entirely new light on the development of the Upper Silurian graptoloid faunas (URBANEK 1970; TSEGELNJUK 1976; PŘIBYL 1983). Especially the studies made on the graptoloid faunas in the EEP (E Poland, Volhynia and Podolia) have provided a substantiation to the view best expressed by JAEGER (1981: p. 27) that "there is indeed a distinct interval that intervenes between the typical Ludlow and Přidoli fauna: this is characterized by Ludlow holdovers and a number of species of their own morphologies not seen before or later". This graptoloid fauna fills the gap in the knowledge of the Silurian sequence, which already existed 20 years ago, and puts an end to our ignorance concerning the developments between the standard *leitwardinensis* Zone on the British Isles and the *ultimus* Zone at the base of the Přidoli in the Barrandian (Bohemia).

The earlier portion of this interval was first adequately described by URBANEK (1970) in the Polish Lowland and the later portion was most completely recognized somewhat later in Volhynia and Podolia by TSEGELNJUK (1976). The present study makes some attempts to resolve the uncertainties which still existed and concerns the relationship between the earlier and the later faunal complexes within this interval, displaying different and entirely new structural types. There is no doubt that this fauna defines a stratigraphic unit comparable to the Gorstian or Přidoli, and that it deserves international recognition in the global standard graptolite zonation of the Silurian.

In contrast to the newly discovered Ludfordian graptoloid fauna, Přidoli monograptids were fairly frequently studied and described, but in most of the earlier papers the figures are, by modern standards, almost useless, and original specimens are frequently badly preserved. Moreover, this fauna was, with a few exceptions, based on flattened specimens, preserved as carbon films. As a consequence, their morphology has remained inadequately known and their taxonomy is in a state of confusion. This is mainly due to the fact that thecal characters, so important for the monograptid taxonomy, are difficult to recognize without an insight provided by specimens etched (isolated) from the matrix by acid treatment. In addition, a rather liberal practice of giving new names to poorly preserved specimens, obscures the real picture of the diversity of this fauna. The present paper is a study of well-preserved and isolated material obtained from the bore-core samples. As such it adds some new facts to our knowledge of the early Přidolian monograptids summarized quite recently by JAEGER (1986) and completes the picture of the lower part of the Přidoli on the Polish part of the EEP (TELLER 1964).

The present paper is primarily focused on: (1) a detailed morphological analysis of recognized taxa, (2) their stratigraphic ranges as revealed by samples from the bore-core, (3) recognition of the affinities within the monograptids of the late Ludfordian and early Přidoli as well as tracing morphological changes in particular lineages, (4) the origin and composition of the late Ludfordian/early Přidoli graptolite fauna, and (5) an analysis of faunal changes at the Ludfordian/Přidoli boundary as can be seen from the graptolite material.

The present description of late Ludfordian–early Přidoli graptoloids from Mielnik-1 wellcore, covers all Monograptina, except for *Linograptus postumus* (Reinhard RICHTER), subject to a separate study in this volume.

GENERAL PART

MATERIAL AND METHODS

The Mielnik-on-the Bug IG-1 deep-boring was designated by the Polish Geological Institute as one of the crucial reference points in the subsurface geology of the Polish Lowland. The coring was therefore almost complete, with a core diameter of 10–12 cm. The bore-core samples ensured an exceptionally good insight into the palaeontology and stratigraphy of the subsurface Silurian in this part of the East-European Platform (EEP).

As in most cases, the graptolite remains show a discontinuous vertical distribution. Thin layers of abundance or even mass occurrences are separated by unfossiliferous strata of varying thickness. Correspondingly, the sampling from the bore-core was in a way biased, as more samples were taken from those sections which contained more abundant graptolite fauna than from the obviously nongraptolitiferous ones. On the average, three samples were taken from each running metre of the core (from its lower, upper and middle portion), where graptolites were observed, while only one control sample was taken from the "barren" beds.

Undoubtedly, such sampling introduces some distortion into the record obtained, but, on the other hand, it proved to be the most efficient way to obtain a maximum number of well-preserved specimens, saving on both chemicals and laboratory operations. Depths are determined approximately, but a possible error in the case of denser sampling should not exceed ±15 cm, while in the less densely sampled portions of the core it does not seem to be more than ±30 cm.

Non-isolated specimens have been used to obtain information on the size and shape of the rhabdosomes and also to compare the material described herein with that discussed by the earlier authors, but the bulk of observations has been made on specimens etched from their matrix (isolated by acid treatment). The isolated specimens were either bleached to study the details of the thecal morphology and astogeny or used to reveal the gross morphology of the rhabdosome with the scanning electron microscope. Standard techniques of etching graptolite remains with chiefly hydrochloric, and only rarely, acetic acid, were applied for dissolving marly or calcareous rock samples. In a few cases a double treatment, involving first hydrochloric and then hydrofluoric acid, had to be used in order to dissolve highly silty samples. After dissolving, repeated washing and decanting served to remove the acid. The dissolved material was next picked up with pipettes of different size and stored in glycerine in Petri dishes.

What has proved to be a particularly effective way of etching graptolites from the high-clay core samples is the submergence of the entire graptolite layer seen on the bedding plane (Pl. 1: 2a, b) in a fairly strong solution of HCl. This easy and quick method usually yields large samples of isolated rhabdosomes.

The isolated graptolite remains were sometimes coated at places (mainly around the aperture) with patches of a residual sediment, firmly adhering to the periderm (Pl. 1: 3). Strong HF or, in some cases, a mixture of HNO_3 with HCl was used to clean the specimens, not always efficiently. The isolated specimens thus obtained were later either bleached to be further examined under the light microscope as transparencies or mounted on stubs with a view of studying their gross morphology with the scanning electron microscope. Bleaching, executed in polystyrene boxes with the help of potassium chlorate and nitric or hydrochloric acid, was followed by a careful washing.

Most transparencies were then mounted in glycerine in translucent polystyrene boxes and drawn with a camera lucida at high magnifications with the Leitz biological microscope. Measurements of bleached specimens were taken with the Wild microscope using a calibrated ocular micrometre.

Before scoping with SEM, specimens were mounted in water droplets at the surface of the stubs covered with a double-faced sellotape and allowed to dry gradually. Later they were coated with gold/palladium (Au/Pd). Most of scanning electron micrographs were taken either at 15 kV with Jeol JSM-35C, Jeol JSM 840 or with Philips 501 B, Philips XL 20 at 15 kV microscopes. Some micrographs were taken with the Coates and Welter field emission microscope at 12 kV.

The graptolite remains encountered in the borehole samples, while flattened to a various extent, are generally well-preserved, their periderm being present and only moderately "carbonized". In some samples, unbleached specimens display growth lines discernible with both the light and scanning electron microscopes (Pl. 1: 7, 9). The degree of their compression is in an obvious way correlated with the clay content in the matrix, as flattening most probably depends on the compaction of the initially loose silty sediments. Three-dimensional or only slightly flattened specimens were obtained from nodules or intercalations consisting of a calcareous sediment with a smaller share of clayey material and therefore showing lesser compaction (Pl. 1: 1). A combination of three-dimensional and flattened specimens can be encountered within one sample. Limestones, making thicker intercalations, seldom yield graptolites, except at the thin boundary layer with the adjacent silty sediments. These places supplied numerous three-dimensionally preserved specimens, suitable for chemical treatment.

In some cases, compaction of silty sediments accounts for certain characteristic preservational features. Two are most common: deep longitudinal folds such as seen in the thecae of *Monograptus (Formosograptus) formosus* (Fig. 22; Pl. 1: 4, pf) and especially conspicuous in their apertural portions, and characteristic protuberances disrupting the thecal walls. The latter may be seen on strongly flattened, ribbon-like specimens of various species (Pl. 1: 6). They were recognized long ago and interpreted in different ways. Thus HABERFELNER (1933) described them as supposed muscle-scars, while OBUT (1947) was convinced that they were carbonized gonads of the zooids. URBANEK (1958) provided evidence that such protuberances were produced by a squeezed free edge of the interthecal septum. The pyriform bodies seen inside the protuberance are thickened, lower (dorsal) margins of the interthecal septa, and as such are regular part of the rabdosome, made of skeletal tissues (Pl. 1: 5, 7, 8, arrowed).

The material illustrated in the present paper is housed at the Institute of Palaeobiology of the Polish Academy of Sciences, Warszawa, Poland, and designated in the collection as ZPAL G.XIX and ZPAL G.XVII.

GEOLOGICAL SETTING OF THE MIELNIK IG-1 BOREHOLE

Location of the borehole — The Mielnik IG-1 deep boring in Mielnik-on-the Bug, E Poland (Fig. 1) was made for the Polish Geological Institute. Coring was discontinued after reaching a depth of 1813.10 m within Precambrian deposits. The Silurian underlain by the Ordovician and overlain by the Permian is confined in the Mielnik IG-1 core to the interval between 1138.40 m (bottom) and 531.80 m (top). The boundary between the Silurian and the Permian rocks is erosional, with both the Devonian and Carboniferous missing. The coring is fairly complete (see Fig. 3 for the late Ludfordian–early Přidoli section of the bore-core).

Mielnik IG-1 is one of the key-wells that played an important role in establishing the main features of the subsurface geology of the Polish Lowland (TOMCZYK 1962). The significance of this borehole is accounted for by two factors: its location in the Podlasie Syneclise, one of the structural elements of the EEP, described in this volume (p. 16) by TELLER , and its position within the marly lithofacies belt of the Silurian. Due to the latter fact, it combines the features of different life-zones of a marine palaeoecosystem (mixed biofacies).

Facies composition and lithology — Upper Silurian deposits within the Podlasie Syneclise display a characteristic pattern of facies belts which were observed by TOMCZYK (1962, 1970) and characterized lithologically by LANGIER-KUŹNIAROWA (1974). From east to west, one encounters successively: (1) a carbonate lithofacies belt developed as marly limestones and marls, frequently dolomitic with a rare pyrite and bituminous admixture. Sporadic lenses of grey pellitic-crystalline limestone occur (Białowieża, Krzyże); (2) a marly lithofacies belt penetrated by the Mielnik borehole, with predominant marls, pellitic and organodetritic limestones and clays. In the central part of the belt, the proportion of marly limestones is still fairly high, up to 40 per cent of the total thickness. NW of Mielnik (in Tłuszcz), the marly lithofacies grades into (3) a clay lithofacies belt with claystones and clay shales as the dominant lithology featuring also scarce marly nodules and intercalations; and (4) a clay and silty lithofacies belt recognized further west (the Żebrak-1 and numerous other boreholes). Clay sediments are predominant there, chiefly in the form of dark-grey clay shales, but marly and dolomitic intercalations and nodules are also quite frequent. Representing open-sea sediments (pelagic and hemipelagic), belt (4) is the main facies as regards both the horizontal and vertical distribution. TOMCZYK (1964) compared belts 2 and 3 with the neritic zone while belt 1 may probably be compared with the shelf proper. However, a comparison with the detailed biofacies belts recognized in the Baltic area (EINASTO *et al.* 1986) has never been made for this part of the platform and their course may only be roughly approximated (see TELLER this volume, p. 10, Fig. 2 therein).

The Mielnik deep boring is situated in the marly lithofacies belt, close to its western boundary. The section studied in the present paper comprises the upper part of the Siedlce Formation and the lower part of the Podlasie Formation.

According to LANGIER-KUŹNIAROWA (1976), the Siedlce Formation as recorded in the Mielnik borehole is made up of marls, pellitic and organodetritic (sometimes dolomitic) limestones, and claystones, both

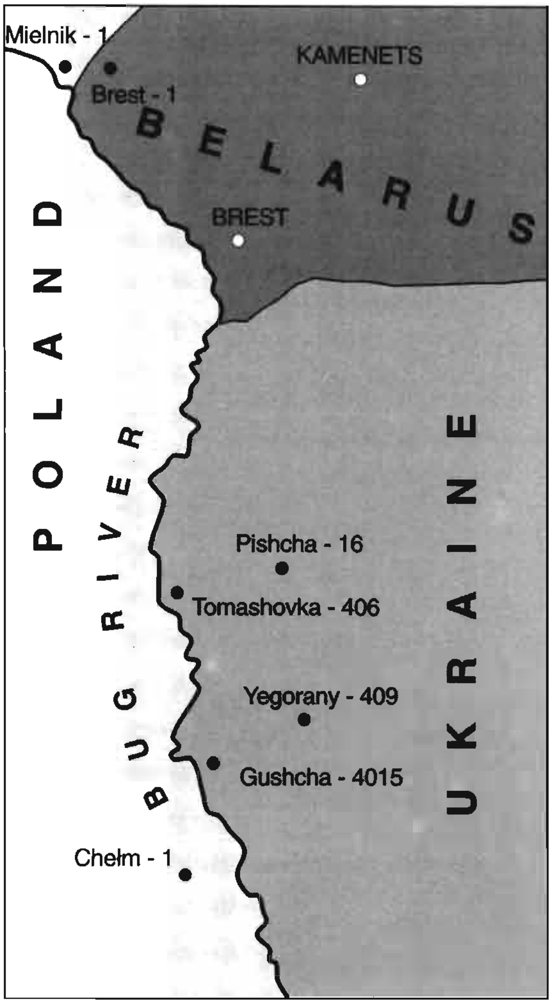

Fig. 1
Location of the Mielnik IG-1 (Mielnik-1) deep boring (E Poland) and some other key wells of the East European Platform.

in light and dark tinted microfacies but with the dark ones predominating. Carbonate rocks mainly contain an accumulation of phosphates, dispersed iron oxides, pyrite, and bituminous material. Rocks are frequently laminated, the laminae varying in thickness from a fraction of a millimetre to a few millimetres. Such laminae occur in claystones (dark tinted microfacies), in pellitic and organodetritic limestones, and also in marls. Some layers are silicified, probably as a result of epigenetic transformations of pyroclastic material. Five intercalations of bentonites were recorded within the Siedlce Formation of the Mielnik section by LANGIER-KUŹNIAROWA (1979, 1981).

In the Podlasie Formation, claystones, marls and pellitic limestones comprise the main lithology. Limestones are slightly dolomitic, sometimes laminated and bituminous. The top of the Silurian beds in the Mielnik borehole is weathered yellow and red due to the presence of ferric compounds. Weathering came as a result of denudation during the Devonian and Carboniferous (LANGIER-KUŹNIAROWA 1971, 1976).

From the above it follows that there is no significant difference in the overall lithology of the Siedlce Formation and the lower part of the Podlasie Formation. As compared with other deep borings in this facies belt, Mielnik displays a rather high carbonate, as well as a relatively high pyroclastic, content even in the rocks classifeid as claystone.

Late Ludfordian sediments show abundant evidence of intense volcanic activity through this interval, mainly in the form of bentonite layers. Five such layers mentioned by LANGIER-KUŹNIAROWA (1967) in her lithological study may be referred to the early phase of the late Ludfordian (depth 823.00–819.70 m), the others being found somewhat higher, at a depth of 763.40 m, within the *acer–spineus* Interval. The thickest bentonite layer (35 cm) is located at a depth of 820.10–819.65 m, which stratigraphically corresponds to the *latilobus–balticus* Zone. Another bentonite layer at 823.00 m (only 4 mm thick) immediately precedes the appearance of the *latilobus–balticus* assemblage and may be used as a local lithological marker of the lower boundary of this interval. However, the source of this abundant pyroclastic material has not been established.

The Mielnik borehole is situated in the Podlasie Depression, one of the structural elements of the western marginal zone of the EEP. Its origin and main stratigraphic and facies components are described by TELLER (this volume, p. 16). The western part of the depression, situated in Poland, is just a closure of a large megastructure of the Epigothic EEP which stretches through Belarus and Ukraine (the Pripyat–Dnieper–Don Depression, *fide* TOMCZYK 1968). For political and administrative reasons, the studies of the Silurian on both sides of the state border between Poland and the former Soviet Union were parallel and largely independent. This obscures the fact that the Podlasie Depression extends immediately eastwards into what, in the literature published in Russian, is called the Brest Depression. Silurian deposits were penetrated there by numerous boreholes, both structural and prospective, which supplied ample data concerning graptolites and stratigraphy. Some of these boreholes are situated in close vicinity of the Mielnik boring (e.g. the Novoselki-1 and the Vysokoe-1 borehole are only 15 km away in a straight line), and essentially repeat the sequence encountered and described in Mielnik.

PAŠKEVICIUS and PUSHKIN (1988) have made an attempt to correlate the Ludlow beds developed on the Polish and Belarus side of the Podlasie–Brest Depression. They produced a facies map showing an extension of the main facies belts in the south-eastern direction (Fig. 2).

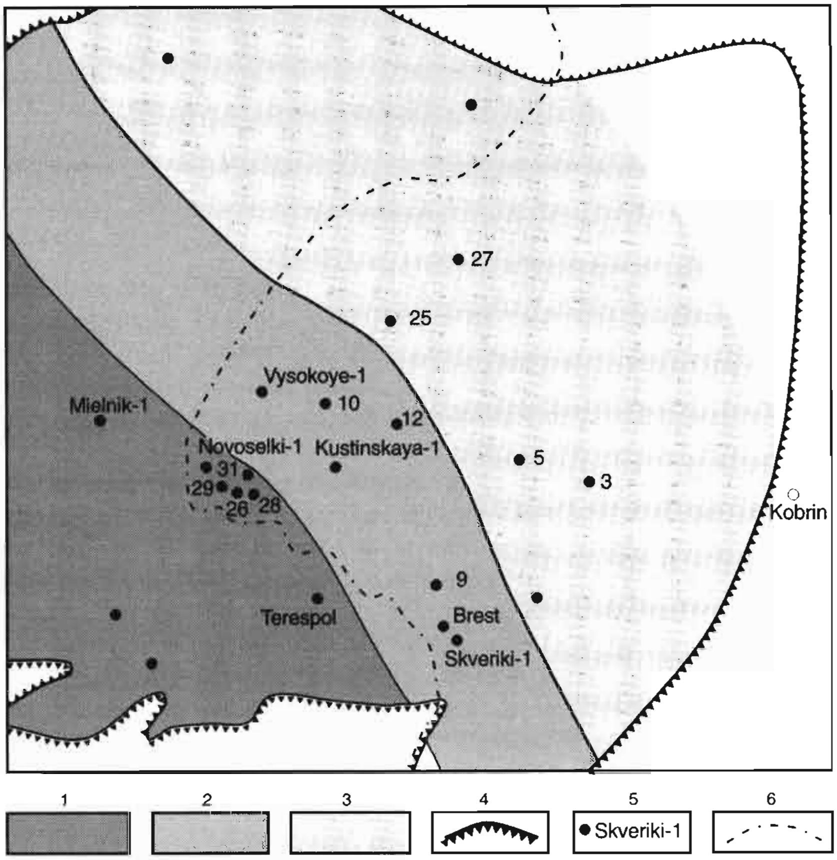

Fig. 2
Situation of Mielnik-1 deep borig in relation to lithologic-facies zones within the Polish and Belarus part of Podlasie Depression: 1 – zone with limestone and inferior marly intercalations; 2 – zone of limestone lenses and nodules intercalated with green-gray (rarely dark grey) marls; 3 – zone of intercalation of green-gray and dark gray (argillite-like) marls with nodules, lenses and thin layers of limestone; 4 – contemporary limit of Silurian deposits; 5 – studied borehole sections; 6 – state boundary (based on data by TOMCZYKOWA and TOMCZYK 1979 and PAŠKEVICIUS and PUSHKIN 1988, after PAŠKEVICIUS and PUSHKIN 1988).

GRAPTOLITE ZONATION OF THE LATE LUDFORDIAN–EARLY PŘIDOLI STRATA IN THE MIELNIK BORING

Most of the graptolite zones distinguished in the present paper are range-zones. I follow the widely used practice of recognition of the successive-appearance zones, that is intervals defined by the first appearance of the name-giving taxon and the first appearance of the immediately succeeding zone fossil. Hence, they are frequently shorter than taxon-range zones that are defined by the total range of a given index fossil. The successive-appearance zones were termed "practical zones" by JAEGER (1986: p. 315) and used for the biostratigraphic subdivision of the type Přidoli. Both in the Barrandian area and Mielnik-1 sequence, such zones are usually separated by gaps characterized by the absence of both index species. Some range-zones are lineage zones (*acer–spineus* Zones, *parultimus–lochkovensis* Zones). I would like to emphasize the significance of lineage zones, based on the history of a group displaying phyletic evolution. The regular and directional nature of changes and mutually exclusive vertical distribution of taxa may be used as a safe guide for subdivision and correlation. In this respect I share DZIK's (1995) opinion about the exceptional value of phyletic transitions within evolutionary lineages as an evolutionary measure of geological time. The only assemblage zone was distinguished at the base of the late Ludfordian, and therefore such units play a minor role in the biostratigraphy proposed herein. However, assemblage zones may be extremely useful in other instances (RICKARDS 1995). When describing the section, I also make use of the notion of interzone (interregnum) to define the intervals with a strongly impoverished fauna. Such intervals are highly characteristic of certain portions of the core. Being probably, in most cases, of purely local significance, they may sometimes reflect wide-spread phenomena.

The sequence of monograptid species encountered in the Mielnik borecore section (Fig. 3) permits recognition of 6–7 graptolite zones within the late Ludfordian–early Přidoli time-span. The zones proposed for the late Ludfordian part of the sequence may for the present be considered regional biostratigraphic zones, although we believe that most of them will eventually be accepted as international stratigraphic units. The early Přidoli part of the sequence can be subdivided in much the same way (with only one difference) as the type Přidoli of the Barrandian (JAEGER 1986: p. 315).

Late Ludfordian graptolite sequence. — In the early period of investigations of the subsurface Silurian in the Polish Lowland, TOMCZYK (1962) assigned a series of strata that locally may be over 1000 m thick and characterized by the occurrence of a number of species "from the group of *Monograptus formosus*" to a single stratigraphic unit. The presence of such series with numerous but yet undescribed species has been widely accepted as a unique feature of the development of the Silurian in the Polish part of the EEP (TOMCZYK 1968; TELLER 1966, 1969).

In the light of the present study this preliminary conclusion may be considerably refined. *M. (Formosograptus) formosus* has indeed a long vertical range in beds of great thickness, displaying some acme horizons. However, within this range the species in question remained very uniform, producing no descendant species. The preliminary reports on numerous species "from the *M. formosus* group" were therefore illusory, probably based on lumping a number of species with similar overall morphology (e.g. a distinct dorsal curvature), such as *M. (Uncinatograptus) acer–M. (U.) aculeatus, M. (U.) protospineus* and *M. (U.) spineus*. Nevertheless, TOMCZYK (1962, 1970) correctly recognized characteristic features of this fairly abundant and, in many ways, unique fauna. His series with the "*M. formosus* group" is a regional equivalent of the late Ludfordian, developed in the graptolitic facies.

The Mielnik late Ludfordian succession begins with a highly characteristic assemblage of newly and abruptly appearing species occurring in a rapid succession (Fig. 3). They include: (1) *Pseudomonoclimacis latilobus* (TSEGELNJUK), FA at a depth of 823.00 m; (2) *Monograptus (Wolynograptus) hamulosus* TSEGELNJUK, FA at a depth of 822.90 m; (3) *Pristiograptus dubius fragmentalis* BOUČEK, FA at a depth of 821.00 m; (4) *Monograptus (Slovinograptus) balticus* TELLER, FA at a depth of 819.85 m; and (5) *Monograptus (Formosograptus) formosus* BOUČEK, FA at a depth of 819.40 m. The most characteristic species of the assemblage zone distinguished herein are the first and the fourth ones. Correspondingly, I suggest naming this zone the *latilobus/balticus* Zone (Fig. 3).

The appearance of the next selected index graptolite, *Monograptus (Uncinatograptus) acer* TSEGELNJUK, is separated by a relatively thick series of strata (approximately between 814.00 and 800.00 m) containing an impoverished graptolite assemblage with predominant *Pristiograptus dubius* s.l. This event, whether of a local or a more general nature, will be referred to as the ingresion of the first *dubius* fauna (see the discussion below).

The frequent occurrence of *Monograptus (Uncinatograptus) acer* TSEGELNJUK through an interval, some 20 m thick, in the Mielnik sequence (depth 794.60–774.50 m) marks a distinct zone. The *acer–-protospineus–spineus* sequence almost certainly contains successive links of a lineage that morphologically and temporally grade into each other (URBANEK 1995). In spite of the fact that the occurrence of *Monograptus (Uncinatograptus) protospineus* is limited only to a narrow band (some 40 cm thick) in the Mielnik sequence, the recognition of an eponymous zone is suggested. Conspecific forms seem to occur both in Volhynia and in Central Asia and the suggested index species may easily be identified.

The next biostratigraphic unit distinguished in the Mielnik bore section is therefore the *spineus* Zone defined by the vertical range of highly characteristic *Monograptus (Uncinatograptus) spineus* TSEGELNJUK (depth 763.80–760.20 m, Fig. 3). The FA of this zonal fossil is separated from the LA of the preceding index fossil, *M. (U.) acer* TSEGELNJUK, by an aproximately ten-meter interval. It coincides, however, with a horizon of a mass occurrence of *Monograptus (Formosograptus) formosus* BOUČEK, that replaces locally almost all the other species and produces huge, practically monospecific, accumulations. Whether these acme horizons are no more than a local phenomenon or a widely distributed event is unknown.

Moreover, the vertical range of the previously mentioned *Monograptus (U.) acer* TSEGELNJUK is interrupted and divided into an earlier and a later part (Fig. 3) by an invasion of the second *dubius* fauna (see discussion below).

Several isolated thecae identified as *"Monograptus" lebanensis* TELLER, 1966 were found within an interval of 794.55–790.90 m. Although the state of preservation (an extremely attenuated and strongly

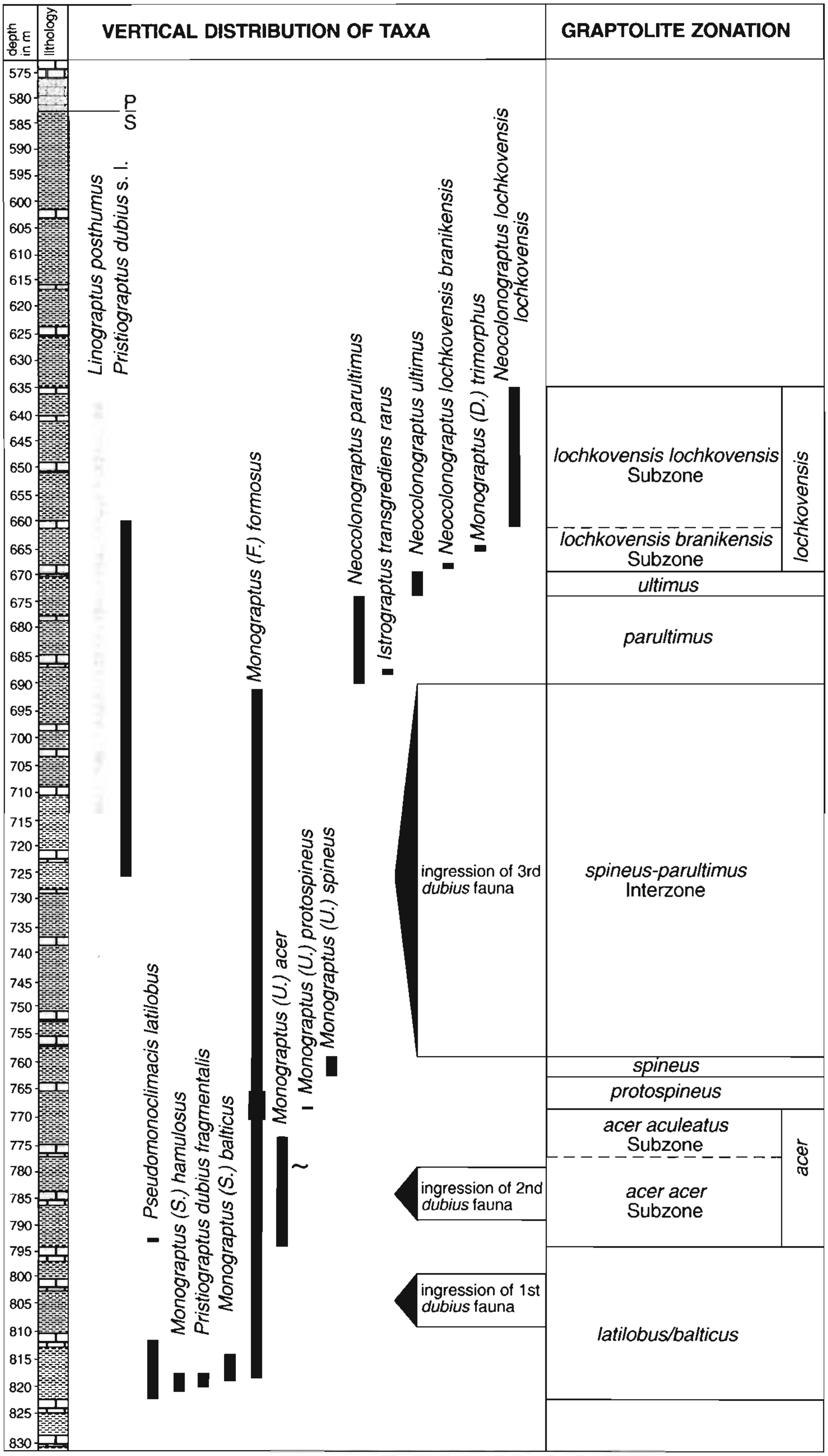

Fig. 3

Simplified lithological section, vertical ranges of graptoloid taxa and zonal subdivision as encountered in Mielnik-1 wellcore. A solid black line within the range of *Pristiograptus dubius* s.l. marks the interval with the *labiatus* morphotype, while wavy line ~ denotes the arbitrary limit between two subspecies of *M. (U.) acer*.

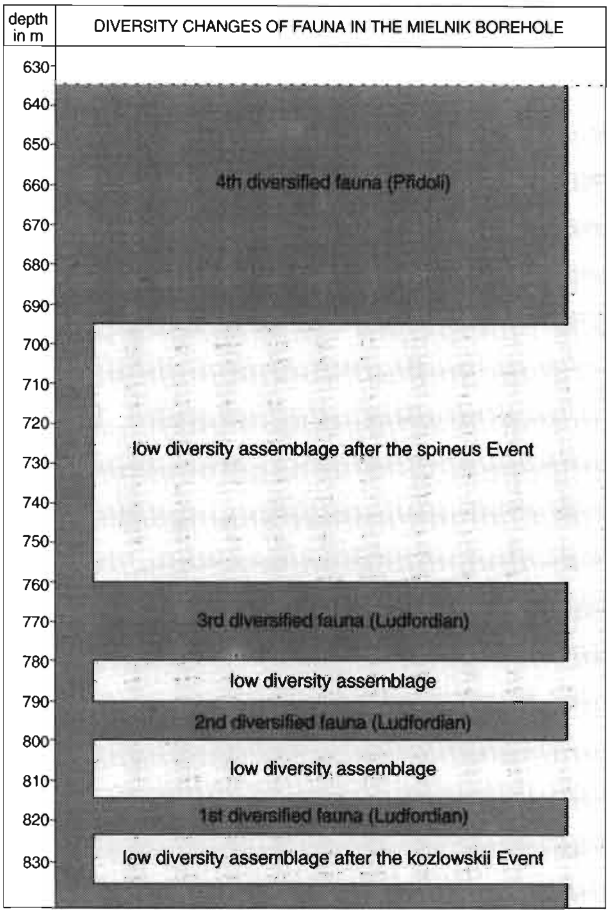

Fig. 4
Diversity changes of the graptoloid fauna in the late Ludfordian–early Přidoli segment of the Mielnik-1 wellcore. Low diversity assemblages-dotted, diversified faunal assemblages – dark. Continuous dotted right margin – presumable area with permanently impoverished fauna; continuous grey left margin – presumable area with permanently high diversity fauna. Futher explanations in text.

flattened periderm) makes it impossible to study their morphology in detail, the Mielnik findings permit the stratigraphic level of *M. lebanensis* to be defined as the *acer* Zone. This confirms TELLER's earlier conclusions concerning its occurrence between the ranges of *M. balticus* and *M. protospineus* (= *M.* cf. *formosus* in TELLER 1966) within Łeba-3 borehole.

The top of the *spineus* Zone closes the sequence of the late Ludfordian index monograptids. The strata above the LA of this species are again characterized by an impoverished graptolite aseemblage yielding rare *Pristiograptus dubius* s.l. and *Linograptus posthumus* (R. RICHTER). *Pristiograptus* displaying the *fragmentalis* morphotype is absent, having been replaced by another morphotype, showing no substantial difference from Lower Ludlow (Gorstian) *P. dubius frequens* except for an extremely thick apertural lip. Therefore, the recognition in the Mielnik section of a separate *fragmentalis* Zone (corresponding to that in the Barrandian or in Central Asia) is unjustified. It is replaced in the EEP by a low diversity interzone of some 70 m thick, probably representing an immediate effect of an extinction event at the top of the *spineus* Zone (KOREN', personal communication) and preceding sudden immigration of *Neocolonograptus parultimus* (JAEGER) (Fig. 3).

An alternative subdivision of the late Ludfordian strata in the Mielnik bore section would involve recognizing a single local *Monograptus (Formosograptus) formosus* BOUČEK Biozone. That species is present throughout practically the entire thickness of these beds [with the FA at a depth of 819.40 m and the LA, at 692.50 m, only some 50 cm below the base of the *N. parultimus* Zone (Fig. 3)]. It, however, shows a discontinuous vertical distribution, displaying a 4-meter-thick band of mass occurrence (at a depth of 770.45–766.45 m, in the *spineus* Zone and the underlying *acer–spineus* Interzone). This epibole coincides with a distinct increase of clay content in the sediments and probably also with a temporary deepening of the basin.

While the *formosus* Zone as defined above seems to be an adequate unit for the entire interval of the late Ludfordian on a regional scale, it can hardly be a suitable internationally recognized standard zone because of its long vertical range passing through the Ludfordian–Přidoli boundary. The mere presence of *Monograptus (Formosograptus) formosus* is not enough, it may be indicative of either early Přidoli or late Ludfordian age. The recent proposal of KOREN' (1986, 1992) to distinguish the *formosus–spineus* Zone as a unit of the global standard zone characteristic of the late Ludfordian is also controversial. Although both monograptid species are morphologically well-defined, it is the second one alone that is confined to the Ludfordian. After all, the type stratum of *M. (F.) formosus* is the *ultimus* Zone, and not long ago JAEGER (1977: p. 343) was convinced that it represents an associated index fossil, by which this zone may be easily recognized.

Ingressions of low diversity assemblages. — The Mielnik section features three intervals of low diversity, punctuating the development of more diversified graptolite faunas (Fig. 4). In this way depauperate faunal assemblages, composed chiefly of *P. dubius*, shadow the evolution of the remaining monograptids, splitting the sequence, as traced at this single point, into three "shadow lines" (ingressions of the *dubius*-predominated depauperate fauna) and four "windows" (reappearance of higher diversity assemblages, see Fig. 4).

The first ingression of the *dubius* fauna is recorded at a depth of 814–800 m. Being basically monospesific and having a standard *"frequens"* habitus, *P. dubius* assemblages are closer to Gorstian forms than to the Ludfordian *fragmentalis*. Still they possess an unusual feature: a strangely modified virgula transformed into a tubular structure (see pp. 157–158 herein).

The second ingression of the *dubius* fauna (at a depth of 790–780 m) is represented, as above, by pristiographtids with a standard appearance, rarely associated with the remains of the Crustoidea (depth 784.20 m), e.g. cysts and stolons, as well as with some enigmatic plant remains and scarce *Linograptus posthumus* (Reinhard RICHTER). The spectrum of the associated forms is thus completely different from that in the vast majority of the assemblages observed.

The third ingression of the *dubius* fauna (at a depth of 760–692 m) is partly associated with an unusual habitus of *P. dubius* displaying hypertrophy of the apertural lip and recognized therein as *P. dubius labiatus* subsp. n. In the somewhat higher strata, *P. dubius* reverts to a standard appearance. That course of events, which might seem paradoxical, is discussed on p. 159 of the present paper. A sample bearing Rhabdopleurida (stolons and cysts) has been found at a depth of 692.55 m. Remains of Eurypterida and scolecodonts are rather frequent associates. The last of the three ingressions follows the extinction of *M. (U.) spineus* TSEGELNJUK and precedes the FA of *Neocolonograptus parultimus* (JAEGER).

In consequence of the second invasion of the *dubius* fauna, the vertical occurrence of *Monograptus (U.) acer* TSEGELNJUK is divided into a lower and an upper part. This may be viewed as an instance of the Lazarus effect on a small scale – the disturbance produced is shorter than the duration of a single index species.

The first ingression of the *dubius* fauna results in the disappearance of the *latilobus–balticus* assemblage replaced by a monotonous and depauperate association. Except for a spurious occurrence of *Pseudomonoclimacis* cf. *latilobus* at a depth of 787.00 m, none of the representatives of the older association reappears above the first *dubius* band.

Such dramatic shifts in the suite of community species may be explained, at least tentatively, in the light of the recent studies on marine systems (BARRY and DAYTON 1991). They reveal that in certain areas, climatic variations account for the abundance of some and disappearance of other species, the latter being replaced by different forms. Changes in the quantity of macroplankton, i.e. its decrease or disappearance, occur in period cycles, following a pattern longer than decadal. A similar explanation was offered by WATKINS and BERRY (1977), namely water mass control of graptolite distributional patterns. The retreat of "graptolitic water mass" would be responsible in this case for the tendency towards exclusive occurrence of monospecific assemblages.

Thus the local retreat of the Mielnik graptoloid fauna to either depauperate or monospecific *dubius* assemblages was probably caused by similar, but much longer, environmental disturbances (with a duration of 10^4–10^5 years). This is especially true for the first and second ingressions of the *dubius* fauna, as defined above, which were shorter than the average period of the evolutionary turn-over of graptolite species (the thickness of corresponding strata is 10–14 m). The third ingression was longer (the respective thickness being 70 m) and occurred in a particularly unsuitable environmental situation which is immediately related to the *spineus* Extinction Event. The results observed at this stage are far-reaching; i.e. true monograptids (with hooded thecae) disappear from the sequence until the *lochkovensis* Zone.

A largely similar explanation may be offered for an abrupt numerical increase of *Monograptus (Formosograptus) formosus* BOUČEK as observed at a depth of 770.45–766.45 m (the *formosus* acme horizon). The mass occurrence of the above species (in the form of the so-called "graptolite carpets", Pl. 1: 2) as almost monospecific assemblage, associated with scanty *Linograptus posthumus* and, in one sample, with rare *Pristiograptid dubius*, is indicative of the severity of the environment in respect to most co-eval species.

Graptolite succession of the early Přidoli. — The FA of *Neocolonograptus parultimus* (JAEGER) delineates, at a depth of 691.95 m (~692 m!), the Ludfordian/Přidoli boundary (Fig. 3). It marks the base of the well-defined *parultimus* Zone, some 17 m thick (LA at 675.65 m). *N. parultimus* is followed by the closely related *Neocolonograptus ultimus* (PERNER) (FA at a depth of 674.95 m, LA at 671.55 m), defining the *ultimus* Zone.

The next index species is *Neocolonograptus lochkovensis branikensis* (JAEGER). Accepting a subspecific rank for *N. branikensis* JAEGER (see p. 169 for discussion), I propose to subdivide the thick *lochkovensis* Zone into two units, the earlier and very thin *branikensis* Subzone and the later, much thicker, *lochkovensis* Subzone (the FA of *Neocolonograptus lochkovensis lochkovensis* at a depth of 662.75 m), the two subspecies being separated by a single appearance of *M. (Dulebograptus) trimorphus* TSEGELNJUK

(FA and LA at 665.80 and 664.74 m). *N. lochkovensis lochkovensis* is the last index graptolite encountered in the Mielnik section, its last occurence being at a depth of 634.15 m.

The graptolite succession in the early Přidoli Beds of the Mielnik section is homotaxial with that in the type area (Barrandian), the first re-appearing *Monograptus* species being, however, different (see the comparison herein, p. 100).

COMPARISON AND CORRELATION WITH OTHER AREAS

Volhynia and Podolia. — The Upper Silurian graptolite faunas of Volhynia and Podolia as well as those of the adjacent territory of Belarus (the Brest Region) are exceptionally rich and well-recognized (TSEGELNJUK 1976, 1981). Silurian deposits are largely naturally exposed or were penetrated by numerous deep borings (24 bore holes in Volhyno-Podolia and a few more in Belarus) from which graptolite remains have been isolated and studied.

Within the Ludfordian interval abounding also in shelly faunas, TSEGELNJUK (1983a) has identified the following graptolite assemblage: *Tamplograptus formosus* (BOUČEK), *Uncinatograptus caudatus* TSEGELNJUK, *U. rectus* TSEGELNJUK, *Dulebograptus bresticus* TSEGELNJUK, *Pseudomonoclimacis haupti* (KÜHNE), *P. medius* TSEGELNJUK, *Bugograptus spineus* (TSEGELNJUK), *B. aculetus* (TSEGELNJUK), *Neolobograptus auriculatus* URBANEK, *N. egregius* URBANEK, *Cucullograptus aversus aversus* (EISENACK), *C. aversus rostratus* URBANEK, *Monograptus balticus* TELLER, *Bohemograptus tenuis* (BOUČEK), *Neocucullograptus kozlowskii unicornus* URBANEK, and others. On the basis of graptolite and especially brachiopod faunas, TSEGELNJUK (1983, 1983a) advanced his concept of the Ulich superhorizon (Ulichian) as a so-far "lost", "missing" or rather neglected stage in the evolutionary and historical development of the Silurian organic world. Essential for the understanding of this stratigraphic unit is TSEGELNJUK's (1983: p. 50) opinion that Ulich age corresponds to the post-Ludlow–pre-Skala interval, which on the scale of evolutionary changes in brachiopods, graptolites and chitinozoans is comparable with both the Ludlow Series (redefined by him) and the Skala (Přidoli) phase.

In spite of the richness of the graptolite assemblage, the graptolite facies of the Ulichian superhorizon have been subdivided in only two graptolite zones: the *Neocucullograptus kozlowskii unicornis* Zone (the Tagrin horizon) and the *Monograptus* (*Uncinatograptus*) *caudatus–Monograptus* (*Wolynograptus*) *balticus* Zone (the Meton horizon). Thus, an exceptionally diversified monograptid fauna, etched from numerous borecores, has been lumped into just two biozones. In my opinion this zonation does not make full use of the discrete time belts defined by the vertical ranges of the monograptid species recognized in the area. TSEGELNJUK's (1981) remarkable caution in distinguishing graptolite zones within the Late Silurian of Volhyno-Podolia (only six zones as compared to about twenty such units in adjacent Eastern Poland) is by no means accidental. It evolves from his elaborate philosophy, according to which most of the "small" zones distinguished in Poland, e.g. the *Neodiversograptus nilssoni* Zone, the *Lobograptus progenitor* or the *Lobograptus scanicus* Zone are practically co-eval, whilst their alleged index species are no more than markers of a single large biozone (TSEGELNJUK 1981: p. 51). His approach, however, contradicts the by-now well-established international practice, as the above-mentioned zones have been gaining recognition in a growing number of regions.

Moreover, TSEGELNJUK (1981) maintains that small discrete biozones (such as those recognized by URBANEK 1966, 1970) are "in fact only partial zones ("Teilzones"), which provide a false impression that graptolites appeared in the fossil record only to become extinct, soon after they were fixed by a palaeontologist". Although TSEGELNJUK (1981) insists that his "attitude to zonal subdivision does not differ from the generally accepted one", the diversity of the Ludfordian graptolite fauna, largely described by him, has not been mirrored in his version of the zonal subdivision. Recent studies on the equivalent strata in the Polish part of the EEP permit a much finer biostratigraphic zonation.

Practically all species recognized from the early Ludfordian of the Polish part of the EEP (URBANEK 1970) together with almost every species from the Ludfordian beds of the same area described in the present monograph have also been encountered in Volhynia and Podolia (listed after TSEGELNJUK 1983a). One could expect therefore very similar ranges and order of appearance of the index species over the entire southern part of the EEP (including Eastern Poland, Volhynia and Podolia). Nevertheless, in a number of cases TSEGELNJUK (1976, 1981) indicates a substantial overlap or concurrence for those monograptid species which, in the Mielnik section, occupy distinctly different horizons.

Some of TSEGELNJUK's claims (such as the concurrence of *Cucullograptus* URBANEK and *Neococullograptus* URBANEK, see TSEGELNJUK 1981: fig. 9) were proved to be erroneous and based on a misinterpretation of the sections, some others may be equally misleading because of the low resolution of his methods of correlation of the sections from the various boreholes. Thus according to TSEGELNJUK (1981: p. 27 and his fig. 4), *Heisograptus acer* [= *Monograptus (Uncinatograptus) acer* TSEGELNJUK in this paper] and *Bugograptus aculeatus* as well as *B. spineus* [probably the first two are conspecific and, as such, referred in this paper, to *Monograptus (Uncinatograptus) acer* (TSEGELNJUK)], are co-eval and occur roughly between bentonic layers M_6–M_1. The Mielnik sequence is indicative of a distinctly earlier appearance of *M. (U.) acer* and a much later origination of *M. (U.) spineus*, to say nothing of TSEGELNJUK's taxonomy obscuring the fact that most probably the two species are immediately related (URBANEK 1995). The unusual persistence of *Bohemograptus bohemicus* (BOUČEK) as high as the Skalian, "without however reaching the metabentonite C_6", may also be accounted for by a similar misidentification of this species' stratigraphic position.

A substantial source of uncertainty was most probably introduced by his use of individual bentonite intercalations as reference points for regional correlation. More than that, emphasizing the inherent incompleteness of the biostratigraphic data and their random character, TSEGELNJUK (1981: p. 7), in his correlations of the outcrops and borings within Volhyno-Podolia, gave priority to intercalations of volcanic ashes which were correspondingly named and numbered within each stratigraphic unit (e.g. B_1–B_6, M_1–M_{13}, C_1–C_{11}, etc.). All FA's and LA's were defined in relation to a given bentonite layer: "2 m below T_l" or "5 m above M_2". This was made to ensure greater accuracy in tracing isochronous lines between different sections and to overcome imperfections of the routine palaeontological method assuming that the presence of the same index fossil implies synchroneity. TSEGELNJUK believes that a given layer of bentonite intercalations may be identified because of its stable position within a certain pattern of a succession of such intercalations in the area. There is a considerable risk, however, of an erroneous interpretation. According to LANGIER-KUŹNIAROWA (1976), bentonite intercalations recognized in the Polish part of EEP cannot be used as stratigraphic markers because of their small thickness, monotonous composition and probably patchy distribution.

The graptolitic facies of the Skalian, which is roughly the regional equivalent of the Přidoli, yields *Skalograptus ultimus* (PERNER), *S. vetus* TSEGELNJUK, *Dulebogratus trimorphus* TSEGELNJUK, *Tamplograptus formosus* (BOUČEK), *Uncinatograptus similis* (PŘIBYL), *U. bouceki* (PŘIBYL), *U. perneri* (BOUČEK), *U. angustidens* (PŘIBYL), *Heisograptus difficilis* TSEGELNJUK, *H. canaliculatus* (TSEGELNJUK), *Ludensograptus parultimus* (JAEGER), *L. podolicus* (TSEGELNJUK), and *Istrograptus transgrediens* (PERNER).

Due to TSEGELNJUK's highly individual attitude towards systematics and nomenclature, his generic and specific names obscure the basic similarity between the Skalian assemblage and the sequence of graptolite zones in the Barrandian type area as well as those observed in the Polish part of the EEP. Anyhow, the graptolite succession of Volhynia and Podolia as interpreted by TSEGELNJUK seems rather undervalued. For instance, he does not emphasize the stratigraphic significance of *Monograptus* (*Uncinatograptus*) *spineus* TSEGELNJUK – a point correctly recognized by KOREN' (1992) on the basis of her studies of the graptolite fauna of Tien Shan. There is little doubt that subsequent studies will provide further justification for introducing a graptolite zonal subdivision of the Ulichian similar to that proposed in the present paper for the equivalent strata of the Polish part of the EEP.

Lithuania and the Baltic Region. — The graptolite sequence in the subsurface Silurian of Lithuania has been studied and synthesized by PAŠKEVICIUS (1974, 1979, 1986). The equivalents of the early Ludfordian are represented by the *Monograptus tauragensis* Zone, the index species being most probably synonymous with *Pseudomomnoclimacis dalejensis* (BOUČEK) (= *M. haupti* KÜHNE). In the regional stratigraphic scheme, the *P. "tauragensis"* Zone corresponds to the lower part of *the* Pagegiai Formation. As the diagnostic species *Saetograptus leintwardinensis* has not been recorded, the Gorstian/Ludfordian boundary cannot be precisely defined. Moreover, *P. dalejensis* makes its first appearance and is quite common in the underlying Gorstian in Eastern Poland and in some erratic boulders of the Baltic origin (KUEHNE 1955; URBANEK 1958). Therefore the lower boundary of the *P. "tauragensis"* (= *dalejensis*) Zone may only be delimitated by the disappearance of the lobogratid fauna. The zonal species is associated with an impoverished fauna composed of bohemograptids and *Pristiograptus* ex gr. *dubius*.

The *balticus* Zone is considered to be the second link of the Pagegiai Formation which, in the South-East Peribaltic area, also contains the overlying *formosus* Zone – the terminal unit of the Ludlow part of the succession. The vertical ranges of the *M. (S.) balticus* and the *M. (F.) formosus* overlap considerably and, what is more, there is some uncertainty in the understanding of the associated species.

Beds of early Přidoli age (the Minija Formation in the regional stratigraphy) are characterized by the presence of *Neocolonograptus parultimus*, *N. ultimus*, and also *N. lochkovensis*. Thus, they resemble the sequence observed in the Mielnik section in the early Přidoli part of the borecore.

The graptolite zonal subdivision of the Late Silurian which has been established on the basis of some key-wells in the Kalinigrad Region (Russian Federation) and in the Baltic syneclize of Lithuania, looks less refined as compared with that on the adjacent territory of Eastern Poland. Nevertheless it has recently been used for the entire Eastern Baltic area and applied to Belarus (the Podlasie–Brest syneclize; PAŠKEVICIUS and PUSHKIN 1988). It was also employed in an attempt to correlate the Silurian deposits in the Polish and the Belarus part of the above syneclize (PAŠKEVICIUS and PUSHKIN 1988, see also p. 92 herein).

As compared with Eastern Poland and Volhynia, the graptolite assemblages above the *scanicus* Zone of the Baltic area seem impoverished, in spite of our knowledge of them being fairly complete. The occurrences of graptolite fauna were also carefully correlated with the facies belts, the assemblages of shelly fauna and the distribution of conodonts (PAŠKEVICIUS 1986; EINASTO *et al.* 1986). BASSET, KALJO and TELLER (1989: fig. 118) made an attempt at a correlation of the Silurian lithostratigraphic and regional chronostratigraphical units in the Baltic Region.

Barrandian. — The graptolite sequence in the upper part of the Kopanina Formation was insufficiently known until PŘIBYL (1983) put forward its revision stimulated by new graptolite finds in that interval and also by the progress of knowledge on the co-eval faunas in the EEP (URBANEK 1966, 1970; TSEGELNJUK 1976). Recent findings leave no doubt that in addition to the *linearis*, *longus*, and *inexpectatus* graptolite zones recognized in the Kopanina Formation by PŘIBYL (1983), the sequence also includes the *kozlowskii* Zone. The presence of this index species, reported by URBANEK from Čertovy schody as early as 1970, has recently been confirmed by newly discovered material coming from the *Acantholomina minuta* Beds in the Kosov Quarry near Beroun (ŠTORCH 1995). *Neocucullograptus kozlowskii* is associated there with numerous *Polonograptus podolensis* (PŘIBYL). The profusion of *Polonograptus* is a remarkable feature of the early Ludfordian faunas in the Barrandian, whereas PŘIBYL's *longus* Zone, based unfortunately on non-diagnostic pristiograptid species, corresponds to the period of flowereing of bohemograptids (the "*Bohemograptus* proliferation Zone" according to URBANEK 1970) as well as to the *B. cornutus* Zone. There is every reason to believe that the Kopanina Formation includes all the main graptolite zones recognized in the lower part of the Siedlce Beds in Eastern Poland (URBANEK 1970), and the earlier opinions about the incompleteness of the Barrandian equivalents to the Polish sequence or about the presence of stratigraphic hiatuses there stemmed from an insufficient knowledge of the Bohemian sections.

Kopanina Formation. — Graptolites of late Ludfordian age recognized in the Kopanina Formation are rare and little diversified in comparrison with Volhynia or Eastern Poland. In the post-*kozlowskii* beds, PŘIBYL (1983) was able to distinguish the *insignitus* Zone as well as the *fecundus* and *fragmentalis* Zones. *Saetograptus* (*Colonograptus*) *insignitus* PŘIBYL is a junior synonym of *Ludensograptus latilobus* TSEGELNJUK (see p. 161 herein). Thus PŘIBYL's biozone corresponds to our *Pseud. latilobus/M. (U.) balticus* Zone, the basal late Ludfordian graptoloid fauna in the EEP. The Bohemian late Ludfordian fauna, however, is much more impoverished than that of Volhynia or Eastern Poland. Although *Monograptus (Wolynogaptus) abhorrens* PŘIBYL and *Monograptus (Formosograptus) formosus* BOUČEK are found in the oldest and the youngest zones respectively, true monograptids are scarce, mainly because of the lack of the *acer–spineus* lineage. In the upper beds of the Kopanina Formation, underlying the Přidoli formation in the stratotype area, graptolites are rare and non-diagnostic. They are mostly represented by pristiograptids, such as *Pristiograptus fecundus* PŘIBYL whose presence in the Silurian of other areas has not been established reliably, or by *P. fragmentalis* (BOUČEK). The latter, differing from typical *P. dubius* (SUESS) in a few quantitative features, marks a gap-filling zone, immediately below the *parultimus* Zone (see p. 96 herein). Future studies may bring discoveries of new faunal elements, but the facies development of the upper beds of the Kopanina Formation (coarse organodetritic limestones) is not particularly promising.

Přidoli. — From the evolutionary viewpoint the graptoloid fauna of the early Přidoli has been amply discussed herein, p. 105. The sequence starts with a sudden appearance of *Neocolonograptus parultimus* (JAEGER), and except for *Monograptus (Formosograptus) formosus* BOUČEK, a survivor from the underlying Kopanina Formation, no true monograptids are initially present. This monotonous assemblage of bilobate types (*ultimus, transgrediens*) is somewhat enriched by the reappearance of *Monograptrus (Uncinatograptus) pridoliensis* PŘIBYL, that either forms a subzone within the *lochkovensis* Zone (JAEGER 1986) or, in some sections, even precedes the appearance of the *Neocolonograptus lochkovensis*. In the Barrandian, *M. (U.) pridoliensis* frequently displays a mass occurrence, forming monospecific populations; surprisingly enough, it is reliably known only from Central Bohemia. In view of its mass occurrence, the endemism of *M. (U.) pridoliensis* has no obvious reasons. However, *Heisograptus difficilis*, described from Volhynia by TSEGELNJUK (1976), may be a senior synonym of PŘIBYL's species (KOREN', personal information).

Monograptids which reappear in the *lochkovensis* Zone of the EEP are represented by different species (and subgenera, see p. 106 for an attempt to provide a theoretical evaluation of the reappearance of the monograptids in the Přidoli).

Another remarkable feature of the graptolite fauna of the Přidoli in its type area is a considerable proportion of the Dendroidea in the assemblages. Less common or rare in the Kopanina Formation, dendroids occur abundantly in the Přidoli (BOUČEK 1957: p. 157), where they are associated with graptoloids in typical graptolite shales. The Přidoli and Lochkov dendroids were equal, or superior to, graptoloids (Monograptina) in their species richness. This is another remarkable feature of the latest Silurian and earliest Devonian graptolites assemblages in the Barrandian, a feature which has no parallel in other areas and may be considered one of the few examples of provincialism (or local ecological control) against the background of the otherwise cosmopolitan and exceptionally uniform global graptoloid fauna of this age.

Kazakhstan. — The late Ludlow and Přidoli deposits in Kazakhstan were intensively studied by numerous researchers and the results obtained summarized by KOREN' (1983, 1986, 1989). The age interpretation of the upper Akkan horizon (regional stage) is beyond doubt, being characterized by the *B. bohemicus tenuis* and *Neocucullograptus kozlowskii* Zones. The overlying *Monograptus (F.) formosus/Monograptus bessobaensis* Zone has been one of the most debatable units in the Late Silurian sequence. Initially, *M. bessobaensis* was identified as *Monograptus similis* PŘIBYL (= *M. pridoliensis* PŘIBYL) which is indicative of a Přidoli age for the zone (KOREN' 1983). Later studies revealed that the monograptid in question is not conspecific with *pridolensis,* a species diagnostic for the corresponding biozone in the Prague Basin. It is a new and so far endemic species (*Monograptus bessobaensis* KOREN').

In a recent report, KOREN' (1989) refers her *formosus/bessobaensis* Zone to the late Ludfordian, rather than to basal Přidoli as was assumed earlier. It also marks the bottom of the Tokrau horizon (regional stage), whose position within the standard Silurian is still uncertain. This especially concerns the Ludfordian/Přidoli boundary that cannot be recognized in the section because of a 150 m-thick gap in the presence of index graptolites and the absence of such diagnostic species as *parultimus–ultimus* and *pridolensis* together with an unusual composition of the remaining graptolite fauna. Along with the species characteristic of the Přidoli (*Neocolonograptus lochkovensis* PŘIBYL, *Monograptus bouceki* PŘIBYL, and *Monograptus perneri kazachstanensis*), the Tokrau fauna comprises new monograptids revealing different morphological types, which are either unique (*"Monograptus" anerosus* KOREN', *Pseudomonoclimacis* sp.) or similar to the earlier, Ludfordian assemblages (*Monograptus beatus* KOREN'and *Monograptus supinus* KOREN'). That is why "the Tokrau faunas at all stratigraphic levels are much more diverse than the Přidoli associations" (KOREN' 1989: p. 153). Interpreted as being of Přidoli age because of the presence of the three index species mentioned above, the Tokrau faunas remain in many ways unique.

The degree of provincialism displayed by the fauna remains exceptional, since normally, as was emphasized by JAEGER (1978), Late Silurian and Early Devonian graptoloid faunas show no detectable provincialism and thanks to that can be used for very accurate worldwide stratigraphic correlations.

Turkestan-Alai (Kirghizia). — The sections of Silurian deposits outcropping on the northern slopes of the Turkestan and Alai Range (Tian Shan) have been developed in pelagic and hemipelagic facies and represent a continuous series of the Upper Silurian strata. Preliminary results of careful zonal collecting and studying their rich and diversified graptolite fauna (KOREN' 1992) convincingly show that the sections are of crucial value for the understanding of the sequence and correlation of Upper Silurian graptolite faunas.

The Ludfordian fauna is well-developed, containing an almost complete sequence of zones recognized in Volhynia and Eastern Poland (URBANEK 1970; TSEGELNJUK 1976). *Saetograptus (S.) linearis* BOUČEK is accompanied by the last cucullograptids [*Cucullogrtus aversus* (EISENACK)] and by new monograptid species with an *uncinatus*-like type of apertures. Some other index species of the early Ludfordian were also identified, e.g. *Bohemograptus cornutus* URBANEK. According to KOREN' (a preliminary report, 1993), true monograptids (*Monograptus* s.s.) reappear here earlier than in Volhynia (TSEGELNJUK maintains that they are absent from the Tagrin horizon and do not reappear until the Meton horizon of his Ulichian), or Eastern Poland where they reappear in the *latilobus/balticus* Zone. KOREN' (1993) has noted in her sections an increasing density of monograptids with the *uncinatus*-type thecae "starting immediately above the *linearis* Zone".

In the post-*kozlowskii* part of the Ludfordian (late Ludfordian in the understandig of the present paper), KOREN' (1992) mentions *Monograptus (W.) balticus* TELLER and *Pristiograptus fragmentalis* BOUČEK, but emphasizes a special significance of the *formosus/spineus* Zone as defined in her regional biostratigraphic scheme. Both index species are highly characteristic and easy to recognize (cf. p. 96 herein). Judging from the already published data (and personal communications KOREN' 1993), the sequence in Tian Shan repeats the essential features of the graptolite zonation recognized earlier in Volhynia (TSEGELNJUK 1976) and recently in Eastern Poland (URBANEK, this volume). The range of individual index species may, however, be somewhat different [e.g. *Monograptus (F.) formosus* BOUČEK and *Monograptus (U.) spineus* TSEGELNJUK are shown with the same FA's while in Eastern Poland the former appears much earlier].

The Přidoli has been best recognized within the Kursala Formation of Southern Tian Shan. The sequence established there fully corresponds to that described by JAEGER (1986) in the type Přidoli of the Barrandian. A sudden appearance of *Neocolonograptus parultimus* (JAEGER) marks the eponymous zone of a small thickness, followed by the *ultimus* Zone, with *Monograptus (F.) formosus* being an associate in both cases. In the overlying *branikensis* Zone the assemblage becomes impoverished due to the extinction of *M. (F.) formosus* and *Pristiograptus fragmentalis* at the top of the underlying zone. KOREN' (1993: p. 40) considers the *parultimus–ultimus–branikensis* graded series a single phyletic lineage.

The sections of the Turkestan-Alai Range comprise all graptolite zones recognized in the upper part of the Přidoli type area (the *lochkovensis, bouceki, perneri,* and also the *transgrediens* Zone). *Istrograptus transgrediens,* lending its name to the last zone, already appears here, just as in the type Přidoli, in the *branikensis* Zone, but becomes a monospecific assemblage towards the end of the Přidoli. The ranges of the *bouceki* and the *perneri* Zone have not yet been established in detail. Neither *M. (U.) pridolensis* nor *M. (Dulebograptus),* characteristic of the Barrandian and the EEP, respectively, have been mentioned by KOREN' (1992).

After more data have been published, the South Tian Shan section will probably become one of the reference sections of the Upper Silurian on the global scale.

Northern and Arctic Canada. — A recent comparison and correlation of Ludlow and Přidoli graptolites in the Arctic Islands and northern Yukon have been provided by LENZ (1990). The sequence recognized above the *Saetograptus linearis* Zone and below the earliest Přidoli zone comprises the *Bohemograptus bohemicus tenuis* Zone alone. According to LENZ (1990: p. 1078), its zonal period "would appear to represent the flowering of bohemograptids". Although northern Yukon yielded *Bohemograptus praecornutus, B.* cf. *cornutus,* and also *"Bohemograptus" helicoides,* its fauna seems to be depauperate. Particularly striking is the absence of *Neocucullograptus* and the scarcity of specialized *Bohemograptus* species in the early part of the Ludfordian. Among the late Ludfordian faunal elements one could mention *Monograptus* cf. *balticus* TELLER in northern Yukon (referred, however, to the *tenuis* Zone), while *Monograptus (Formosograptus) formosus* BOUČEK is reported from the *parultimus* Zone. Hence, equivalents of a diversified late Ludfordian fauna as found in the EEP have not been recognized so far.

The Přidoli part of the sequence is more fully developed than that of the highest Ludlow. In a broad sense, it corresponds to the European stratigraphic zones. LENZ (1990: p. 1082) mentions the scarcity or absence of such Přidolian species as *Monograptus (U.) pridolensis* PŘIBYL, *Monograptus perneri* PŘIBYL, and *Neocolonograptus lochkovensis* PŘIBYL, while JACKSON (1978) recognized in Yukon the *Istrograptus (T.) chelmiensis* Zone. The above picture of the development of the Ludlow and Přidoli graptolite faunas may, however, be incomplete as the studies are steadily progressing.

Remarks on standard classification of the Silurian. — The present subdivision of the Silurian System was shaped by the work of the Subcommission on Silurian Stratigraphy (1975–1985), reviewed by HOLLAND (1989). The long and thorough work of SSS proceeded, however, under the burden of history and the influence of the heritage of investigations (compare HOLLAND 1980b). In the present author's opinion not enough attention was paid to the proper evaluation of the entirety of the new data available, especially those concerning the development of the graptolite fauna at the Wenlock/Ludlow boundary as well as between the Ludlow proper and the Přidoli sequence. Instead of looking from a wider comparative viewpoint, the majority of the Subcommission was clearly influenced by regional and historical reasons (see also JAEGER 1991). A similar point of view was expressed by TSEGELNJUK (1983) who emphasized a preoccupation with the geological history of the British Isles on the side of the majority of SSS, leading to a certain undervaluation of the progress in the knowledge made in other areas. This is why the final outcome is in certain aspects rather controversial and has met criticism. Thus JAEGER (1980) disagreed on the usage of series and stages by SSS majority and argued that Llandoverian, Wenlockian, and

Ludlovian should be ranked as stages. Regarding them as series (HOLLAND 1980) introduces a superfluous category into the stratigraphic classification of the Silurian and reduces the newly defined stages into narrow units. JAEGER insisted that stage be regarded as an important category, defined by a number of graptolite zones, recognizable around the globe and having an adequate size. I agree with the above arguments and share the opinion that the stratigraphic classification, accepted by the SSS and aproved by International Geological Congresses (Paris 1980, Moscow 1984), is unnecessarily complicated.

Still more important, however, are inconsistencies which may be seen between the accepted stratigraphic boundaries and the natural intervals observed in the development of the graptolite fauna. Some instances of such incongruities are particularly striking. Due to the redefinition of the Wenlock Series its newly recognized Homerian Stage envelops both the late Wenlock fauna (within the *C. lundgreni* Zone), its mass extinction episode as well as the early recovery phase of an entirely new assemblage. From the standpoint of the development of the graptolite fauna, the Homerian stage is such a heterogeneous set of graptolite zones that in fact it is meaningless as a stratigraphic unit! It is *malum neccessarium* and we use it only because it is an internationally recognized standard. I therefore share criticism expressed in this connection by JAEGER (1991: pp. 311–331), who also emphasized a rather paradoxical fact, that the conservative stance regarding the Wenlock/Ludlow boundary follows at the same time a modern approach, and sets the boundary in a close relation to the event of the first order (the *lundgreni* Event), whilst the boundary approved by the SSS pays no attention to it.

The next obvious imperfection in the standard classification of the Silurian, is the recognition of the Ludfordian Stage, clearly a premature decision. At its type area, the Ludfordian contains only one graptolite – *Saetograptus leintwardinensis,* which was used to define the base of the stage (LAWSON and WHITE 1989). In this way this boundary goes through the continuous lines of development of saetograptids, cucullograptids and retiolitids (see URBANEK, this volume, p. 38). Hence, the Ludfordian at its type area is devoid of a rich graptolite fauna, already described by the time the SSS decision was made (HOLLAND 1980a), from the EEP (URBANEK 1970; TSEGELNJUK 1976). I concur with JAEGER (1980, 1991) that the boundaries and the content of the Silurian stages should be defined in terms of graptolite biozones. In this respect Ludfordian as currently understood is an "empty" stage. TSEGELNJUK (1983) was essentially right, speaking of a "lost stage" in the recent subdivision of the Silurian, and having in mind the "postLudlow–preSkala" interval (compare his interesting concept of the Ulichian superstage discussed herein, p. 98). This regrettable situation could perhaps be improved, by a redefinition of the Ludfordian on the basis of graptolite zonation, and selection of an alternative reference section (a parastratotype) developed in the graptolitic facies or in a mixed biofacies. The importance of the graptolite based zonation is emphasized not merely to observe the principle of orthostratigraphy (otherwise rather undervalued by the SSS), but because of the exceptional significance graptolites play in intercontinental and global correlation, as well as in the high resolution regional stratigraphy.

GRAPTOLITE FAUNAS OF THE LATE LUDFORDIAN AND THE EARLY PŘIDOLI

The development of the graptolite faunas in the late Ludfordian and Přidoli reveals a number of remarkable similarities in the general course of events and their repetition as well as in an exceendingly high degree of homeomorphy. In both cases, the development starts from a recovery, represented by an acme of new species which originated from local survivors (in the late Ludfordian, by a massive occurence of *Pseudomonoclimacis* ex gr. *latilobus* (TSEGELNJUK) and in the early Přidoli, by an equally massive occurrence of *Neocolonograptus parultimus* (JAEGER) and *N. ultimus* (PERNER)). These elements represent similar morphologies and the same adaptive type which may be called the bilobate type (as defined below). Therefore each of the faunal cycles was initiated by a strikingly similar speciation event.

Moreover, the graptolite assemblages of the late Ludfordian and early Přidoli are marked by the presence of homeomorphic pairs of species featuring an exceendingly high degree of resemblance. Thus the Ludfordian *latilobus* group pairs with the Přidolian *ultimus* group and also with the *transgrediens* one, sharing with them a number of characters in thecal morphology and in the overall appearance of the rhabdosome. A similar homeomorphic pair among the *Monograptus* species is produced by Ludfordian *M. (U.) acer* TSEGELNJUK and *M. (U.) hornyi* JAEGER from the Přidoli. They have the same characteristic shape of the apertural lobe and even a common tendency to produce antero-lateral processes upon the lobe! The general morphological spectrum of the graptolite fauna is, however, predominated by pristiograptid-like species with paired apertural lobes, especially characteristic of the Přidoli but also present in the basal part of the late Ludfordian (see the bilobate adaptive type below). They are not only similar to each other, but at the same time reveal a great resemblance to Gorstian *Colonograptus* PŘIBYL.

THE ORIGIN OF THE LATE LUDFORDIAN GRAPTOLITE FAUNA

The graptolite fauna within the Ludfordian stage reveals a distinctly bipartite composition due to the *kozlowskii* Event, which wiped out the faunal assemblage of the early Ludfordian and opened the possibility for the development of a radically new graptolite fauna. It is characterized by a modest share of new species, which originated from indigenous survivors, and by the predominant role of the Lazarus and cryptic immigrants.

The late Ludfordian fauna was formed as a result of the recovery which followed the *kozlowskii* Event, or C_3 in URBANEK's terminology describing the biotic crises in the Upper Silurian (URBANEK 1970, 1993). As recorded in the Mielnik deep boring, the event is marked by the extinction of the last neocucullograptid, *Neocucullograptus kozlowskii*, and the late bohemograptids associated with it. The last occurrence of this fauna is overlain by a series, about 25 metres thick, containing a relic assemblage made up of *Pristiograptus dubius* s.l. and *Linograptus posthumus.* Neither of the survivors displays proliferation (mass occurrence). In line with the concept proposed recently by URBANEK (1993), the local survivors did not respond to the ecological release by a population burst, showing no signs of what he has called the post-event syndrome. Hence, they missed an opportunity to a massive re-radiation by means of speciation from indigenous survivors. Some new species, namely *P. dubius fragmentalis*, usually considered to be an index species for the upper part of the late Ludfordian, did, however, appear through splitting from the *Pristiograptus dubius* stem-lineage. The *Pseudomonoclimacis latilobus*, a probable derivative of the early Ludfordian *P. dalejensis,* produced a horizon of proliferation (acme zone) thus marking the beginning of the late Ludfordian in much the same way as the *parultimus–ultimus* group marks the beginning of the Přidoli.

The recovery, however, came essentially as a result of immigration of alien faunal elements. The succession encountered in the Mielnik borecore allows distinguishing three or four invasions of such elements, the earliest newcomer being *Monograptus hamulosus* TSEGELNJUK, almost immediately followed by *M. balticus* TELLER associated with the first representatives of the *latilobus* group. They define the base of the late Ludfordian and the beginning of the recovery (see Fig. 3). *M. balticus*, a slender monograptid representing *M.* (*Slovinograptus*), deserves to be classified as a Lazarus taxon (for definition see JABLONSKI, 1986 and herein, p. 105). It was quite common for some time, leaving no immediate followers in the Mielnik wellcore or in other EEP sections Nevertheless, its relation to younger gracile monograptids was suggested by some authors, e.g. by KOREN' (see p. 133 herein). The next to invade the vacant habitat was *M. (Formosograptus) formosus*, a species with a distinct morphology showing a remarkable similarity in its thecal characters to the Telychian *Oktavites spiralis. M. (F.) formosus*, which should be best regarded as cryptic (cryptogenetic), remains for some time very rare, then later exhibits a mass occurrence and defines a distinct acme horizon (Pl. 2: 2). In the EEP and especially in the Baltic area, the appearance of *F. formosus* is, as a rule, related to a widespread transgressive event (BASSET *et al.* 1989). In Barrandian (JAEGER, 1986), *M. (F.) formosus* appears in the Kopanina Beds, displaying a discontinuous distribution and never featuring an acme horizon. Thus the range of *F. formosus* on the EEP is extensive, as it almost reaches the bottom of the *parultimus* Zone.

In both cases this species disappears after some time, in all probability leaving no descendants. In the course of the faunal succession, the third species *Monograptus (Uncinatograptus) acer* TSEGELNJUK, a possible descendant of *M. (U.) hamulosus* TSEGELNJUK, makes its appearance, producing a distinct zone in the Mielnik succession. Not unlike *M. balticus*, it manifests the reappearance of "true" monograptids, which have been absent from all the sequences studied on the EEP since the end of the *nilssoni–colonus* Zone. *M. acer* is probably ancestral to the *M. (U.) spineus* TSEGELNJUK lineage. The primary species of this lineage have an *uncinatus*-like apertural apparatus (simple lobes), later transformed into a more complex lobate-spinose type. The latter type represented by *M. (U.) spineus* TSEGELNJUK is in most respects homeomorphic to the late Wenlock spinose monograptids of the *priodon* group (URBANEK 1995), representing against the background of coeval fauna an unusual element.

The reappearance in the Ludfordian–Přidoli of *uncinatus*-like true monograptids has been ascribed by URBANEK (1993) to the Lazarus effect. This is by no means a trivial event, as was rightly emphasized by BULMAN (1971, 1978). He was convinced that their reappearance could be explained by migration of the pelagic graptolite fauna from some mid-ocean "reservoir". In order to substantiate their long absence from all known successions, URBANEK (1993) suggested that BULMAN's "reservoirs" might correspond to Central Water masses isolated by gyres. The latter concept has been recently developed in oceanography (see VAN DER SPOEL 1986) and could be applied to explain Lazarus effects in the pelagic macrozooplankton of the Early Palaeozoic. The hypothesis advanced by RICKARDS *et al.* (1977: p. 78) that the Late Silurian–Early Devonian representatives of *Monograptus* s.s. "evolved independetly from a pristiograptid ancestor" seems far less probable, at least for the Ludfordian–Přidoli interval, in light of the widespread recognition of the role of Lazarus effect in graptoloid biotic crises. However, *de novo* appearance of hooded monograptids cannot be excluded for Early Devonian faunas. PORĘBSKA (1984) provided convincing evidence that *"M." aequabilis* developed from Přidoli pristiograptids of *dubius* or *kosoviensis* type. Her observations, however, provide no support for the coalescence theory of the origin of hoods as postulated by RICKARDS *et al.* (1977), and hoods were formed through the continuing growth of the dorsal wall of the theca (see p. 156 herein).

The reappearance of *uncinatus*-like monograptids had far-reaching consequences as their descendants constituted a large portion of the Late Silurian graptolite faunas. (This was convincingly demonstrated by JAEGER 1978, 1986). Some of the *uncinatus*-like monograptids must have been temporarily less successful (e.g. *M. balticus),* some had better luck (as *M. acer* which established a persistent lineage). Generally speaking, it was the reappearance of true monograptids [*Monograptus* (*Uncinatograptus*)] as a result of the Lazarus effect that shaped the major features of the graptoloid history in the Late Silurian and Early Devonian. Whilst the earlier authors saw the reapperance of *uncinatus*-like forms only at the base of the Přidoli, recent studies provide evidence for their much earlier reimmigration and flourishing in the late Ludfordian and probably even earlier as indicated by the latest findings of KOREN' (personal information). She has recognized three types of true *Monograptus* within the *leintwardinensis* Zone in the Kursala Formation of Tien Shan. Another early reappaearance of *uncinatus*-type monograptids is that of *Monograptus ceratus,* recognized in the *leitwardinensis* Zone of northern Yukon and Canadian Arctic Islands (LENZ 1988, 1990).

The meaning of the *uncinatus* type of theca needs, however, a certain redefinition. In the light of recent knowledge, the view that the bulk of Late Silurian and Early Devonian monograptids represent a uniform *uncinatus* type of theca (JAEGER 1978, 1986) is no longer tenable. Not only some Devonian lineages show a clearly separate origin (e.g. the *aequabilis* lineage, PORĘBSKA 1984), but also some earlier groups [e.g. *M. (Dulebograptus)* TSEGELNJUK] display specializations, sufficient to make any immediate derivation from *M. (U.) uncinatus* impossible. Nevetheless, the majority of Ludfordian–Přidoli hooded monograptids reveal enough similarity to have been derived from a common ancestor, or from a core group of which *M. (U.) uncinatus* is a typical representative. Its thecal characters are shown on Pl. 2: 7–9. Hence, the present paper uses the term "*uncinatus* type of theca" in this restricted sense. The Devonian hooded monograptids, which according to JAEGER (1986: p. 315) represented the peak in the evolution of the *uncinatus* Group, are in fact a heterogenous assemblage whose affinity with *M. (U.) uncinatus* is either lacking or difficult to perceive.

Summing up, the late Ludfordian fauna owes its origin mainly to migration in which both the cryptic and Lazarus taxa took part, whereas the indigenous contribution to the new lines was negligible. Some of the migrants established themselves as permanent elements of the fauna, starting new trends that would become fully operative within the stage (e.g. the *acer–spineus* lineage). In its development, the late Ludfordian fauna displays a substantially different pattern from that associated with the recovery after the *lundgreni* and *leintwardinensis* Events (C_1 and C_2 in URBANEK's 1970 wording). After C_1 and C_2, the lead in the recovery was taken by indigenous speciation and adaptive radiation of local survivors. Subsequently, developments in the late Ludfordian are mimicked by the course of events after the *perneri* Event (C_4), when the great Silurian/Devonian turnover involved a mass invasion of alien faunal elements with a negligible participation on the part of the local survivors.

THE ORIGIN OF THE PŘIDOLI GRAPTOLITE FAUNA

In the Mielnik boring, a 60 m thick series of sediments was encountered above the top of the *spineus* Zone, containing an impoverished graptolite assemblage with *P. dubius* and *P. dubius labiatus* subsp. n.

along with rare *Linograptus posthumus*. This *dubius* Interregnum corroborates KOREN's (personal communication) view that the late Ludfordian fauna displays a distinct discontinuity in its development, which should be recognized as an extinction event, namely the *spineus* Event. Previous studies on the type Přidoli (JAEGER 1986: p. 314), demonstrate a relatively high distinctness of this stratigraphic stage as far as its graptolite fauna is concerned. This is especially well seen when we trace the hold-overs from the underlying Kopanina Beds. There are only four such species (*P. dubius* s.l., *P. fragmentalis*, *F. formosus*, and *L. posthumus*). The large majority of the species are confined to the Přidoli, and either developed from the local survivors after the *spineus* Event, or appeared through immigration. The latter source accounts for the appearance of *Monograptus (Uncinatograptus)*, which displays a Lazarus effect (it disappears for some time from the succession and is absent from the sequence until the *lochkovensis* Zone). The same is true for the Mielnik core sequence, where the first true monograptids reappear only in the *lochkovensis* Zone, being represented by *Monograptus (Dulebograptus) trimorphus*, instead of *M. (U.) podoliensis* as in the type Přidoli. The EEP sections (E Poland, Volhynia) show differences in composition as compared with Barrandian, but the Lazarus effect in the distribution of hooded monograptids across the Ludfordian/Přidoli boundary is common to all three areas. Their reappearance and later development added to the diversity of the assemblages.

On the whole, however, the early Přidoli graptolite fauna looks impoverished and featureless as compared with the late Ludfordian faunal assemblage. This is especially clearly seen when comparing Přidolian and Ludfordian graptolites recognized recently on the EEP. In Barrandian, the scantiness of graptolites in the underlying Kopanina Formation, as well as their inadequate knowledge, gives the early Přidoli fauna the look of a prolific assemblage. In fact, it was predominated by a single morphological type, defined herein as the bilobate type, which was prevailing in the Přidoli and disappeared with the *transgrediens* Zone (JAEGER 1986).

This significant trend in the morphological evolution appeared in the early Přidolian as *Neocolonograptus parultimus*, which initiated the *parultimus–lochkovensis* lineage. In the type Přidoli, monograptids from this group constitute numerically the bulk of the fauna and define the prevailing morphological type of early Přidolian graptolites. This is also true for the Mielnik borecore where *N. parultimus* forms a distinct horizon, some 17 m thick, with abundant index species, occurring monospecifically or associated with scanty *Linograptus*. The appearance of *parultimus* defines the base of the Přidoli in Barrandian, a boundary which, in the Mielnik sequence, can be established approximately at a depth of 692 m. The previously published data (URBANEK 1970: p. 177) placing this boundary at a depth of 823.00 m are incorrect and were caused by a misidentification of the fauna at this early stage of the study. It should be noted that in the Kazakhstan sections, *parultimus* has not been recognized so far (KOREN' 1983).

The appearance of *parultimus* represents a borderline case between immigration and local speciation. Since its immediate ancestor has not been recognized within the established assemblages, *parultimus* can be interpreted as an immigrant. But it is only in a few minor traits that it differs from pristiograptids of the *dubius* type – a group common in all sequences studied. One can reasonably assume that *parultimus* evolved through parapatric speciation with but a few changes needed to form a new species. URBANEK (1993: p. 35) proposed the term "semicryptic origin" for such borderline cases on the ground that the ancestral group could be reliably established, but the transition stages are still unknown. It now seems that late Ludfordian *Pseudomonoclimacis latilobus* (TSEGELNJUK), although displaying a remarkable overall similarity to the *ultimus* group of the early Přidoli, was already too specialized to be considered an ancestor of the last named group (see below, p. 164).

THE COMPOSITION OF THE LATE LUDFORDIAN GRAPTOLITE FAUNA

As a result of intense immigration and thanks to a certain contribution from local speciation of indigeneous survivors, the late Ludfordian graptoloid fauna comprises the following elements:

(1) taxa which reappeared as a result of the Lazarus effect and are represented by *Monograptus (Uncinatograptus)* or *Monograptus (Slovinograptus)*, e.g. *M. (S.) hamulosus* TSEGELNJUK, *M. (S.) balticus* TELLER. Some of these species established lineages that developed through the late Ludfordian (see 3 below);

(2) cryptic (cryptogenetic) immigrants, such as *Monograptus (F.) formosus*, representing a distinct adaptive type, which to some extent may be considered an analogue of "triangulate monograptids" among the Ludfordian–Přidolian fauna. It seems to have disappeared without leaving descendants;

(3) the *acer–spineus* lineage. Having started from an ancestor which appeared as a Lazarus taxon (see 1, above), it produced a highly elaborate lobate-spinose apertural apparatus manifesting a distinct adaptive type. This lineage evolved through local speciation, as traced in the sequence (URBANEK 1995). *M.* (*U.*) *spineus* is a highly characteristic index fossil for the late Ludfordian, recognized so far on the EEP (E Poland, Volhynia) and in Central Asia (Tien Shan, Alai Range). That is why KOREN' (1992, 1993) recognizes the *formosus/spineus* Zone both in her regional biostratigraphic zonation and in the global standard;

(4) bilobate monograptids with distinct ventral excavations, represented by *Pseudomonoclimacis latilobus* TSEGELNJUK, probably related to *P. dalejensis* (BOUČEK) from the underlying early Ludfordian beds. It appeared as a result of local speciation and is strongly homeomorphic to the *parultimus–ultimus* group of the Přidoli. As *P. dalejensis* itself had most probably a pristiograptid ancestry, *P. latilobus* may be seen as an indirect derivative of the *dubius* stem-species;

(5) conservative or slowly evolving survivors of the *kozlowskii* Event, namely *Pristiograptus dubius* s.l. and *Linograptus posthumus* (Reinhard RICHTER). The stem-species represesented by *P. dubius* produced a robust, rapidly widening variety usually considered to be a separate species (*P. fragmentalis* BOUČEK), although a subspecific rank seems more appropriate. In the Mielnik core, it appears in the basal part of the late Ludfordian, while in the Kopanina Formation of Barrandian, it is considered the index species for the uppermost part of the formation, thus immediately preceding the *parultimus* Zone. *Linograptus posthumus* within the Ludfordian had already attained all its species-specific characters (a multiramous pattern, presence of a virgellarium), displaying later gradual changes through the Přidoli (URBANEK 1993 and in this volume).

THE COMPOSITION OF THE EARLY PŘIDOLI GRAPTOLITE FAUNA

As a result of the processes described above, the Early Přidoli fauna comprises the following elements:

(1) indigenous survivors of the *spineus* Event, e.g. *Linograptus posthumus* and *Pristiograptus* ex gr. *dubius*;

(2) immigrants representing Lazarus taxa, namely monograptid relics from the Ludfordian: *Monograptus (Dulebograptus) trimorphus* (on the EEP) or *Monograptus pridoliensis* (in the type Přidoli), the latter showing a considerable speciation potential;

(3) two distinct lineages evolved locally from either source 1 (indigenous survivors) or source 2 (Lazarus taxa, *uncinatus*-like monograptids), namely:

3a, the *pridoliensis–hornyi* lineage traced in the type Přidoli by JAEGER (1986),

3b, the *parultimus–lochkovensis* lineage. Its immediate ancestor though still unknown should not be too remote from the conservative pristiograptid stem (see above),

3c, the parallel *transgrediens* lineage.

Lineages 3b–3c developed a distinct bilobate adaptive type whose gradual evolution can be traced in the Mielnik sequence (however, see below a different opinion presented by TSEGELNJUK, p. 168).

In terms of numerical abundance, the significance of each of these elements in the composition of the fauna varies considerably. Nevertheless, the components listed above as 3a and 3b–3c predominate and define the morphological spectrum of the fauna.

TRENDS AND ADAPTIVE TYPES

The term "trend" is used in this paper in an operative sense. It means a certain direction of morphological change, leading to the appearance of a given condition (a morphoecological or adaptive type), characterized by a stable complex of features. A trend may affect several lineages being in this way responsible for the essential similarity of graptolite faunas of different age and ancestry. A trend may also be defined as a tendency towards achieving a certain morphological type by a number of evolutionary lines either within a certan span of time or within different intervals.

Trends are largely responsible for the morphological and ecological spectrum of graptolite faunas, especially for the reappearance of similar structural (and adaptive) types. Such understanding of the term "trend" corresponds to its usage by other graptolite workers (RICKARDS *et al.* 1977). The late Ludfordian–

early Přidoli faunas display operation of three prevailing trends, responsible for three distinct adaptive types: bilobate, lobate-spinose and lobate. Two first trends are discussed in some details below, while the third one is only briefly mentioned.

The bilobate trend and adaptive type. — The bilobate adaptive type is characterized by the development of paired apertural lobes, described figuratively by JAEGER as "blinders" (undulating aperture of RICKARDS *et al.* 1977). The corresponding morphoclines in the Ludfordian and Přidoli essentially repeat the events which occurred in Homerian–Gorstian *Colonograptus* (cf. considerations in URBANEK 1960 and their criticism in JAEGER 1978a). In the late Ludfordian fauna, this adaptive type is represented by *Pseudomonoclimacis latilobus* TSEGELNJUK, attaining a degree of lateral lobe elaboration comparable with that in the advanced morphs of *Neocolonograptus ultimus* (PERNER) from the Přidoli. There is no doubt, however, that a bilobate aperture developed independently in both cases, representing a clear case of homeomorphy. A probable ancestor of *P. latilobus* may be seen in *Pseudomonoclimacis dalejensis* (BOUČEK) (= *M. haupti* KUEHNE), a Gorstian–Ludfordian representative of the pristiograptid-like types, provided, with distinct excavations of the ventral wall of the thecae. This feature is shared by *P. latilobus* which is distinguished by more or less developed lateral lobes (lappets). *P. dalejensis* is particularly common in the assemblages of early Ludfordian age in the Mielnik boring, and it is reasonable to suppose that it was subject to morphological transformations during the environmental crisis at the time of the *kozlowskii* Event. The ideas of TSEGELNJUK (1976, 1978) to assign his *latilobus* to the genus *Ludensograptus* TSEGELNJUK, erected to include the late Homerian and early Gorstian bilobate types, seem unconvincing. Such a generic taxon would be too heterogeneous phylogenetically and has little sense stratigraphically. For the time being, the application of the generic name *Pseudomonoclimacis* seems more justified in view of the thecal morphology and a possible derivation of *P. latilobus* TSEGELNJUK from *P. dalejensis* BOUČEK. Late Ludfordian *P. latilobus* forms a homeomorphic pair with *Colonograptus*? *gerhardi* (KÜHNE) from the late Homerian as a result of the combination of ventral excavations and lateral apertural elevations.

The Přidoli morphocline leading to bilobate forms started from gentle lappets or even elevations in the *Neocolonograptus parultimus* thecae. These structures became distinctly pronounced in *N. ultimus* and, eventually, transformed into strongly developed paired lobes in *N. lochkovensis* (Figs 6 and 8). The link represented by *ultimus* is bridged by *branikensis,* a morphological and temporal "intermediary" between *ultimus* and *lochkovensis*, although it is morphologically closer to the last of the two (JAEGER, 1986). In extreme cases, the apertural structure of *ultimus* resembles the lappets in juvenile *lochkovensis,* while the early growth stages of the latter reveal a great similarity with *branikensis* in the shape of the rhabdosome. Thus the particular temporal species of the *parultimus–lochkovensis* lineage are interconnected by transients which leave no doubt that apertural lappets originated *de novo* and developed gradually during the early Přidolian.

Moreover, this course of events resembles, in its essential features, the development of paired apertural lobes in the Homerian–Gorstian monograptids, as initiated by *praedeubeli* and followed by more advanced species like *gerhardi, colonus* or *roemeri* (Fig. 7B_1, B_2). The above sequence forms the *Colonograptus* trend characterized by the development of apertural elaborations strikingly similar to Přidoli bilobate monograptids. In view of this resemblance they deserve to be named "neocolonograptids" (Fig. 7C–C_3). This rather unusual case of homeomorphy is further discussed below.

The empirical data do not confirm TSEGELNJUK's (1978) speculative hypothesis concerning the ancestry of the *parultimus–lochkovensis* lineage. He derived the forerunners of this lineage from the *uncinatus* group of monograptids (his *Uncinatograptus*) through a critical phase represented by his *Dulebograptus.* This trimorphic transient form has a few proximal thecae provided with apertural lobes only partly notched, several medial thecae with completely paired lobes, and some distal ones with simple "pristiograptid" apertures. TSEGELNJUK assumed that the *ultimus* group (his *Skalograptus*) was derived as a result of the splitting of the initially undivided apertural lobe (hood). In my opinion, the differences in the specialization trends existing between *Dulebograptus* and late representatives of *Neocolonograptus* (such as *N. lochkovensis*) exclude their immediate phylogenetic relations (see also p. 156), although the course of events posited by TSEGELNJUK (1978) is theoretically plausible (see URBANEK 1956 for a discussion on the possibility of the splitting of the hooked aperture into paired apertural lobes). The decisive criterion would be the presence of a morphocline linking these two structural types. Such a morphocline has not been recognized yet, and there is every reason to believe that the actual phylogeny chose, in the case in question, entirely different pathways. In his considerations, TSEGELNJUK neglects the progression (gradual elaboration) of the lateral lobes in *parultimus–ultimus* as described by JAEGER (1975, 1986). The morphology of *parultimus* clearly indicates that its presumed ancestor resembled the conservative pristiograptid of the *dubius* type. *N. ultimus* and *N. lochkovensis* also display astogenetic and phylogenetic intergradation and appear to represent a single evolutionary line (cf. the opinion of KOREN' 1992). In view of this evidence, TSEGELNJUK's idea of separating *N. lochkovensis* and ascribing it a quite separate ancestry is not convincing.

The lobate-spinose trend and adaptive type. — The discovery of numerous well-preserved lobate-spinose monograptids from beds of Ludfordian age (TSEGELNJUK 1976) added an entirely new element to this fauna. While homeomorphic to late Wenlock spinose monograptids (*priodon–flemingi* Group), they differ in minute structural details (see p. 112 herein). What is even more important, Ludfordian spinose monograptids [*M. (Uncinatograptus) protospineus, M. (U.) spineus*] appeared as terminal products of a lineage defined by URBANEK (1995) as the *acer–spineus* lineage. Their evolution was traced in time and they comprise their own morphocline, entirely different from that in earlier lobate-spinose monograptids. This gap in time is the best criterion of their independent origin, in spite of the homology in the structure of the apertural apparatus. In the Mielnik borehole, lobate-spinose monograptids of the species *Monograptus (U.) spineus* make up quite rich assemblages through some 3 m of thickness, and are closely related to the underlying lobate species. Their forerunners include *Monograptus (U.) acer acer* TSEGELNJUK and *M. (U.) acer aculeatus* (TSEGELNJUK), as well as a transient link described by URBANEK (1995) as *Monograptus (U.) protospineus*. Forming a distinct lineage composed of *M. acer*, *M. protospineus*, and *M. spineus*, the lobate-spinose monograptids constitute a highly characteristic, although so far undervalued, component of the Ludfordian fauna. They must have developed from the conservative stem of *Monograptus uncinatus* whose reappearance as a Lazarus lineage marks one of the remarkable events in the late Ludfordian (see URBANEK 1995 for an analysis of morphological changes in the above mentioned lineage). The lobate-spinosity may be defined as a simultaneous presence of hooked (hooded) apertural lobes and lateral spines, resembling those in the *priodon–flemingi* group of Wenlock monograptids. But the adaptive type discussed in the present paper developed independently and secondarily during the Přidolian. This can be deduced from the specific position of the spines: in the Přidolian forms, it is antero-lateral in contrast to the Wenlock species, e.g. *M. (Monograptus) priodon, M. (M.) flemingi* or *Testograptus testis*, whose spines are situated laterally (cf. URBANEK 1958, 1995; URBANEK and TELLER 1974; TELLER, 1986; LENZ 1990).

While the general appearance of Wenlock and late Ludfordian lobate-spinose monograptids is strikingly similar, there are obvious differences in minute structural details as shown in Fig. 5A–C. The antero-lateral processes (alp) of the dorsal apertural lobe, although present in the Wenlock forms, do not serve as a base for the spines which are placed beneath, on the lateral margins (Fig. 5B_1, B_2, lp). The picture is quite different in the Lower Přidolian taxa, where spines are located directly on the antero-lateral processes and the lateral margins of the dorsal apertural lobes remain free (Fig. 5C_1, C_2, alp). It clearly follows from the above that lateral apertural spines are not homologous in the two groups in question. In spite of their general resemblance, each of the types was acquired independently, displaying homoiology rather than homology. The lateral spines of Ludfordian lobate-spinose monograptids originated in the *acer–spineus* lineage through an intermediate stage represented by *protospineus* (p. 148), which was doubtlessly a novelty acquired in Ludfordian time. The antecedents of the last named taxon (*acer, hamulosus*) had non-specialized spineless apertural lobes, resembling in their ancestral features the lobes of *Monograptus uncinatus* (the *nilssoni* Zone of the Gorstian). This allows one to infer that lobate-spinose monograptids developed from the *uncinatus* group, assuming the impact of the Lazarus effect and the later reappearance of relatively non-specialized descendants of the stock in the late Ludfordian [e.g. *Monograptus (U.) acer*]. Such generalized monograptids of the *uncinatus* group subsequently underwent specialization and gradually evolved into lobate-spinose forms (URBANEK 1995).

The well-known lobate-spinose monograptids of the Upper Wenlock were therefore too highly specialized to be ancestral for the similar Ludfordian forms. Moreover, they manifested a different trend in specialization as can be seen from distinct differences in the position of the spines in relation to the homological points of the dorsal apertural lobe (marked *x*, *y* in Fig. 5A–C). In spite of its later occurrence, *Monograptus (U.) uncinatus* represented a less specialized character state and may safely be considered an ancestral form in respect of the Ludfordian lobate-spinose lineage (Fig. 5A_1, A_2).

It seems that, notwithstanding the above structural differences, Upper Wenlock and Late Ludfordian lobate-spinose monograptids represented essentially the same adaptive type with their lateral apertural

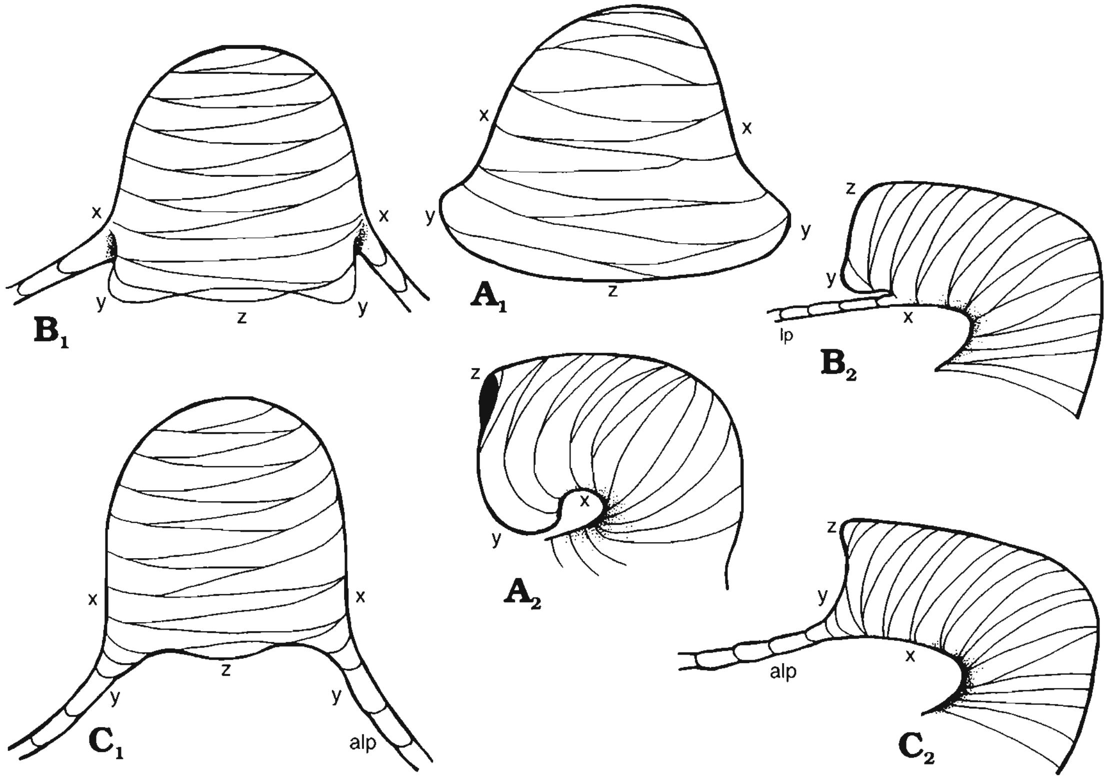

Fig. 5

Comparison of apertural apparatus (A$_1$, A$_2$) in *Monograptus uncinatus* Tullberg from the *nilssoni* Zone (Ludlow, Gorstian) representing a nonspecialized, ancestral type of structutre, with late Wenlock (*M. priodon–M. flemingi* group, **B**$_1$, **B**$_2$) and late Ludfordian [*M. (U.) spineus*] lobate-spinose monograptids (C$_1$, C$_2$). All seen in ventral and lateral aspects; *x*, *y*, *z* are homological points on the dorsal apertural lobe. Note that lateral processes (lp) in late Wenlock forms were situated at *x*, while their analogues (alp, anterolateral processes) in Ludfordian forms were palced at *y*. Point *z* was transformed in the latter group into a projecting edge (promontorium). After Urbanek 1996.

spines functioning in the same (although not quite obvious) way. They must have responded to essentially the same demands posed by the environment in a similar, though not identical (!) way owing to a stable morphogenetic potential preserved within the monograptid stock during at least 5 Ma of their history (see recent estimationsin Hughes 1995).

Significance of other trends in thecal morphology. — Among the other trends having great significance for the late Ludfordian and early Přidoli graptoloid faunas, one should mention: (1) pristiograptid trend, characterized by essentially straight thecae provided with simple apertures [as in *Pristiograptus dubius* (Suess) and related species like *P. dubius fragmentalis* (Bouček) or *P. dubius labiatus* sp. n.]. The importance of this conservative and non-specialized trend for the evolution of Late Silurian monograptids was exceptional (Rickards *et al.* 1977; Koren' and Urbanek 1994). Its double phylogenetic role consisted of its exceendingly high survival value without significant changes combined with the ability to produce, in certain situations, new and progressive lines of evolution, branching off the main stock (Urbanek 1993, 1994; Koren' and Urbanek 1994). The latter ability is commonly described by palaeontologists as evolutionary plasticity.

According to Koren' (1983) and Jaeger (1986), the last representatives of the *dubius* line are observed in the *perneri* Zone. One could hypothetize that by elimination of this phyletic line, monograptids strongly reduced their potential for prospective evolutionary change. This factor, along with some others recently specified by Urbanek (1993), may be responsible for the lack of an adequate evolutionary response on the side of the monograptids to the changing environment in the early Devonian times, and in the last instance, for their extinction.

The next trend (2) of great significance wäs represented by standard lobate monograptids commonly referred to as *uncinatus*-like or *uncinatus*-type monograptids. The importance of their reappearance and their role in the Upper Silurian faunas were discussed in various aspects above (herein, p. 105). However, they are not unique for the discussed time-span and pass into the Early Devonian. Differences in expressivity and penetrance as well as different styles of their main character, namely apertural hoods, leaves no doubts that, phylogenetically, this trend was represented by a number of independent lineages. Along with conventional monograptids, provided with a simple and entire apertural hood, the Late Silurian saw at least two lines of specialization: one leading to the lobate-spinose adaptive type as discussed above (p. 109) and the second, represented by *Dulebograptus* TSEGELNJUK The latter line developed notched apertural lobes, especially in the most proximal thecae, resulting in a biform or even triform rhabdosome (TSEGELNJUK 1976, 1978, 1988). The notched apertural lobes are a highly characteristic trait, not seen before Přidoli time. The origin of monograptids with a *Dulebograptus* habitus might, however, precede the appearance of notched forms, and early representatives of the group may be encountered among *Monograptus* s.s. recognized by KOREN' as low as the *leitwardinensis* Zone of the Kursala Formation, Tien Shan (unpublished). Speculations concerning the supposed role of *Dulebograptus* as an ancestor of some Přidoli "neocolonograptids" (TSEGELNJUK 1976, 1978) are discussed on p. 156 herein.

Thecal characters of some important index species of the Přidoli, such as *Monograptus bouceki* PŘIBYL and *Monograptus perneri* PŘIBYL, were not recognized with any certainty. A number of descriptive terms such as "clawlike" were used to describe the shape of the apertural apparatus in the former species, but they refer only to different preservational features and are misleading as a description of the real structure. Observations on well-preserved semiflattened or three-dimensional specimens of *M. bouceki* seem to indicate the presence of standard hooded apertures, not unlike those in *M. pridoliensis* PŘIBYL. The latter species seems to be akin to *M. bouceki* through the *M. hornyi* JAEGER transient link. The thecal characters in some other frequently identified and described species will not be defined until isolated material is available. Especially enigmatic are Přidoli spinose monograptids, such as "*M*". *willowensis* described by BERRY and MURPHY (1975) from the beds assigned to the Přidoli in Central Nevada.

JAEGER (1986: p. 316) recalls a poorly preseved *Monograptus* sp. gr. *willowensis*, which "was found in a 1/2 cm-thick layer within the *lochkovensis* Zone", as "the sole spinose species in the type Přidoli". JAEGER (*ibidem:* p. 315) compares this form with paired spines to the spinose monograptids of the lower Ludlow and finds some resemblance to *Seatograptus fritchi linearis* from the Leitwardinian of Europe (see BERRY and MURPHY 1975: p. 80). However, the real relationship of *willowensis,* its generic assignement and origin remain obscure. Recently, conspecific or closely similar forms were described from the *perneri* Zone of the Tokrau horizon of Kazakhstan (KOREN' 1983), which leaves no doubt that spinose monograptids are a regular albeit rather little-known constituent of Late Silurian graptolite faunas. Until now, however, there is no evidence of their presence on the EEP.

The last trend to be mentioned is that of Late Silurian "triangulate" monograptids, represented by only one species: *Monograptus (Formosograptus) formosus* (BOUČEK). Its origin remains obscure (see above, p. 104).

HOMEOMORPHY AND ADAPTIVE REPETITIONS IN THE HISTORY OF UPPER SILURIAN GRAPTOLOIDS

Homeomorphy as a descriptive-analytical category embracing parallelism and convergence was discussed in the light of moderm evolutionary concepts by GEORGE (1962) and reviewed recently by WEBB (1994). The material studied in the present paper leaves no doubt that homeomorphy (especially heterochronic parallelism and iterative evolution) was common in the history of Late Silurian graptoloid faunas (p. 114 herein). I also share WEBB's (1994: p. 185) opinion that homeomorphy "poses major problems in phylogenetic reconstruction".

A remarkable feature of the evolution of Upper Silurian graptoloids consists in multiple repetitions of certain developmental trends leading to a heterochronic appearance of analogous adaptive types (Fig. 6). Thus the Gorstian and the Ludfordian saw reradiation of the "operculate" adaptive type represented in succession by cucullograptids (*Lobograptus* and *Cucullograptus*) and neocucullograptids (*Neolobograptus*, *Neocucullograptus*). Having a strikingly similar overall morphology, they display differences in the kind of fabric of which their homeomorphic apertural apparatus are made: normal and microfusellar tissue, respectively (URBANEK 1966, 1970). After the extinction of the last cucullograptids in the *leintwardinensis*

Zone, *Bohemograptus*, a survivor related to the former stock by a common ancestor (most probably *Lobograptus*? *sherrardae* from the *praedeubeli* Zone), must have had its morphogenetic potential similar enough to recreate the operculate adaptive type. One may assume, on one hand, that the environmental conditions during Ludfordian time again opened an opportunity for the existence of an "operculate" niche. On the other hand, the morphogenetic potential of the survivors had to be capable of responding adequately to the demands of the environment. That is why the "operculate melody" sounded twice, in the Gorstian and during the Ludfordian. The *kozlowskii* Event eliminated the last bohemograptids and neocucullograptids. Operculate monograptids were never recreated, their place being taken by quite different morphoecological types. These, however, were not fully novel or unique, as they resurrected upper Wenlock and lower Ludlow themes. The former involved lobate-spinose forms and their forerunners, while the latter was represented by members of the lineage leading towards bilobate species. The spinose-lobate morphological type is strikingly similar to the upper Wenlock spinose *priodon–flemingi* group. The bilobate trend is a less perfect imitation of lower Ludlow *Colonograptus*, but even here the resemblance is so strong that at one time PŘIBYL did not hesitate to assign *lochkovensis* to the genus *Colonograptus*. From a formal-morphological point of view his decision is justified, although we know that the key-characters in the two groups in question appeared independently and heterochronously.

Figs 5 and 7 provide a comparative analysis of the crucial anatomical features in the older models and in their younger mimic forms. Their resemblance cannot be explained as a random coincidence for it involves a number of common structural principles. The development within the bilobate trend is illustrated by the succession of events in the *parultimus–ultimus–lochkovensis* lineage (Fig. 7C_1–C_3). A gradual increase of the lateral lobes from gentle elevations to large structures, covering to a great extent the aperture, essentially repeats the course of events seen in the Ludlovian colonograptids and their forerunners (Fig. 7B_1, B_2).The final effects are largely similar although not quite identical. The same is true for the Ludfordian lobate-spinose monograptids. The ancestral structures which may be observed in *M. hamulosus* and *M. acer* resemble the simple hooded apertural lobe inherited from *M. uncinatus* (Fig. 5A_1, A_2). The appearance of *Monograptus spineus* is indicative of a lobate-spinose condition attained through a transient link of *Monograptus (U.) protospineus* with elaborated antero-lateral processes. *M. spineus* shows a striking resemblance to the spinose monograptids of the late Wenlock (*priodon, flemingi, testis*), its spines, however, are situated on the antero-lateral lobes (Fig. 5C_1, C_2) and not on the lateral margins as is the case with the Wenlockian forms. (Fig. 5B_1, B_2). This is, indeed, *la petite difference* between the upper Wenlock and the late Ludfordian lobate-spinose monograptids! Both produced strikingly similar spines superimposed on apertural lobes, but in each case these spines are differently situated in relation to the homological points (or so-called landmarks) denoted as x, y, and z in Fig. 5 (see discussion above). The spines of the Ludfordian monograptids were formed gradually and a comparative analysis reveals, in *Monograptus spineus*, some components inherited from *uncinatus*-like ancestors and acquired at the *protospineus* and *spineus* stages of evolution (URBANEK 1995: fig. 5).

In a very broad sense, the development of the graptoloid fauna in the late Ludfordian and early Přidoli may be seen as the re-establishment of an essentially late Wenlock–early Ludlow spectrum of morphological diversity. This is indicated by the presence of hooked and spinose monograptids as significant constituents of the fauna, along with an extraordinary profusion of Přidolian "colonograptids". *M. (Formosograptus)* seems to be the only genus to be inspired by still earlier Llandovery patterns.

Such heterochronic appearance of similar morphological types may probably be explained on two assumptions: (1) the morphological system in monograptids displayed a relatively high rigidity, being capable of only a limited number of structural patterns, and (2) there was a relative stability of the adaptive zone occupied by the graptoloids as the dominating group in Early Palaeozoic macrozooplankton.

The environment, except during the disturbances, challenged its inhabitants to repeatedly solve essentially the same problems, to which monograptids could offer only a limited number of solutions. Most of them were already used in similar situations with only a few representing entirely novel propositions in response to the environmental demands (see linograptids). This, at least partially, may explain a high frequency of repetitive appearances of strikingly similar structural patterns in the history of Silurian monograptids (Fig. 6).

They were not unique in this respect, however, and STEBBINS (1967) found numerous instances of what he termed "adaptive reversals" in his study on the adaptive radiation of angiosperms. What he implied by this was basically the recurrence of certain morphological and adaptive themes in evolution. However, the evolution of the Upper Silurian monograptids, represents a rather different case, and instead of reversal of existing specializations and adaptations, we observe an iterative (repetitive) appearance of adaptive

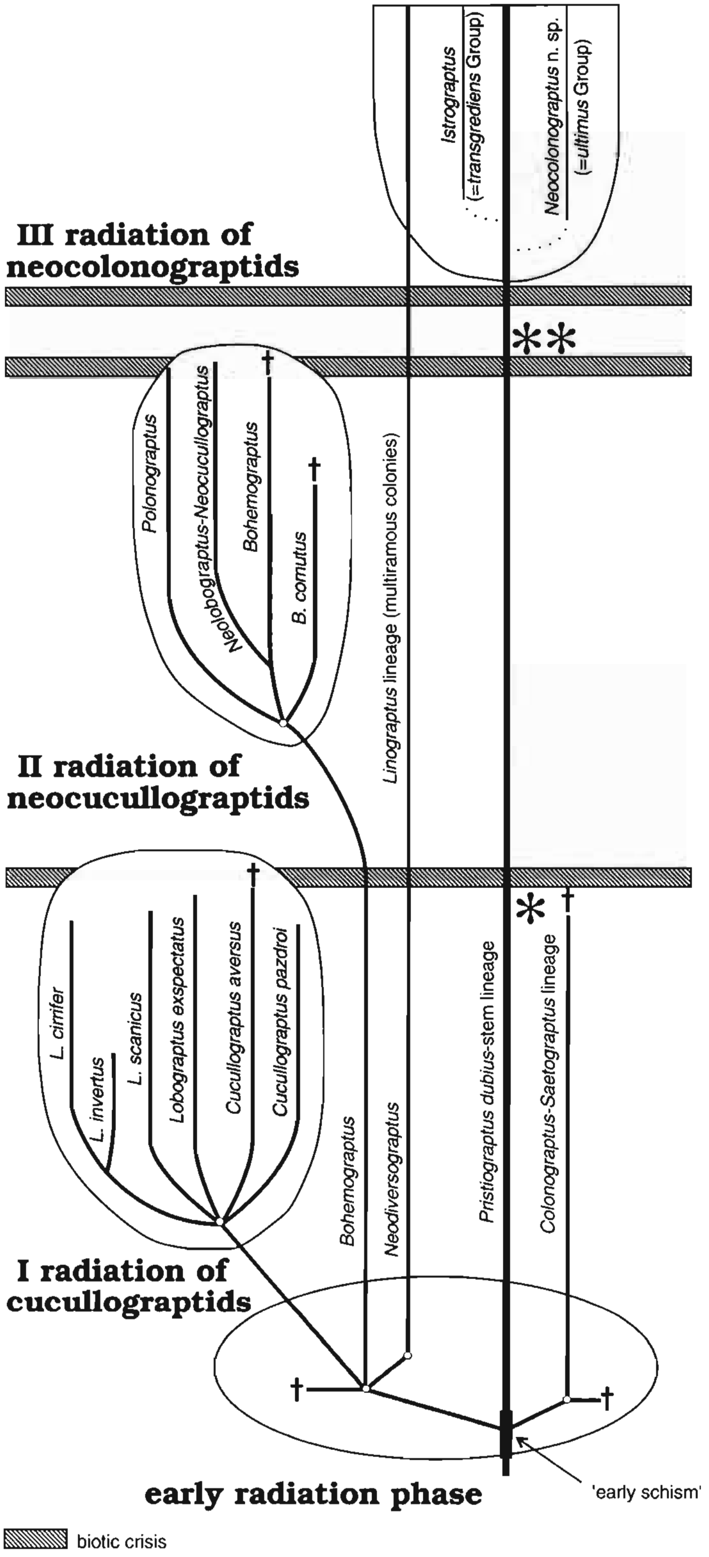

Fig. 6

Simplified history of *Pristiograptus dubius* (SUESS) and related lineages in the Late Silurian. Subject to adaptive radiation in the late Homerian, *P. dubius* stem lineage remains conservative until early Přidoli, when a new splitting take place, (III radiation phase) producing *Neocolonograptus* and *Istrograptus*, homeomorphic with *Colonograptus–Saetograptus* lineage of Gorstian. Meanwhile its descendant lines, which appeared in the early radiation phase, produced in the Gorstian (I) and in the early Ludfordian (II) secondary radiations including strikingly similar adaptive themes. Minor speciation events are marked with asterisks: * – in Gorstian and ** – in late Ludfordian. Further explanations in text. After URBANEK 1996, modified.

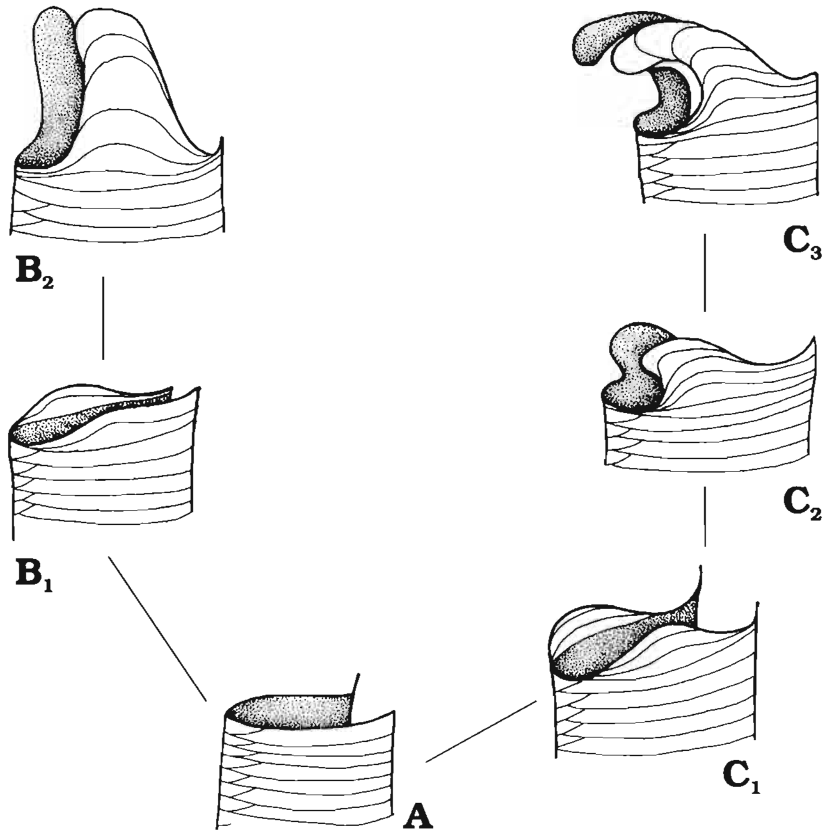

Fig. 7

Comparison of the morphological evolution of bilateral apertural lobes in the proximal thecae of Ludlow colonograptids, as illustrated by *Colonograptus praedeubeli* (JAEGER) (**B**$_1$, *praedeubeli* Zone) and *Colonograptus colonus* (BARRANDE) (**B**$_2$, *nilssoni* Zone), with Přidoli neocolonograptids represented by *Neocolonograptus parultimus* (JAEGER) (**C**$_1$, *parultimus* Zone), *N. ultimus* (PERNER) (**C**$_2$, *ultimus* Zone) as well as with *N. lochkovensis* (PŘIBYL) (**C**$_3$, *lochkovensis* Zone). Final products of both lineages display a remarkable resemblance, although they developed heterochronously and independently from the persistent stem lineage of *Pristiograptus dubius* (SUESS) with straight apertural margins. After URBANEK 1996.

types, resembling that known from the past, but descending from conservative stem lines. The application of the term "adaptive reversal" would be inadequate in the case in question. Moreover, the suggested terminology seems superior as compared to RICKARDS' (1988) recent attempt to introduce such notions as "heraldic", "anachronistic" and "echoic" as descriptive categories in the analysis of the sequence of graptoloid faunas. "Heraldic evolution" is characterized by an early appearance of certain morphological types which reappear and flourish again at a much later time. A classical example may be Telychian *Oktavites spiralis* preceding (and "heralding") a much later occurrence of *M. formosus*. This seems to me rather a literary approach that has little explanatory force and essentially repeats the concept of "Vorformen" or "Vorpostenformen" used by German palaeontologists. I am convinced (URBANEK 1996) that the occurrence of repeatedly evolving characters in some groups of Late Silurian monograptids can be explained within the framework of notion and concepts developed by phylogenetic systematics (e.g. "canalized evolutionary potential" suggested by SAETHER 1983 or "rampant parallelism" introduced by Gosliner and Ghiselin, 1984 and Sluyter, 1989). I also assume a close genealogical affinity of the groups in question due to the effect of *oligophyly*, which is defined herein on p. 124.

Due to the above pattern of evolutionary change, homeomorphy is a distinctive feature of the Upper Silurian graptoloids. This is expressed in the growing number of generic names, containing the prafix *neo-*, *pseudo-*, thus emphasizing the resemblance to earlier taxa. Some of the homeomorphic traits fulfill the criteria of homology, but were acquired in a different time, although morphoclines produced could be strikingly similar. That is why in addition to criteria of ancestry and transient forms, a time parameter, defining e.g. when a given apomorphic feature was acquired (if it appeared more than once!) is also needed. For instance lateral apertural elevations (*e*, or "blinders", see p. 112), were acquired by pristiograptid-like ancestors in the Homerian (*eH*, e.g. *Colonograptus*? *ludensis*, KOREN' and URBANEK 1994) and again in the early Přidoli (*eP*, herein p. 112) by *Neocolonograptus parultimus–N. ultimus*. Moreover, such a trait appeared in the lateral branch of pristiograptids, classified as *Pseudomonoclimacis*. This happened in Ludfordian (*eL*, *P. latilobus*, herein, p. 164). Synapomorphies based on such heterochronously acquired traits, cannot be used as a basis for (mono)phyletic groups, as it was suggested by PŘIBYL (1983), who has lumped two of the above mentioned species (representing *eL* and *eP*) into *Saetograptus (Colonograptus)*. Therefore WEBB (1994) is right when he emphasizes that parallelism may not be always resolved by cladistic techniques which are poorly suited to distinguish homeomorphs.

Only the tracing of the real history of the lineages may solve the problem of relations among such taxa. The approach outlined above makes use of those criteria of parallelism or iterative evolution, which were termed "non-biotic data" (WEBB 1994). Separation of originations in time or space may serve for recognition of parallel lines of evolution. However, in view of cosmopolitan distribution of most graptoloid species, stratigraphic gaps play the crucial role as the criterion.

A number of descriptive terms are used by palaeontologists and stratigraphers to denote the common occurrence of strikingly similar monograptid species at different horizons separated by unbridged gaps. Thus the forms appearing in surprisingly low horizons and resembling much later species are said "to foreshadow" them (e.g. BULMAN 1970: p. V106). These and similar phrases usually do not imply the ancestry or affinity but merely a repetition of a similar morphology.

Such a close homeomorphy among different monograptids of the Late Silurian (and the Early Devonian) is the primary cause of the differences of opinions as to their affinities and ancestry. The best example was provided by RICKARDS and PALMER (1977) who suggested that early Ludlow monograptids had Devonian affinities. They especially stressed the resembleness between some Ludlow forms from the *scanicus* Zone having more or less distinct climacograptid thecae (or "geniculum") and sometimes also thecal hoods (e.g. *"M." dalejensis* = *"M." haupti* and also *"M." micropoma*) and such Devonian monograptids as *M. ramstalensis* JAEGER. RICKARDS and PALMER (*ibidem*) advanced a view that either (1) some late monograptids from the *hercynicus* group in the Early Devonian "have their origin quite low in the Ludlow" or (2) monograptids of the "Devonian aspects" developed several times from their pristiogratid ancestors. In the latter case, some lower Ludlow monograptids represent a very early and rare attainment of those features "which were to become commonplace in the Devonian".

JAEGER (1978) denied the Ludlow ancestry of the Devonian monograptids. According to him, both the incipient apertural hoods in *haupti* observed in the senile growth stages of its rhabdosome and the apertural lobes present in *micropoma* are morphologically different from the standard *uncinatus*-like apertural lobes in the *hercynicus* group. They are also astogenetically delayed, being formed secondarily on the mesial edge of the thecae, wheras the hoods of the *hercynicus* group like those of all *uncinatus*-like monograptids, are completed before the growth of the next theca begins. It should be noted, however, that JAEGER (1978) missed the point that the Ludlow species, especially *micropoma*, have their hoods or flanges made of microfusellar tissue (URBANEK 1958, 1976), whilst the *uncinatus*-like monograptids have lobes composed of standard fusellar tissue. Moreover, JAEGER insisted that *micropoma* had not evolved from Wenlock *Monoclimacis*, a view invalidated by the discovery of *Monoclimacis praemicropoma* in the *lundgreni* Zone (TELLER 1988), from which true *micropoma* of the *scanicus* Zone can be easily derived assuming the Lazarus effect (URBANEK 1993). Thus *micropoma* can be assigned to *Monoclimacis* and can be thought of as a Wenlock relic among a Ludlow fauna. The erection of a separate genus, *Heisograptus* (TSEGELNJUK 1976) seems superfluous, and obscures real affinities with the earlier taxa. JAEGER's (1978: p. 306) main conclusion that the Late Silurian–Early Devonian lineages did not evolve directly from the early Ludlow species is, however, by all means correct. There were certain unit characters responsible for a close resemblance in the general habitus between the given forms which certainly did evolve many times during the Late Silurian–Early Devonian time, a phenomenon of great signifcance for the evolution and phylogeny of late graptoloid faunas.

Another interesting case of such phenomena is *"M." petri* described by KOREN' (in print) from beds immediately below the FA of *Neocolonograptus parultimus* in Kursala Formation (Tien Shan, Kirghizia). Its short rhabdosome is made of thecae displaying a uniform, well developed paired apertural lobes. In the degree of expression of this trait, *"M." petri* rather closely resembles *N. ultimus* (PERNER), and therefore is too advanced to be considered an ancestral species, either to *parultimus–ultimus–lochkovensis* lineage (*Neocolonograptus* gen. n.) or to *transgrediens* lineage (*Istrograptus* TSEGELNJUK). Nevertheless all these forms (Fig. 8), are products of a similar trend towards development of bilobate apertural apparatus, operating in about the same time but with a different rate and leading to a differential evol-

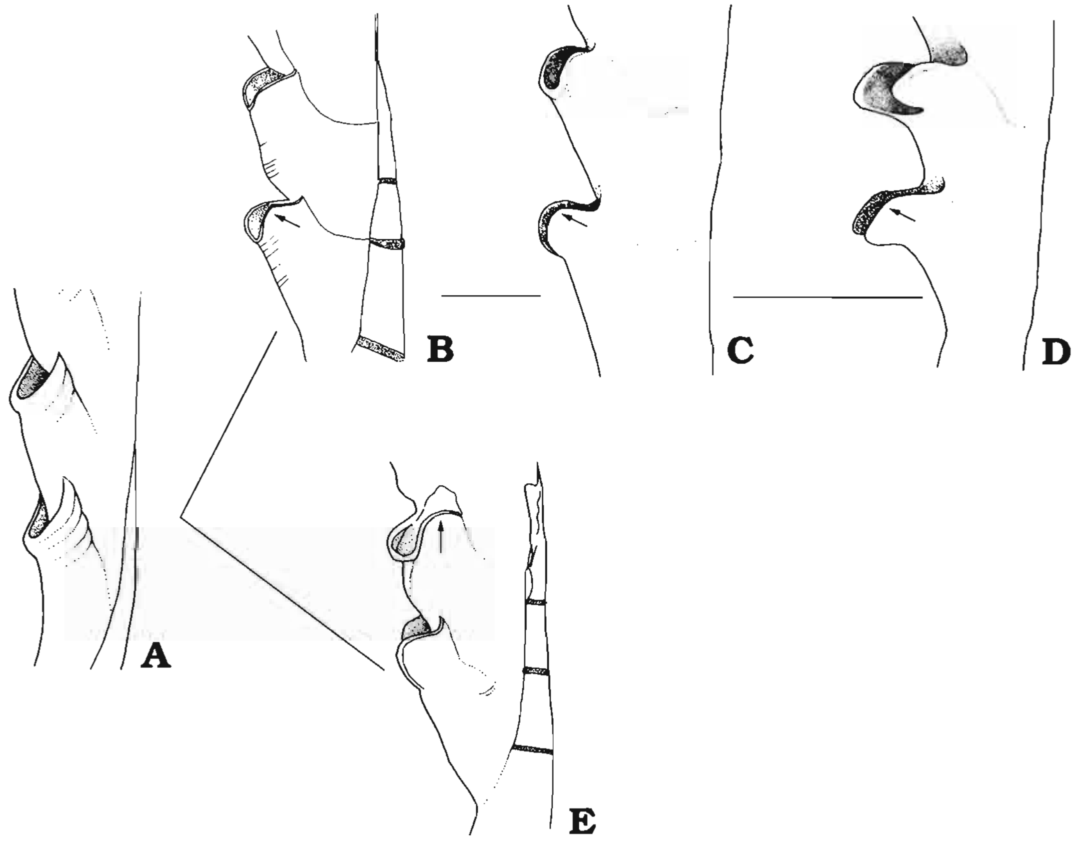

Fig. 8
Morphological change in proximal thecae of Přidoli bilobate pristiograptids, representing *Neocolonograptus* gen. n. (**B–D**) and *Istrograptus* TSEGELNJUK (**E**): **A**, *Pristiograptus dubius* cf. *frequens*, a presumable common ancestor; **B**, *Neocolonograptus parultimus*; **C**, *Neocolonograptus ultimus*; **D**, *Neocolonograptus lochkovensis branikensis*; **E**, *Istrograptus transgrediens rarus*. Note the different directions in growth of apertural undulations and lobes (arrowed) in each lineage. Not to scale.

utionary success. Thus *"M." petri* may be considered representative of a short-living lineage, displaying a tachytelic rate of evolutionary changes (as defined by SIMPSON 1944), or even being a result of "quantum speciation". Mutations involved in this process instantly exhibit a high expressivity and penetrance, although this rapid innovation failed to produce a lasting success. Much more successful were attempts by the *transgrediens* lineage to develop at a very slow rate, essentially the same trait (bilobate apertural processes). The course of events in this lineage is analytically described by TELLER (this volume, p. 74). It deserves to be classified as a bratyletic line (SIMPSON 1944). The *parultimus–ultimus–branikensis–lochkovensis* lineage represented an intermediate, "average" rate of evolutionary change in essentially the same direction. As such, it may fit the horotelic rate of morphological change, as defined by SIMPSON (1944). The details of the processes involved are shown on Fig. 8. A differential rate of morphological change was probably a common feature of evolution in parallel lines.

The case of *"M." petri* resembles another instance of a precocious form, namely *"M." insperatus*, described from late Homerian (KOREN' 1991; KOREN' and URBANEK 1994). It anticipates advanced *Colonograptus* from much younger beds (*nilssoni/colonus* Zone) and represents a short living, cryptogenetic species which left no known descendants. Such species were observed even earlier and characterized usually as taxa "before its time". They obviously represent a distinct analytical category related to the operation of a certain trend with different rate and intensity. They commonly characterize short, side lines of evolution, "a less successful attempt to achieve the same thing" (RICKARDS *et al.* 1977: p. 61).

Repetitive evolution in graptoloids, producing an effect of heterochronous homeomorphy, may also be considered a good illustration of the contingent nature of evolutionary change. While the overall morphology seems to be defined by largely deterministic factors (morphological constraints, repetition of environmental situations), minute details seem to be contingent. In this sense repetitive evolution resembles historical experiments, the "re-runs" according to GOULD (1989) that each time produce similar but not identical results (e.g. the position of spines in lobate-spinose monograptids of the Wenlock and the Přidoli). If I understand his intentions correctly, GOULD was inclined to emphasize the differences in the outcome in order to expose the role of chance in evolution. On the contrary, the history of graptolites highlights, in my opinion, a greater role of deterministic factors. The other aspect of the Přidolian case is in providing certain arguments against the now widely propagated cladistic attitude toward stem species and stem lineages. The doctrine demands that stem species after its speciation event should be considered a new species and correspondingly be renamed. The *dubius* and *uncinatus* lineage demonstrate the preservation of essentially the same evolutionary potential in spite of flow of time and speciation events which occurred in the meantime. A specific evolutionary potential is certainly an important criterion in the definition of an evolutionary species (SIMPSON 1961). This is one of the reasons, why we prefer herein a non-cladistic approach to the taxonomy of the stem species (compare KOREN' and URBANEK 1994; URBANEK 1996).

EARLY DEVELOPMENT AND ITS ABNORMALITIES

Preservation of the monograptid pattern. — The early development of Late Silurian monograptids follows the orthodox monograptid type, defined by a nonresorption porus (primary notch) and upward growth of the initial bud. Preservation of this pattern is demonstrated e.g. by the developmental stages studied in details in such late Ludfordian species as *M. (F.) formosus*, *M. (U.) acer*, and *Pseudomonoclimacis latilobus* or in such early Přidoli species as *Neocolonograptus parultimus* and *N. lochkovensis* (see the description of the sicula and its growth stages in the above-mentioned species herein, and also JAEGER, 1986). This remarkable stability of the early development of various monograptid genera and lineages in their late phase of evolution presents an interesting phenomenon and may probably serve as an instance of a morphogenetic constraint. It seems that in the production of the first blastozooid in the colony, the timing of its budding and the behaviour of both the parental siculozooid and the initial bud were rigidly controlled by the genome and followed a strictly defined succession of events (formation of the *sinus*, the primary notch, then the *lacuna* stages of EISENACK 1942, and finally an upward growth of the initial bud). The course of the development was evidently centered on the realization of the norm, and any deviations in the morphogeny were consistently eliminated. Innovations were tolerated only if they did not interfere with the formation of the primary stipe, according to the fundamental monograptid pattern (as for instance sicular cladia invented by linograptids, see URBANEK in this volume). This conservation of the norm, so deeply rooted in the organization of the monograptid colonies, was most probably the source of their future weakness. One could ascribe the lack of evolutionary plasticity demostrated by the Early Devonian monograptids to this rigid morphogenetic control of the early development.

Nevertheless, Late Silurian monograptids provide new evidence that within certain limits, the sicula and its development were subject to directional changes and even certain restructuring.

Late Silurian restructuring of the sicula. — One novel feature of the early development in late Ludfordian and early Přidoli monograptids is the reduction in the number of sicular annuli ("black" rings) and a small amount of observed variation in their number and position. In the majority of otherwise unrelated species within the above time-span, either two or three rings were observed: the first (r_1) situated at the aperture of the prosicula, and the second (r_2) placed somewhere at 1/3 of the length of the metasicula. The third ring (r_3), when present, is placed at the primary notch.

Such a stable number and position are observed in both phylogenetic elements of Late Silurian graptoloids, namely in the *dubius*-derived taxa (*dubius* Group) as well as in the non-*dubius* taxa (*uncinatus* derived Group as well as truly cryptogenetic taxa, Fig. 9). The common ancestor of the *dubius* Group is *Pristiograptus dubius* (SUESS), whose early development is known mainly from the studies on abundant populations from Baltic erratic boulders (*scanicus* Zone, Gorstian). According to WALKER (1953) and URBANEK (1953, 1958), the number of rings is commonly 5–7, although both a smaller (3–4) and a greater (up to 9) number were observed within a single sample (Fig. 9A–C). The last ring is usually associated with the primary notch (the bud ring). Therefore the changes within the *dubius* Group were expressed in the strong reduction in the number of the true rings (to 2), the bud ring being preserved, however, as

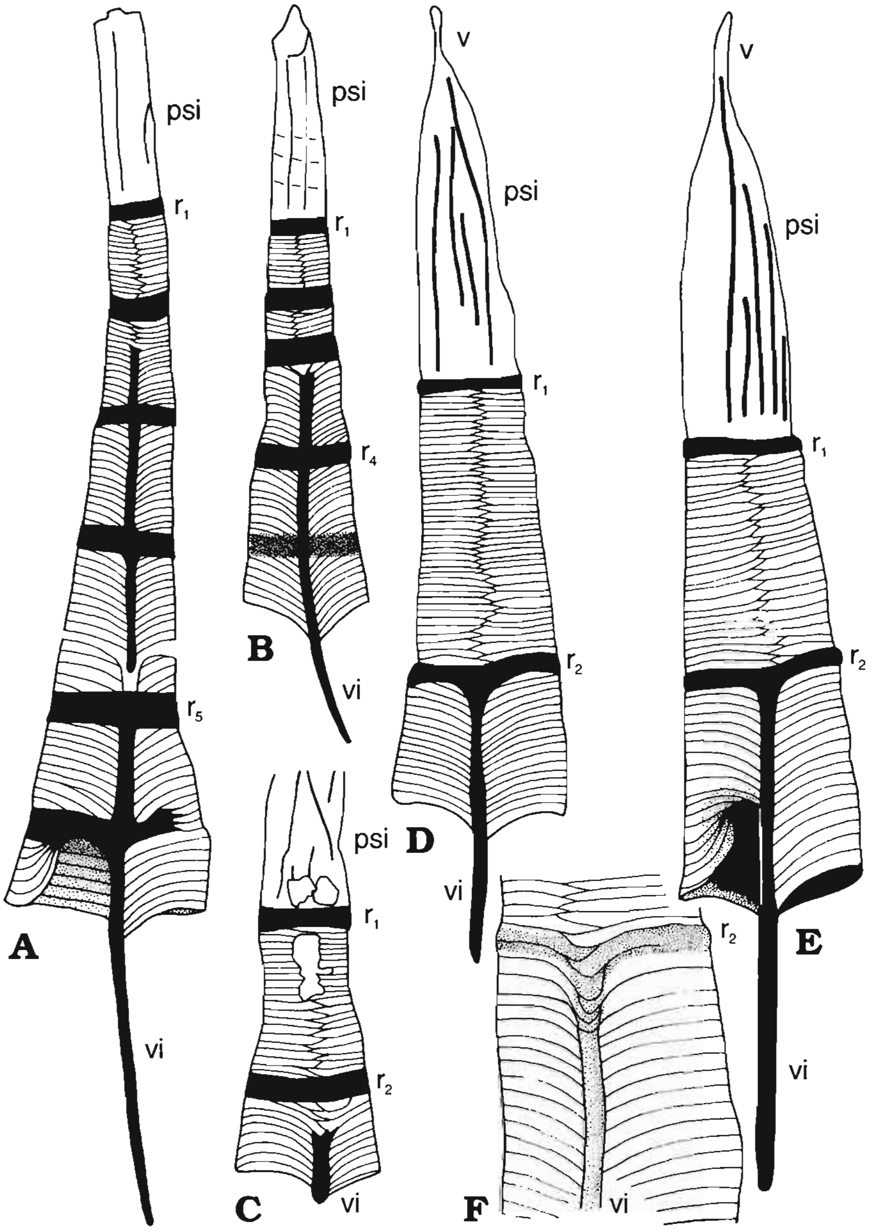

Fig. 9

Variation in the number of sicular rings as observed among late Silurian monograptids: **A–C**, multiannular condition as observed among Gorstian pristiograptids; **D**, **E**, pauciannular condition as seen in Ludfordian *M. (U.) acer acer* (TSEGELNJUK), **F** shows the coincidence between r_2 position and the origin of virgella (vi) in Přidolian *N. lochkovensis lochkovensis* (PŘIBYL). Note the variable relation of metasicular rings to the origin of virgella as shown in **A–C**. **A–C** from WALKER 1953, remaining original.

a supplementary (r_3) one. The earliest forms of *P. dubius* with a fixed number of three sicular rings were observed in the Mielnik wellcore at a depth of 786.50 m within the *acer* Zone (Fig. 43). These specimens represent the second invasion of the impoverished *dubius* fauna as defined above (p. 97). Hence, it is probable that the "pauciannular" *dubius* morph made its first appearance still earlier, soon after the *kozlowskii* Event, but sufficient evidence is not available yet. The three-ringed condition was later preserved within the lineages derived from the *P. dubius* stem lineage. This holds for *Istrograptus* TSEGELNJUK (*transgrediens* Group) as well as for *Neolobograptus* (*parultimus–lochkovensis* lineage). Such conditions can also be encountered in the late Ludfordian *Pseudomonoclimacis latilobus* (PORĘBSKA 1984; JAEGER 1986; and data herein p. 161).

A possible common ancestor for some representatives of the non-*dubius* Group may be seen in *Monograptus uncinatus* of Gorstian age, but the Ludfordian and Přidoli *uncinatus*-like monograptids reappeared as a result of the Lazarus effect, their immediate ancestry remaining somewhat enigmatic. Taking *M. uncinatus* as a plausible model of an ancestor, we observe a certain reduction in the number of annuli (from 4 in the ancestor to 2 in late Ludfordian and Přidoli hooded monograptids, Fig. 9D–F). This is combined, however, with a complete elimination of the bud ring, which in *M. uncinatus* was especially strongly developed (URBANEK 1958: p. 48).

Although the initial conditions and the style of the reduction in the number of sicular rings was different in each of the major phyletic groups of Late Silurian monograptids, the overwhelming trend was uniform and well-defined. This becomes particularly conspicuous when comparing early and late Ludfordian representatives of the *dubius* phyletic Group. The early Ludfordian monograptids resemble those of the Gorstian in the great number of rings and the amount of observed variation (URBANEK 1970). It seems therefore that, at least statistically, Late Silurian monograptid faunas display a distinct shift towards a reduction in the number of sicular rings. This trend was operative both in the *dubius*- and *uncinatus*-phyletic Groups and set at the beginning of the late Ludfordian. *Monograptus (F.) formosus*, a cryptogenetic taxon, clearly unrelated to *M. uncinatus*, also regularly displays only two rings (Figs 19, 20; Pl. 4: 1–5). The same is true for *M. (Dulebograptus) trimorphus*, another species of an uncertain ancestry, displaying, nevertheless, two rings in the sicula (Fig. 42A, B). The two-ring pattern in hooded monograptids cannot, however, be claimed to be universal in late graptoloid faunas. This clearly follows from PORĘBSKA's (1984) work on Early Devonian monograptids. Her precise studies on a well- preserved, flattened material, lead to the recognition that the characteristic number of rings was commonly three (e.g. in the *praehercynicus–hercynicus* lineage), with very little variation. It may be concluded, therefore, that the essential feature of the late monograptid faunas is the restriction of variation rather than any particular count of sicular rings. Nevertheless, the sicula with two or three rings presents the most common developmental plan for the latest Silurian and earliest Devonian hooded monograptids.

Another remarkable feature, already observed by JAEGER (1986: p. 319) in Přidoli monograptids, is the invariable origin of the virgella at the level of the second ring (r_2). In Gorstian mononograptids, the virgella appears much earlier (closer to the prosicula) and its formation is not obviously related to one of the rings (Fig. 9B, C herein; WALKER 1953; URBANEK 1953). In late Ludfordian monograptids such as *M. (F.) formosus* (Pl. 4: 1, 2, r_2, vi and Fig. 20B$_2$) or *M. (U.) acer* (Fig. 26B) as well as in the Přidoli *N. lochkovensis* (Fig. 49A), the virgella appears by a modification of the ventral zig-zag suture just at the level of r_2, even when one more ring is present (r_3). This stable relation between the origin of the virgella and the position of r_2, is a novel feature which appeared for the first time in the late Ludfordian fauna. The early Ludfordian monograptids still do not reveal any clear relation between these two traits of the sicula (URBANEK 1970).

Thus the developmental plan of the sicula in latest Silurian monograptids is defined by a reduction in the amount of variation and in the number of sicular rings as well as by the establishment of a steady morphogenetic relation between the origin of the virgella and one of the rings (r_2).

One might hypothetize that a new trend, expressed in the reduction of the number of annuli and in setting a steady relation between one of them (r_2) and the formation of virgella, started to operate in the late Ludfordian and continued throughout the rest of the Silurian. The observed change has probably the nature of an anagenetic trend resulting in a structural grade (as defined by HUXLEY 1958, and applied to the graptolite evolution by BULMAN 1963), that represents a certain structural level attained independently by coeval but phylogenetically unrelated lineages. JAEGER (1986) pointed to this relationship as an example of "programme" evolution, advanced by BULMAN (1933). It certainly combines aspects of both these ideas, each pertaining to a number of causal factors which potentially could be taken into account. It is certainly probable that for some reasons the "pauciannullar" version of the sicula was more efficient in the late Silurian pelagic environment than the "multiannullar" one. In my opinion, the advantage of the former version may be seen not so much in some specific function of sicular rings *per se*, but more reasonably, in the morphogenetic mechanisms responsible for the reduction of variation and fixation of the ring number. These mechanisms may be best described in terms of an increased morphogenetic control of the development and production of the norm with a greater accuracy. Why such changes in the morphogenesis were adaptive, remains rather obscure. One of the reason might be increasing instability of the environmental change, and the need for a greater independence from the external influences in the course of astogeny. Moreover, one can posit that such rigid control of the norm was one of the factors responsible later for the evident loss of evolutionary plasticity exhibited in the dull morphological uniformity of the Lower Devonian monograptids.

Abnormalities of the development. — Almost every large sample of isolated graptolites contains besides normal rhabdosomes, different forms of abnormality or malformation.

Some of these abnormalities are distinctly related to injuries due to various accidents which affected developing colonies, usually in their juvenile stages. The resulting deviant phenotypes were classified as regenerative morphoses (URBANEK 1963), as they present obvious instances of repair (or regulation) of serious injuries. The study of the effects of injury and regeneration in graptoloid colonies proved to be of great importance for a better understanding of morphogenesis (breaking of the colony and subsequent regeneration was used by URBANEK 1963, and URBANEK and UCHMAŃSKI 1990 as a natural experiment) or the life cycle of the colony (the significance of fragmentation in the graptoloid life cycle, URBANEK 1990a).

The new material analyzed herein mainly reveals injuries resulting in minor disturbances of the normal development of the colony. Nevertheless, even such cases provide information that the environmental conditions were relaxed enough to allow the existence of injured colonies and that repair of damages was an important element in the survival strategy in graptoloid colonies. Some of the observed malformations may be ascribed, however, to spontaneous disturbances of astogeny.

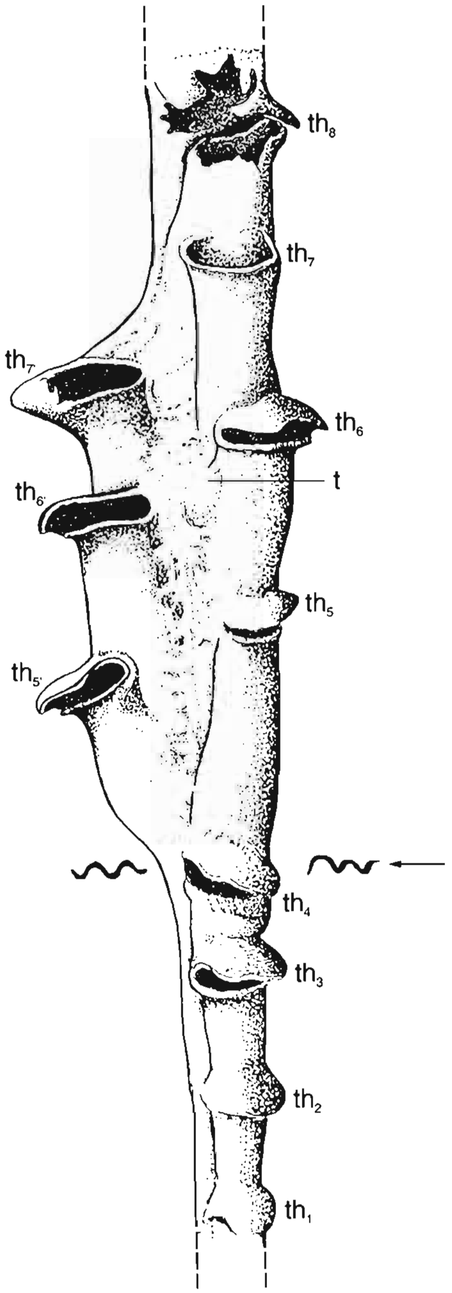

Fig. 10
Abnormality in the course of astogeny in *M. (S.) balticus* TELLER, involving a change from monoserial (th$_1$–th$_4$) to a biserial (th$_5$–th$_7$) arrangement of thecae, and again a return to monoserial condition (th$_8$). Thick wavy line and arrow indicate place where specimen was broken during the attempts to make a SEM. Further explanations in text. Mielnik, depth 819.40 m, *latilobus/balticus* Zone.

The specimen in Fig. 10 represents one of the most interesting teratologies ever found in monograptids. It illustrates an obviously spontaneous change from the monoserial condition into a biserial one and next the return to a monoserial pattern of growth. By its thecal characters, *teratum* may be assigned to *Monograptus (S.) balticus,* a species common in the sample discussed (depth 819.40 m, *latilobus/balticus* Zone). The initial portion composed of three thecae has a normal monograptid appearance. However, the fourth theca widens at its aperture to produce besides its normal successor (th$_5$), an additional theca (th$_5$) placed somewhat laterally. The latter initiates a parallel series made of three thecae (th$_5$'–th$_7$') adnate to the primary stipe and fused along the dorsal surface. The additional thecal series was, probably, devoid of its own virgula (or pseudovirgula), since it was connected with the lateral wall of the primary stipe by a special skeletal material (Fig. 10, t). The thecae of the additional series are normally built displaying all species specific characters of the aperture, but they are staggered in relation to the primary stipe. As the additional theca 7' lost the ability to produce its own daughter theca, the short biserial portion of the rhabdosome ends abruptly, while the primary stipe continues to grow by normal monograptid budding. The preserved distal monoserial portion is made up of another three thecae.

It seems that the additional series originated by means of apertural budding, comparable to the cyrtograptid pattern of cladial generation rather than to the formation of a true dicalycal theca as observed in the early development of diplograptids. In spite of this difference, the biserial portion of the rhabdosome is remarkably "diplograptid" in appearance. Such teratological morphoses could potentially be a source

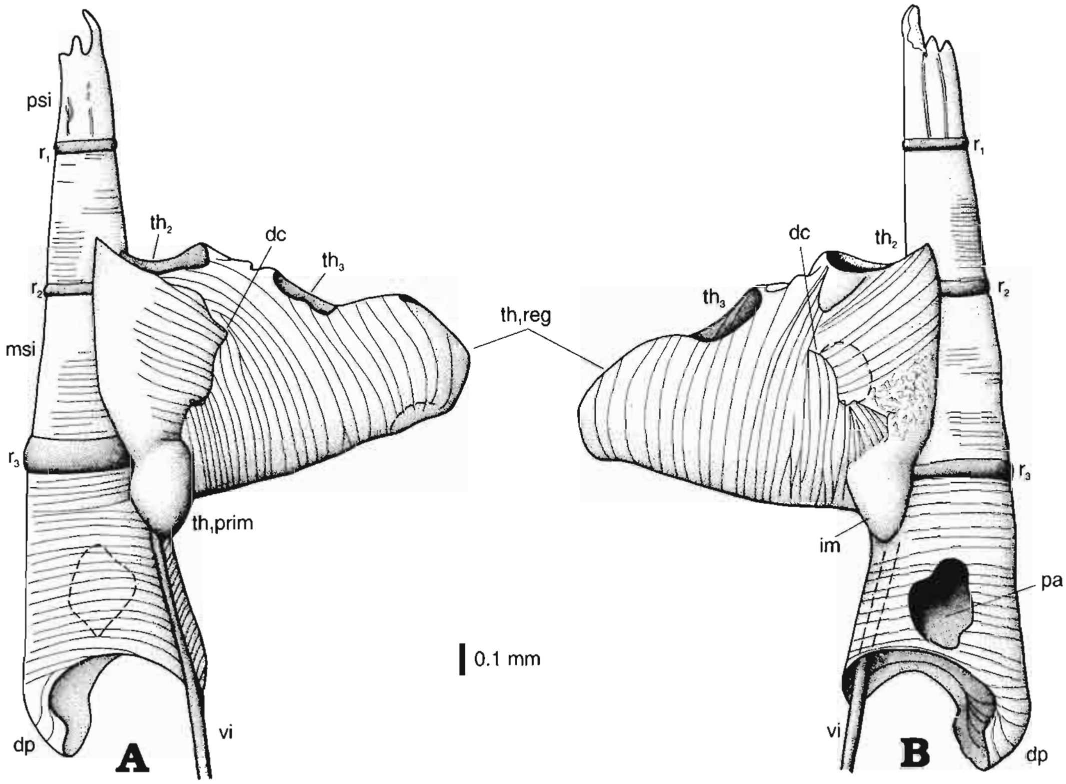

Fig. 11
Abnormal proximal end development in *Neocolonograptus lochkovensis* (PŘIBYL) due to injury of growing th_1, seen in reverse (**A**) and obverse (**B**) view. Note the disconformity in fusellar systems of the primary (th_1 prim) and regenerative (th_1 reg) part of the first theca. Further explanations in text and Fig. 12. Mielnik, depth 659.50 m, *lochkovensis* Zone.

of taxonomic misidentifications, especially if a disturbance will appear in the proximal end of the colony and a parallel series continues over a longer distance. This may offer an alternative explanation to the remarkable finding of a sole specimen identified as *Climacograptus* sp. in the *hercynicus* Zone of the Carnic Alps reported by JAEGER (1978: p. 509), but illustrated only recently by FLÜGEL *et al.* (1993: p. 14). KIRK (1978: pp. 539–540) suggested that the extreme scarcity of this late *Climacograptus* must have been due to severe competition offered by uniserial, adaptively more efficient forms. However, in view of the uniqueness of this form (a single specimen!) and an unusually late occurrence for a diplograptid (Early Devonian), an assumption of its teratological or atavistic nature cannot be excluded *a priori*. JAEGER (1978) was convinced that the specimen in question represented a late survivor of the diplograptid stem, a relic being a sort of "a fossil living fossil".

The biserial portion of the rhabdosome in *M.* (*S.*) *balticus* probably appeared as a result of a localized and non-genetic change in the tissues of a zooid. This is evidenced by its spurious effect. One could imagine, however, lasting consequences of such a morphogenetic change leading to the preservation of the biserial growth pattern within a given rhabdosome (monoserial-biserial mosaic pattern). Still it is unlikely that such changes could be transmitted to the next generation because of their obvious somatic nature.

The specimen which might be assignable to *Neocolonograptus lochkovensis* (Fig. 11), represents an injury to the growing th_1, resulting in an excessive stimulation of budding, and leading to an abnormal proximal end development. Despite the extent of the disturbance, the monograptid pattern of development and the direction of growth were preserved. The bleached specimen seen in both aspects on Fig. 11A, B, may be interpreted along the lines suggested by the diagram in Fig. 11A–C. The chimney-like th_1 is composed of the remnants of the primary th_1 (th_1prim, im) as well as of a newly formed, regenerative portion (th_1reg). There is a distinct discordance of fusellar systems on both sides of th_1 (dc). Besides its terminal aperture (assigned to the regenerated zooid of th_1) and the prothecal opening for the next theca (th_2), th_1 is also provided with a supernumerary opening situated on the distal wall of the thecal tube (th_3, s). Moreover, there is an additional opening situated on the obverse side of the meta-

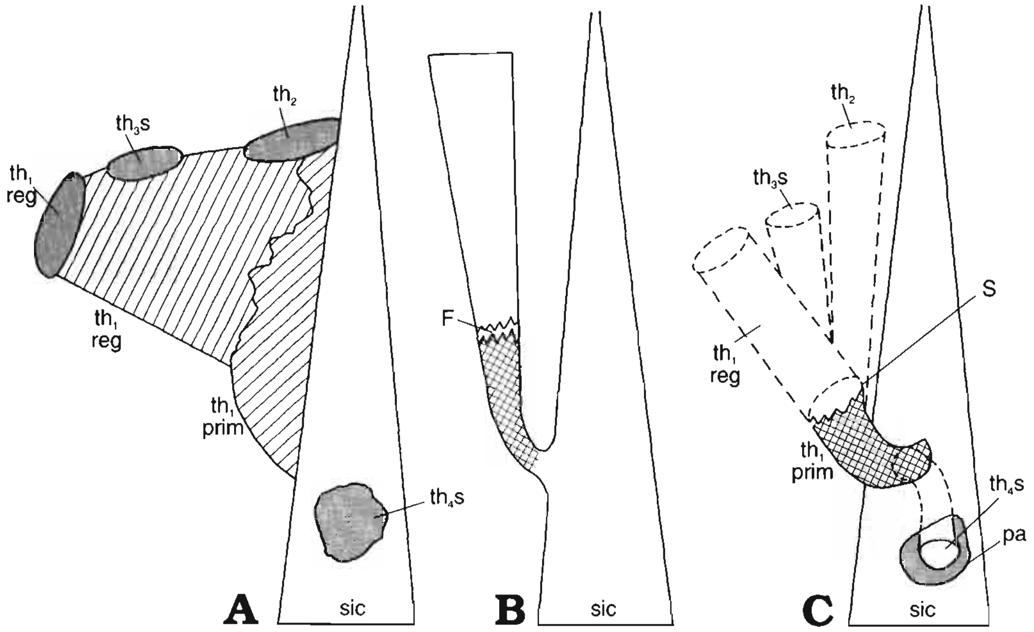

Fig. 12

Ideogram showing the possible interpretation of proximal end abnormality illustrated on Fig. 11: **A**, diagram of observed situation emphasizing the discordance between the presumably primary (th_1prim) and regenerative (th_1reg) portion of the first theca, the presence of supernumerary openings (th_3s, th_4s) in addition to normal prothecal opening (th_2) and thecal aperture (th_1); **B**, possible interpretation of the injury (wavy line) resulting in fracturing (F) of the primary th_1; **C**, reconstruction of the regeneration process involving the production of four zooidal buds (th_1reg, th_3s, th_2 as well as th_4s). The latter bud was growing inside the sicula (sic) and giving its way out through the perforation (resorption?) of its wall (pa). Remnants of the primary portion of th_1 are visible as a scar (s).

sicula, close to its aperture, and formed by perforation or rather resorbtion as indicated by its smooth edges (pa in Fig. 11B).

The diagram (Fig. 12B, C) illustrates the attempts to restore the possible course of events. The growing first theca was injured and its upper portion fractured (Fig. 12B, F). The fragmented zooid that was left in the preserved portion of th_1 was stimulated to intense regeneration (Fig. 12C) and produced a regenerated zooid within th_1reg, the normal bud for the successive th_2 and also two supernumerary buds – one growing up (th_3, s) and one making its way out through perforation (th_4, s). The prosicular apex is also broken off, but it is difficult to judge whether this injury occurred during the lifetime or *post mortem.*

The timing of the breaking off of the prosicular apex as seen in *Monograptus (U.) spineus* (Fig. 13d), is clear – it occurred during life and before the formation of th_2. The damage also involved the incipient portion of the primary nema, later replaced by an asymmetric regenerative one. The formation of an abnormal regenerative nema has been described in many graptoloids (EISENACK 1941; URBANEK 1953, 1958; and summarized in BULMAN 1970), and as such monstrosities occur fairly frequently in fossil assemblages. In this case, the asymmetry in the position of the regenerative nema might have caused the "humped" apppearance of the rhabdosome, but otherwise probably did not adversely affect the fitness of the colony. The repair of this particular structural deficiency seems to be rapid and effective, which shows that the graptoloid colonies were evidently conditioned to frequent damage of this vital part of the colony.

The presence of trumpet-like siculae in *Neocolonograptus lochkovensis* (Fig. 51B), might be interpreted either as a monstrosity or an extreme expression of variation (deviation). It may represent a purely phenotypic or genetically conditioned variation. However, the morphological effects are nontrivial, as the siculae in question resemble the *hercynicus* sicular type characteristic for the majority of Devonian monograptids. What is abnormal in the early Přidolian becomes a norm for a large group of later monograptids. It is worth mentioning that siculae of the *hercynicus*-type were recognized within the populations of Přidolian *Neocolonograptus ultimus* (JAEGER 1986) and in some representatives of Ludfordian *Bohemograptus* (URBANEK 1970) – in both cases as deviants without phylogenetic consequences. Moreover, *Colonograptus*? *deubeli* of the late Homerian reveals this type of sicula as a species-specific but phylogenetically precocious feature (JAEGER 1959, 1991).

MAJOR PHYLOGENETIC ELEMENTS AMONGST THE LATE SILURIAN MONOGRAPTIDS

Recent progress in the knowledge of the evolution and affinities of the Late Silurian monograptids speaks in favour of the view that the bulk of the post-*lundgreni* monograptids are descendants of a single species – *Pristiograptus dubius* (RICKARDS *et al.* 1977; but especially KOREN' 1992; KOREN' and URBANEK 1994; URBANEK 1994). They constitute a (1) *dubius*-related phyletic group which, being monophyletic, is exceptionally diversified morphologically and taxonomically. This group is composed of such genera as: *Pristiograptus, Colonograptus, Saetograptus, Neocolonograptus* gen. n., *Istrograptus, Lobograptus, Cucullograptus, Bohemograptus, Neolobograptus, Neocucullograptus, Polonograptus, Neodiversograptus, Linograptus, Abiesgraptus,* and probably also *Pseudomonoclimacis.* In the late Wenlock, the entire stock was represented, in addition to *P. dubius,* by only two evolutionary lines showing a small degree of divergence ("the early schism", KOREN' and URBANEK 1994). The late Ludfordian and Přidoli representatives of this group are either derivatives of the so-called A-line (*Linograptus*), or immediate products of the iterative splitting from the *dubius*-stem lineage (*Neocolonograptus* gen. n., *Istrograptus*, and probably also *Pseudomonoclimacis*) (Fig. 6).

While the significance of the A-line derivatives markedly decreases in the uppermost Silurian, because of earlier massive extinctions caused by the *leitwardinensis* and *kozlowskii* Events, the *dubius* phyletic group is represented chiefly by descendants of the stem lineage. This latter, as in the Homerian, is again phylogenetically active. This is a remarkable shift in the phyletic composition of the late Silurian monograptid fauna. The hey-days of the A-line, so characteristic of the Gorstian and early Ludfordian, are over.

The second major phyletic element is made up of taxa that might reasonably be derived from *Monograptus uncinatus* TULLBERG, 1883, a Lazarus taxon (URBANEK 1993) that appeared in the *nilssoni* Zone and strongly resembles non-specialized Wenlock hooked monograptids. The (2) *uncinatus*-related phyletic group includes the following genera or subgenera: *Monograptus (Uncinatograptus)* and *Monograptus (Slovinograptus)* subgen. n. The lobato-spinose *Monograptus* of the Ludfordian may, in spite of its unique morphology, also be placed within the former subgenus (URBANEK 1995 and p. 109 herein). It is rather uncertain whether all Late Silurian monograptids, technically assigned to the morphological group with *uncinatus*-like apertural lobes and called also sometimes "hooded" monograptids, are related to *M. uncinatus.* The group may comprise also elements of a different ancestry. I believe that most Ludfordian and Přidoli monograptids [probably including also *M. (Dulebograptus)* !] have *uncinatus* affinities. Also some fraction of Devonian hooded monograptids has *uncinatus* affinities but probably not all of them. It is true that all Devonian monograptids have thecae of the *uncinatus*-type, but they display great differences in the penetrance of this trait. The minimum is one hooded theca in a rhabdosome (*M. aequabilis, M. ato-*

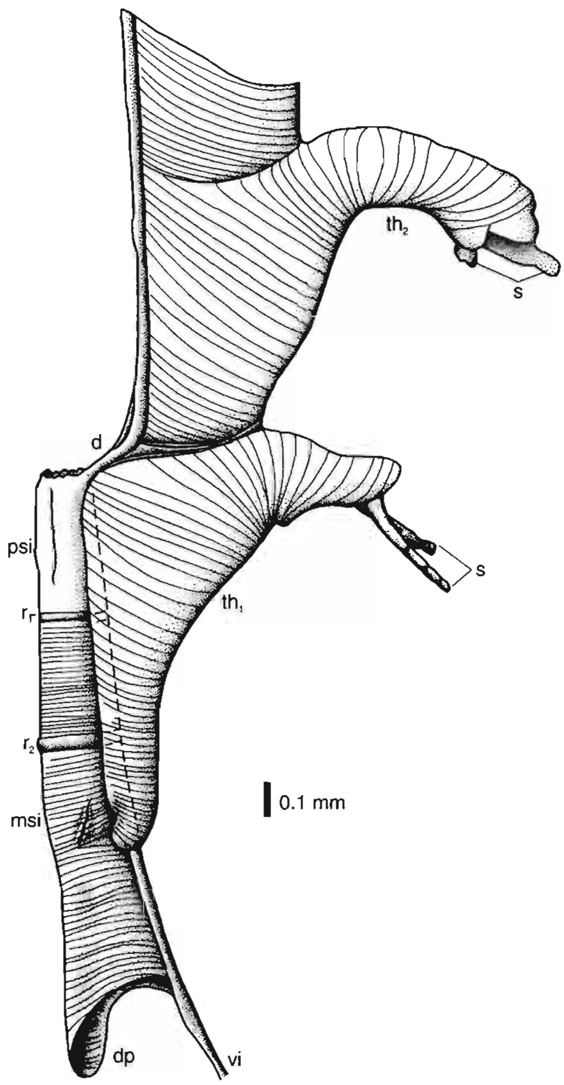

Fig. 13
Monograptus (Uncinatograptus) spineus TSEGELNJUK. Proximal fragment of the rhabdosome showing an abnormal growth due to the damage (d) and subsequent regeneration of the apex of the prosicula, resulting in a "humpback" rhabdosome. Mielnik, depth 760.15 m, the *spineus* Zone, × 80.

pus), the maximum reveals a complete penetrance. Those forms that have only one fully developed hood may, at least theoretically, be suspected of a novel origin of their thecal shape from a simple, non-hooded ancestor. JAEGER (1978) suggested such an ancestry for his *M. ramstalensis* and PORĘBSKA (1984) provided evidence for the pristiograptid ancestry of *M. aequabilis*. In any case, a considerable penetrance variation is a new feature in the latest hooded monograptids, not shared by earlier representatives of this thecal type, which as a rule display a complete penetrance (*M. uncinatus, M. acer, M. balticus, M. hamulosus*). Therefore, Devonian hooded monograptids present a more heterogeneous assemblage. Although on the whole I do not share the suggestions (RICKARDS *et al.* 1977: pp. 61–62) that Late Silurian hooded monograptids evolved secondarily from pristiograptid ancestors and consequently *Monograptus* s.s. is polyphyletic, a convergence toward *uncinatus*-like types among some Devonian lineages cannot be excluded. Such a view is, however, untenable for earlier faunas. The incompletness of the record around the *ludensis* Zone and the reappearance in the *nilssoni* Zone may be explained, in view of the obvious Wenlock affinities of *M. (U). uncinatus,* by the Lazarus effect (URBANEK, 1993). The same explanation is probably true in respect of the second gap, between the *nilssoni* and the *leitwardinensis* Zone (see p. 105, herein). That is why I consider the bulk of the Late Silurian hooded monograptids related in one way or another to *uncinatus*. This seems also true in respect of *M. (Dulebograptus)*, which, although characterized by unique notched apertural lobes, reveals nevertheless an *uncinatus*-like th$_1$, thus displaying an astogenetic recapitulatory effect pointing to its ancestry. TSEGELNJUK (1978) also related his *Dulebograptus* to uncinatograptids. An alien element, which technically may be defined as *Monograptus* s.l. (see below), is really present, but these forms cannot be derived from the pristiograptid stock either.

The third analytical category, the (3) non-*uncinatus* Group, can hardly be defined as a phyletic unit, being a highly heterogenous assemblage, composed of cryptogenetic elements with an uncertain affinity. Some, as *Monograptus (Formosograptus)* represent a roughly "hooded" type of morphology, due to the presence of some sort of a single apertural lobe. This feature, however, combined with such traits of specialization, makes their derivation from the *uncinatus*-stem untenable. Otherwise they are clearly unrelated.

Still more enigmatic are such taxa as *"Monograptus" lebanensis* TELLER, 1966, *"Monograptus" willowensis* (BERRY *et* MURPHY, 1975) or *"Monograptus" supinus* KOREN', 1983, which occupy entirely isolated positions against the background of the remaining Upper Silurian monograptid fauna. Their morphology is inadequately known, while their similarity to some earlier taxa is clearly deceptive.

Nevertheless, one can speak about a relatively very high degree of phylogenetic uniformity in the Ludlow and post-Ludlow monograptid faunas. Due to a severe bottle-neck effect caused by the *lundgreni* Extinction Event, these faunas are dominantly composed of descendants of a single surviving species, contaminated by the products of another survivor which re-appeared from some refuge, plus by a very small fraction of the species with an enigmatic ancestry. In order to describe this situation I propose to introduce a new term: *oligophyly* (from Gk *oligos* few, scanty and *phylon* tribe, race) having in mind a recovery based on scanty ancestry, which causes an unusually close affinity within descendant groups. Such a close relatedness is in turn responsible for frequent morphological repetitions of evolutionary themes expressed as abundant parallelism, homoplasy and in general – homeomorphy, so characteristic a feature of the Late Silurian monograptid fauna (see also p. 111).

REMARKS ON THE GENERIC CLASSIFICATION OF MONOGRAPTIDS

While representing the same structural grade and a remarkably stable type of the proximal end development (compare p. 117 herein), monograptids reveal a great diversity in thecal morphology and rhabdosomal shape. Because of their essential structural stability, it is tempting to use only a single generic name, *Monograptus* GEINITZ, 1852, for the bulk of the representatives of the family. On the other hand, the diversification in the thecal morphology and, to a lesser extent, the overall shape of the colony, provide a basis for the subdivision of *Monograptus*. Every palaeontologist dealing with monograptids has been tempted either to give a separate name to each morphological group or to preserve the broadly understood genus *Monograptus* GEINITZ, 1852, as a portmanteau name. The recent generation is no exception in this respect. While JAEGER (1986) needed only two generic names (*Monograptus* and *Linograptus*) in order to describe the diversity of the entire Přidoli graptoloid fauna in the type Barrandian, TSEGELNJUK (1975,

1988) suggested its subdivision into some 8 genera. His classification of the Upper Silurian (Gorstian–Přidoli) graptoloid fauna in the SE part of the EEP, introduces as many as 21 generic names. Although more and more generic names are proposed for particular groups of *Monograptus* s.l., and the need for a soundly based subdivision of that genus seems irresistible, the current practice is by no means satisfactory. The subdivision is too frequently based on species with an imperfectly known thecal structure or on erroneously derived phylogenetic relations. This situation was rightly criticized by BULMAN and RICKARDS (1970), proponents of a conservattive attitude to the problem in question. They have warned taxonomists against any attempts at a premature subdivision of *Monograptus* s.l. BULMAN was convinced that the erection of new genera should be accompanied by some addition to our knowledge on the structure and phylogeny of a given group of monograptids and in each case the morphology of the type species should be perfectly understood before a taxonomic decision is made. His conservative stance was by no means dogmatic – BULMAN gradually (1955, 1970) accepted more and more genera as convincingly designated (*Rastrites, Monoclimacis, Pristiograptus, Saetograptus, Lobograptus*, and *Cucullograptus*), but he still considered most of the newly suggested genera ill-defined or of a dubious value.

BULMAN convincingly exposed the dangers stemming from the premature erection of new genera. Splitting of the genus into too numerous new genera could only be the source of confusion for stratigraphers, especially when new genera are ill-defined or based on misunderstood phylogenies.

However, the conservative atttitude toward the subdivision of *Monograptus*, has its own negative consequences – it masks the real diversity of a given fauna. The use of a sole generic name would result e.g. in an apparent uniformity of the graptolite faunas of Wenlock, Ludlow or Přidoli age, when traced above the species level. In order to describe the taxonomic effect of faunal changes one is compelled to recognize instead of the genera a number of more or less natural species groups. This practice could scarcely be regarded as more parsimonious than the standard procedure of giving generic names to such groups.

Although the crucial significance of thecal characters for the generic subdivision of monograptids can hardly be doubted, simple thecal characters such as genicular bending or paired lateral elevations, do not provide *per se* a reliable basis for a generic classification. Theca-based monograptid genera may include forms of independent origin, which at different time acquired a given morphological trait that became decisive for their assignement to a particular "form genus". BULMAN (1970: pp. 103, 107) provided convincing evidence for such a process within *Diplograptus* s.l. He called it "transition". In my opinion, a more precise term would be "generic transition". Generic transitions are meant as gradations from one genus defined by certain thecal characters to another determined by the acquisition of a new (usually simple and frequently "silhouette") trait. Such generic transitions may occur repeatedly and in both directions, as the newly acquired character may be later obliterated or lost. Among Late Silurian monograptids, *Pseudomonoclimacis* seems to represent such a unit, being composed of species which evolved in different times but share a common thecal character, namely a more or less conspicuous genicular bending and the presence of a ventral excavation in the thecae. In the case of *Pseudomonoclimacis* which belongs to the *dubius* phyletic group (defined above, p. 123), they probably also share a common ancestor, which was *Pristiograptus dubius* s.l., a conservative, long-lasting stem species. In this sense they are monophyletic. However, the species representing *Pseudomonoclimacis* were relatively shortlived offshoots that appeared at different time or at least came from geographically different populations of the ancestral species. In this respect, this genus is a bundle of lineages, composed of homeomorphic taxa. Nevertheless it is accepted herein as a compromise between the phylogenetic and the morphological criteria in generic classification.

Generic transitions can also be reversible as the result of the reduction of a novel character as illustrated by the fate of thecal genicular bending within the *N. parultimus–N. lochkovensis* lineage. Present in early members (*N. parultimus–N. ultimus*), this trait was later lost (*N. lochkovensis*). Hence, we observe the following morphological changes: presumably straight tubular thecae (in ancestral *P. dubius*) → thecae with ventral excavation (*N. parultimus, N. ultimus*) → straight tubular thecae (*N. lochkovensis*). However, paired apertural lobes which developed in the meantime within the terminal members of the lineage are not subject to reduction.

One can conclude that studies on Late Silurian monograptids point to the significance of considering their evolution in terms of homeomorphy (see p. 111 herein) and generic transition. Both prove to be descriptive-analytical categories with important implications for the understanding of repeated patterns in both numerous lineages and subsequent radiations from surviving species. The classification of the groups in question should also reflect the importance of the repetitive patterns.

A REVISED CLASSIFICATION OF LATE LUDFORDIAN AND PŘIDOLI MONOGRAPTIDS

Recent papers by LENZ (1990), KOREN' (1983, 1986), MIKHAJLOVA (1975), PŘIBYL (1940, 1948, 1983), and TSEGELNJUK (1976) contain ample material concerning the generic subdivision of Upper Silurian *Monograptus* s.l. (Přidolian monograptids included). Even the adherents of a conservative approach, especially JAEGER (1986), provide certain guidelines for a generic subdivision inasmuch as they either recognize species groups made up of closely related species, or outline convincing phylogenies. The same holds for the morphological groups discriminated by KOREN'(1983, 1986).

The present preliminary attempt to provide a subdivision of *Monograptus* focuses on late Ludfordian and early Přidoli species with a view to elaborating a practical classification scheme applicable, in the first instance, to the taxa described herein. Therefore this is no more than a preliminary arrangement of the species selected with no ambition to provide a comprehensive systematic treatment. However, the author is convinced that a gradual improvement in the generic classification of the Monograptina could only be achieved by such partial attempts which might be eventually culminated in a complete and comprehensive scheme. Instead of being based on the outline appearance of flattend specimens, such partial revisions should involve, if feasible, the study of isolated specimens.

TSEGELNJUK's (1976) far-reaching concepts of the subdivision of *Monograptus* s.l. provide a convenient starting point for a revised classification of the Přidolian graptoloid fauna. For the time-being we will focus on his generic classification, postponing our comment on his phylogenetic ideas until later.

The designation of *Uncinatograptus* TSEGELNJUK (with *Monograptus uncinatus* TULLBERG as the type species) seems to me an acceptable idea, especially because thus defined, this genus shows a clear distinction from the late Wenlock representatives of *Monograptus* and also because of the great role played by the *uncinatus*-like monograptids in the Late Silurian and Early Devonian. I would rather rank this taxon as a subgenus of a broadly understood *Monograptus*, that is *Monograptus (Uncinatograptus)* (see Table 1). It distinctly differs from the late Wenlock (Homerian) true *Monograptus (Monograptus)*, represented by the biform and spinose *priodon–flemingi* group [with *M. (M.) priodon* as the type species]. Further revision will probably expose Wenlock ancestors of *M. (Uncimatograptus)* thus clearing the infrageneric taxonomy of hooked monograptids in genetral. The erection of *Wolynograptus* TSEGELNJUK to accommodate gracile monograptids with an attenuated proximal end and elongated thecae seems also justified, although TSEGELNJUK (1976) designated his genus on badly defined (probably preservational) characters with *Wolynograptus valleculosus* as the type species. Such monograptids differ, however, from the co-eval uncinatograptids and appear to continue in the *microdon* group. I suggest replacing TSEGELNJUK's ill-conceived taxon by a new one, namely *Monograptus (Slovinograptus)* subgen. n., with *Monograptus balticus* TELLER 1966 as its type species. Not unlike the previous case, *Slovinograptus* is treated as a subgenus (see Table 1).

TSEGELNJUK's *Tamplograptus* is a junior synonym of *Formosograptus* BOUČEK, MIHAJLOVIĆ *et* VESELINOVIĆ, 1976 (as established by PŘIBYL 1983). Its extreme distinctiveness against the background of the associated monograptid fauna (see also KOREN' 1986) together with a fairly striking resemblance to the remote triangulate monograptids of the Lower Silurian provide justification for the erection of this genus. Also RICKARDS (1989: p. 272) is convinced that *M. formosus* had an independent origin, unrelated to *uncinatus*. However, in its thecal character, *Formosograptus* is closely related to hooked or lobate monograptids, and regarding it as a subgenus in *Monograptus* seems preferable (see Table 1).

TSEGELNJUK's genus *Acanthograptus* is an invalid name, a junior homonym of *Acanthograptus* SPENCER, 1878, a well-known dendroid graptolite (cf. also PŘIBYL 1983: p. 150). This name was replaced by a valid name *Bugograptus* (TSEGELNJUK, 1988). The main reason for the erection of this genus was the need to accommodate the species (like *"A." spineus* TSEGELNJUK) with lobate-spinose thecae, a conspicuous feature of the late Ludfordian fauna. *"Acanthograptus"* sensu TSEGELNJUK and *Wolynograptus* TSEGELNJUK were included in the subfamily Wolynograptinae TSEGELNJUK. From the present study it becomes clear, however, that lobate-spinose monograptids represent a derivative of *Monograptus (Uncinatograptus)* and correspondingly belong to the latter subgenus (URBANEK 1995 and p. 151 herein).

To conclude the first part of the present survey embracing all hitherto described genera of late Ludfordian and Přidoli (or rather Post-Ludlow) monograptids, I would like to stress the importance of a great "comeback" of *Monograptus*, which reappeared due to the Lazarus effect and was highly prominent in the the Late Silurian and Early Devonian fauna. It is represented by the following subgenera: *Mono-*

graptus (Uncinatograptus), Monograptus (Slovinograptus) subgen. n. and *Monograptus* (*Formosograptus*). A higher ranking of these taxa (as independent genera) would obscure the *Monograptus* comeback, a fact of prime significance for stratigraphy. Moreover, there is possible that some of these subgenera [especially *M. (Uncinatograptus)*] may represent a certain structural or adaptive type, rather than coherent systematic groups.

The second important constituent of the late Ludfordian- Přidoli fauna is made up of species preserving an essentially pristiograptid foundation of the rhabdosome in combination with a new acquisition – a bilateral apertural processes (see p. 108 herein). Because of a great silhouette resemblance to the Gorstian *Colonograptus* PŘIBYL, 1943, these species were assigned by PŘIBYL either to *Colonograptus* (PŘIBYL 1940) or even to *Saetograptus (Colonograptus)* (PŘIBYL 1983). That was a misleading practice because the Ludfordian and Přidolian forms doubtlessly developed independently and *de novo*, their resemblance to the Gorstian genera (or subgenera) *Colonograptus* and *Saetograptus* being of a homeomorphic nature (see p. 108 herein). They were a classical example of the so-called "form genera", as PŘIBYL had applied purely typological criteria neglecting the possibility of an iterative appearance of roughly identical thecal characters and paying no attention to a considerable stratigraphic gap in the vertical distribution of the taxa (cf. also the opinion of RICKARDS 1989: p. 272, about their independent origin).

The Ludfordian species of the *latilobus* group have been included herein into the genus *Pseudomonoclimacis* MIKHAJLOVA, 1975. By introducing this name, she was emphasizing the "glypto-" or "climacograptid" appearance of the thecae in such Late Silurian species as *Monograptus dalejensis* BOUČEK (= *Monograptus haupti* KÜHNE) and *Ludensograptus latilobus* TSEGELNJUK, although the type species she designated was *Pseudomonoclimacis elegans* (from the Tokrau horizon, Kazakhstan). While the presence of a sort of a geniculum is a common feature for these forms, they differ in the absence or presence of apertural lobes. This probably explains why KOREN' (1983: p. 412) tends to limit the scope of *Pseudomonoclimacis* MIKHAJLOVA to the forms provided with some climacograptid thecal excavations but devoid of any apertural additions. She also suggested (in LENZ 1990, footnote on p. 1082) that the species *parultimus* and *ultimus* (having both the geniculum and the apertural elaborations) should not be assigned to the genus *Pseudomonoclimacis*, an opinion with which LENZ disagrees. On the other hand, KOREN' suggested that at present the Přidoli forms with lateral lobes or with more complicated apertural structures (*transgrediens, lochkovensis*) can only be referred to *Monograptus* s.l. This provisional solution is hardly satisfactory and may even be a source of confusion.

An entirely different classification of this group was proposed by TSEGELNJUK (1976). His concept is based on a speculative phylogeny assuming the splitting up of the hooked apertural lobe in *Monograptus*-like ancestors to produce a transient biform monograptid (genus *Dulebograptus*) with hooked proximal and bilobate distal thecae. Thinking along these lines, he suggests that further progress of such processes could produce representatives of *Skalograptus* whose colony is composed throughout of thecae with paired apertural lobes (the type species *S. vetus* TSEGELNJUK is either a junior synonym of *M. ultimus* PERNER or a representative of its somewhat more advanced variety). In the present paper, we proceed from empirical data that provide reliable evidence that the Přidoli bilobate taxa developed *de novo* and gradually from the ancestral pristiograptid foundation (TSEGELNJUK's hypothesis is evaluated herein, p. 172). On the basis of this evidence, TSEGELNJUK's genera can only be considered as quite impracticable.

In my considerations, I will follow KOREN's suggestion and use *Pseudomonoclimacis* in a restricted sense, namely to accommodate the Late Silurian pristiograptid-like forms with a more or less distinct bending of the ventral wall. Apart from *Pseudomonoclimacis dalejensis* (BOUČEK) (= *M. haupti* KÜHNE) and *Pseudomonoclimacis latilobus* (TSEGELNJUK), from the early and late Ludfordian, such forms are known at present only from the Tokrau horizon of Kazakhstan (*P. elegans, P. bandaletovi, P. cinctutus* – all described by MIKHAJLOVA 1975 and KOREN' 1986).

On the other hand, a group of closely related species such as *parultimus* JAEGER, *ultimus* PERNER, and *lochkovensis* PŘIBYL must be accommodated elsewhere, no matter whether a geniculum is present or not. They are included in a newly erected genus *Neocolonograptus* gen. n. The praefix *neo-* conveniently emphasises the iterative nature of the evolution of the thecal characters in the Late Silurian monograptids, while the root of the generic name manifests their unusual resemblance to the Ludlow forms, a resemblance which previously proved to be misleading for some of the taxonomists. Early representatives of the lineage display a distinct geniculum on the ventral wall of their thecae (*parultimus, ultimus*), this character becoming less distinct in *lochkovensis*. Neocolonograptids may possibly be derived from a conservative pristiograptid stock, *via* still unknown monoclimacid-like transient forms (the appearance of a geniculum or a ventral excavation, p. 166 herein). This characteristic phylogenetic acquisition is repeated in the astogeny of the early representatives of neocolonograptids. The type species of *Neocolonograptus* gen. n. is *Monograptus lochkovensis* PŘIBYL, 1940. TSEGELNJUK'S (1988) last proposals to consider *M. parultimus* JAEGER a late survivor of *Ludensograptus*, without any relation to *Pristiograptus lochkovensis* PŘIBYL, being in his opinion a direct descendant of *Dulebograpus* (p. 156 herein), are purely speculative and hardly convincing. The same holds for his idea of the collective nature of *M. ultimus* PERNER, which he suggested should be split into two completely unrelated species ("true" *M. ultimus* which should be assigned to *Istrograptus* TSEGELNJUK with a pristiograptid ancestry, and *Skalograptus vetus*, an advanced variety of *ultimus*, which in his opinion stems from dulebograptids).

The concept of *Neocolonograptus* gen. n. corresponds better to the empirical data and is free of unnecessary speculative reasoning.

The Přidoli faunal assemblage included some representatives of *Pristiograptus* JAEKEL, the foremost among them being the persistent *Pristiograptus dubius* (SUESS) s.l., passing without much change through almost the entire Přidoli (cf. also KOREN' 1986). Analyzed with a higher stratigraphic resolution, it reveals both chronodemes representing a standard morph basically similar to late Homerian–Gorstian *P. dubius frequens* and populations composed of deviant phenotypes. After some time such deviants are again replaced by a standard morph. This variation makes any taxonomic evaluation with the help of standard criteria very difficult (see p. 159 herein).

Alongside the zigzag microevolution of the *dubius* lineage, Přidoli monograptids exhibited more persistent trends which evolved into valid species. One such trend can be illustrated by *transgrediens* PERNER, an interesting case manifesting the appearance of thecal characters remarkably similar to those developed almost coevally in the *parultimus–ultimus* lineage. The similarity is so close that the proximal fragments of the rhabdosomes of the *transgrediens* and *the ultimus* species groups can be mixed up! Thinking in typological terms, PŘIBYL (1983) assigned *transgrediens* to his *Seatograptus (Colonograptus)* because of its elaborate apertural lobes. KOREN' (1983) uses the name *Monograptus transgrediens*, which seems misleading. LENZ (198) temporarily, until a better solution has been found, uses quotation marks in his nomenclature, e.g. *"Pristiograptus" transgrediens.* The use of quotation marks in generic naming signals in the first place that the generic assignment of the species discussed is so far unresolved and that this species occupies an exceptional place within the genus in which it has been tentatively included. The revision of the *transgrediens* Group by TELLER (this volume p. 73) enables us to accept and redefine TSEGELNJUK's (1988) generic name *Istrograptus*. Its type species is *Monograptus transgrediens* PERNER, 1899, and it comprises solely the *transgrediens* group of species (compare also KOREN', in press). I do not accept, however, TSEGELNJUK's speculative assignement of *M. ultimus* PERNER (partim) to this group as well, nor do I share his idea of the latter species' collective nature.

Essential reclassification of the Přidoli monograptid fauna described herein will be conducted using the scheme shown in Table 1. Although our knowledge about the actual phylogenetic relationships remains limited in respect of some forms, the classification and reassessment of the nomenclature are based on isolated material providing safe grounds at least for understanding the morphology. It must be clearly stated that neither intellect nor scrutiny can replace a careful and detailed study of three-dimensionally preserved and chemically etched material.

Table 1
Tentative generic subdivision of late Ludfordian and Přidoli mononograptids.

Genus	**Type species**
Monograptus (Uncinatograptus) TSEGELNJUK, 1976	*Monograptus uncinatus* TULLBERG, 1883
Monograptus (Slovinograptus) subgen. n.	*Monograptus balticus* TELLER, 1966
Monograptus (Formosograptus) BOUČEK, MIHAJLOVIĆ *et* VESELINOVIĆ, 1976	*Monograptus formosus* BOUČEK, 1931
Pristiograptus JAEKEL, 1889	*Pristiograptus frequens* JAEKEL, 1889
Pseudomonoclimacis MIKHAJLOVA, 1975	*Pseudomonoclimacis elegans* MIKHAJLOVA, 1975
Istrograptus TSEGELNJUK, 1988	*Monograptus transgrediens* PERNER, 1899
Neocolonograptus gen. n.	*Monograptus lochkovensis* PŘIBYL, 1940

SYSTEMATIC PART

Family **Monograptidae** LAPWORTH, 1873

Genus *Monograptus* GEINITZ, 1852

Subgenus *Monograptus (Slovinograptus)* subgen. n.

Diagnosis. — Rhabdosome slender in proximal part, thecal apertures provided with globose hoods, adnate to the ventral wall.

Derivation of name: From Slovinians, an ancient Slavic tribe inhabiting Pomerania.

Monograptus (Slovinograptus) hamulosus (TSEGELNJUK, 1976)
(Pl. 2: 1–6, Fig. 14A, C_1, C_2)

1976. *Wolynograptus hamulosus* n. sp. TSEGELNJUK; TSEGELNJUK, p. 112, pl. 33: 6, 7.

Material. — about 20 fragments of rhabdosome including proximal part with sicula.

Description. — Sicula 1.5 mm long and straight, with only the apertural part slightly turned ventrally. Prosicular apex extends to the level of the th_1 aperture. Diameter of the metasicular aperture 0.25 mm. Initial bud in a characteristic low position, placed at a distance of 0.18–0.20 mm from the metasicular aperture. Dorsal process of the metasicula is very indistinct, marked as a slightly protruding margin (Pl. 2: 1, 2; Fig. $14A_1$, A_2).

Thecae displaying a straight or gently sigmoidal ventral wall in the proximal part, becoming increasingly convex distalwards. Apertures provided with a strongly developed apertural hood of the *uncinatus*-type. While most proximal thecae seen ventrally exhibit rounded margins of their apertural lobes, medial and distal thecae are more or less distinctly cordate when seen in this aspect. This cordate appearance is produced by the presence of an angular promontorium in the middle of the free margin (Pl. 2: 6, Fig. $14C_1$, C_2). In some cases this appearance is less distinctly marked. Lateral corners of the apertural lobe form projections, visible both in the lateral as well as in the ventral view (Pl. 2: 5, 6).

$Theca_1$ is 1.6 mm long and displays a very short metathecal segment and a small overlap with the succeeding theca. Both the length of the metatheca and the degree of overlap increase distalwards (Pl. 2: 1, 6).

Stratigraphic distribution. — In the Mielnik-1 borehole *M. (S.) hamulosus* appears soon after the FA of *Pseud. latilobus* at a depth of 822.90 m, being the first hooded monograptid to re-appear after the extinction of *M. (U.) uncinatus* TULLBERG in the *nilssoni* Zone of the Gorstian (compare however p. 105). It is associated with frequent *Pseudomonoclimacis latilobus* and *Linograptus posthumus* but occurs only in a single sample. In Volhynia, the species in question is more numerous and perhaps more widely distributed vertically, but its FA seems again to coincide with the Mielnik record (TSEGELNJUK 1976). Until more is known, *M. (S.) hamulosus* may be regarded as one of the associated species of the *latilobus/balticus* assemblage Zone.

Monograptus (*Slovinograptus*) *balticus* TELLER, 1966
(Pl. 3: 1–12; Figs 14B, C_3, C_4, 15–18)

1966. *Monograptus balticus* sp. n. TELLER; TELLER, pp. 556–558, pl. 1: 6–11, text-fig. 4a, b.
1974. *"Monograptus" balticus* TELLER; PAŠKEVICIUS, p. 126, pl. 15: 1–5, pl. 19: 4–11, pl. 20: 1, 2.
1976. *Wolynograptus balticus* (TELLER); TSEGELNJUK, pp. 111–112, pl. 33: 5.
1979. *Monograptus balticus* TELLER; PAŠKEVICIUS, pp. 168–169, pl. 12: 4–8, pl. 28: 1–12.
1983. *"Monograptus" balticus* TELLER; TSEGELNJUK, pl. 145: 34.
1988. *Monograptus balticus* TELLER; KOREN', RINNENBERG and LYTOCHKIN, pl. 17: 1.

Redefined type horizon: The *latilobus–balticus* Zone of the late Ludfordian, overlying the low-diversity horizon which appeared as a result of the *kozlowskii* Event and underlying the *acer* Zone as defined herein (Fig. 3).

Material. — Twenty five well-preserved three-dimensional and semiflattened or flattened fragments of the rhabdosome, including proximal parts with siculae.

Description. — Sicula (Fig. 15A; Pl. 3: 1, 3, 6–7) elongated (1.6–1.8 mm long) and thin (attaining approximately 0.3 mm at the level of the initial bud), with only a slightly marked dorsal process 0.08–0.10 mm). Prosicular apex reaches to the middle of the metathecal segment of th_1.

Prosicula (psi) with 4–5 indistinct longitudinal threads visible on some specimens is 0.46–0.52 mm long and possesses an apertural ring (r_1). Metasicula (msi) has a length of 1.15–1.30 mm. Its single ring

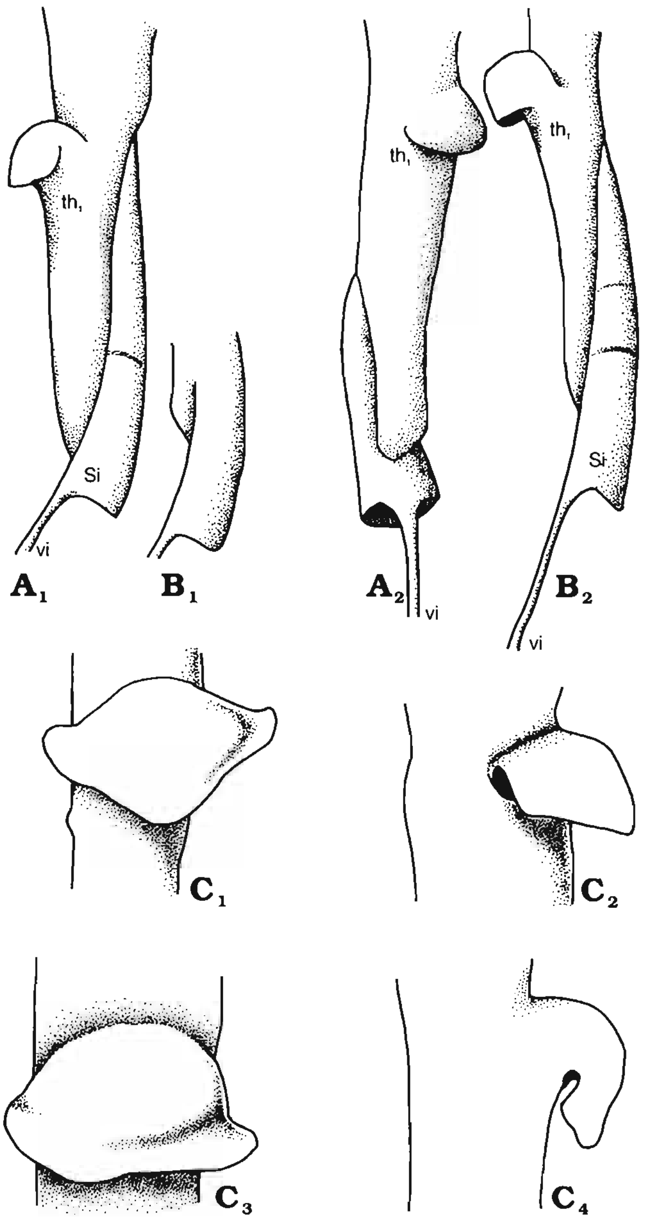

Fig. 14

Diagnostic features of *Monograptus (Slovinograptus) hamulosus* TSEGELNJUK (A_1, A_2, C_1,C_2) and *M. (S.) balticus* TELLER (B_1, B_2, C_3, C_4) as revealed in the structure of sicular part of the rhabdosome (A, B) and thecal characters (C). Mielnik, depth 822.90 m and 814.40 m respectively, both *latilobus/balticus* Zone.

(r_2) is situated approximately 0.5 mm from the sicular aperture. Metasicular aperture rather narrow (0.10–0.17 mm in diameter), with a dorsal process only slightly marked (0.08–0.10 mm long). Initial bud located at a distance of 0.35–0.40 mm from the metasicular aperture (Fig. 14B_1, B_2). Virgella rather thin but long.

Thecae generally long and tubular with a straight ventral wall, displaying a considerable overlap (Fig. 15B; Pl. 3: 9). First theca (th_1) approximately 1.60–1.70 mm long, attaining a width of up to 0.23 mm below the aperture.

The proximal part of the rhabdosome is distinctly attenuated, consisting of elongated and narrow thecae provided with apertural hoods adnate to the thecal tubes (Fig. 15B).

Proximal thecae display prothecae and metathecae of a fairly equal length (0.85–1.00 mm and 0.80–1.00 mm, respectively), the thecae being slender and varying in width from 0.12–0.20 mm in the prothecal part to 0.15–0.28 mm in the metathecal segment.

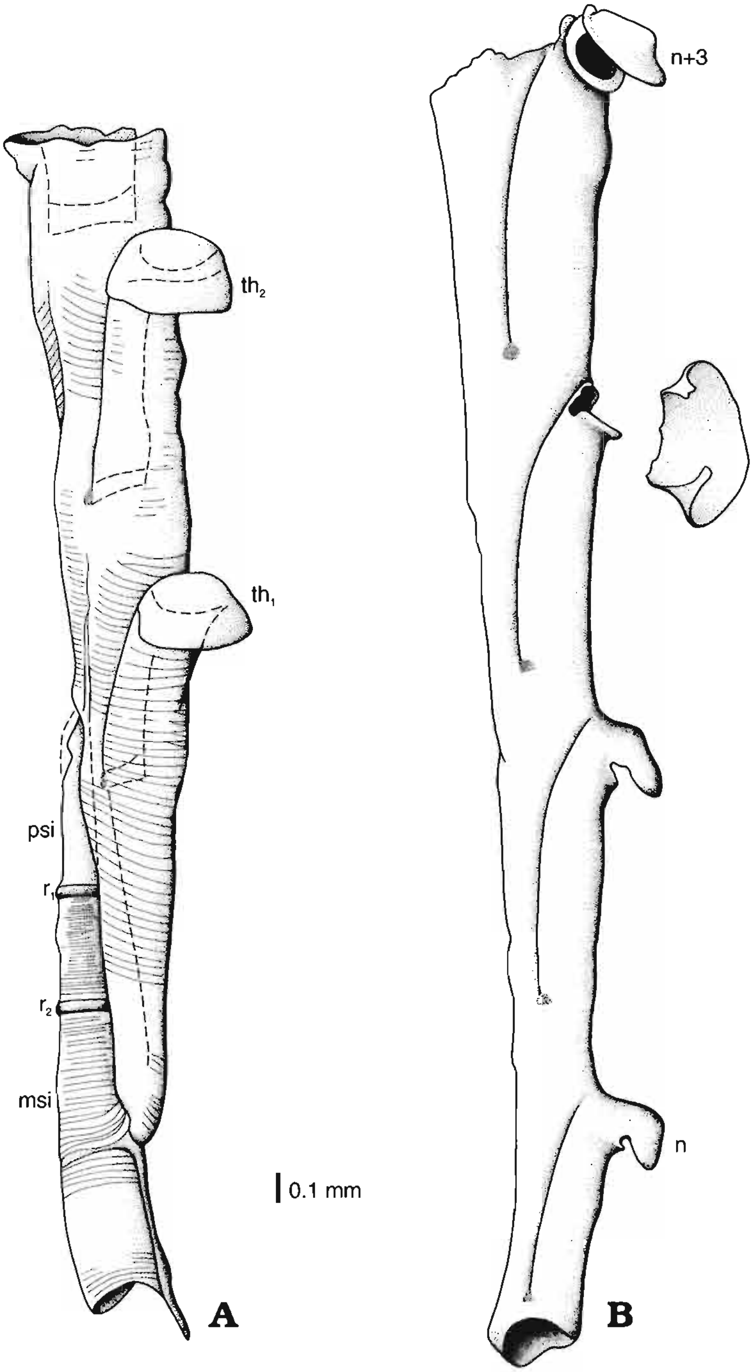

Fig. 15
Monograptus (Slovinograptus) balticus TELLER. **A**, **B**, proximal part of the rhabdosome seen laterally (in reverse aspect); **B** with broken sicular part and traces of healing. Mielnik, depth 820.70 m, the *latilobus/balticus* Zone, × 80.

Distal thecae exhibit a proportional increase of the metathecal segment attaining a length of 2.00–2.15 mm while the protheca is about 1.00 mm long. The respective width of these parts is 0.18 mm and 0.31–0.38 mm. All in all, the protheca/metatheca ratio changes from 1:1 in the proximal thecae to approx. 1:2 in the distal ones (Fig. 18).

Both proximal and distal thecae are provided with an apertural lobe (hood) resembling a bowler hat in appearance (Figs 16A, B, 17) as it has a rounded main part (l) and a narrow brim (Pl. 3: 8–12, Fig. 16A). The main part of the lobe adheres to the ventral wall without producing a neck (Fig. 16D, E) so characteristic of the *acer* group. The anterior margin of the apertural lobe smooth or slightly notched.

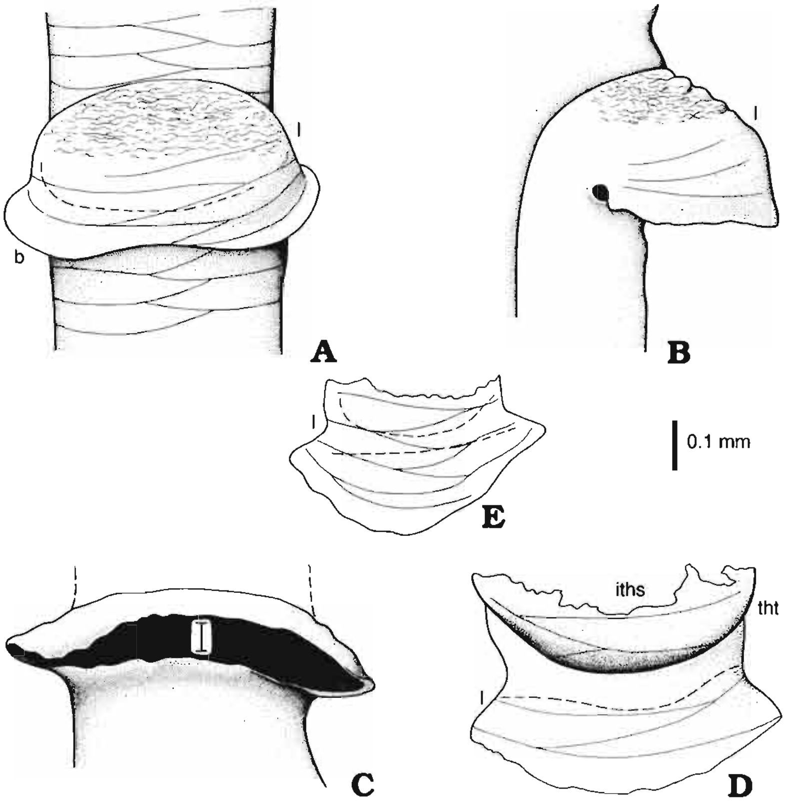

Fig. 16
Monograptus (Slovinograptus) balticus TELLER. Structure of the apertural apparatus: **A**, **B**, in a distal theca seen ventrally and laterally; **C**, apertural slit in a distal theca seen from beneath and showing the width of a single metathecal fusellus (for more information see the text); **D**, **E**, fusellar structure seen on bleached specimens in the top view and showing the stem (**D**) and the free part (**E**) of the lobe apertural margin. Mielnik, depth 820.70 m, the *latilobus/balticus* Zone.

Bleached specimens reveal that the lobe is composed of interdigitating fuselli which form a broad zig-zag suture (Figs 16E, 17A, B). Thecal aperture covers the aperture rather tightly, leaving, from the ventral side, only a slit-like opening that slightly exceeds the width of a single metathecal fusellus (Fig. 16C). Laterally, the aperture is incised, more so in the distal thecae. TELLER's interpretation of the apertural lobe as twisted (1966, Fig. 4 therein) may be explained by the imperfect state of preservation of his material.

Rhabdosome straight as indicated by three-dimensionally preserved sicular portions including thecae th$_{10}$–th$_{12}$. TELLER (1966: p. 557) characterized the proximal part of the rhabdosome as "dorsally

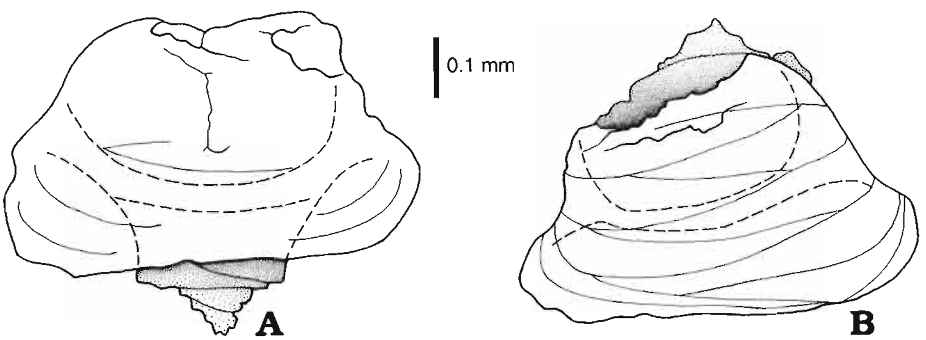

Fig. 17
Monograptus (Slovinograptus) balticus TELLER. Fusellar structure of apertural hoods as seen from ventral side on isolated and strongly bleached specimens (**A**, **B**). Mielnik, depth 820.70 m, the *latilobus/balticus* Zone.

curved from th_7, th_8", but he also mentioned the presence of "some rhabdosomes whose proximal part is not so strongly dorsally curved" (*ibidem:* p. 558). Some of Mielnik specimens even reveal a slight tendency towards the ventral curvature of the sicular part. It is difficult to judge whether and to what extent the variation observed may be accounted for by preservational factors or ascribed to primary intraspecific processes. The width of the rhabdosome is 0.23 mm immediately above th_1 and 0.56 mm above th_5.

N varies from 10–11 in the proximal and medio-distal parts of the rhabdosome to 9 in its distal portion.

Abnormal astogenetic development. — Specimen showing a change from monoserial arrangement of the thecae to biserial one and the return to the normal monograptid pattern is discussed elsewhere (p. 120, Fig. 10).

Taxonomic position. — *M.* (*S.*) *balticus* stands apart among other Ludfordian monograptids because of its slenderness and thecal characteristics. What makes it different from the most similar *M.* (*S.*) *hamulosus* is the high position of the initial bud in relation to the sicular aperture (0.35–0.40 mm instead of only 0.18–0.20 mm in *M.* (*S.*) *hamulosus*, see Fig. 14A, B), greater slenderness and the shape of the apertural lobes as seen in the ventral aspect: bowler-like rather than cordate (cf. Pl. 2: 5, 6 and Pl. 3: 10–12).

The relation between *M.* (*S.*) *balticus* and other slender monograptids of the Přidoli and the Early Devonian needs further study. In the Mielnik-1 borecore and in other EEP sections the species has no immediate followers, and its lineage appears to become extinct. Nevertheless, its relation to younger gracile monograptids was suggested by KOREN' (1983: p. 419). She suggested a graded series: *M. (S.) balticus* TELLER – *M. beatus* KOREN' – *M. microdon* Reinhard RICHTER as a possible lineage. This suggestion is tempting, because of a general morphological similarity of the forms mentioned, which, however, are separated by appreciable time gaps (1. late Ludfordian–middle Přidoli, 2. upper Přidoli–Lochkovian). The nature of these gaps should be somehow elucidated before any conclusion is reached.

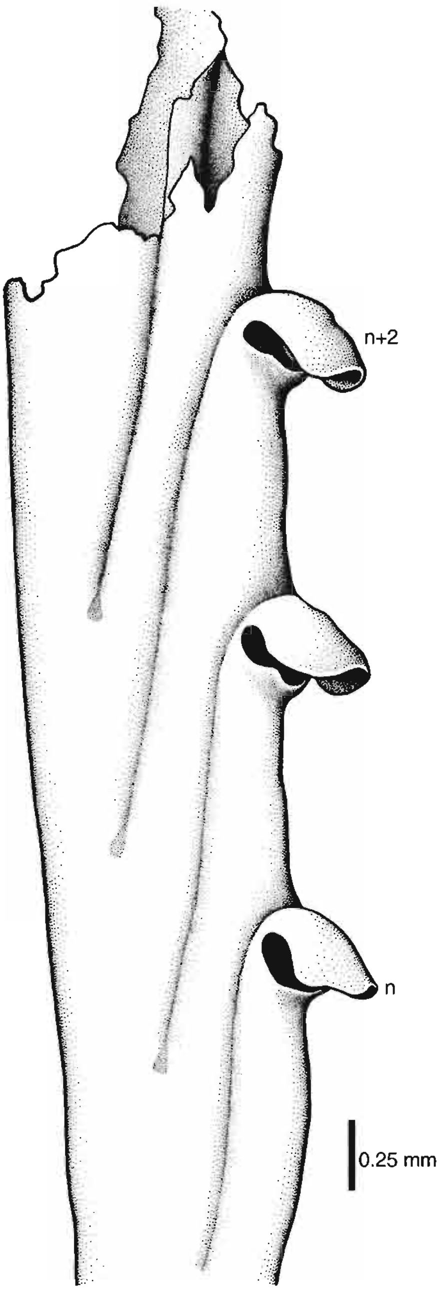

Fig. 18
Monograptus (Slovinograptus) balticus TELLER. Distal fragments of the rhabdosome seen laterally. Mielnik, depth 820.70 m, the *latilobus/balticus* Zone.

Stratigraphic distribution. — *M.* (*S.*) *balticus* was described by TELLER (1966) from the beds with a poorly characterized assemblage (*Linograptus posthumus*, *Pristiograptus dubius*) in the Łeba-3 borecore, some 40 m below the FA of his *M.* ex gr. *formosus*. It was tentatively referred by him (1966: p. 558) to the Upper Ludlow as a potential index fossil "for that part of the section which is characterized in Poland by the occurrence of forms from the *M. formosus* group". These conclusions remain true in spite of the fact that in the light of the present knowledge TELLER's "*M.* ex gr. *formosus*" represents a form that should be assigned to *M.* (*U.*) *protospineus*. This roughly corresponds to the range of *balticus* in the Mielnik borehole where it is confined to the *latilobus/balticus* Zone of the late Ludfordian (FA at a depth of 819.85 m and LA at 814.40 m, see Fig. 3 for range). Its occurrence in the middle of the Pagegiai Series of Lithuania (PAŠKEVIČIUS 1974) and in the Meton horizon of Volhynia (TSEGELNJUK 1976) corresponds to the range observed in the Mielnik core section.

Occurrence. — *M.* (*S.*) *balticus* has been described from N and E Poland, Lithuania (PAŠKEVIČIUS 1974), Volhynia (TSEGELNJUK 1976), and also recently from the Alai Range, Tien Shan, Kyrgystan (KOREN' unpublished).

Subgenus *Monograptus (Formosograptus)* BOUČEK, MIHAJLOVIĆ *et* VESELINOVIĆ, 1976
Monograptus (*Formosograptus*) *formosus* BOUČEK, 1931
(Pls 4–6, Pl. 7: 1–4, Pl. 8: 7, 8; Figs 19–24)

1931. *Monograptus formosus* n. sp. and *Monograptus purkynei* n. sp. BOUČEK; BOUČEK, p. 8, p. 18, text-fig. 9a–d.
1940. *Monograptus (?Spirograptus) convexus* n. sp.; PŘIBYL, p. 73, pl. 1: 4.
1946. *Spirograptus ?formosus* (BOUČEK); PŘIBYL, p. 36, pl. 9: 4.
1962. *Monograptus formosus* BOUČEK; WILLEFERT, p. 33, pl. 2: 18, text-fig. 8.
1962. representative of *formosus* Group, TOMCZYK; TOMCZYK, pl. 3: 1–2, pl. 4.
1967. *Monograptus formosus* BOUČEK; JAEGER, p. 286, pl. 14: b–c.
1969. *Monograptus paraformosus* n. sp. JACKSON and LENZ; JACKSON and LENZ, p. 27, pl. 4: 1, 2, 4.
1973. *Monograptus formosus* BOUČEK; KOREN', p. 151, pl. 1: 13–16.
1974. *"Monograptus" formosus* BOUČEK; PAŠKEVIČIUS, p. 127, pl. 14: 11, 12, pl. 20: 3, 4.
1976. *Formosograptus formosus* (BOUČEK); BOUČEK, MIHAJLOVIĆ and VESELINOVIĆ, p. 85, text-fig. 1a–f, pl. 1: 1–3, pl. 3: 5.
1976. *Tamplograptus convexus* (PŘIBYL), *Tamplograptus formosus* (BOUČEK) and *Tamplograptus paraformosus* (JACKSON *et* LENZ); TSEGELNJUK, p. 114, pl. 35: 1–9.
1979. *Monograptus formosus* BOUČEK; PAŠKEVICIUS, p. 173, pl. 15: 3, 4, pl. 31: 1–3.
1986. *Monograptus formosus* BOUČEK; JAEGER, p. 316, pl. 3: 4, 5, pl. 4: 13, text-fig. 28a–e.
1986. *Monograptus formosus* BOUČEK; KOREN', p. 97, pl. 20: 5–7, pl. 21: 7, text-fig. 16.
1986 a. *Monograptus formosus* BOUČEK; KOREN', p. 154, text-fig. 112H.

Type horizon: Type stratum, namely the *N. ultimus* Zone, is a late occurrence for the species with the Biozone ranging from the late Ludfordian *latilobus/balticus* Zone to the above-mentioned early Přidoli zone.

Material. — A few hundred fragments representing all growth stages of the sicula and displaying a complete astogeny; mostly flattened or semiflattened.

Description. — Sicula straight, 1.42–1.60 mm long, with the prosicular apex distinctly below the level of the th_1 aperture (Fig. 19A, B).

Prosicula 0.51–0.57 mm long, with longitudinal threads (4–6) and traces of a helical line visible on some bleached specimens (Fig. 20A, B_1, C). The aperture of the young prosicula without an apertural ring (Fig. $20A_1$) which appears at later growth stages (Fig. $20A_2$). Metasicula (msi) 0.85–1.06 mm long with an aperture 0.21–0.29 mm in diameter, usually provided with a distinct shovel-like dorsal process (dp) some 0.15–0.23 mm long. (Fig. $20D_2$, D_3). Metasicular dorsal process is subject to substantial variation, but usually is strongly pronounced (Pl. 5: 1–5, dp).

The development of the metasicula follows a standard monograptid pattern including the formation of a primary notch (pn) (*sinus* and *lacuna* stages) and initial bud (ib) situated on adult siculae at a distance of 0.35–0.48 mm from the sicular aperture. Metasicula is provided with a ring (r_2) approximately at 1/3 of its length and 0.30 mm from the apertural ring of the prosicula (r_1). The presence of two rings (r_1, r_2) on the sicula is an invariable feature of all siculae examined (Pl. 4, Fig. $20B_2$, D_1, C).

Thecae, both proximal and distal, vary in shape and proportions. Proximal thecae (th_1–th_3) subtriangular, with a distinctly isolated apertural part (Fig. 19B, Pl. 5) involving the entire metatheca. Distal thecae feature a much lesser degree of isolation with the metatheca almost fully adnate to the rhabdosome (Fig. 21, Pl. 6: 6, 7, Pl. 7: 1).

Most proximal thecae have long (1.20–1.10 mm) and narrow prothecae (0.18–0.20 mm wide at the base). Their metathecae are distinctly shorter (0.55–0.70 mm long), and in th_1–th_3 they are completely isolated. The critical position is occupied by th_4 in which the prothecal and metathecal segments are of equal length (0.90 mm), while almost one third of the metatheca (0.30 mm) is adnate and the remaining two thirds are free (isolated, 0.60 mm).

Starting from this turning point, the metathecal segment becomes longer, attaining a length of 1.34–1.46 mm in the distal part of the rhabdosome, whereas the prothecal one remains stabilized within the range of some 0.77–0.90 mm. At the same time almost two thirds (60 per cent) of the metathecae are adnate and a little more than one third (40 per cent) is isolated. Thus, most proximal and most distal thecae represent contrasting morphological types linked by a smooth intergradation in the course of the astogeny. One of the characters revealing this directional astogenetic change is the width of the rhabdosome which steadily increases, varying from 0.18–0.30 mm at the base of the prothecae in th_1–th_4 of the slender proximal part to 0.77–0.82 mm in truly distal thecae.

Rhabdosome is biform as regards the isolation, overlap and proportions of thecal segments. This aspect of biformity is, however, screened by the relative uniformity of the apertural apparatus which shows only

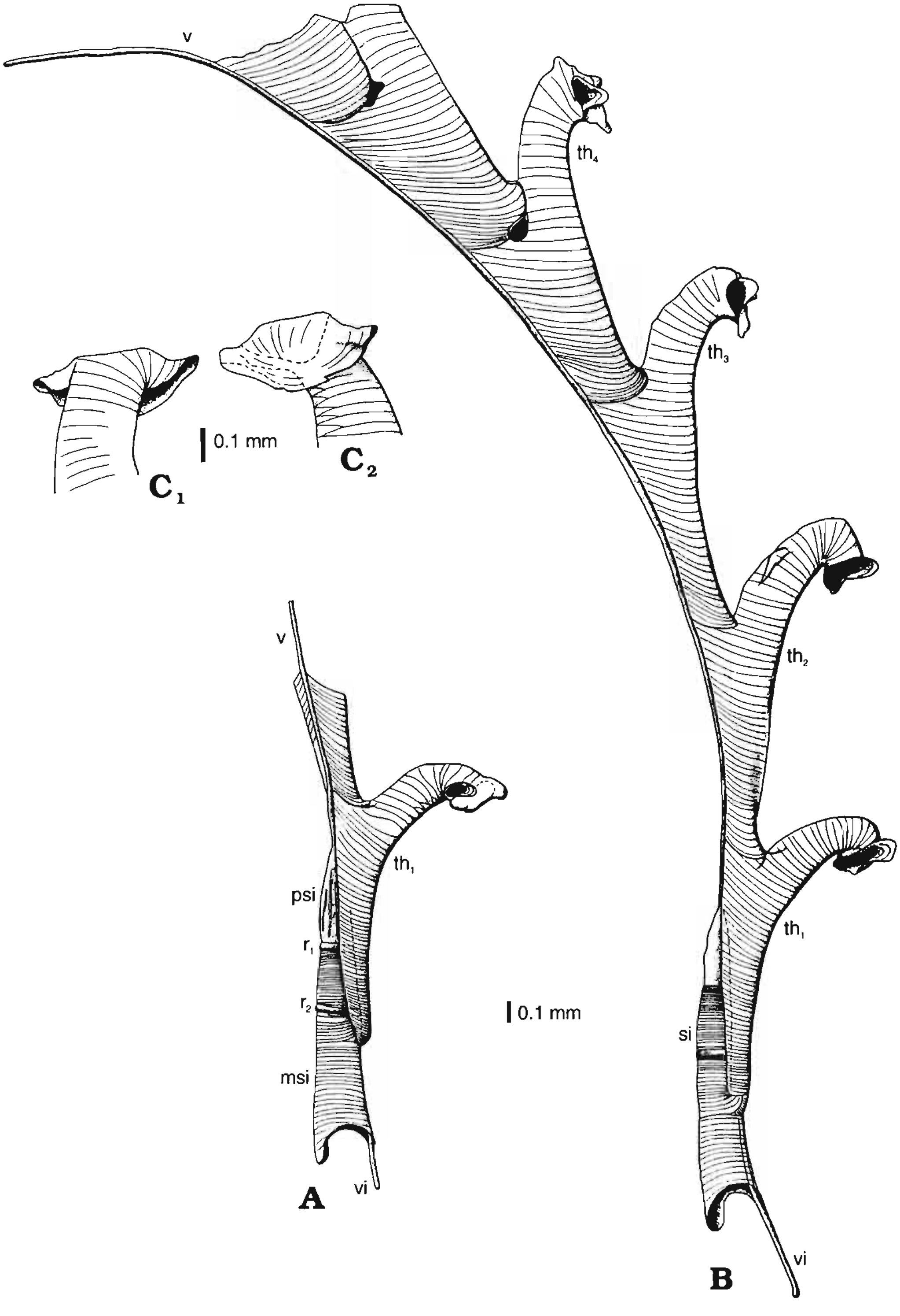

Fig. 19

Monograptus (Formosograptus) formosus (BOUČEK). Sicula with th$_1$ (**A**) and proximal portion of the rhabdosome (**B**); **C**, details of the aperture in th$_1$ seen dorsally (**C**$_1$) and ventrally (**C**$_2$). Mielnik, depth 770.45–769.45 m, the *acer–spineus* Zone.

a minor astogenetic variation. Apertures of thecae are covered by a single apertural lobe (l) which extends into two, left and right, lateral processes (Fig. 22, llp, rlp). These processes are semitubular, with only a narrow slit visible from the dorsal side (Fig. 22B), and end with a turned-out, hoof-like area which I propose to term *auriculum* (a). This area is usually flat, and the degree of its extroversion flattening may be at least partly preservational due to lateral compression (Fig. 22A–B, D a; Pl. 6: 1c, Pl. 7: 2a). Another

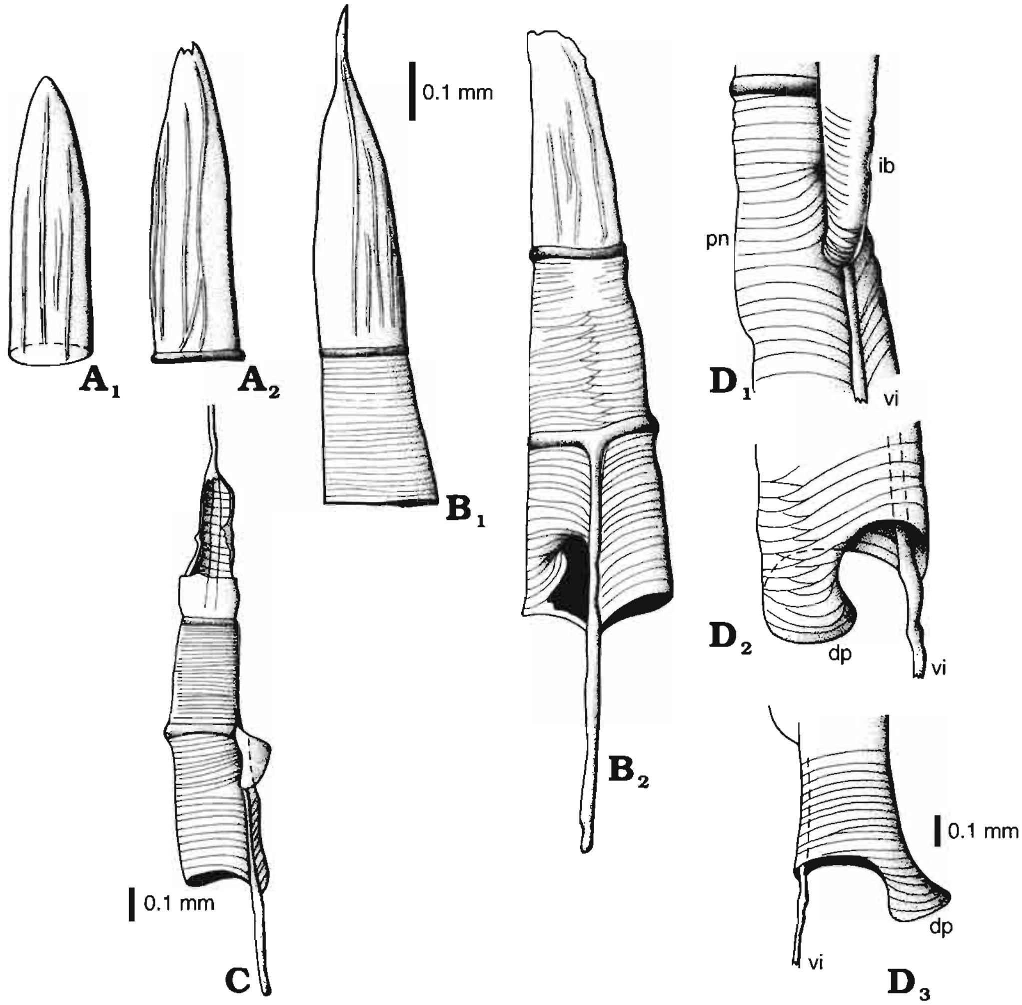

Fig. 20

Monograptus (Formosograptus) formosus (BOUČEK). Development of the sicula and formation of the initial bud. **A**$_1$, **A**$_2$, an early and advanced prosicula; **B**, young and and advanced metasicula; **C**, young sicula with the initial bud; **D**$_1$–**D**$_3$, structural details of a fully grown sicula showing the primary notch and the initial bud area (**D**$_1$) as well as the fusellar structure of the aperture (**D**$_2$, **D**$_3$). Mielnik, depth 770.45–768.00 m, the *acer–spineus* Zone.

obviously preservational character is the presence of a deep infolding (pf) seen on many specimens (Fig. 22A, B, D, E; Pl. 6: 1) as a result of lateral compression. Some naturally preserved specimens (Fig. 22F, G) and needle preparations on bleached fragments reveal the presence of an apertural lip (val), similar to that found in "operculate" Gorstian and early Ludfordian forms (URBANEK 1966, 1970).

Strongly bleached specimens show the fusellar structure of the lobe proper, made of two series of fuselli with their oblique sutures forming a zig-zag line in the middle (Fig. 22D). Semitubular lateral processes are made of a single series of fuselli which, narrowing into strips, converge on the dorsal side to form the ventral apertural lip (Fig. 22B, G). On the ventral side, they end freely, composing the anterior margin of the lobe.

Rhabdosome is strongly dorsally curved, the curvature starting approximately at the level of the th$_1$ aperture, i.e. slightly above the prosicular apex. The angle of deviation, D, measured as shown in Fig. 23A in strongly curved specimens, is approximately 25°. Smaller values were also observed. Dorsal curvature as traced along the dorsal line of the rhabdosome composed of a sicula and 9 thecae is shown in Fig. 23B. The dorsal curvature of the rhabdosome, along with the triangulate shape of the thecae, the slenderness of the proximal part of the rhabdosome, and the complexity of the thecal apertural apparatus, are among the species-specific features of *M. (F.). formosus*. The now obsolete meaning of the *"formous* Group" was based on the overall appearence of the rhabdosome of certain forms, defined by the dorsal curvature and hooded thecae (p. 94).

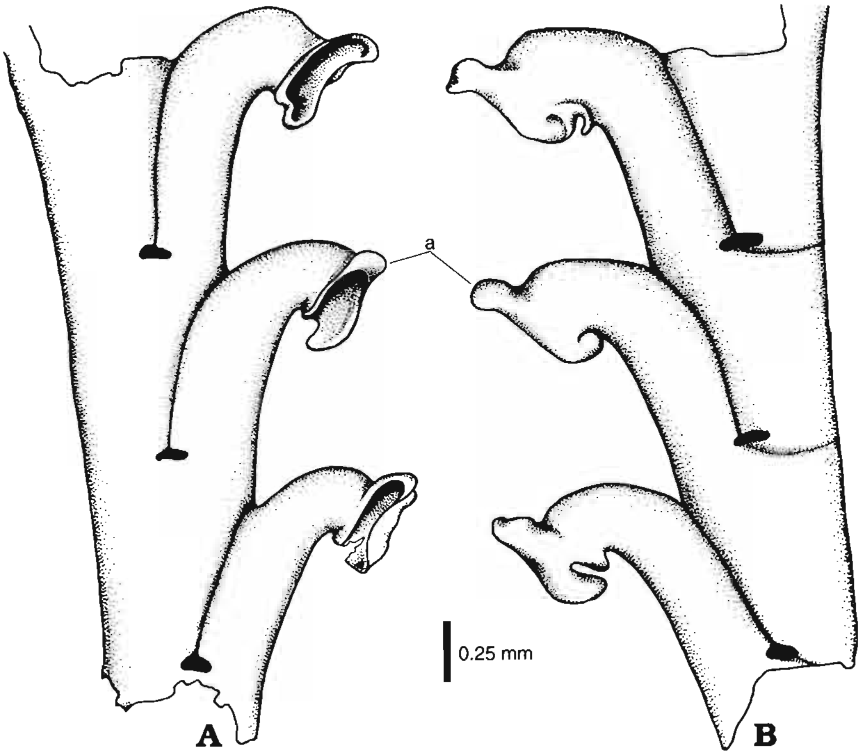

Fig. 21
Monograptus (Formosograptus) formosus (BOUČEK). Distal fragment of the rhabdsosome, reverse (**A**) and obverse (**B**) aspects. Mielnik, depth 766.45 m, the *acer–spineus* interval.

The growth of the proximal part of the rhabdosome may be traced on a series of specimens (Fig. 24A–E). The growth of the metasicula begins before th_1 is completed, while the first fuselli of th_2 are laid down before the formation of the aperture in th_1 is initiated (Fig. 24C, D).

The number of thecae in 10 mm, N, in the sicular part is 9+sicula, in the distal part, 9–11.5, and in the medial part it is as high as 12.

Taxonomic position. — Against the background of the late Ludfordian and early Přidoli graptoloid fauna, *M. (F.) formosus* occupies a quite separate position. Unique in many aspects, it exhibits a remarkable similarity to *Oktavites spiralis* (GEINITZ) from the late Llandovery (Telychian). This resemblance is most conspicuously expressed in thecal characters, less so in the overall shape of the rhabdosome [see Pl. 8: 1–6 and Pl. 8: 8, 7 for comparing the thecae of *O.* aff. *spiralis* and *M. (F.) formosus*]. The rhabdosome of *O.* aff. *spiralis* is, however, strongly coiled, while in *M. (F.) formosus* it is only dorsally curved. Nevertheless the degree of similarity in thecal characters is exceptional and difficuit to interprete. At the same time they differ from "standard" Late Silurian hooded monograptid represented by *M. (U.) uncinatus* (Pl. 8: 9, 10). Heterochronous parallelism seems a more plausible explanation than the Lazarus effect (see URBANEK 1993: for an extended discussion). However, none of the recently known Late Silurian monograptids can be regarded as ancestral to our species which, at the present stage of knowledge, ought to be considered truly cryptogenic.

During its relatively long stratigraphic occurrence over an extensive area of geographic distribution *M.* (*F.*) *formosus* exhibits a remarkable cohesion. *Monograptus paraformosus* JACKSON *et* LENZ, 1969, the only candidate to the role of a closely allied vicarious species (Yukon Territory, Canada), is now considered conspecific with true *formosus* from Barrandian (KOREN' 1986: p. 97; JAEGER 1986: p. 316d). In spite of its obvious biological success, *M.* (*F.*) *formosus* probably left no descendant. TOMCZYK's previous reports (1962, 1962a) on a diversified and abundant "*formosus*" group occurring in the upper part of his Siedlce beds (a regional stage or formation) were partly exaggerated. The present data, confirming the abundance of *M.* (*F.*) *formosus* in these beds, reveal some **acme** horizons, but no other affined species have been found so far, allowing one to think that it was not a speciose taxon (see p. 106 herein).

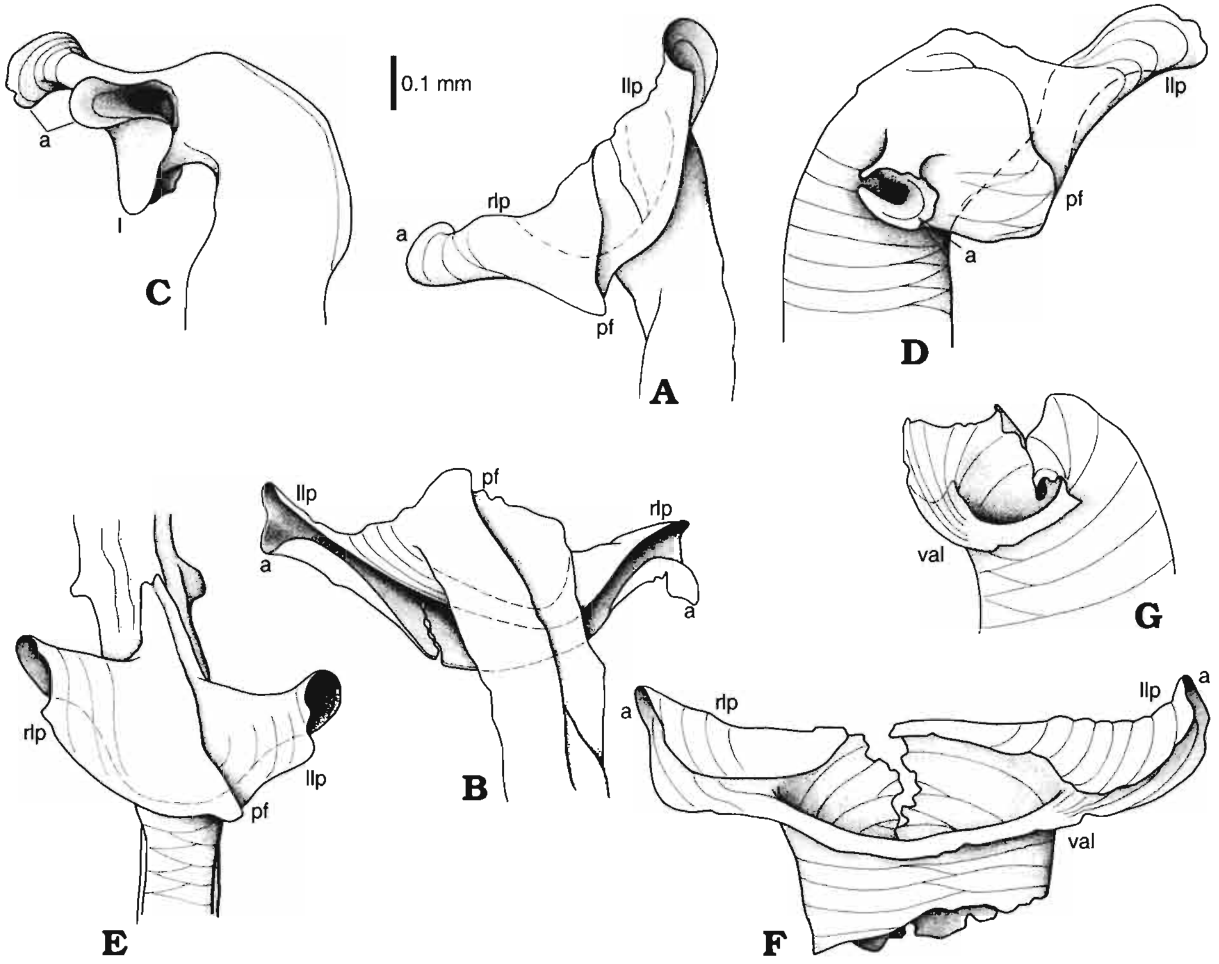

Fig. 22
Monograptus (Formosograptus) formosus (BOUČEK). Structural details of the apertural apparatus in distal and medial thecae. **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, seen ventro-laterally; **E**, ventral view of a medial theca; **F**, **G**, internal structure of the aperture seen ventro-proximally. Mielnik, depth 766.75 m, the *acer–spineus* Zone.

Stratigraphic distribution. — Thanks to its morphological characteristics, *M.* (*F.*) *formosus* can be compared with such distinct and highly representative taxa as *Nemagraptus gracilis, Spirograptus turriculatus*, or *Linograptus posthumus*. The data available permit the *formosus* holozone to be extended from the *latilobus/balticus* Zone to the *ultimus* Zone inclusive, so that it ranges across the Ludlow/Přidoli boundary. The vertical distribution as observed in particular geographic areas as a rule represents only a fraction of this interval (a merozone). Thus, in the Mielnik borehole it extends through the *latilobus/balticus* Zone across the *post-spineus* low diversity interzone and almost to the bottom of the *parultimus* Zone. In Barrandian, it occurs in the *fragmentalis* Zone of the Kopanina Formation and penetrates the Přidoli reaching the *ultimus* Zone (JAEGER 1986: p. 318). In the Canadian Arctic Archipelago, the vertical distribution embraces the *parultimus* Zone, and in the Northern Yukon, its position is "more or less precisely" the same (JACKSON *et al.* 1978; LENZ 1990). In the sections of the Alai Range (South Tien Shan) it appears above the *kozlowskii* Zone and reaches the *parultimus–ultimus* Zone (KOREN' and LYTOCHKIN 1992).

From the above it follows that the mere presence of *M. (F.) formosus* can only serve as an arbitrary basis for the assignment of the given stratum either to the Ludfordian or to the Přidoli. To achieve a more precise discrimination between the two stages one should use true index species, namely the *acer–spineus* group (confined to the late Ludfordian) and the *ultimus* group (the early Přidoli). In his early reports on the stratigraphy of the subsurface Silurian in the Polish Lowland, TOMCZYK (1962), emphasized the abundance of the "*formosus*" group of monograptids and their significance for what he calls the Upper

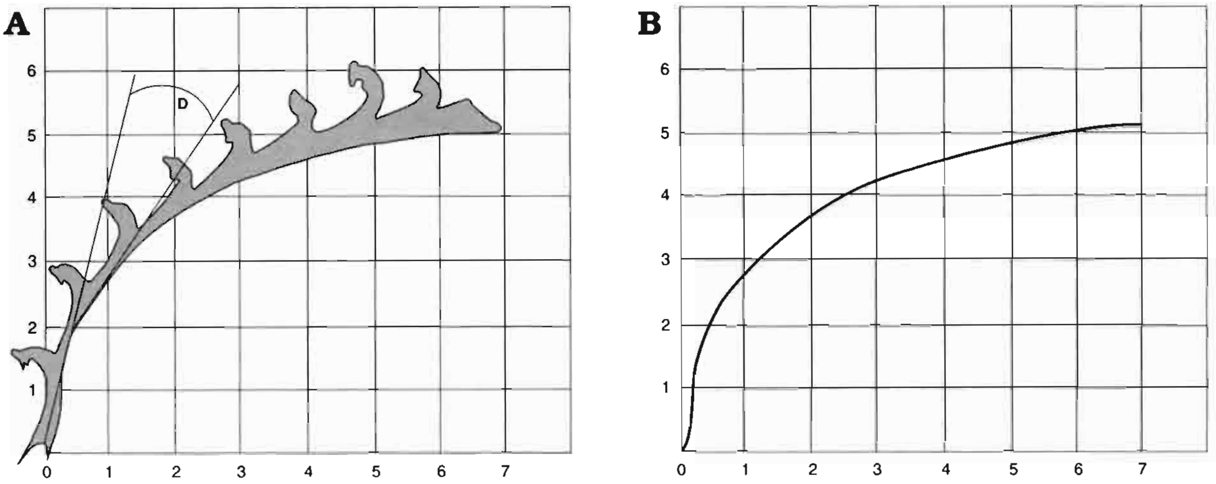

Fig. 23
Proximal part of *Monograptus (Formosograptus) formosus* (BOUČEK) rhabdosome seen on orthogonal grid co-measurable to the scale of magnification of the specimen: **A**, rhabdosome with the dorsal process of sicula placed at 0; **B**, its dorsal line. Mielnik, depth 767.80 m, *formosus* epibole within the *protospineus–spineus* interval.

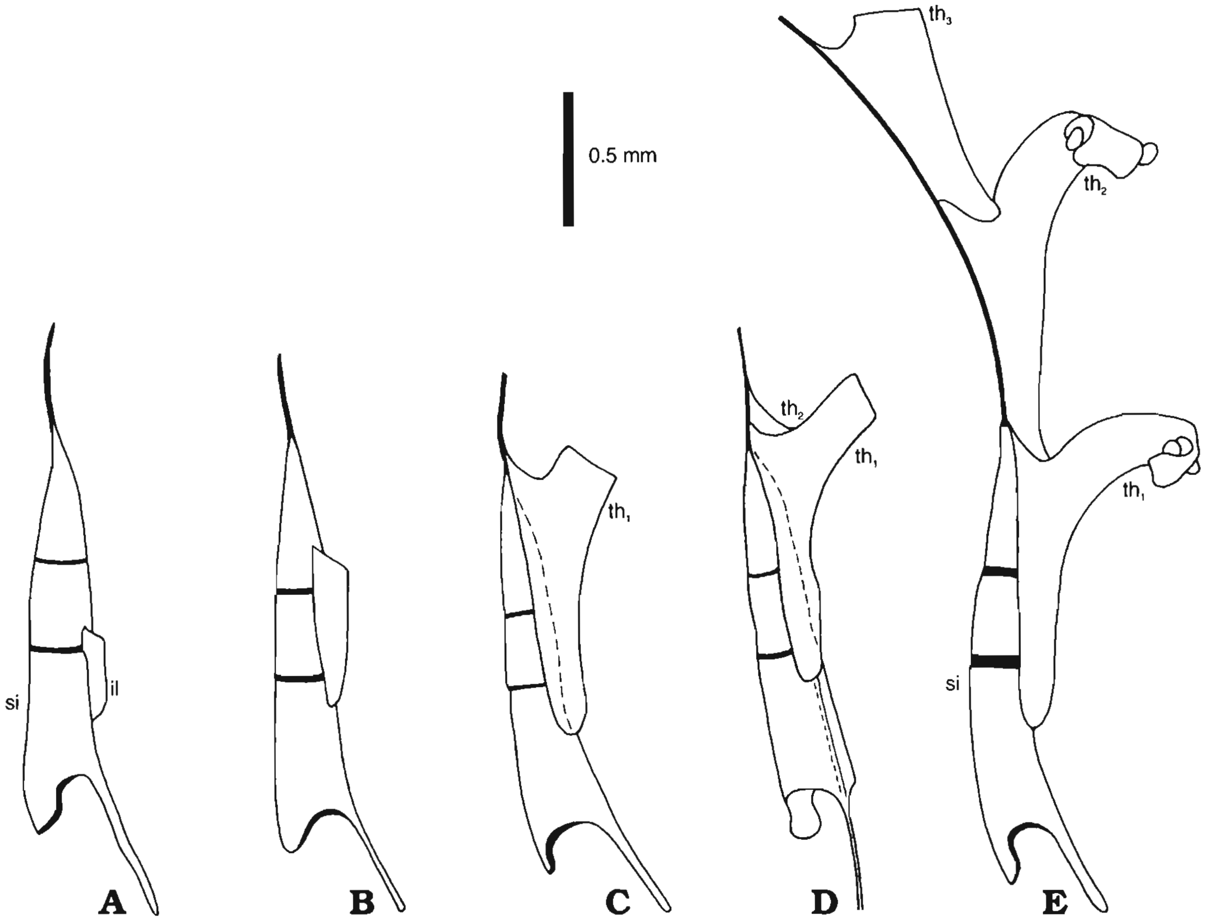

Fig. 24
Monograptus (Formosograptus) formosus (BOUČEK). **A–E**, successive stages of astogeny.
Mielnik, depth 770.45, the *acer–spineus* Zone.

Siedlce Beds (a formation or a regional stage). Although the diversity of the "group" was illusory (see p. 106 herein), there is no doubt that *M. (F.) formosus* is characteristic of those beds, which are more or less precisely equivalent to the late Ludfordian.

Occurrence. — *M. (F.) formosus* is a truly cosmopolitan species, described from all the continents except for South America and the Antarctic (JAEGER 1986: p. 318). In addition to the occurrences quoted above (p. 138 herein), one should mention its findings in NW Africa (Sahara), within the so-called middle Ludlow (WILLEFERT 1962: p. 33) and SE Australia, in the Rosebank Shale of the Yass syncline (New South Wales, JAEGER 1967). *M.* cf. *formosus* was also described from a younger member (Elmside Formation) of the same syncline (JENKINS 1982).

Subgenus *Monograptus (Uncinatograptus)* TSEGELNJUK, 1976

Monograptus (Uncinatograptus) acer (TSEGELNJUK, 1976), *sensu* URBANEK 1995

(Pls 9, 10, Figs 25–32)

1976. *Heisograptus acer* n. sp. TSEGELNJUK; TSEGELNJUK, p. 108, pl. 30: 1, 2 [= *Monograptus (U.) acer acer* (TSEGELNJUK)].

1976. *Acanthograptus aculeatus* n. sp. TSEGELNJUK; TSEGELNJUK, p. 113, pl. 34: 10 [= *Monograptus (U.) acer aculeatus* (TSEGELNJUK)].

1983. *Bugograptus aculeatus* (TSEGELNJUK); TSEGELNJUK, p. 141, fig. 35 [= *Monograptus (U.) acer aculeatus* (TSEGELNJUK)].

Redefined type horizon: The *acer* Zone as defined by URBANEK (1995), and subdivided into the *acer acer* and *acer aculeatus* Subzones.

Material. — About 40 well-preserved fragments, including young stages of astogeny and distal parts of rhabdosome, mostly semiflattened or 3-dimensional.

The concept of *M. (U.) acer–aculeatus* as chronospecies: TSEGELNJUK (1976) placed these two species into different genera (*Heisograptus* and his *Acanthograptus*, respectively), but the analysis of the Mielnik core material has revealed that *M. (U.) ac*er (TSEGELNJUK, 1976) and *M.* (*U.*) *aculeatus* (TSEGELNJUK, 1976) are very closely allied species, or varieties, which have most of the characters in common except for the degree of the dorsal curvature in the proximal part of the rhabdosome (URBANEK 1995). The *acer* morphotype is almost straight, and the *aculeatus* is distinctly curved. In my opinion, the amount of variation displayed in this case does not exceed the intraspecific range obseved in many species of monograptids with a dorsal curvature. What is more, the advance of the morphotype may vary in *M.* (*U.*) *acer* s.l. within a single sample, as it does in the specimen obtained from the lower part of its vertical range of distribution in the Mielnik borehole. This allows the two forms to be considered conspecific, the *acer* morphotype representing one extreme and the *aculeatus* form being at the other end of a continuous spectrum of variation (morphocline). However, the degree of curvature increases remarkably upwards through the sequence, so that in the higher zonal populations distinctly curved forms were predominant. This simple character may easily be identified even in poorly preserved specimens and therefore used for biostratigraphic purposes. On these grounds *acer* and *aculeatus* are distinguished in the present paper as closely allied chronospecies linked by a wide range of intermediate forms (Fig. 25A–D).

In the core of the Mielnik sequence, URBANEK (1994) proposed drawing an arbitrary demarcation line between the two subspecies at a depth of 780.00 m. In view of the recognized, very gradual character of the evolutionary changes involving the shift of the mean, any such limit must of necessity be arbitrary. The same holds for the use of subspecific names. The above concept differs from the original version presented by TSEGELNJUK (1976) who considered the almost straight and curved morphotypes as two distinct but contemporaneous species, paying no attention to the progressive character of the curvature in time or to the presence of intermediate types. Moreover, according to TSEGELNJUK's recent opinion (personal communication), his "*Acanthograptus*" *aculeatus* lacks apertural spines. The structure which he previously took for spines placed on the apertural lobes proved to be intersections of the lobes proper with the bedding plane. Therefore its assignement to a separate genus *Bugograptus*, as suggested by TSEGELNJUK (1983), seems unjustified (see also URBANEK 1995).

Description. — Sicula (Figs 26, 27; Pl. 9: 1, 2, 4, 5) straight or rarely slightly ventrally curved, 1.43–1.66 mm long, with the apex of the prosicula situated somewhat below or at the level of the apertural lobe of th$_1$. Prosicula (psi) with a length of 0.46–0.51 mm shows a distinct apertural ring (r$_1$) 0.15–0.18 mm in diameter. Metasicula (msi), 0.95–1.15 mm long, is provided with a single ring (r$_2$), a normally strong shovel-like dorsal apertural process (dp), and a strong virgella (Pl. 9: 7). In some cases this process is less pronounced being only 0.12–0.15 mm long and the virgella may be strongly deviated (Fig. 28). The diameter of the metasicular aperture is 0.28–0.32 mm, but in some specimens a tendency towards flaring

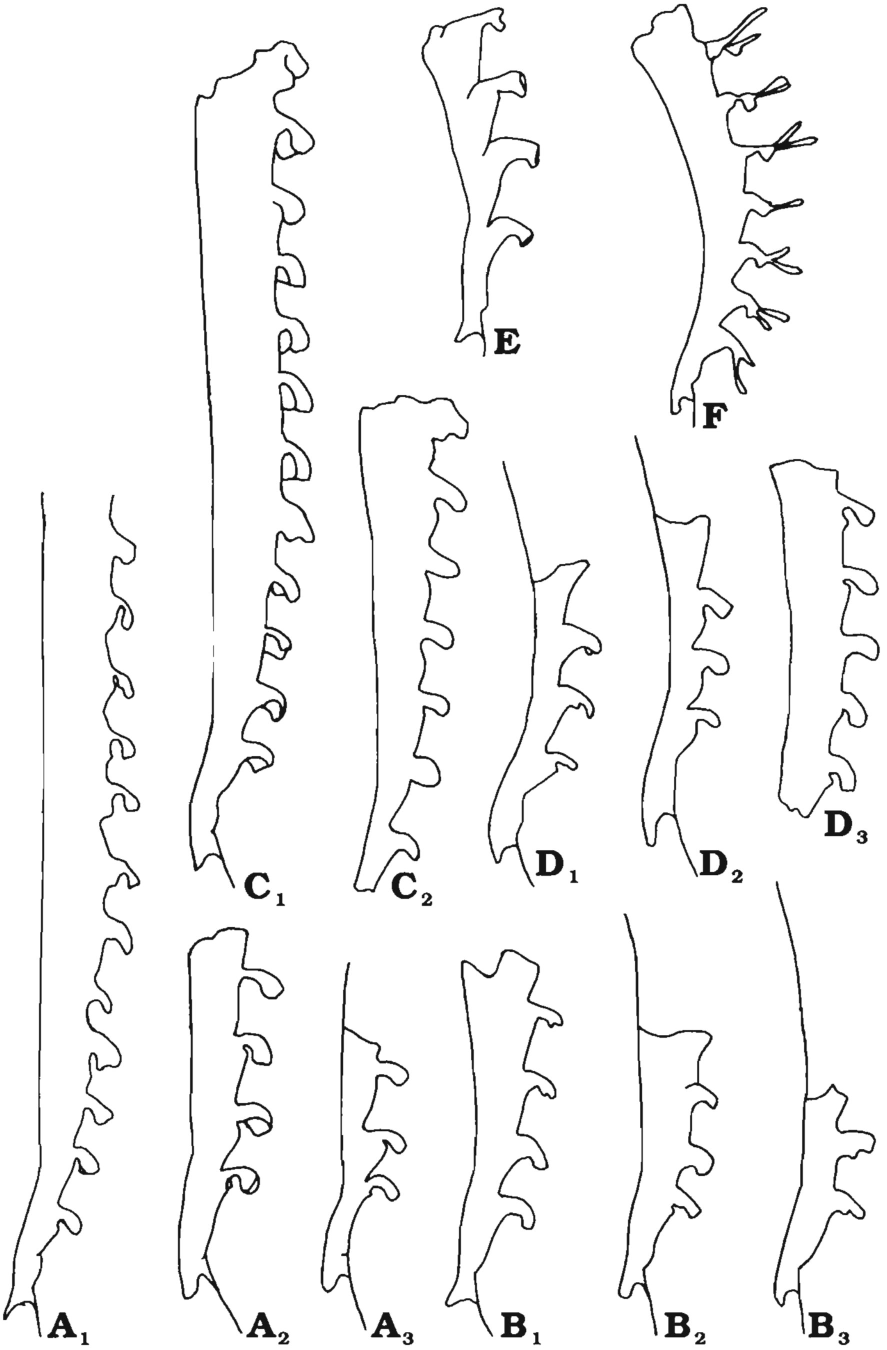

Fig. 25

Change in the degree of the dorsal curvature of the rhabdosome within the *acer–spineus* lineage: **A–C**, *M. (U.) acer acer* (TSEGELNJUK), representative specimens from the depth of 792.70 m, 790.90 m and 790.55 m respectively; **D**, *M. (U.) acer aculeatus* (TSEGELNJUK), specimens from the depth of 774.50 m; **E**, *M. (U.) protospineus* URBANEK, specimen from depth of 773.50 m; **F**, *M. (U.) spineus* (TSEGELNJUK) from the depth of 760.15 m. All specimens from Mielnik-1 wellcore. Note the gradual increase of the dorsal curvature in the proximal part of the rhabdosome within the lineage.

is observed, especially clearly so in the sample from a depth of 770.90 m. Primary bud is situated at a considerable distance (0.30–0.40 mm) from the metasicular aperture.

Thecae in the proximal part of the rhabdosome are subtriangular, with the ventral wall either straight or slightly incised at the base. Th_1 attains a length of 1.00–1.20 mm and its metathecal portion is only 0.21–0.28 mm long. Subsequent proximal thecae are rapidly gaining width (see below). Proximal thecae (th_2–th_3) display prothecae 0.69–0.80 mm long and metathecae 0.30–49 mm long, the total length being

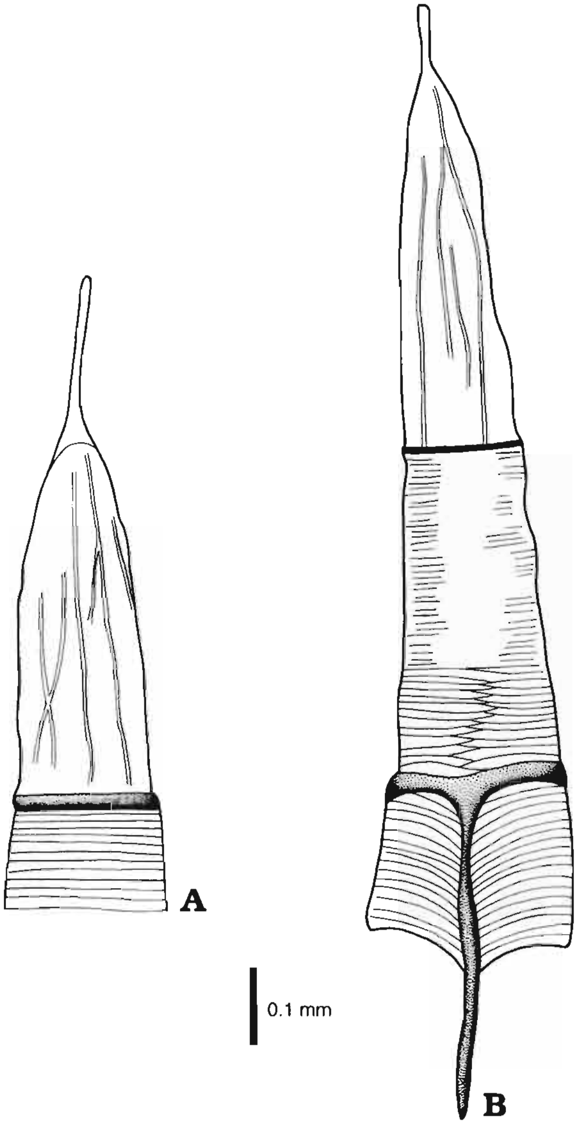

Fig. 26
Monograptus (Uncinatograptus) acer TSEGELNJUK. Early growth stages of sicula (**A**, **B**). Note that virgella starts at the level of the second metasicular ring (**B**) Mielnik-1, depth 792.55 m, the *acer* Zone.

1.00–1.20 mm. The distal ones have prothecal and metathecal segments with a length of 0.85–0.92 mm and 0.82–1.00 mm, respectively. The total length of the thecae in the distal fragments is approximately 1.60 mm. Hence in the astogeny we see a usual change of proportions between the thecal segments due to an increase in the metathaecal share (Figs 29, 30; Pl. 9: 6, 9).

Thecae are provided with characteristic strongly developed apertural lobes, uniform in structure throughout the rhabdosome, but differing in size (Fig. 31; Pl. 10: 6–9). Morphologically, they are composed of a "neck" (n), part of the lobe covering the aperture proper when seen from above (dorso-distally), and the lobe *s.s.* (l), stretching foreward and provided with two more or less pronounced corners, the incipient antero-lateral processes (alp; Fig. 31). The presence of a "neck" is a distinctive speciec-specific feature of the apertural apparatus in *M. (U.) acer*. This distinguishes it from such Ludfordian monograptids as *M. (S.) balticus* or *M. (S.) hamulosus* where the lobe proper is adnate to the thecal tube (see p. 131). The other distinctive feature is its fairly flat shape: the aperture is covered with a kind of a flat roof, without any convexity, characteristic of most hooded monograptids [e.g. *M. (U.) uncinatus, M. (S.) balticus*]. The apertural lobes of *M. (U.) acer* are also fairly large, the length (transv.) of the lobe in th_1 being 0.46–0.49 mm, in th_2 0.49–0.54 mm and in th_3 0.66 mm. In the lobe of a 0.60 mm long median theca, 0.28 mm is occupied by the "neck" and 0.32 mm produces its free part. The length of the apertural lobes in most proximal thecae exceeds the width (transv.) of the rhabdosome at the corresponding level, which accounts for a characteristic appearance of the rhabdosome.

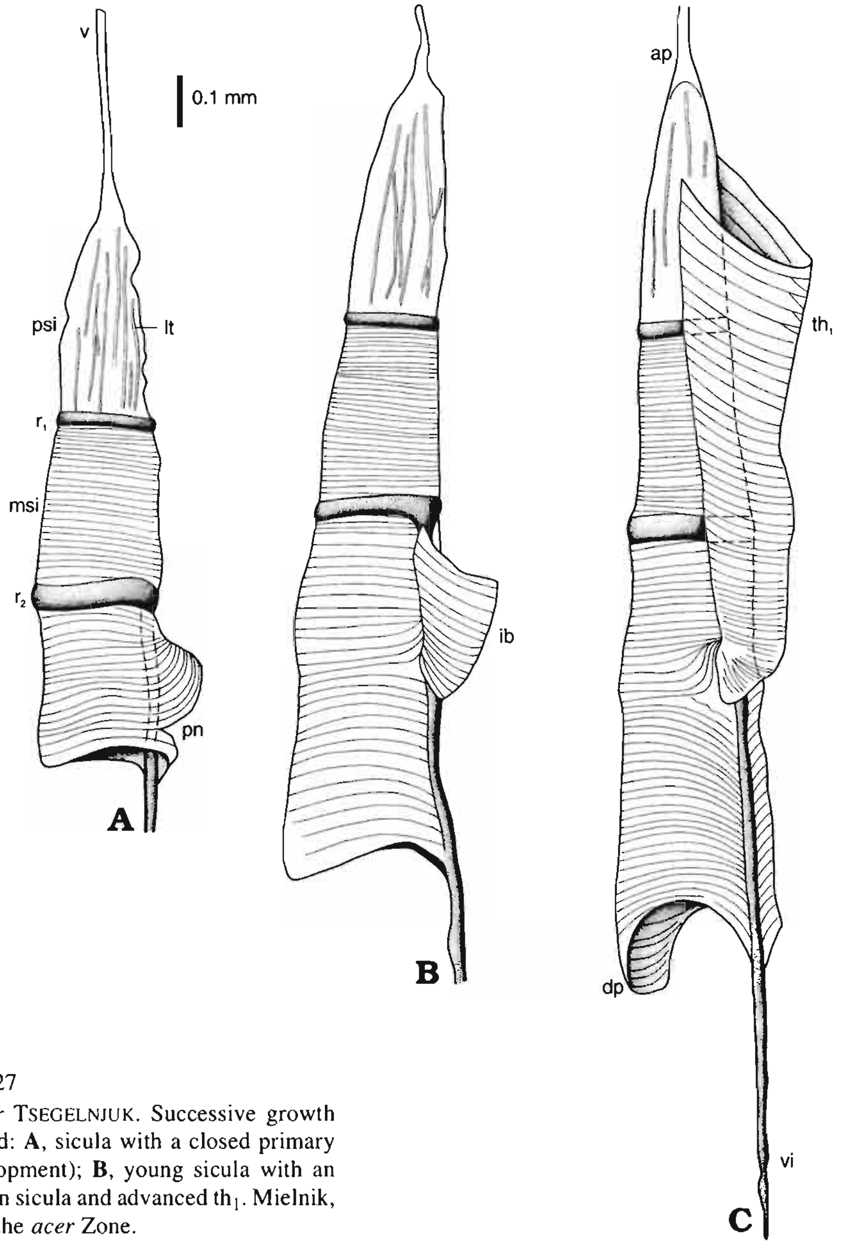

Fig. 27
Monograptus (Uncinatograptus) acer TSEGELNJUK. Successive growth stages of the sicula and the initial bud: **A**, sicula with a closed primary notch (pn, the lacuna stage of development); **B**, young sicula with an incipient initial bud (ib); **C**, fully grown sicula and advanced th$_1$. Mielnik, depth 792.55 m the *acer* Zone.

The free margin of the lobe has a roll-like thickening (Pl. 10: 10, 11m), which in some specimens tends to continue over the ventral lip of the thecal aperture (Pl. 10: 1, 2). Thecae are frequently preservationally distorted (Pl. 10: 1–3), or preserved in a 1/4 turn around the long axis of the rhabdosome (Fig. 29, th$_1$, th$_2$; Pl. 9: 1, 8).

As compared with the structure of *M. (S.) balticus*, the apertural lobes are laterally much more incised, with a slightly protruding apertural margin (Pl. 9: 6, Fig. 30). This, and most of the previously mentioned features were preserved unchanged as a certain foundation in all subsequent members of the *acer–spineus* lineage as defined by URBANEK (1995).

Bleached specimens reveal a fusellar structure of the apertural lobes (Fig. 31A–C). They represent a standard difusellar system, with a broad zig-zag suture in the middle and pronounced anterolateral corners (alp, A, C$_2$), which were to play an important role in the phylogeny of the lineage (see p. 149). Some of the fuselli, especially those of the "neck", converge laterally towards the ventral apertural margin (A$_2$, C$_1$).

In a broad sense such an apertural apparatus may be regarded as representing the *uncinatus* type of lobes (as defined by JAEGER 1978, 1986), although it differs in its overall shape both from *M. (U.) uncinatus* from the Gorstian as well as from other Ludfordian hooded monograptids (as described herein).

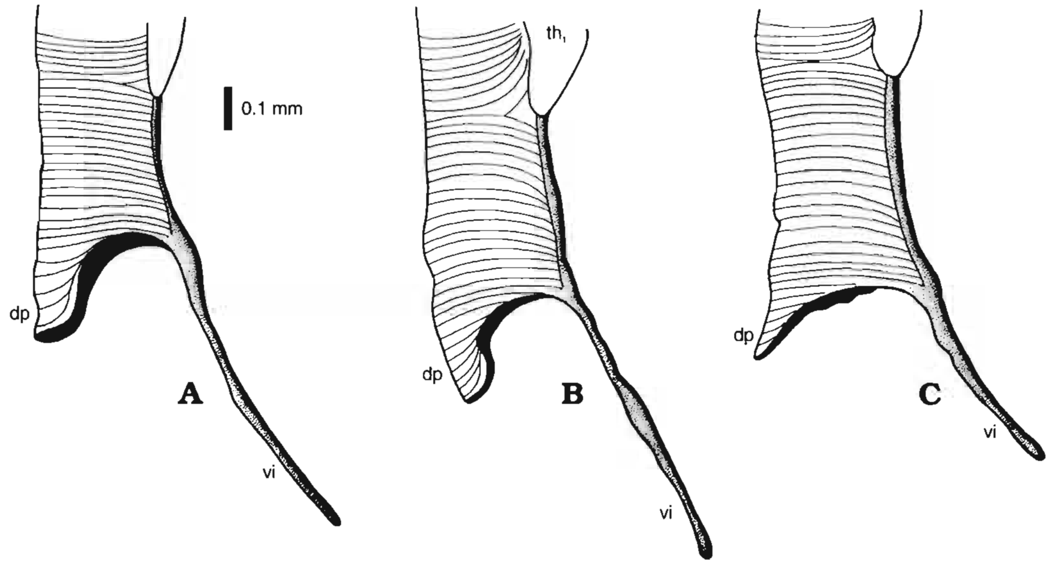

Fig. 28
Monograptus (Uncinatograptus) acer TSEGELNJUK. **A–C**, variation in the shape of the dorsal process (dp) of the metasicular aperture. Mielnik, depth 792.55 m, the *acer* Zone.

Thus one can say that it initated its own style of apertural devices (the *acer* acquisition of URBANEK 1994) preserved in the later phyletic stages of the lineage.

Rhabdosomes, as can be judged from isolated fragments, were fairly long and rather robust (the largest preserved proximal part is 11 mm long, but TSEGELNJUK 1976, mentions rhabdosomes 30 mm long). Rhabdosome widens rather rapidly, attaining ~0.30 mm at th_1, ~0.60 mm at th_3, and ~0.90 mm at th_6, and stabilizes near this value. This rapid increase in width (0.12 mm/theca between th_1 and th_6 is a characteristic feature of the species, in which it resembles *M. hornyi,* but differs from *M. pridoliensis* (both of Přidoli age). The number of thecae (N) in 10 mm of the rhabdosome length is 11–12 in the proximal part, but distal fragments of a comparable size are lacking.

The overall shape of the rhabdosome is defined by the degree of the dorsal curvature. This character is fairly variable ranging from almost straight to slightly bent to distinctly dorsally curved forms (URBANEK 1994). Furthermore, straight or slightly bent rhabdosomes prevail in the samples from the lower horizons within the range of the vertical distribution of *M.* (*U.*) *acer–aculeatus* (Fig. 25A_1–A_3, depth 792.70 m), whereas the degree of curvature increases in the samples from subsequent horizons (Fig. 25B–D, depth 790.90–774–50 m). From the above, it follows that the empirical data summarized in Fig. 25A–D reveal a gradual and uni-directional character of changes in the degree of the dorsal curvature within the population sequence. These changes cannot be traced continuously in the Mielnik borehole because of the gap in the occurrence (the 790.90–780.50 m interval). Nevertheless, this lack of continuity does not produce a significant disturbance in the tracing of the processes discussed. After their reappearance at a depth of 780.50 m, the populations display only some increase in the curvature without producing any jerkiness (see Fig. 25D_1–D_3). According to URBANEK (1995), this speaks for a slow and truly gradual evolutionary change involving the shift of the mean.

Assuming the essential stability of thecal characters, the degree of dorsal curvature (a purely quantitative trait) becomes the main feature distinguishing *M.* (*U.*) *acer* from *M* (*U.*) *aculeatus.* This makes the boundary between the two taxa fairly arbitrary. I suggest that such a limit be established in the Mielnik core at a depth of 780.00 m, some 50 cm after the populations' reappearance.

Taxonomic position. — As understood in the present paper, a single chronospecies with two sequential subspecies, *M.* (*U.*) *acer acer* and *M. (U.) acer aculeatus* initiates the *acer–spineus* lineage as defined by URBANEK (1995). It represents the first phase of the phyletic evolution, displaying slow and gradual changes in the degree of the dorsal curvature of the rhabdosome as well as minor modifications of the shape of the proximal thecae, expressed in the development of shallow incisions at the base of prothecae.

The ancestry of *M. (U.)* is cryptic. It differs from the earlier Ludfordian hooded monograptids (*latilobus/balticus* Zone), by its specific style of the apertural apparatus and by the overall shape of the rhabdosome. In this way the species creates a certain morphological foundation, common to later members

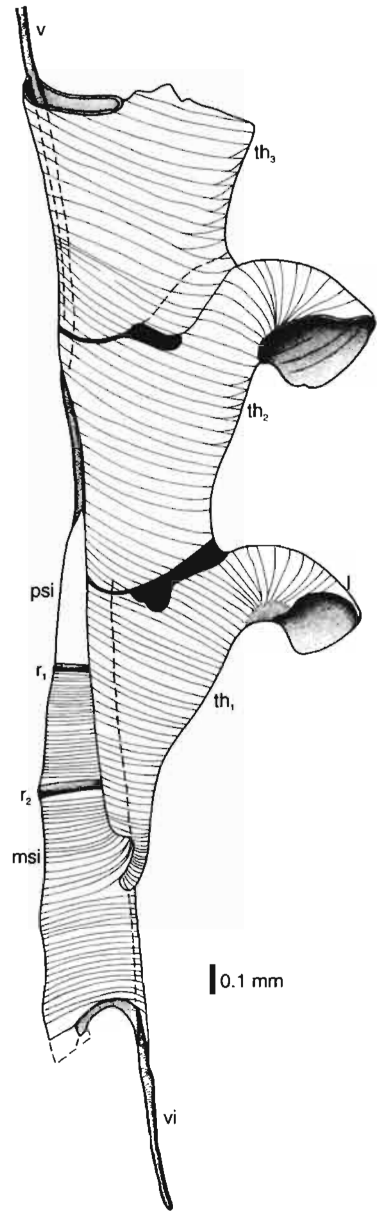

Fig. 29
Monograptus (Uncinatograptus) acer TSEGELNJUK. Proximal part of the rhabdosome, showing thecae slightly distorted. Mielnik, depth 792.55 m, the *acer* Zone.

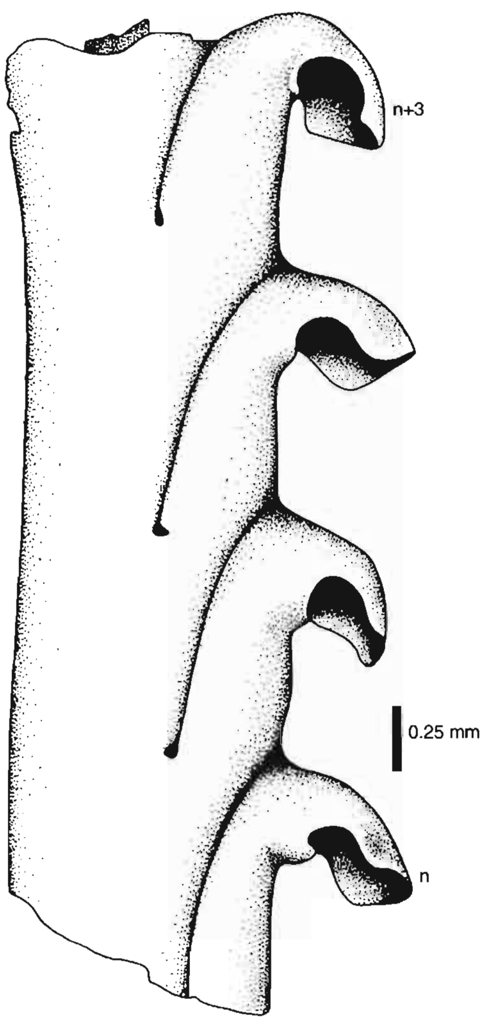

Fig. 30
Monograptus (Uncinatograptus) acer TSEGELNJUK. Distal part of the rhabdosome seen laterally. Mielnik, depth 790.55 m, the *acer* Zone.

of the *acer–spineus* lineage (URBANEK 1994). Its remarkable resemblance to *M. hornyi* JAEGER, 1986 is most probably of the nature of a homeomorphy (see p. 103 herein). A certain similarity to ealier *M. hamulosus* TSEGELNJUK, 1976 is not distinctive enough to draw any conclusion on their common ancestry.

The species includes two temporal subspecies: (1) *Monograptus (Uncinatograptus) acer acer* (TSEGELNJUK, 1976), a lower zonal taxon (Fig. 32A, B), characterized mostly by straight proximal thecae and the degree of curvature, D < 7°, (2) *Monograptus (Uncinatograptus) acer aculeatus* (TSEGELNJUK, 1976), a higher zonal taxon (Fig. 32C), characterized by proximal thecae, either straight or provided with shallow incisions at the base of the protheca, as well as by the degree of curvature, D > 7°.

In view of a purely quantitative nature of the differences between these subspecies and the presence of numerous transients, the assignement of particular specimens to one of them may cause problems.

Stratigraphic distribution. — In the Mielnik core, *M. (U.) acer* marks a well-defined zone, situated above the *latilobus–balticus* assemblage Zone and below the *protospineus* Zone (Fig. 3). Its FA is at a

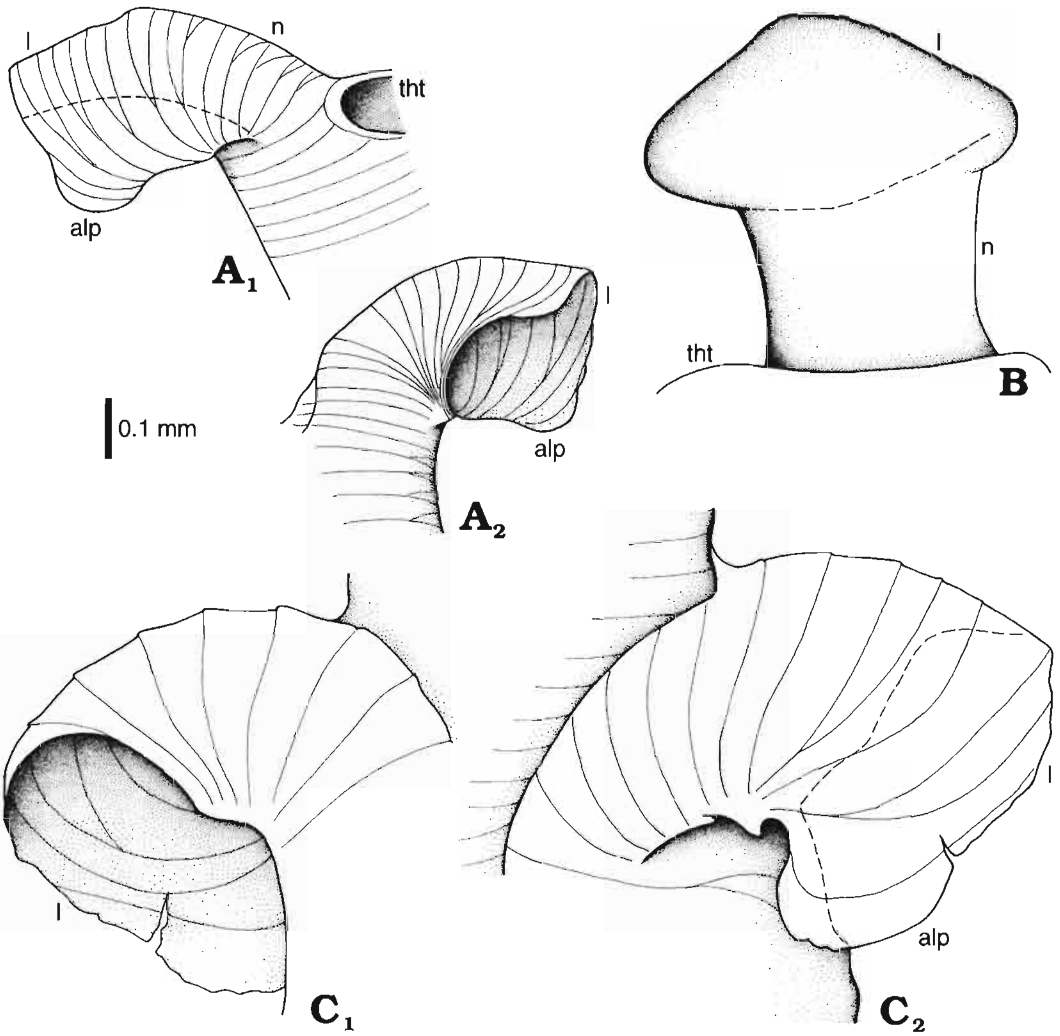

Fig. 31

Monograptus (Uncinatograptus) acer TSEGELNJUK. Thecal morphology and fusellar structure. A_1, A_2, slightly distorted aperture of th_1 seen from both sides; **B**, top view of a proximal theca showing a distinctly isolated apertural portion ("neck", n); **C**, fusellar structure of the aperture as seen on a distorted distal theca. Mielnik, depth 792.55–790.55 m, the *acer* Zone.

depth of 794.60 m and LA at 774.50 m. However, its vertical distribution is discontinuous, displaying a gap within the depth interval of 790.90–780.50 m. This gap is obviously related to the drastic drop of diversity of the graptolite assemblage, described above as the second ingression of the *dubius* fauna (see p. 97, Fig. 3). The impoverishment of the assemblage and the temporary dissappearence of some taxa may probably be ascribed to a local or regional period of unfavourable environmental conditions. URBANEK (1995) proposed to draw a demarcation line between the *M. (U.) acer acer* lower zonal populations and the *M. (U.) acer aculeatus* higher zonal populations at a depth of 780.00 m, some 0.5 m above the level of the species reappearance. The *acer* Subzone comprises the beds between 794.60 and 780.00 m while the *aculeatus* Subzone occupies the interval of 780.00–774.50 m.

TSEGELNJUK (1976, 1983) distinguished none of the two zones within his ample core material from Volhyno-Podolia. Instead, he described both taxa as co-occuring within a single assemblage zone, namely the *caudatus/balticus* Zone. KOREN' has described, from the Kursala Formation of the Southern Tien Shan (Kyrgystan), a distinctly curved form identified by her as *M. aculeatus* (TSEGELNJUK) and accommodated within her broadly understood *formosus–spineus* Zone. She does not, however, mention *M. acer* either in association or below the range of *M. aculeatus.*

Occurrence. — Relatively newly erected species *M. acer* (TSEGELNJUK) and the *M. aculeatus* (TSEGELNJUK) subspecies were so far recognized in the EEP (TSEGELNJUK 1976, and this paper). The latter is also known to occur in the Tien Shan, the Alai Range (Kyrgystan, KOREN' in press).

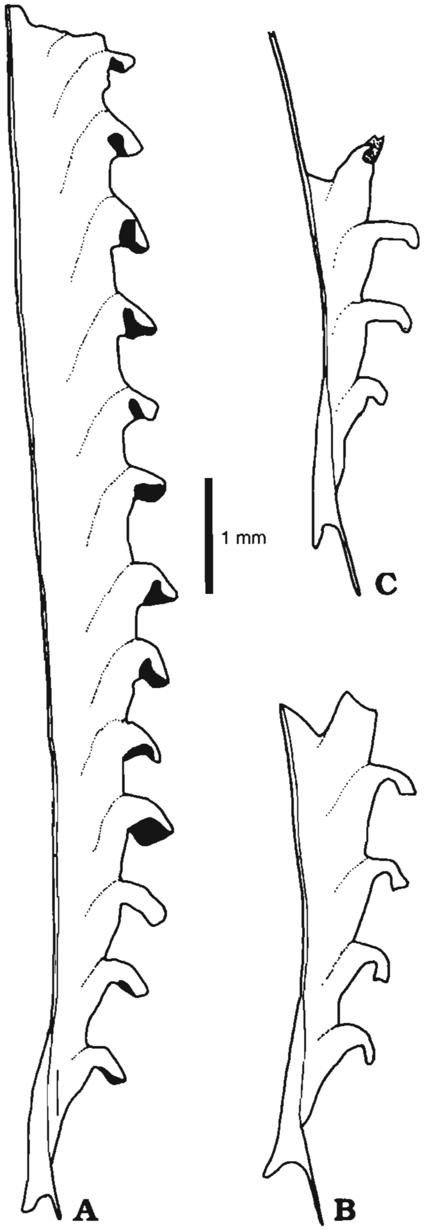

Fig. 32
Outline drawings of rhabdosomes: **A**, **B**, in *Monograptus (Uncinatograptus) acer acer* (TSEGELNJUK) and **C**, in *Monograptus (Uncinatograptus) acer aculeatus* (TSEGELNJUK). Mielnik, depth 792.55 m, 790.90 m and 774.50 m respectively, the *acer* Zone.

Monograptus (Uncinatograptus) protospineus URBANEK, 1995
(Pl. 11: 1, 2; Figs 33, 34)

1966. *Monograptus* cf. *formosus* BOUČEK; TELLER, fig. 12.

1995. *Monograptus (Uncinatograptus) protospineus* sp. n.; URBANEK, p. 13, figs 1B, C, 6A–E, 7A, B.

Holotype: Specimen figured by URBANEK 1995, fig. 7A, ZPAL G.XVII/1.

Type stratum: The eponymous zone, overlying the *acer aculeatus* Subzone and underlying the *spineus* Zone, late Ludfordian, Late Silurian.

Material studied. — Six isolated, flattened or semiflattened specimens, including the proximal portion with a sicula, and short distal fragments of the rhabdosome.

Description. — Sicula (Fig. 33) approximately 1.50 mm long, with the apex of the prosicula situated immediately above the apertural lobe of th_1. Prosicula (psi) 0.53 mm long, with an aperture 0.18 mm in diameter, provided with an apertural ring (r_1). Faint traces of some 3 longitudinal threads visible on the prosicula.

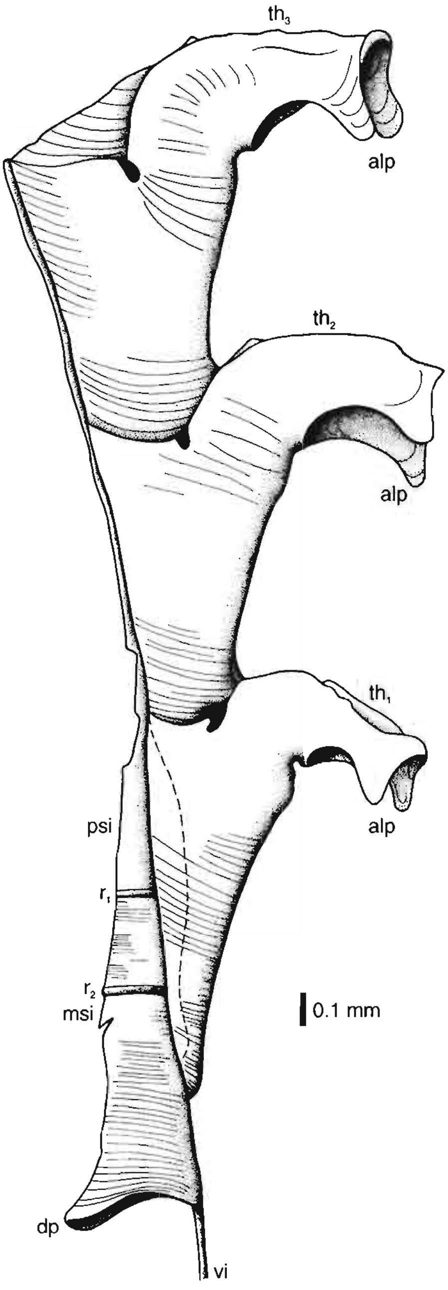

Fig. 33
Monograptus (Uncinatograptus) protospineus URBANEK. Sicular part of the rhabdosome with fusellar structure only partly visible. Note the characteristic anterolateral processes (alp) on apertural lobes of the thecae. Mielnik, depth 773.50 m, *protospineus* Zone.

Metasicula (msi) 0.95–1.00 mm long, with a single ring (r$_2$) situated approximately at 1/3 of the total length of the metasicula. Metasicular aperture 0.41 mm in diameter, provided with a protruding dorsal process (dp), 0.12 mm long. Initial bud placed at a distance of 0.30 mm from the margin of the metasicular aperture. Virgella strong, 0.80 mm long.

Thecae rather uniform in shape throughout the rhabdosome, narrow at the base of the protheca (0.30 mm at th$_1$, 0.45 mm at th$_3$, up to 0.52 mm in medial thecae), and rapidly widening towards the aperture (metathecae displaying a width of 0.28 mm in proximal thecae and 0.48 mm, in distal ones). The ventral wall of the theca is gently sigmoidal or almost straight. Proximal thecae (th$_1$–th$_2$) are 1.15–1.18 mm long, with the prothecal segment and the metathecal one attaining a length of 0.90–1.15 mm and 0.15–0.28 mm, respectively. Overlap in most proximal thecae very small, increasing distalwards to some 1/3.

Apertural apparatus uniform throughout the rhabdosome and composed of a long (transv.), horizontally oriented and strongly protruding apertural lobe (l) featuring characteristic paired anterolateral processes (alp) made up of 3–4 arcuately bent fuselli (Fig. 34; Pl. 11: 1, 2). The roof of the lobe is flat and the aperture of the theca somewhat extruded ventrally, which closely resembles the overall morphology observed in *M. (U.) acer aculeatus.* Apertural lobe proper (transv.) is 0.50 mm long in th$_1$, 0.66 mm in th$_2$, and 0.69 mm in th$_3$. The length of the apertural lobe measured in distal thecae is 0.80 mm. The length (long.) of the anterolateral processes is 0.08 mm in th$_1$, 0.15 mm in th$_1$–th$_3$, and some mm in distal thecae. The presence of these processes is a species-specific feature. (Fig. 34B$_2$). Readily discernible on embedded specimens, it may serve as a diagnostic feature for distinguishing it from other species of the *acer–spineus* lineage (URBANEK 1995).

Rhabdosome distinctly dorsally curved (dorsally concave), with the curvature starting at the apex of the prosicula. The deviation angle (D) measured as in other members of the *acer–spineus* lineage (see diagram in URBANEK 1995, Fig. 4) is D=12°. The rhabdosome gains width rather rapidly, being at the aperture of th$_1$ 0.53 mm, at th$_2$ 0.57 mm, and at th$_3$ 0.69 mm wide. It attains 0.80 mm in width at the apertures of distal thecae. The overall shape of the rhabdosome resembles that of both *M. (U.) acer aculeatus* and *M. (U.) spineus.*

Taxonomic position. — Morphology and stratigraphic occurence define *M. (U.) protospineus* as a transient link between the earlier *M. (U.) acer aculeatus* and the later *M. (U.) spineus*, within the *acer–spineus* lineage (URBANEK 1995). The directional and gradual character of changes speaks in favour of phyletic evolution as the mode of evolution within the lineage. The small number of the specimens recorded and the short time-span of its occurence (as indicated by the small thickness of the interval it occupies in the Mielnik-1 borehole), might suggest that *M. (U.) spineus* populations were small in size and subject to rapid phylogenetic transformations. This interpretation needs to be confirmed by data from other sites.

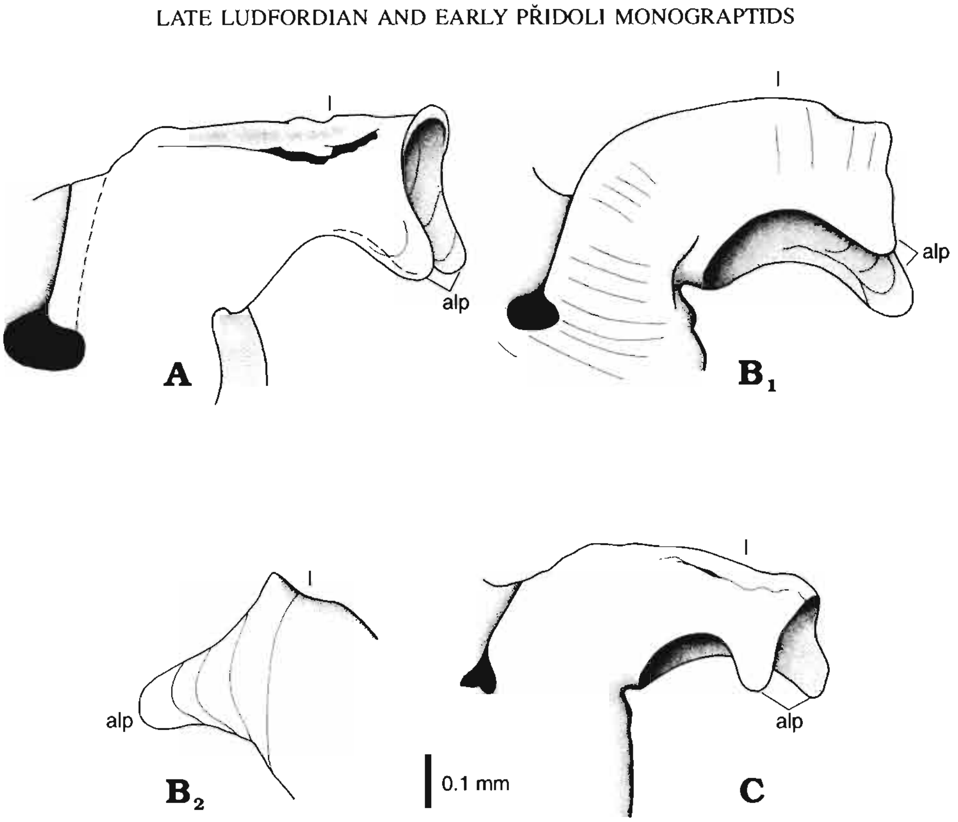

Fig. 34
Monograptus (Uncinatograptus) protospineus URBANEK. Structural details of apertural lobes (l) in th_1–th_3 (A–C) and their antero-lateral processes (alp). Mielnik, depth 773.50 m, *protospineus* Zone.

While the overall shape of the rhabdosome and the foundations of the apertural apparatus were inherited without significant changes from the ancestral *M. (U.) acer aculeatus*, a species-specific novelty is represented by anterolateral processes, these being in turn incipient structures for elaborated apertural spines so characteristic of closely affined *M. (U.) spineus*.

Occurrence. — Known from the EEP and Tien Shan (KOREN', in press).

Monograptus (Uncinatograptus) spineus (TSEGELNJUK, 1976)
(Pl. 11: 3–6; Pls 12, 13, Figs 13, 35–41)

1976. *Acanthograptus spineus* sp. n. TSEGELNJUK; TSEGELNJUK, p. 113, pl. 34: 6–9.
1983. *Bugograptus spineus* (TSEGELNJUK); TSEGELNJUK, p. 145, fig. 34.
1988. *Monograptus spineus* (TSEGELNJUK); KOREN', RINNENBERG, and LYTOCHKIN, p. 17: 8.
1995. *Monograptus (Uncinatograptus) spineus* (TSEGELNJUK); URBANEK, p. 3, figs 1d, 2, 7C–E.

Type horizon redefined: The eponymous zone overlying the *protospineus* Zone and underlying a low diversity horizon immediately below the *parultimus* Zone, late Ludfordian, Late Silurian. Its zone is sometimes also defined as the *formosus/spineus* Zone.

Material. — 30 well-preserved and isolated, although in most cases flattened or semiflattened fragments of the rhabdosome. Numerous siculae, proximal and distal parts of the rhabdosome.

Description. — Sicula (Figs 13, 35, 36; Pl. 12: 1–4, 7) straight or very gently ventrally curved, 1.37–1.62 mm long, usually with a well-developed dorsal process and a strong virgella. The apex of the prosicula situated distinctly distally of the apertural lobe of th_1.

Prosicula (psi) 0.46–0.54 mm long, provided with a distinct apertural ring (r_1). Metasicula (msi) 0.85–1.07 mm long, with a single ring (r_2), situated approximately 0.35–0.40 mm from the aperture of the prosicula. The aperture of the metasicula widens normally, attaining a width of 0.30 mm (Fig. 35), or is somewhat flared — 0.35 wide, because of the tongue-like expansion of the dorsal process (Fig. 35B, dp), which may be as long as 0.15 mm. Initial bud situated at the distance of 0.35–0.40 mm from the margin of the metasicular aperture. Virgella strong.

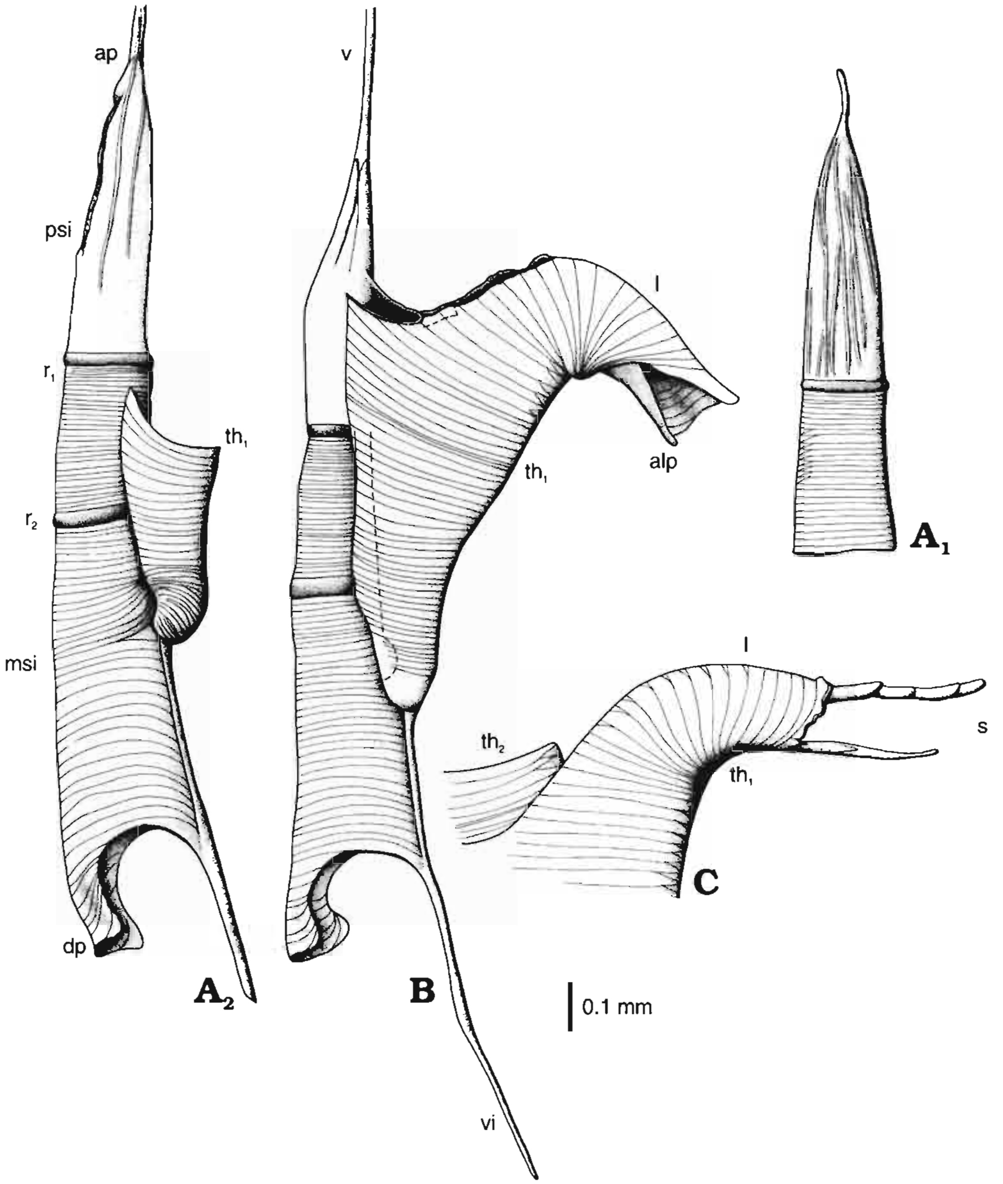

Fig. 35
Monograptus (Uncinatograptus) spineus TSEGELNJUK. Sicula and first theca. **A**, fully grown sicula and incipient th$_1$; **B**, sicula and th$_1$ with an incomplete (juvenile) aperture; **C**, fully grown apertural apparatus in th$_1$. Mielnik, depth 760.15 m, the *spineus* Zone.

Thecae in the proximal part of the rhabdosome reveal a subtriangular base made of the protheca and the subapertural segment of the metatheca and are provided with strongly developed apertural lobes, oriented nearly horizontally (Fig. 36; Pl. 12: l, 2). Ventral wall of proximal thecae is slightly sigmoidal, with a narrow "neck" (immediately above the aperture of the preceding theca), and a somewhat expanded upper part of the prototheca (forming a "belly"). The length (transv.) of the lobe proper in proximal thecae attains 0.18–0.23 mm while in distal ones it is 0.53–0.58 mm and equals or exceeds the width (transv.) of the rhabdosome, measured immediately above the given aperture.

Apertural lobe proper is made of two series of fuselli, interdigitating in the middle to produce a broad zig-zag suture (Fig. 37A, C$_1$, C$_2$). The anterior margin of the lobe, situated between the bases of antero-lateral spines, always forms a somewhat protruding area, which I propose to name *promontorium* (p). It is either gently rounded (Fig. 38C$_1$, p) or angular and pointed (Fig. 38C$_2$, p). This situation may be indicative of a certain tendency in variability, never fully realized in the phylogeny, to develop a trispinose condition (Pl. 13: 6–8). The overall shape of the lobe proper is very similar to that in closely affined

M. (U.) protospineus and *M. (U.) acer aculeatus*, but the presence in both the proximal and distal thecae of long, paired apertural spines (Figs 37–40; Pl. 13: 1–2s) gives the thecae a characteristic and even bizarre appearance. Spines, situated in the antero-lateral corners of the lobe proper, are made of a number of superimposed fuselli (Figs 38A, B, 39A, B). They attain a length of approximately 0.31–0.32 mm in th$_1$, 0.28–0.37 mm in proximal thecae, and some 0.50–0.58 mm in distal thecae. However, one cannot be sure whether they are completely preserved. SEM micrographs reveal that spines are hollow, (Pl. 13: 12h), but this feature might be preservational due to the leaching of the fusellar content of the spines. Owing to flattening, apertural lobes display two different states of preservation: they are either squeezed between the spines and oriented downward or pushed upward (Fig. 40A, B), which results in a quite different outline of the same structure (Pl. 13: 3-5, 10; Fig. 41).

Rhabdosome is distinctly dorsally curved (dorsally concave), with the curvature starting at the prosicular aperture. The angle of deviation (D), measured between the long axis of the sicula and the dorsal wall of the rhabdosome along th$_2$–th$_3$ (see diagram in URBANEK 1995: fig. 4) is approximately 20–25°. Spinosity and distinct dorsal curvature are characteristic features of the species. Although preserved fragments are incomplete, it appears that *M. (U.) spineus* had a moderately long rhabdosome (observed maximum length is about 10 mm).

Taxonomic position. — In the light of URBANEK's (1995) considerations, *M. (U.) spineus* may be considered the terminal and most specialized link (chronospecies) of the *acer–spineus* lineage. Its immediate forerunner was represented by *M. (U.) protospineus* having almost identical features, except for the absence of true apertural spines. The latter are the main acquisition attained at the *spineus* stage of the phyletic evolution (URBANEK 1995).

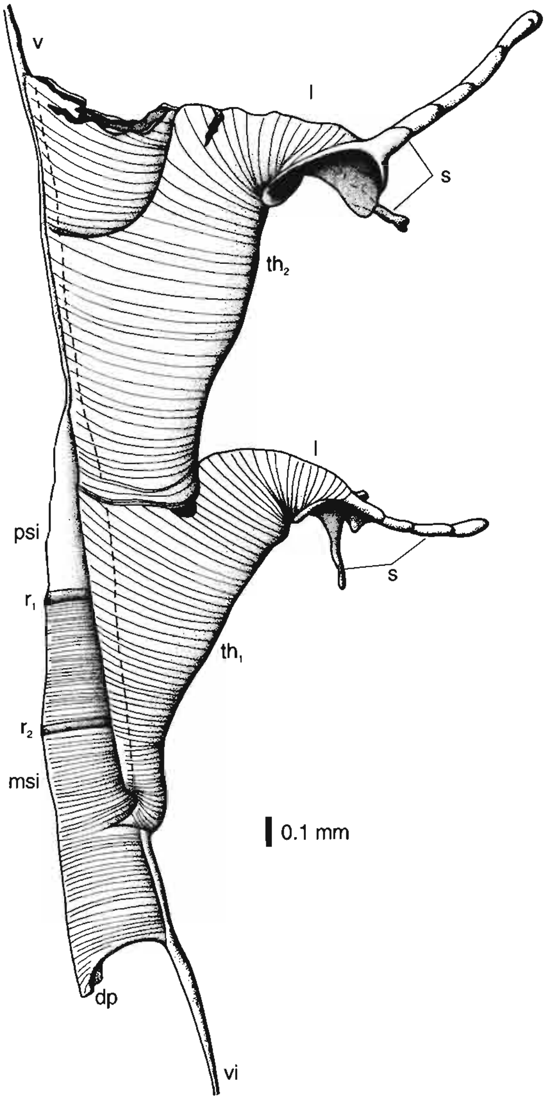

Fig. 36
Monograptus (Uncinatograptus) spineus TSEGELNJUK. Proximal part of the rhabdosome as seen on a bleached specimen. Mielnik-1, depth 760.15 m, the *spineus* Zone.

The lobate-spinose apertural apparatus in *M. (U.) spineus* is homeomorphic to the *priodon–flemingi* group of Wenlock monograptids, but differs in the antero-lateral location of the spines. Therefore being essentially homological with the Wenlock spinose representatives of *Monograptus* s.s., it is not identical in the structural plane ("style") – for details see an extended discussion p. 109 herein. These minute differences and the morphocline represented by the *acer–spineus* lineage leave no doubts that the species in question and its thecal characters originated *de novo*, in the Ludfordian, from the *uncinatus*-like ancestors. That is why I assign the species in question to *Monograptus (Uncinatograptus)*.

Occurrence. — *M. (U.) spineus* has previously been found in the Meton Horizon of the boreholes in Volhynia (TSEGELNJUK 1976, 1981) as well as in the Kursala Formation of Tien Shan (KOREN' 1992).

Stratigraphic distribution. — Common and morphologically distinct, *M. (U.) spineus* is a magnificient index fossil of the late Ludfordian (KOREN' 1992; URBANEK 1995 and herein, p. 96). However, the concept of the *formosus/spineus* Zone as advanced by KOREN'(1986, 1992) is controversial. While *spineus* defines a discrete time belt, confined to the upper part of the late Ludfordian, *formosus* crosses the Ludfordian into the Přidoli. Therefore the concept of a conventional *spineus* Zone is preferred in this paper.

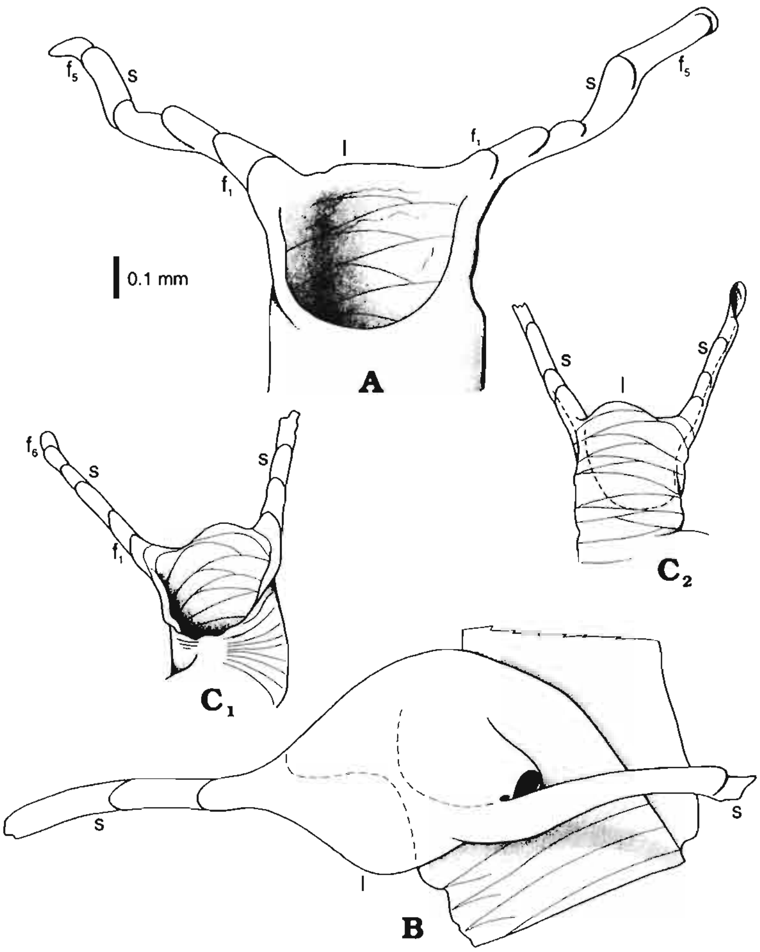

Fig. 37
Monograptus (Uncinatograptus) spineus (TSEGELNJUK). Structure of the apertural apparatus as seen in different aspects and states of preservation. **A**, flattened apertural lobe in a distal theca seen from the ventral side; **B**, semiflattened apertural lobe in a distal theca, ventral view; **C$_1$**, **C$_2$**, apertural lobe of a proximal theca, ventral and dorsal views. Mielnik, depth 760.15 m, the *spineus* Zone.

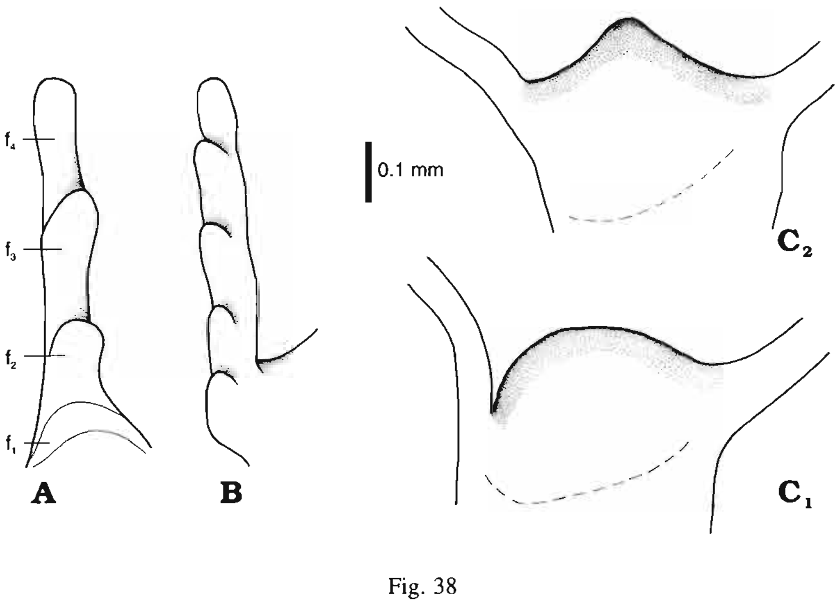

Fig. 38
Monograptus (Uncinatograptus) spineus (TSEGELNJUK). Fusellar structure of the apertural spine (**A**, **B**) and variation in the shape of the promontorium (**C$_1$**, **C$_2$**) in two adjacent thecae (n, n+1). Mielnik, depth 760.15 m, the *spineus* Zone.

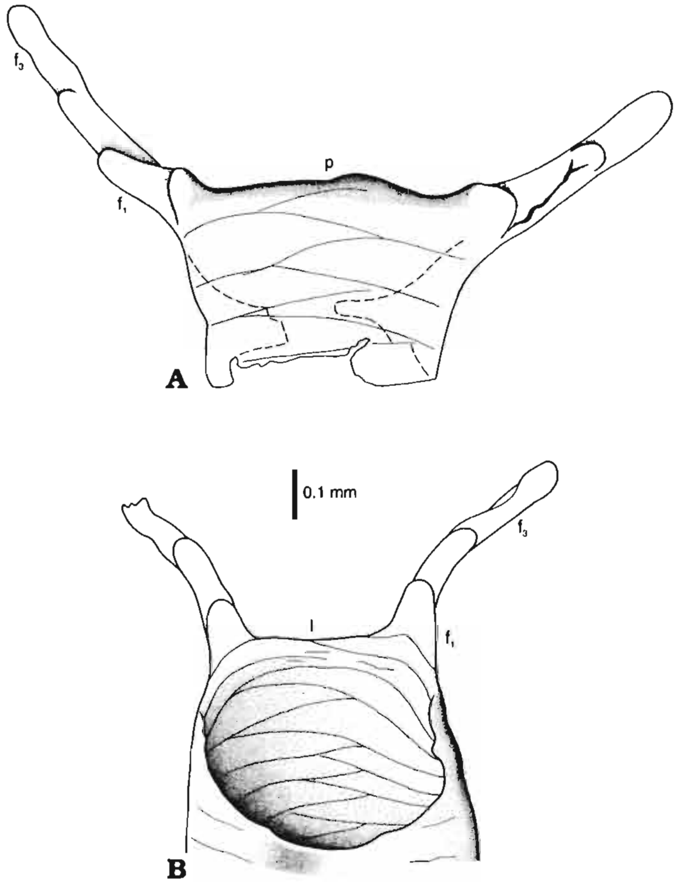

Fig. 39
Monograptus (Uncinatograptus) spineus (TSEGELNJUK). Fusellar structure of the apertural apparatus examined from the dorsal (**A**) and ventral (**B**) sides. Mielnik, depth 760.15 m, the *spineus* Zone.

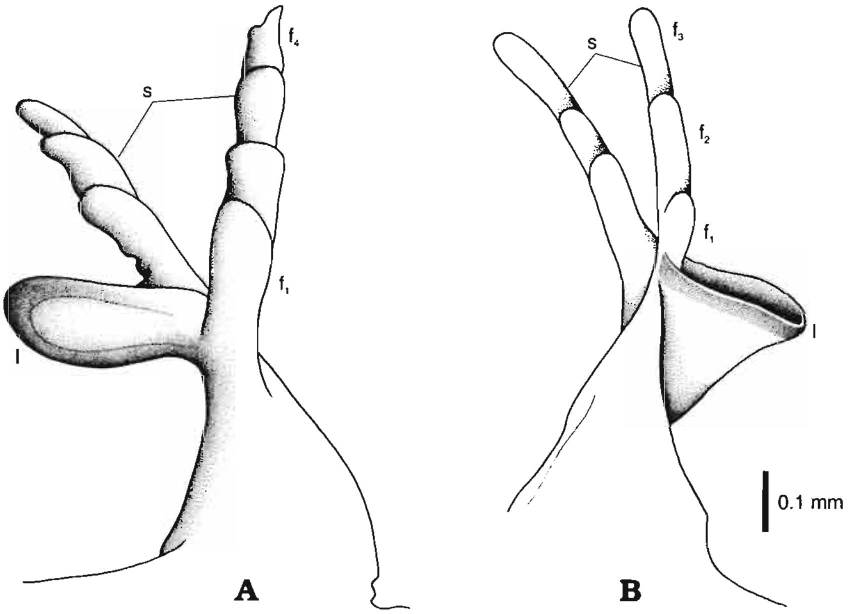

Fig. 40
Monograptus (Uncinatograptus) spineus TSEGELNJUK. Apertural lobes (l) with paired antero-lateral spines (s) flattened upwards (**A**) and downwards (**B**). Note the "telescopic" appearance of the spines made of fuselli (f_1–f_4). Mielnik, depth 760.15 m, the *spineus* Zone.

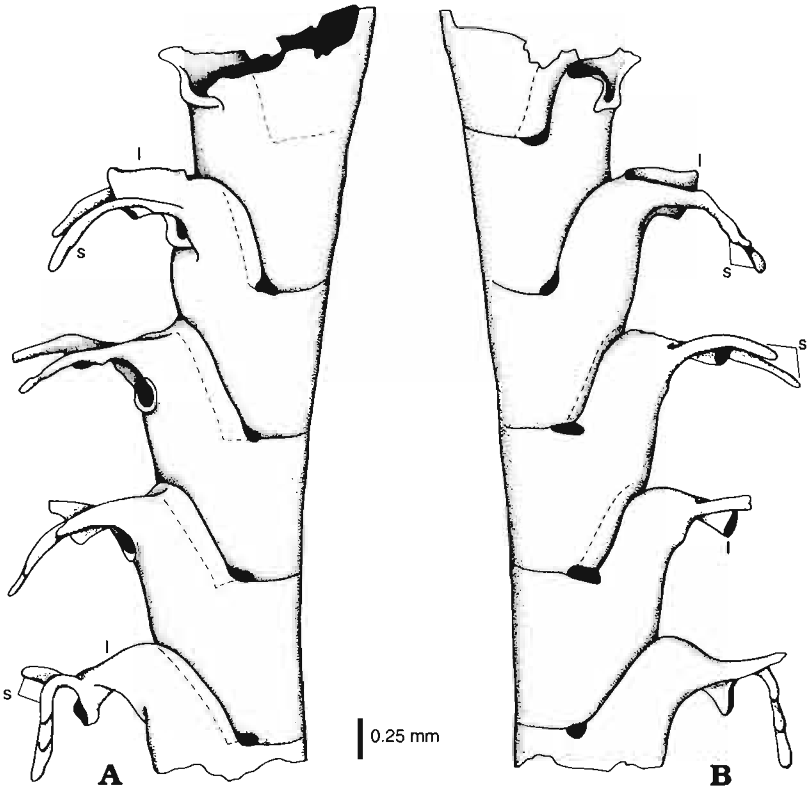

Fig. 41
Monograptus (Uncinatograptus) spineus TSEGELNJUK. A distal fragment of the rhabdosome in the reverse (**A**) and obverse (**B**) view. Mielnik, depth 760.15 m, the *spineus* Zone.

In the Mielnik-1 borehole *M. (U.) spineus* makes its FA at a depth of 763.00 m, and its LA at a depth of 760.20 m. Its zone is thus 2.80 m thick). There is, however, another but doubtful occurrence at a depth of 753.30 m. The stratigraphic range is given in Fig. 3.

Subgenus *Monograptus (Dulebograptus)* TSEGELNJUK, 1976
Monograptus (Dulebograptus) trimorphus TSEGELNJUK, 1976
(Pl. 14, Fig. 42)

1976. *Dulebograptus trimorphus* n. sp. TSEGELNJUK; TSEGELNJUK, p. 100, pl. 32: 1.
1978. *Dulebograptus trimorphus* TSEGELNJUK; TSEGELNJUK, p. 90, pl. 2: 1, 6, pl. 3: 1, 3, 5.
1988. *Dulebograptus trimorphus* TSEGELNJUK; TSEGELNJUK, p. 85, pl. (2): 6, 7.

Material. — About 20 fragments of rhabdosome, from a single sample, all semiflattened or flattened, usually laterally but some dorso-ventrally. Proximal parts with sicula present.

Description. — Sicula (Fig. 42A, B; Pl. 14: 3) moderately long (1.56–1.74 mm, including the dorsal process of metasicula), in the middle of the metasicular portion slightly curved ventrally. Aperture provided with a distinct dorsal process of the metasicula (0.10–0.12 mm long). Apex of prosicula reaches to the middle of th$_2$ Prosicula (psi) with a distinct apertural ring (r$_1$) is 0.42–0.58 mm long. Metasicula (msi) is usually provided with a single ring (r$_2$), although on one specimen a thin additional ring (r$_3$) was seen. Aperture of the metasicula measures 0.12–0.16 mm in diameter and is provided with a strong virgella and a distinct dorsal process. Initial bud situated rather close to the metasicular aperture, at a distance of 0.19–0.20 mm.

Thecae rather short, first theca being roughly triangular in outline and some 0.83 mm in length (TSEGELNJUK 1976: p. 100 mentions 1.1 mm). Remainig thecae display a more or less distinct genicular bending of the ventral wall (Fig. 42; Pl. 14: 4) and an increasing degree of overlap distalwards. Medio-distal theca is approximately 2.00 mm long, prothecal segment being some 0.90 mm in length, while the

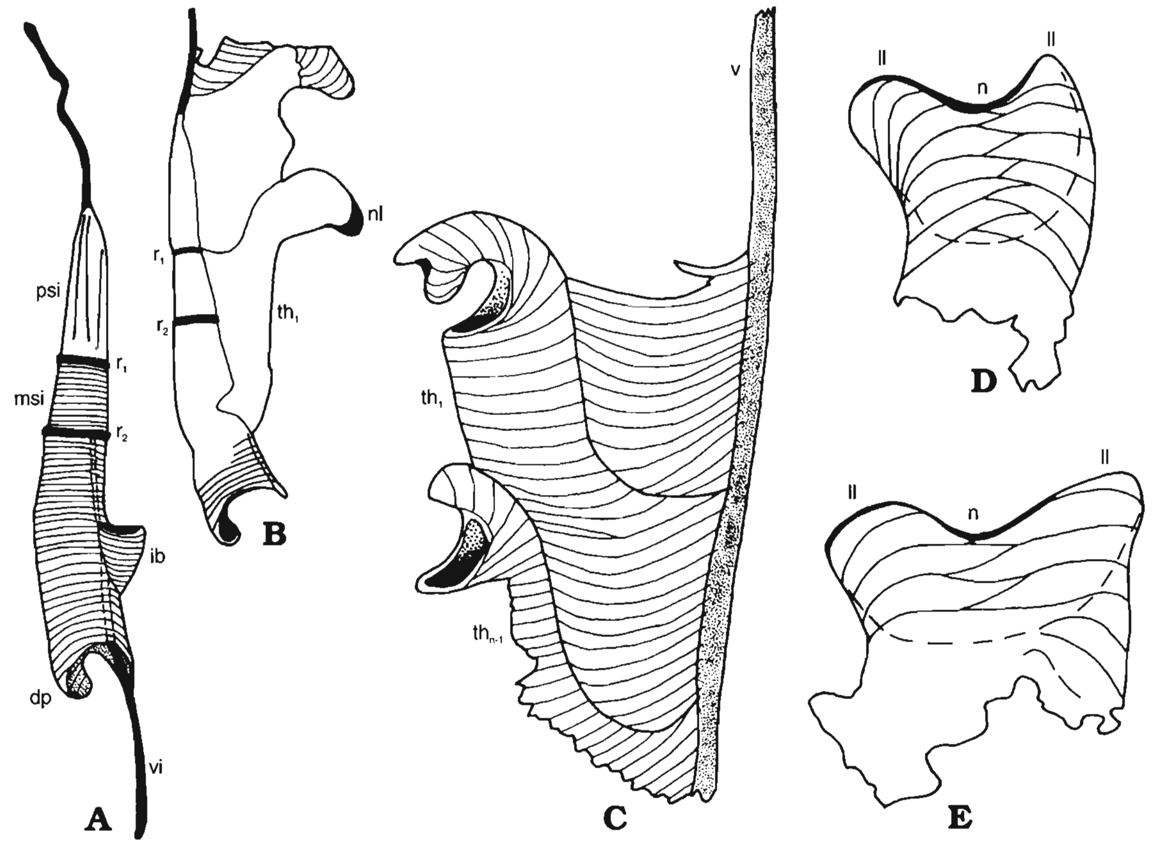

Fig. 42
Monograptus (Dulebograptus) trimorphus (TSEGELNJUK). Structural details of sicula and proximal thecae (**A**, **B**) as well as distal thecae (**C**); **D**, **E**, fusellar structure of apertural lobe in proximal (**D**) and medial (**E**) thecae as seen on detached and strongly bleached lobes in dorsal view. Mielnik, depth 664.80 m, *lochkovensis* Zone.

metathecal one is 1.10 mm long. Thecae are provided with characteristically modified (notched) apertural lobes, which otherwise are of an uncinatograptid appearance.

While notched apertural lobes are a characteristic feature of *M. (Dulebograptus)* TSEGELNJUK, their considerable astogenetic variation is a species-specific character of *M. (D.) trimorphus* TSEGELNJUK. First theca displays an almost regular uncinatograptid shape of the apertural lobe (Pl. 14: 1, th$_1$), whereas, successive proximal thecae (th$_2$–th$_4$) show a distinct median incision (notch), reaching its maximum at th$_3$. Apertural lobe is there almost bilobate due to a deep notch separating two lateral lappets (Pl. 14: 2, th$_3$). Distal of th$_3$ the median notch becomes shallower and wider, while the apertural lobe itself is gradually reduced to a short, roof-like structure (Pl. 14: 4, 1). Th$_7$ has its notch reduced to a shallow incision on the border, and the same is true for the more distal thecae (Pl. 14: 1, 51).

TSEGELNJUK (1976, 1978) mentions a complete division of the apertural lobe into paired lateral lobes within the proximal part of *M. (D.) trimorphus* rhabdosome as well as the presence of simple pristiograptid thecae in its medial and distal parts. Such radical astogenetic changes were not observed in the material from the Mielnik-1 borecore. Notched apertural lobes always exhibit a rudiment of the free dorsal wall (e.g. Pl. 14: 1, th$_3$ or Fig. 42C), while most of the distal thecae observed are still provided with a short brim-like apertural lobe, some 0.25 mm wide (Pl. 14: 4, 5).

Studying the fusellar structure of the notched aperural lobes in *M. (D.) trimorphus* proved to be a difficult task, mainly because of the preservational fold due to compression (Pl. 14: 6f). This fold obscures the structural details of the central portion of the lobe. From a great number of apertural lobes, which were detached with a needle from strongly bleached rhabdosomes, only two revealed satisfactorily their microstructure (Fig. 42D, E). Both the proximal and the medial thecae feature the presence of a more or less distinct notch (n) between two lateral lobes comprising 2-3 fuselli (ll) and of the lobe proper with a zig-zag suture in the middle. The first theca alone has a regular structure of the *uncinatus* type, showing an entire apertural margin.

The degree of the incision, measured by the depth of the notch (n) in the apertural lobe, displays an irregular astogenetic variation: th_1 shows no incision, th_2 exhibits a shallow notch (0.06 mm) and th_3 is deeply notched (0.22 mm). The succeeding thecae show again a decrease in the degree of incision: th_4 has a notch 0.13 mm deep, and th_5 displays a notch only 0.06 mm deep. More distal thecae reveal notches some 0.06–0.05 mm deep. Therefore, in the degree of incision they are comparable to th_2. The ancestral, unmodified structure of th_1 may speak for a distal introduction of the novel trait (notch), although the expressivity of this trait does not follow a single gradient as does the majority of other thecal characters.

Rhabdosome is straight except for a slight ventral curvature of the sicular part. The width of the rhabdosome at the apertural level of th_1 is 0.42 mm, while the widest observed distal parts measured 0.87 mm.

Taxonomic position. — TSEGELNJUK (1976, 1978) considered his *Dulebograptus* a derivative of the *uncinatus* stock. This view seems well-grounded and is supported by the structure of most proximal thecae having a distinct *uncinatus*-like appearance. This resemblance of most proximal thecae to the presumed ancestor may be explained as a recapitulatory effect in the astogeny (compare Pls 7, 8: 9 and Pl. 14: 1).

TSEGELNJUK (1976, 1978, 1988) advanced a hypothesis ascribing his *Dulebograptus* an important phylogenetic role, namely the role of the ancestor of some advanced Přidoli neocolonograptids. In view of the latest version of this hypothesis (TSEGELNJUK 1988), *M. (D.) trimorphus* is considered the immediate ancestor of *Neocolonograptus lochkovensis* as well as of morphologically advanced varieties of *N. ultimus* (distinguished by TSEGELNJUK as a separate species, namely his *vetus*). Such advanced neocolonograptids were envisaged by TSEGELNJUK as representatives of genus *Skalograptus*, in contrast to less specialized forms (such as *parultimus* and *ultimus* s.s.) classified as a new genus *Istrograptus*. Therefore, according to TSEGELNJUK, *Duleboraptus* is an intermediate link between true lobate uncinatograptids and bilobate *Skalograptus*. The latter is believed to have appeared by the splitting of the notched apertural lobe of *Dulebograptus*.

A quite different view on the relationship between bilobate and hooded Přidoli monograptids was expressed by RICKARDS *et al.* (1977: p. 78). According to them, hooded biform and uniform rhabdosomes originated by dorsal coalescence of paired lateral lappets observed in the *ultimus* Group. This view may easily be extended onto *M. (Dulebograptus)* interpreting them as an immediate effect of such coalescence. The presence of *Dulebograpus*-like phenodeviants in *N. lochkovensis* rhabdosomes is suggestive of morphogenetic equivalence between bilobate and hooded apertural devices (see discussion, p. 108 herein).

It is difficult to evaluate these two contradictory view points on the phylogeny of Late Silurian monograptids. Both fit some morphologic and astogenetic data and therefore seem possible for formal, comparative anatomical reasons, but none is sufficient to explain the real phylogenetic relations. The problem is, however, which of the two suggested pathways was realized in the course of the evolution. Neither of the hypotheses in question is supported by an unbroken sequence of changes (a morphocline), thus providing an empirical evidence of its verity.

The hypothesis of the splitting of the primarily single, difusellar apertural lobe into paired apertural lobes, as advanced by TSEGELNJUK (1976, 1978, 1988) seems tempting based solely on *M. (D.) trimorphus*. Seen against a wider background, it proves to be unsatisfactory. First of all *M. (D.) trimorphus* appears too late to be considered an ancestor of advanced neocolonograptids – the latter appear earlier than their presumed forerunner. Moreover, *M. (D.) trimorphus* displays some specialization in the thecal structure (genicular bending), which prevents its being regarded the immediate ancestor of *N. lochkovensis*. The former also exhibits the presence of two black rings on the sicula, whereas the porus ring characteristic of the siculae in *N. lochkovensis* is lacking. This fact seems to indicate a different trend in the evolution of the sicula. TSEGELNJUK's reasoning pays no attention to the important evidence presented by JAEGER (1975, 1986) on a very early appearance of incipient paired lateral lappets and their gradual development within the *parultimus–ultimus–lochkovensis* lineage.

Also KOREN' and LYTOCHKIN (1992) interpreted these species as a single evolutionary line. In view of this evidence, TSEGELNJUK's idea on separating *lochkovensis* from the rest of the lineage and ascribing it a quite separate ancestry seems unconvincing to me.

On the other hand, the coalescence theory is theoretically possible and seems partly supported by the finding of *Dulebograptus*-like deviants in *N. lochkovensis* rhabdosomes (see p. 179). There is little doubt, however, that such monstrosities represent only phenodeviants and *per se* cannot be regarded as the material for a future evolutionary change. The crucial evidence for the theory in question, namely a morphocline bridging the gap between bilobate and lobate monograptids in the Přidoli, has not been recognized yet, and I consider *Dulebograptus* and *Neocolonograptus* as unrelated and representing separate lineages.

Stratigraphic distribution. — *M. (D.) trimorphus* was described from the Skala Stage (Skalian) of Volhynia and Podolia. TSEGELNJUK (1976) mentioned it from the Gushcha-4015 boring and referred the species to the upper part of the Milovanov suite.

In the Mielnik-1 borecore, *M. (D.) trimorphus* made its first appearance at a depth of 665.80 m, within the well-defined *lochkovensis* Zone. It occupies a narrow band, approximately 1 m thick. It is the first hooded *Monograptus* to reappear after the *spineus* Event, which resulted in a distinct Lazarus effect for this group of monograptids. The same role in Barrandian was played by *M. (U.) pridoliensis,* which appears within the *lochkovensis* Zone and subdivides the zone into lower and upper Subzones (JAEGER 1986).

Occurrence: Dulebograptids are known only from the EEP, they were not found in the Barrandian and are not mentioned in faunal assemblages from the Tien Shan by KOREN' and LYTOCHKIN (1992).

Subfamily **Pristiograptinae** GÜRICH, 1908

Genus *Pristiograptus* JAEKEL, 1889

Pristiograptus dubius dubius (SUESS, 1851) *s.l.*

(Pl. 15: 1–4, 7; Fig. 43)

1851. *Graptolithus dubius* n. sp.; SUESS, p. 115, pl. 9: 5a, b.
1933. *Monograptus dubius* (SUESS); COX, pp. 421–425, text-figs 1–16, pl. 11.
1943. *Pristiograptus dubius* (SUESS); PŘIBYL, p. 4, pl. 1: 4–6.
1953. *Pristiograptus (P.) dubius* cf. *dubius* (SUESS); URBANEK, pp. 101–102 (French text), text-fig. 8.
1953. *Monograptus dubius* (SUESS); WALKER, pp. 365–370, text-figs 2, 3.
1955. *Monograptus dubius* (SUESS); KUEHNE, pp. 360–365, text-fig. 2.
1958. *Pristiograptus dubius* (SUESS); URBANEK, p. 83, pl. 5, text-figs 1, 2, text-pl. 7, text-fig. 57.
1991. *Monograptus dubius frequens* (JAEKEL); JAEGER, p. 314, fig. 25: 9, 11, 15.

Material. — A few dozens of specimens, mostly proximal and medial parts of rhabdosome, flattened, semiflattened and 3-dimensional.

Description. — The species in question has been described many times, including isolated specimens (COX 1933; WALKER 1953; URBANEK 1953, 1958; KUEHNE 1955; JAEGER 1991). In most of the features, specimens from the late Ludfordian of the Mielnik wellcore are similar to the *frequens* morphotype characteristic for Gorstian populations and therefore are described tentalively as cf. *ferquens*.

Sicula (Fig. 43C–D, Pl. 15: 1, 2), gently ventrally curved or almost straight, is 1.80–2.2 mm long. Its prosicular apex reaches up to the level somewhat above the aperture of th_1.

Prosicula, 0.38–0.46 mm long, is provided with a distinct apertural ring (r_1). Metasicula with a length of 1.41–1.48 mm attains a width of 0.30–0.33 mm at its aperture featuring a moderate dorsal process, 0.13–0.15 mm in length. Remarkable features of the sicula are its fixed 3-ring pattern (Fig. 43A–D) and a steady relation of the point of the virgella origin to the second ring (r_2, Fig. 43A, B). Position of the sicula within the proximal part of the rhabdosome is shown in Fig. 43C, D. Initial bud is situated at a distance of 0.20–0.23 mm from the margin of the metasicular aperture.

Thecae are tubular, rather long and narrow with their apertures slightly oblique to the long axis of the rhabdosome (Pl. 15: 1–3). First theca 1.15 mm long, with the diameter of the aperture 0.30 mm. Apertural margins are obliquely placed in relation to the main rhabdosome axis and have only a narrow thickening.

Rhabdosome straight, slowly gaining in width (0.5 mm above th_1 and 0.80 mm above th_5). Periderm, evidently without a thick cortical deposit, frequently reveals the fusellar structure without bleaching (Pl. 15: 1, 3, 4).

Stratigraphic distribution. — This ubiquitous and long-lasting species, which made its first appearance in the *riccartonensis* Zone of the early Wenlock (middle Sheinwoodian), continues through the entire Ludlow and reaches as high as the *perneri* Zone in the late Přidoli (KOREN' 1986a; JAEGER 1991). In the Late Silurian, it is commonly associated with almost every species as an accessory element of the assemblage, being a dominant or subdominant species in characteristic, impoverished assemblages usually also containing *Linograptus posthumus* and called in the present paper "*dubius* fauna" (p. 97). Common or numerous in the late Ludfordian, it is rather rare within the *parultimus–lochkovensis* interval of the Přidoli.

More or less clearly defined zonal variants are produced due to the appearance of minor traits, characteristic of certain horizons. These zonal variants, usually recognized as subspecies, were recently discussed by JAEGER (1991: pp. 313–316). Some such forms are, however, merely astogenetic and preservational variants. In the material presented herein, the appearance of forms with a robust, rod-like

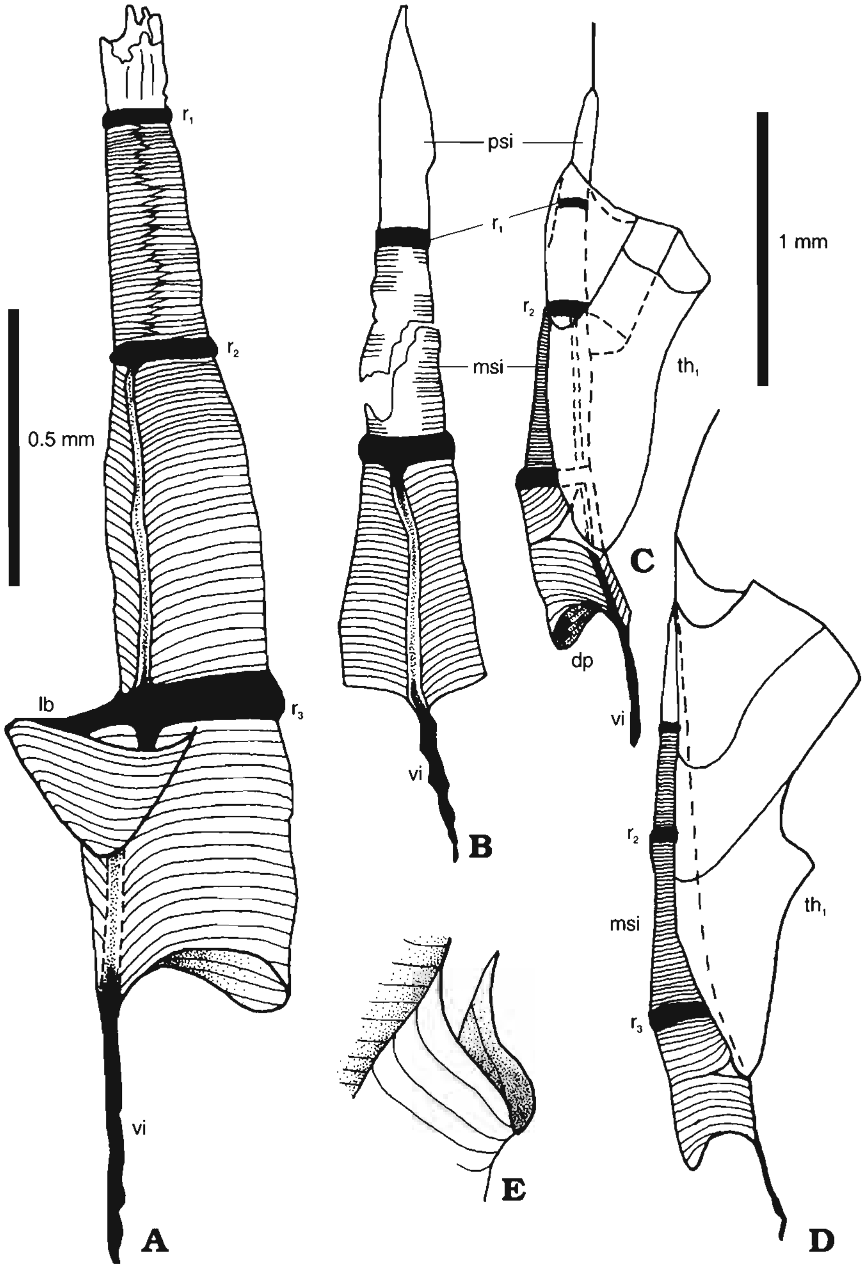

Fig. 43
Pristiograptus dubius cf. *frequens* JAEKEL. Growth of sicula (**A**, **B**) and early stages of astogeny (**C**, **D**) as well as an apertural border of theca (**E**). Note the fixed 3-ring pattern of sicula (r_1–r_3). Mielnik-1, depth 786.50 m, *acer* Zone.

or tubular virgula (Pl. 15: 7a, b, v) is characteristic of the interval of 815.10–802.70 m (*latilobus/balticus* Zone, ingression of the 1st *dubius* fauna as defined above, p. 97). Some intervals display the predominance of rather robust morphotypes or forms with a strikingly thick apertural margin, followed later by the re-appearance of standard *dubius* morphotypes which do not differ from the Gorstian ones, commonly regarded as *P. dubius frequens* and representing a gracile morphotype (e.g. *labiatus* case described below). Statistically, these latter forms are most common in the majority of assemblages. The only noteworthy difference is the number of sicular rings (annuli, see below) by which late Ludfordian populations of *P. dubius* differ from the Gorstian ones. This gracile morphotype is defined in the present paper as *P. dubius* cf. *frequens* (Fig. 43), but more studies are needed to define its taxonomic position.

The presence of this species in association with various monograptids together with its presence in low diversity assemblages may reflect its eurybiotic nature and lack of specializations.

Systematic position. — *P. dubius* played an important role in the phylogeny of Late Silurian monograptids due to its double role of a conservative survivor and the ancestor of new evolutionary lineages (KOREN' and URBANEK 1994; URBANEK 1996). Through most of its stratigraphic range *P. dubius* frequently occurs without undergoing any significant changes. This stability of phenotypic traits and persistence through time, provide substantion for the *dubius* stem lineage concept (KOREN' and URBANEK 1994). The prolonged stasis condition gives way to short periods of speciation (splitting of the stem lineage), producing more or less defined descendant species or subspecies (especially after the *lundgreni* Event when the so-called "early schism" initiated a true adaptive radiation, KOREN' and URBANEK 1994; and to a lesser degree after the *kozlowskii* Event and the *spineus* Event, URBANEK 1995). A simplified history of the *P. dubius* lineage seen in the light of recent studies is shown in Fig. 6.

Otherwise, during the periods of stasis *P. dubius* populations reveal quite an amount of variation, expressed i.a. in the degree of robustness of the rhabdosome. These changes did not achieve any evolutionary significance, as the relatively gracile morphotype, which does not differ much from those characteristic of Gorstian populations, would re-appear after the relatively long intervals dominated by more robust types. This would appear to exemplify the zig-zag mode of microevolution, with oscillating shifts of the mean value in time, although the migration of different ecotypes or microgeographic races onto the given area may also be responsible for the effect in question. More studies are necessary for any definite conclusion on this phenomenon.

There is, however, one remarkable difference between late Ludfordian and stratigraphically older populations of *P. dubius,* namely in the number of black rings (annuli) in the sicula. While Gorstian populations are characterized by a great amount of variation in this respect (0–8 rings in a sicula!) with a distinct predominance of multiannular forms, the late Ludfordian populations display a uniform presence of only three rings, r_1 situated at the boundary of pro- and metasicula, and r_3 placed close to the primary notch area (Fig. 43A, C, D). The significance of this condition is discused on p. 117. Moreover, the 3-ringed sicula is preserved in *P. dubius* derived taxa, behaving as a token, an "emblem-trait" of the latest Silurian pristiograptids.

A widely used practise to identify this species as *P. dubius* s.l. is justified in view of its considerable variation in minor traits combined with the preservation of its main features. Some of these traits, such as extreme robustness or extremely thickened apertural margins are accepted in the present paper as diagnostic characters of separate subspecies (*P. dubius fragmentalis*, *P. dubius labiatus* subsp. n.). Although the overall differences are small, they are segregated in time, which makes these taxa useful stratigraphically.

Pristiograptus dubius fragmentalis (BOUČEK, 1936)
(Pl. 15: 5, 6)

1936. *Monograptus fragmentalis* sp. n. BOUČEK,; BOUČEK, p. 7, text-fig. 1l–n .

1943. *Pristiograptus fragmentalis* (BOUČEK); PŘIBYL, p. 25, text-fig. IIR–5.

1976. *Pristiograptus fragmentalis* (BOUČEK); BOUČEK, MIHAJLOVIĆ and VESELINOVIĆ, pp. 88–91, pl. 2: 1–7, pl. 3: 1, text-fig. 2a–e.

1986. *Monograptus fragmentalis* BOUČEK; JAEGER, p. 316, pl. 2: 14–18, 20, 21.

1988. *Pristiograptus fragmentalis (*BOUČEK); KOREN', RINNENBERG and LYTOCHKIN, p. 17, text-fig. 14.

Material. — Several fragments of adult rhabdosomes, mostly semiflattened, juvenile growth stages rare.

Description. — Sicula 1.80–2.20 mm long, with an aperture 0.40 mm in diameter and a dorsal process 0.15 mm in length. Apex of the sicula reaches just above the aperture of th_1. Thecae as in the *P. dubius* standard morph. Rhabdosome straight, robust with a width of 0.65–0.80 mm immediately above th_1 and 1.25–1.30 mm immediately beyond th_5 (measured on semiflattened specimens).

Systematic position. — The close relationship of *P. dubius fragmentalis* to typical *P. dubius* is beyond any doubt. The subspecies differs from the type subspecies in the overall size, a greater maximum width and a more rapid increase in width in the growth of the rhabdosome. JAEGER (1986: p. 316) characterizes *P. dubius fragmentalis* simply as a giant *dubius* and emphasizes that the juvenile stages of both taxa cannot be discriminated.

This purely quantitative nature of specific charactes implies a subspecific rank of *P. fragmentalis*. This taxonomic decision by no means undermines its relatively high stratigraphic value, as the *fragmentalis* morphotype (large and robust *dubius*-like form) is highly characteristic of the latest Ludlow beds.

After its origination from the conservative *dubius* stem lineage, it attained probably no more than a semispecies stage, and its divergence from the ancestral taxon was a modest one.

Stratigraphic distribution. — In Mielnik-1 borecore, rhabdosomes with a "fragmentalis" appearance are confined to the *latilobus–balticus* Zone (FA at a depth of 821.00 m and LA at a depth of 819.40 m). They are not particularly abundant. In the Kopanina Formation of the Prague Basin and in Kursala Formation of the Alai Range, the subspecies is much more abundant and in some horizons even dominant. In Barrandian, it is a characteristic fossil for the uppermost zone of the Kopanina Formation. It is even recorded in association with *N. parultimus* in Serbia (Bouček *et al.* 1976) and in Central Asia (Koren' in print) and therefore crosses the Ludlow/Přidoli boundary.

Occurrence. — *P. dubius fragmentalis* is known from Europe (Barrandian, the Ruj Mountains in Serbia) and from Central Asia (Turkestan, the Alai Range).

Pristiograptus dubius labiatus subsp. n.
(Pl. 16: 1–11, Fig. 44A–D)

Holotype: Specimen figured on Pl. 16: 1, 2, ZPAL G.XIX/1.

Type stratum: The *spineus* Zone and the *spineus–parultimus* Interzone.

Diagnosis. — Pristiograptus from the *dubius* group, with exceedingly thickened apertural margins of the thecae, forming a kind of brim.

Derivation of name: From L. *labium*, lip.

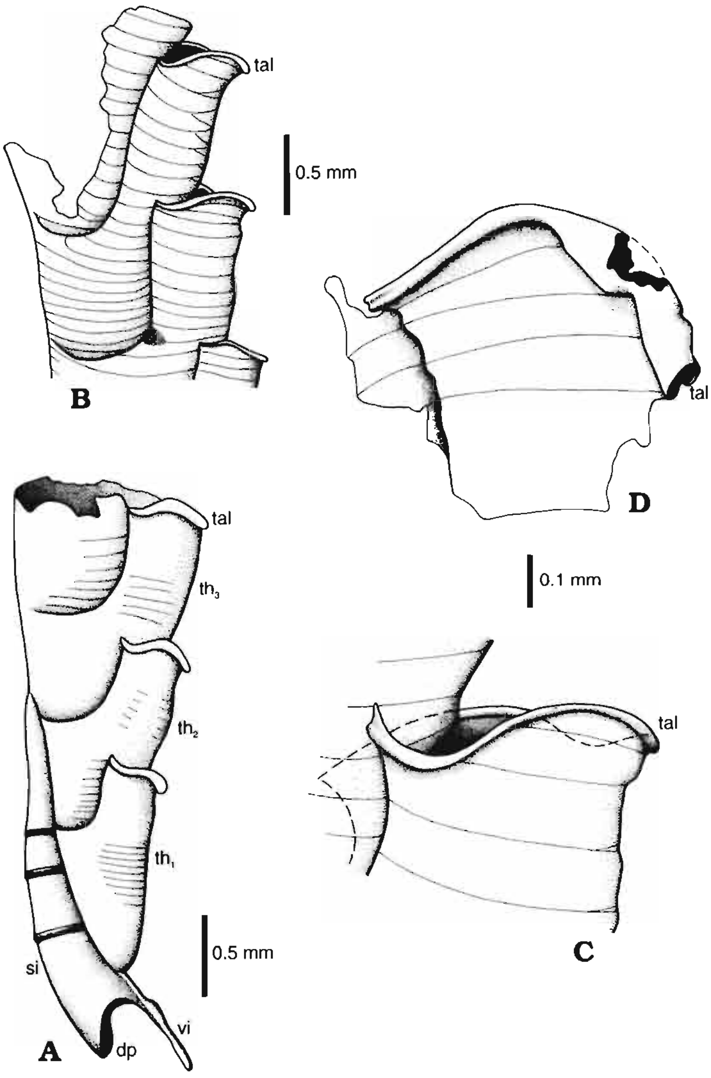

Fig. 44

Pristiograptus dubius labiatus subsp. n. Proximal (**A**) and distal (**B**) part of the rhabdosome, as well as the details of the thickened apertural lip (tal; **C**, **D**). Mielnik, depth 759.50 m, the *spineus* Zone.

Material. — A few dozens of specimens, mostly semiflattened, rarely 3-dimensional, including growth stages of the sicula, and proximal and distal fragments of the rhabdosome.

Description. — Morphology, proportions and dimensions do not differ from standard *P. dubius* s.l. as described above (Pl. 16: 1, 2, Fig. 44A, B), except for the presence of unusually strongly developed apertural margins of thecae (Pl. 16: 3–9, m, Fig. 44C, D, tal) and, to a lesser degree, the apertural margin of the metasicula (Pl. 16: 5). These thickened apertural lips are made of a heavy cortical deposit, which in higher magnification SEM's may be resolved into coarse cortical fibrils, oriented normally to the surface of the lip (Pl. 16: 10, 11, m, fb). They are distinctly thicker than apertural lips seen in standard *dubius* morph (compare Pl. 16: 12) and are considered the main diagnostic feature of the subspecies. Moreover, in most cases apertural border appears gently undulated (Fig. 44A–D).

Taxonomic position. — The overall morphology leaves no doubt that *P. dubius labiatus* subsp. n. is a little-specialized derivative of the *dubius* stem lineage. The 3-ring pattern of sicula (Fig. 44A, sic) and its FA (depth 760.60 m, *spineus* Zone) leave no doubt that ancestral populations should be assigned to *P. dubius* of the late Ludfordian type, after the "sicular revolution". The biological status of *P. dubius labiatus* subsp. n. is difficult to define. It is distinguished herein as a subspecies in view of its morphological characteristics and stratigraphic confinement to a certain interval.

Stratigraphic distribution. — Pristiograptids with the *labiatus* morphology were recognized in the Mielnik wellcore in the interval between 761.75–727.70 m, overlapping the *M. (U.) spineus* TSEGELNJUK range, and the lower part of the 3rd ingression of the *dubius* fauna as defined above. From the beginning, this impoverished faunal assemblage is composed of *P. dubius labiatus* subsp. n. In some layers, *P. dubius labiatus* subsp. n. displays a mass occurrence (e.g. at a depth of 757.15 m. and in its LA). Like other *P. dubius* subspecies, the new subspecies locally defines a clearly cut time interval, being preceded and replaced by the standard *dubius* morph (see Fig. 3).

Genus *Pseudomonoclimacis* MIKHAJLOVA, 1976
Pseudomonoclimacis latilobus (TSEGELNJUK, 1976)
(Pls 17–19, Figs 45–47)

1976. *Colonograptus latilobus* n. sp. TSEGELNJUK; TSEGELNJUK, p. 109, pl. 29: 9–11.

1983. *Saetograptus (Colonograptus) insignitus* n. sp. PŘIBYL; PŘIBYL, p. 160, pl. 1: 3–8, pl. 4: 11–13.

1988. *Ludensograptus latilobus* (TSEGELNJUK); TSEGELNJUK, p. 82, text-fig. 3.

1988. *Monograptus latilobus* (TSEGELNJUK); KOREN', RINENBERG and LYTOCHKIN, p. 17, text-figs 9–10.

Material. — Some 30 fragments of rhabdosomes, semiflattened and 3-dimensionally preserved, including early stages of astogeny.

Description. — Sicula long (1.80–2.12 mm), slightly ventrally curved, with its apex reaching to the level of the th_2 aperture. Prosicula (psi) measuring 0.45–0.60 mm in length, provided with an apertural ring (r_1). Metasicula (msi) 1.52–1.59 mm long, with a usually rather short and blunt dorsal process (0.09 – 0.15 mm long), sometimes stronger and pointed. Diameter of the metasicular aperture 0.36–0.45 mm, initial bud situated at a distance of 0.18–0.27 mm from the metasicular aperture. Metasicula provided with two (r_2, r_3) or a single apertural ring (r_2) and a fairly strong virgella, 0.6 mm long. (Figs 45A, 46; Pl. 17: 1–4).

Thecae, having an essentially pristiograptid appearance, displaying quite an amount of variation in the degree of expression of a number of characters which are species-specific. For descriptive purposes one could distinguish (1) a less advanced (Pl. 19) and (2) a more advanced morphotype (Pls 17, 18). Gerontic growth stages (Pl. 19: 6), with a robust appearance due to heavy secondary deposits and obliteration of some thecal characters add an additional dimension to the variation observed.

In three- dimensionally preserved specimens, th_1 is tubular, in flattened ones, somewhat triangular in outline. Its aperture in (1) has a gently undulated margin (Pl. 19: 1–5), while in (2) it is provided with distinct paired lobes (Pl. 17: 1, 2, 5; Pl. 18: 1–4). Its ventral wall and, in some cases, the ventral walls of th_2–th_3 are straight. However, starting from th_2, thecae exhibit to various degrees an excavation (e) of the ventral wall, comparable with that in Wenlock *Monoclimacis* or Gorstian–early Ludfordian *Pseud. dalejensis (= M. haupti)*. This excavation is bordered by a hoof-shaped angular thickening (Pl. 17: 7–9e, ex). Due to the ventral excavation, thecae display a gentle genicular bending situated at the level of the pro- and metatheca boundary and especially well seen on naturally split rhabdosomes (Pl. 15: 8, ex), where it is emphasized by a roll-like thickening. Distal, mature or gerontic thecae show, in the their upper parts,

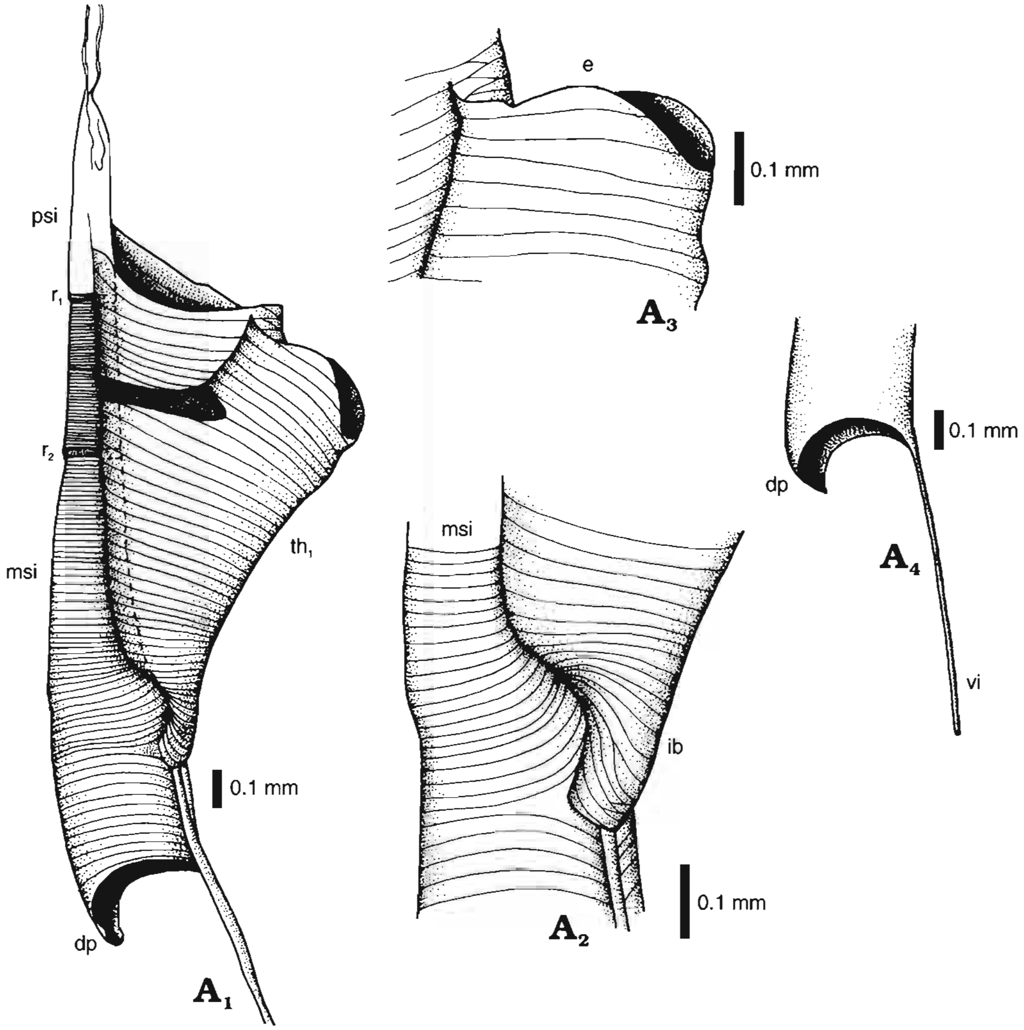

Fig. 45

Pseudomonoclimacis latilobus (TSEGELNJUK). Sicular part of a growing rhabdosome (**A**$_1$) and details of the fusellar structure: of the initial bud (A$_2$), aperture of th$_1$ (**A**$_3$) as well as the shape of metasicular aperture (**A**$_4$) with a distinct dorsal process (dp). Mielnik, depth 820.30 m, *balticus/latilobus* Zone.

above the ventral excavation, a flat surface, a kind of a shield bordered by a thickening with a hoof-like outline (Pl. 17: 7–9). This structure produces an appearance characteristic of this species.

Aperture is characteristically elaborated due to undulations (elevations) of the apertural margin, bordered by a single ventral notch and paired lateral incisions (Pl. 17: 7–10; Pl. 19: 14; Fig. 47e, n, ln). While the ventral notch (n) is usually shallow, lateral incisions (li) are distinctly deeper. Their presence is also a characteristic feature of *Pseud. latilobus* thecal aperture, which distinguishes it from the Přidoli *ultimus* Group. The degree of expression of undulation decreases distalwards in the given rhabdosome, until it acquires the form of a gentle elevation (Pl. 17: 5, 6, Pl. 18: 7, 8, Fig. 47).

Astogenetic changes are also expressed as a gradual elongation of thecae. While th$_1$ is 1.14 mm long, the distal thecae measure 1.90 mm from their base to the lower armpit of the lateral incision, and some 2.60 mm from the base to the ventral border of the aperture.

Moreover, in spite of a considerable variation observed in each sample, there is no progression in the degree of undulation upwards in the stratigraphic column. Quite to the contrary, earlier populations (Mielnik-1 borecore, depth 821.60 m) exhibit a higher expressivity of thecal characters, e.g. a strong development of undulations of the aperture, deep excavations etc.). Most proximal thecae, especially th$_1$, resemble the apertural lappets seen in *Colonograptus colonus* (URBANEK, 1958) or in *Neocolonograptus ultimus* (JAEGER, 1986). There is no question, however, about the homeomorphic nature of these resemblances.

Stratigraphically younger samples (depth 819.25 m) represent morphologically the less advanced morphotype. Th$_1$–th$_3$ show only a gentle undulation of the aperture, and th$_2$–th$_3$ display a very slight ventral excavation. While the size of the apertural lateral elevations remains unchanged, they become better expressed due to a deeper ventral and lateral incisions. The general habitus of such morphotypes resembles to some extent *N. parultimus* from the earliest Přidoli, although there is no doubt about their specific distinctness (see p. 106).

It is difficult to judge how much attention should be given to the observed "reverse" order of morphological changes in the Mielnik-1 material. The most probable explanation seems to be that they represent random statistical fluctuations (errors in sampling) due to the limited size of core samples. Most probably, natural populations of *Pseud. latilobus* always included large spectrum of variation, being composed of the more and less advanced morphotypes as defined above.

The thecal characters described above are subject to profound gerontic changes. Due to the deposition of ample secondary skeletal material (probably in the form of cortical bandages), rhabdosomes were changing their appearance and size, becoming more robust (Pl. 19: 6) with age. As in many other monograptids, such gerontic specimens may be difficult to identify because of the obliteration of some diagnostic features.

Rhabdosome is straight, quickly gaining in width: the width of the rhabdosome above th$_1$ is 0.7–0.8 mm, measuring 1.1 mm above th$_5$) and reaching 1.15 mm in the distal part (TSEGELNJUK 1976 mentions 2.3–2.6 mm for the most distal portion observed).

Taxonomic position. — Specimens from the Mielnik-1 borecore identified herein as *Pseud. latilobus* TSEGELNJUK reveal a close similarity to the TSEGELNJUK's specimens described from Volhynia (1976: pl. 29: 9–11 and especially 1978: pl. 1: 4, 6) both in the thecal characters and in the essential size parameters. Moreover, comparative studies on PŘIBYL's (1983) original material from Velki vrch Hill near Koneprusy (Barrandian, Central Bohemia) as well as on some additional material from this locality made avaiable by Dr. P. ŠTORCH (1993) clearly indicate that *Saetograptus (Colonograptus) insignitus* PŘIBYL 1983 is a junior synonyme of TSEGELNJUK's species. Hence, the *insignitus* Zone distinguished within the Kopanina Formation by PŘIBYL (1983: p. 154) is an equivalent of the *latilobus/balticus* Zone as defined above.

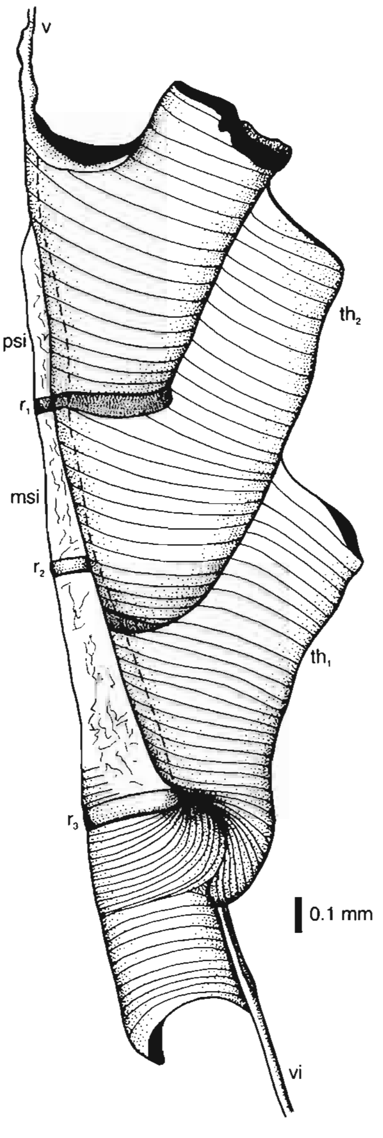

Fig. 46
Pseudomonoclimacis latilobus (TSEGELNJUK). Proximal part of the rhabdosome as seen on a bleached specimen. Mielnik, depth 820.30 m, *latilobus/balticus* Zone.

The ancestry of *Pseud. latilobus* is unclear. It either represents a derivative of the conservative *dubius* stem lineage (URBANEK 1995) or originates from *Pseud. dalejensis* (BOUČEK 1936). For the time being the latter hypothesis has been given preference in the present paper (see p. 108) because of the greater parsimony of evolutionary steps needed to transform the hypothetical ancestor into the descendant *Pseud. latilobus*. Especially the genicular bending and excavation could be transmitted and not invented *de novo*. However, JAEGER (1978) observed that rare gerontic specimens of *Pseud. dalejensis* developed certain unexpected traits (secondary apertural hoods or rims), which he considered features of specialization. At the present state of knowledge it is difficult to evaluate the phylogenetic significance of gerontic thecal characters (*Pseud. latilobus* itself displays advanced gerontic growth stages, see above). But it is true that the origin of *Pseud. dalejensis*, if not cryptic, poses certain problems. URBANEK (1958) was convinced that because of its ventral excavations *Pseud. dalejensis* represented a Wenlock relic affined to *Monoclimacis* FRECH. At some time this view was forcefully criticised by JAEGER (1959) who emphasized the incompletness of the *Monoclimacis* record across the *lundgreni–ludensis* interval. However, after the recognition of the Lazarus effect (JABLONSKI 1986) and its role in the faunal turn-overs in graptolites (URBANEK 1993), this argument lost its previous significance.

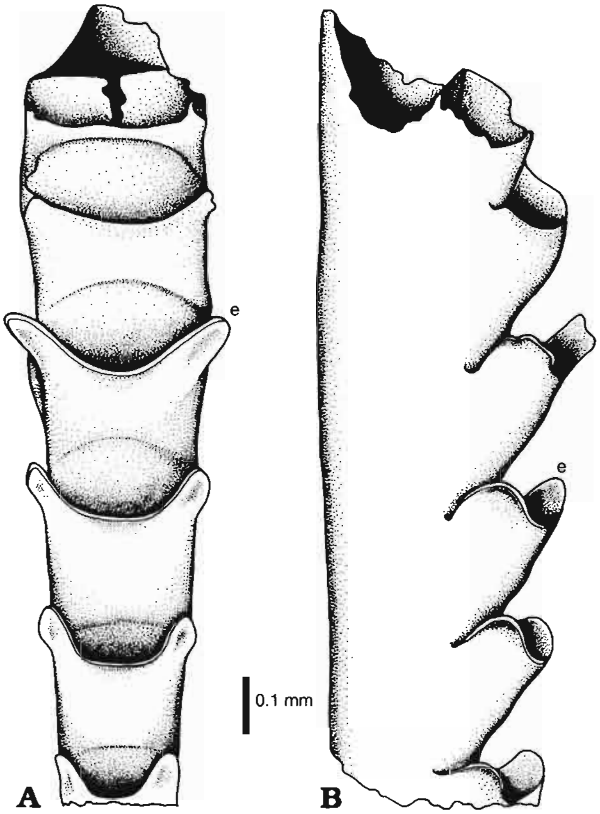

Fig. 47
Pseudomonoclimacis latilobus (TSEGELNJUK). Medial fragment of the rhabdosome seen in ventral (**A**) and lateral (**B**) view. Mielnik, depth 820.30 m, *latilobus/balticus* Zone.

Moreover, in the meantime we have also learned how easily such traits as the ventral excavation may be independently acquired in non-related lineages (compare p. 127). Thus, *Pseud. dalejensis*, which differs from *P. dubius* mainly in a certain reduction of size and in the appearance of the ventral wall, may equally well be derived from the conservative *dubius* stock, the source of many new lineages throughout the Late Silurian (KOREN' and URBANEK 1994; URBANEK 1995). It is, however, now quite clear that the *micropoma* Group of Ludlow monograptids represents a Lazarus taxon which escaped mass extinction in the Homerian (URBANEK 1993). Whether *dalejensis* is related to this group is an open question.

For the reasons already stated (p. 108), I consider the assignement of *Pseud. latilobus* to TSEGELNJUK's (1978) genus *Ludensograptus* unjustified. Also PŘIBYL's (1983) assignement of this species to *Colonograptus* is based on obsolete data.

A deceptive homeomorphy of *Pseud. latilobus* to the *ultimus* Group of Přidoli monograptids was the source of quite a number of erroneous opinions. URBANEK (1970: p. 182) for example, identified, at the preliminary stage of his studies on Mielnik-1 material, *Pseud. latilobus* as *N. ultimus* (PERNER). The same standpoint resulted in the incomplete understanding of the succession of faunal elements through the Ludfordian/Přidoli boundary in URBANEK's (1993) paper, dealing with biotic crises in the history of the Upper Silurian graptoloids (see also p. 104 herein). As a matter of fact, *Pseud. latilobus* is very similar to *N. parultimus–N. ultimus* group of species in its overall appearance, but differs from it in structural details (the former is more robust, it widens more rapidly and has distinct lateral incisions at the aperture, that are lacking in the latter). *Pseud. latilobus* is also too specialized (advanced) to be considered the ancestor of the early Přidoli bilobate species. Moreover, the development of the monograptid fauna across the Ludfordian/Přidoli boundary is punctuated by the *spineus* Event (p. 106 herein).

Stratigraphic distribution. — In the Mielnik-1 core, *Pseud. latilobus* in association with *Pristiograptus dubius fragmentalis* (BOUČEK, 1936) and *M. (Slovinograptus) hamulosus* TSEGELNJUK, 1976 makes its FA at a depth of 893.00 m. In this way it initiated the ingression of a new, late Ludfordian graptoloid fauna, after the *kozlowskii* Event. Its LA is observed at a depth of 809.15 m, while its single still higher occurrence (depth 787.00 m) is uncertain as far as the identification is concerned. Thus practically the entire range of *Pseud. latilobus* falls below the *M. (U.) acer* range and is separated from it by a certain gap (Fig. 3 herein and URBANEK 1995: fig. 3). It is frequently associated with *M. (S.) balticus* TELLER, 1966 and *M. (F.) formosus* BOUČEK, 1931. It therefore seems convenient to consider the species in question to be one of the index species of a single assemblage zone, namely the *latilobus/balticus* Zone (URBANEK 1995). A similar stratigraphic range of *Pseud. latilobus* is observed in Volhyno-Podolia (TSEGELNJUK 1976, 1981), where the associated monograptid fauna is even richer, as well as in the Kursala Formation of the Alai Range in Tien Shan (KOREN' and LYTOCHKIN 1992).

Occurrence. — *Pseud. latilobus* has been reported from a few regions only, namely from the EEP and from the Kopanina Formation, Barrandian [described by PŘIBYL 1983: p. 160, as *Saetograptus (Colonograptus) insignitus*], as well as from Central Asia (the Kursala Formation of the Alai Range, Tien Shan, KOREN' and LYTOCHKIN 1992; KOREN' and SUYARKOVA 1994).

Genus *Istrograptus* TSEGELNJUK, 1976
Istrograptus transgrediens rarus (TELLER, 1964)
(Pl. 20: 1–5, Fig. 8E)

1964. *Pristiograptus rarus* n.sp.; TELLER, p. 38, pl. 9: 10–12, text-fig. 3a–c.
1976. *Skalograptus rarus* (TELLER); TSEGELNJUK, p. 102, pl. 32: 6–9.

Material. — Several specimens, mostly flattened.

Description. — Sicula (Pl. 20: 1–5), rather robust, is 2.00–2.45 mm long, slightly ventrally curved and provided with a fixed number of three sicular rings. Prosicular apex reaches up to the level of th_2 aperture.

Prosicula, 0.60 mm long, has a distinct apertural ring (r_1). Metasicula is 1.40–1.85 mm in length and displays two rings (r_2, r_3), a fairly wide aperture (0.47 mm) and a strong dorsal apertural process (0.30–0.45 mm long). Initial bud is situated at a distnce of 0.25–0.30 mm from the apertural margin of the metasicula.

Thecae approximately triangular in outline. First theca (th_1) usually with a characteristic concave profile (Pl. 20: 2, 3). of its ventral wall, being inclined toward the long rhabdosome axis at 60° in its basal part and at 70°, at its apertural portion. This shape of th_1 is a "token" of the *transgrediens* group of species (*Istrograptus* TSEGELNJUK). The apertural margin of th_1 has a roll-like thickening and a gentle lateral undulation due to the presence of bilateral elevations, some 0.12 mm high, separated by a shallow ventral notch. Similar elevations, decreasing in size, are present in th_2–th_4. Long axes of these elevations are oriented postero-ventrally, which is another characteristic feature of the *transgrediens* lineage (Fig. 8E, arrowed). Apertures of th_5 and the succeeding thecae are nearly straight.

Rhabdosome straight, gradually gaining in width (0.7 mm above the level of th_1 and 0.9 mm, above th_5).

Taxonomic position. — The morphology and stratigraphic occurrence define this form as an early representative of the *transgrediens* group, with the greatest similarity to *P. rarus* TELLER, 1964. The nature of this monograptid has been recently revised by TELLER (this volume, p. 74), and it is now considered to be the initial member of the *transgrediens* lineage. Evidence that this lineage started to operate as early as the *ultimus* Zone, was presented by JAEGER (1986: p. 328). He also considered it likely that the long-lasting *transgrediens* stock was represented by more than one zonal variety. This view has been developed by TELLER (this volume) who recognized *rarus–chelmiensis* and *samsonowiczi* as successive links of the lineage terminating with true *transgrediens*. TSEGELNJUK (1988) assigned both *"Pristiograptus" rarus* and *"P." transgrediens* to his genus *Istrograptus*, which, in my opinion, is a valid decision, as they share a number of common traits and at the same time differ from *ultimus* group. Specimens showing strongly elaborated apertural margins (Pl. 20: 6a–c) and identified herein as *Istrograptus transgrediens* cf. *rarus*, may in fact represent a more advanced mnorphotype of the *transgrediens* lineage.

Stratigraphic distribution. — In the Mielnik wellcore, *Istrograptus transgrediens rarus* has been found in a sample at a depth of 689.55 m, within the *parultimus* Zone. Stratigraphically younger specimens with a *transgradiens* appearance are too fragmentary to be identified and described.

Occurrence. — EEP and probably Central Asia.

Genus *Neocolonograptus* gen. n.

Derivation of the name: Praefix from Gk. *neo*, new.

Diagnosis. — Pristiograptids with bilobate apertural elaborations, ranging from gentle undulations to strong lappets oriented antero-ventrally. Ventral walls of thecae sigmoidal or straight.

Neocolonograptus parultimus (JAEGER, 1975)
(Pl. 21, Fig. 48)

1899. *Monograptus ultimus* n. sp. PERNER; PERNER, p. 13, pl. 16: 4, 5 (non fig. 14 a, b = *Neocolonograpus ultimus).*
1940. *Monograptus (Pristiograptus) ultimus* PERNER; PŘIBYL, pl. 1: 9, 10.
1975. *Monograptus parultimus* n. sp. JAEGER; JAEGER, p. 119, pl. 2: 4, 8, text-fig. 4.
1976. *Pseudomonoclimacis ultimus* (PERNER); TSEGELNJUK, p. 106, pl. 30: 10–12.
1976. *Pseudomonoclimacis podolicus* n. sp TSEGELNJUK; TSEGELNJUK, p. 106, pl. 31: 1–3.
1979. *Monoclimacis parultimus* (JAEGER); PAŠKEVICIUS, p. 160, pl. 10: 1–5, pl. 24: 16–19, pl. 25: 1–5.
1983. *Ludensograptus parultimus* (JAEGER); TSEGELNJUK, pp. 94, 145.
1988. *Ludensograptus parultimus* (JAEGER); TSEGELNJUK, p. 83, pl. (1): 5.

Material. — A few dozens of rhabdosome fragments, flattened, semiflattened and 3-dimensional, including early astogenetic stages.

Description. — Sicula 1.41–1.76 mm long, metasicular part gently ventrally curved. Sicular apex reaches just the level of the th_2 aperture (Pl. 21: 1, 2, 4, 8, Fig. 48A). Prosicula, 0.36–0.49 mm in length, is provided with a distinct apertural ring (r_1).

Metasicula is 1.00–1.27 mm long, attaining a width of 0.36–0.40 mm at its aperture. Two metasicular rings (r_2, r_3) invariably present, and the origin of the virgella related to the r_2 level. Dorsal process of the sicula (dp) strong (length 0.14–0.20 mm), frequently ventrally incurved and producing a kind of "heel" (talon). Initial bud situated at a distance of 0.19–0.20 mm from the aperture of the metasicula.

Thecae display a gentle excavation at the ventral side of their base and in consequence are somewhat sigmoidal (Pl. 21: 4, 7, 8). This gives them a "pseudomonoclimacid" appearance. Most proximal thecae exhibit, in addition, incipient, sometimes hardly discernible, lateral undulations, separated by a shallow ventral notch (Pl. 21: 3, 5, 8; Fig. 48C). Upwards in the Mielnik section, there is a distinct increase in the expressivity and penetrance of this trait. Therefore the youngest populations display more pronounced undulations, especially well seen in th_1 (Pl. 21: 8). Th_1 is 0.83–1.05 mm long and 0.20 mm wide at the aperture, displaying a lateral apertural undulation 0.11–0.13 mm high. Successive 2–3 thecae show a decreasing degree of undulation of the apertural margin. In most specimens th_4 and the following thecae have almost straight apertures, which, similar to the previous ones, are only moderately thickened at the border (Pl. 21: 3, 6). A few specimens of th_1 show an abnormally strong development of their lateral apertural undulations, resembling true *ultimus*.

Rhabdosome straight and short, 0.41 mm wide immediately above th_1 and 0.83 mm, above th_5.

Taxonomic position. — This species was described by JAEGER (1975) as an immediate forerunner of *N. ultimus* (PERNER), as indicated by its morphology and stratigraphic position. Some authors (e.g. PŘIBYL 1983) although distinguishing *N. parultimus* as a separate species, nevertheless, recognized the *ultimus* Zone as the base of the Přidoli, obviously believing that *N. parultimus may* be considered an early zonal form of *N. ultimus.* The differences are, indeed, small, purely quantitative, and bridged by transient forms. Both species "grade into each other, so the assignement of transient specimens to either species becomes an arbitrary decision" (JAEGER 1986: p. 320).

The origin of *N. parultimus*, considered by JAEGER (1986: p. 320) to be cryptic, has been defined by URBANEK (1993: p. 35) as "semicryptic" because of its doubtless and close relation to the *P. dubius* stem lineage. One can hypothetize that *N. parultimus* originated somewhere by parapatric or allopatric speciation from the *dubius* populations of the latest Ludlow, and later spread by migration. This is indicated i.a. by the 3-ring pattern of the sicula, a token of the Ludfordian *P. dubius* derived taxa (p. 118 herein). Therefore, the resemblance of *Pseudomonoclimacis latilobus* and *Pseud. dalejensis* to *N. parultimus* is deceptive and purely homeomorphic. The former is too specialized and the latter separated by too large a time gap to be considered an ancestor. As the earliest representatives of *N. parultimus* in the Mielnik wellcore display sigmoidal thecae but only negligible apertural elevations, one could hypothetize that the immediate ancestor lacked any apertural undulations but revealed a certain degree of ventral excavation of the thecae. Technically, such a pristiograptid might be assigned to *Pseudomonoclimacis*, and the case may be described in terms of generic transition as discussed above (p. 125).

Stratigraphic distribution. — In the Barrandian area, the first appearance of *N. parultimus* defines the basal zone of the Přidoli (KŘIŽ *et al.* 1986). Likewise, in the Mielnik wellcore, FA of *N. parultimus* at a depth of 691.95 m is considered the lower boundary of the Přidoli segment of the core. The beds with *parultimus* are 16.30 m thick (LA at a depth of 675.65 m), which is a large thickness as compared to the maximum attained in Barrandian (2 m) or in the Tien Shan (30 cm!). As in the type area, *N. parultimus*

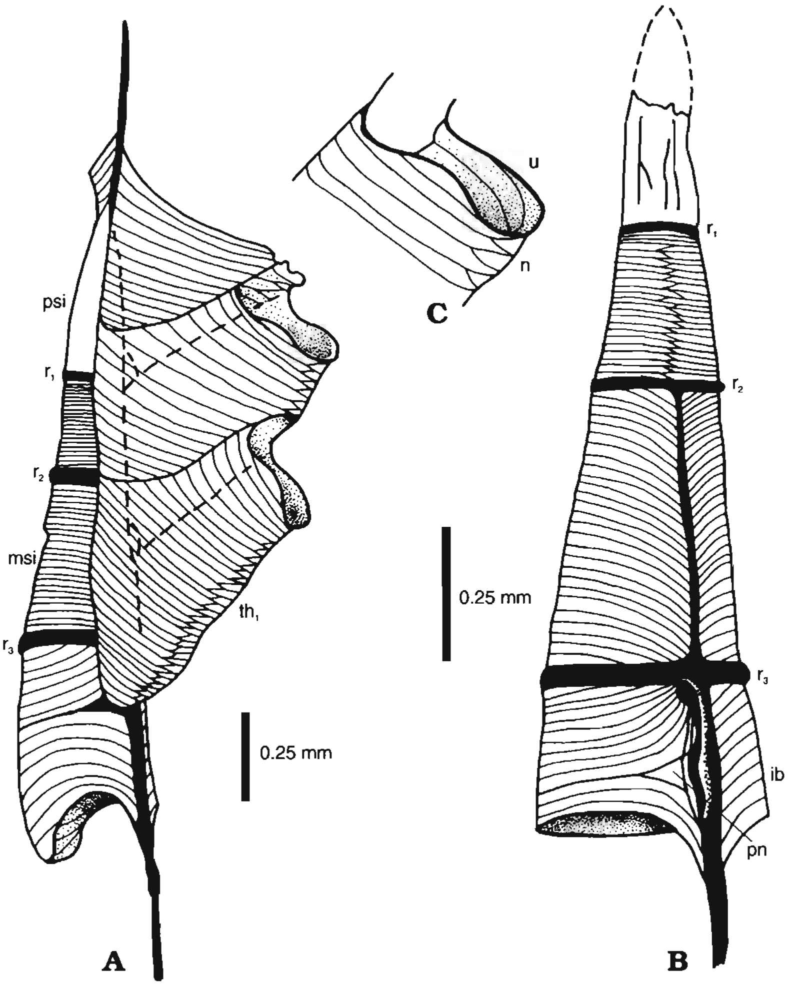

Fig. 48
Neocolonograptus parultimus (JAEGER). Early stage of astogeny (**A**), the origin of virgella (**B**) and the aperture of th$_1$ (**C**). Note the 3-ring pattern of sicula and the origin of virgella related to r$_2$. Mielnik, depth 686.80 m, *parultimus* Zone.

occurs in the Mielnik section in abundance, displaying a gregarious habit and crowding in monospecific assemblages in certain layers. Sample from a depth of 690.25 m represents a "centrotype", a standard morph comparable with the specimens described by JAEGER (1975) from the type stratum in Barrandian. The last sample with *N. parultimus* is represented by clearly more advanced forms.

Occurrence. — Outside Barrandian, *N. parultimus* is known from deep borings in the EEP (Volhynia, Lithuania, Eastern Poland), from the Carnic Alps, E. Serbia and from the Tien Shan and in Arctic Canada (JAEGER 1986; BOUČEK *et al.* 1976; KOREN' in press; LENZ 1990). In E Serbia, Tien Shan and the Canadian Arctic Islands it is associated with *M. (F.) formosus* and *P. dubius fragmentalis*,or some other Ludlow species, which indicates the overlapping ranges of the late Ludfordian and early Přidoli index graptolites.

Neocolonograptus ultimus (PERNER, 1899)
(Pl. 22, Fig. 8C)

1899. *Monograptus ultimus* n. sp. PERNER; PERNER, p. 13, text-fig. 14a, b (non pl. 16: 4, 5 = *N. parultimus* JAEGER).
1975. *Monograptus ultimus* PERNER; JAEGER, p. 119, text-fig. 4b.
1976. *Monograptus vetus* n. sp. TSEGELNJUK; TSEGELNJUK, p. 101, pl. 32: 2–5.
1977. *Monograptus ultimus* PERNER; JAEGER, p. 339, text-fig. 2A.
1978. *Monograptus ultimus* PERNER; JAEGER, p. 44, text-fig. 12.
1986. *Monograptus ultimus* PERNER; JAEGER, p. 321, pl. 1: 3, 4, 7, 11, 13, pl. 2: 7, 8, text-figs 35a–b, 36a–c, 37a–d, 38.
1990. *Pseudomonoclimacis ultimus* (PERNER); LENZ, p. 1080, text-fig. 4V–Z.

Material. — Several fragments of 3-dimensionally preserved rhabdosomes, mostly medial and distal.

Description. — Sicula, 1.85 mm long, slightly ventrally curved and provided with a distinct dorsal process (0.10 mm in length) and a relatively strong virgella (Pl. 22: 2, si). Diameter of the metasicular aperture is 0.32 mm, while the initial bud is situated at a distance of 0.24 mm from the metasicular aperture. Prosicular apex extends to the level of the th_2 aperture.

Thecae having a pristiograptid foundation but provided with elaborated apertures forming either paired lobes (th_1, th_2) or more or less conspicuous undulations (elevations) of the apertural border, separated by a deep ventral and a shallow dorsal apertural notch. Th_1 subtriangular in shape, 0.90–1.00 mm long, with its ventral wall slightly concave. Its aperture exhibits elaborated paired apertural lobes (lappets) rising 0.25 mm above the margin, directed antero-ventrally and separated by a "V"-shaped ventral notch (Pl. 22: 4, 5). Remaining thecae are tubular with a hardly discernible gently sigmoidal ventral wall (this character is less pronouced than in *N. parultimus*). Their apertures are provided with gradually decreasing undulated margins forming paired lateral elevations (u), approximately 0.20 mm high in th_2 and 0.15 in th_3. They are directed postero-distally (Pl. 22: 4, 5, arrowed). The height of these undulations, gradually decreases in successive thecae (distalwards). Each elevation is separated by a "U"-shaped ventral notch and by a shallow dorso-lateral notch. The latter is much shallower as compared with the conditions observed in *Pseudomonoclimacis latilobus* (p. 162 herein).

Rhabdosome straight, attaining a width of 0.5 mm immediately beyond th_1 and 0.75, above th_5.

Taxonomic position. — There has been considerable confusion over the true nature of this species in the past, primarily as the result of an underestimation of the role homeomorphy played in the monograptid evolution (assignement to *Monograptus, Pristiograptus*, and *Skalograptus* were proposed). In the light of the careful studies by JAEGER (1977, 1978, 1986), *N. ultimus* should be regarded as the immediate descendant of *N. parultimus,* appearing through intergradation. The evolutionary changes involved were primarily related to an increase in size and of modifications in the shape of the apertural lobes and elevations. The change was achieved through addition of a greater number of fusellar growth bands to the incipient undulations seen in ancestral *N. parultimus.* This is especially true in respect of th_1 and th_2 which show the highest expression of the character and, in extreme cases, mirror the conditions observed at the *lochkovensis* structural level. Moreover, a sample from a depth of 671.55 m contains specimens which could still be classified as *N. ultimus* but are transient to *N. lochkovensis branikensis* (JAEGER) in the size and shape of the lobes.

JAEGER's (1986) studies on the material etched from the successive horizons in Barrandian reveal a great amount of variation in expressivity and penetrance of the apertural undulations, observed both within the same rock sample and in the stratigraphic succession. The progression from *N. parultimus* towards *N. ultimus* was far from uniform either (JAEGER 1986: pp. 322–323). Nevertheless, TSEGELNJUK's (1978, 1988) suggestion to identify the advanced morphotypes found by JAEGER (1986: e.g. fig. 37a) within the *ultimus* populations as a seperate morphospecies (*Skalograptus vetus),* intermediate in characteristics between the centrotype of *ultimus* and true *lochkovensis,* seems unnecessary. It misinterpretes the phylogeny, which in this case most probably involved the appearance of an advanced morph and an increase of its abundance in populations. Morphs with essentially *lochkovensis* features still belonged to the *ultimus* level of evolution as they were outnumbered by less advanced morphotypes (JAEGER 1986: p. 323).

Stratigraphic distribution. — In Barrandian, this species defines a distinct zone with a maximum thickness of some 4 m. In Mielnik-1 borecore, it defines a rather narrow band (some 3.40 m thick, with FA at a depth of 674.95 m and LA at a depth of 671.55 m). It overlies the *N. parultimus* Zone and underlies the *N. lochkovensis* Zone, both of a much greater thickness (Fig. 3).

Occurrence. — Numerous sites in Europe are listed in JAEGER (1986). It was found also in N Africa (Morocco) and its presence in N America (Canada, Yukon Territory) is considered almost certain by JAEGER (1986: p. 324), who considers *Monograptus bugensius* described by JACKSON and LENZ (1969) as a synonym of *N. ultimus.* LENZ described it from Canadian Arctic Islands, within well developed zone.

Neolobograptus lochkovensis branikensis (JAEGER, 1986)
(Pl. 23, Fig. 8D)

1986. *Monograptus branikensis* n. sp.; JAEGER, p. 325, text-fig. 40, pl. 1: 10, 12, 14.

Material. — Several specimens mostly 3-dimensionally preserved.

Description. — Because of the essential resemblance to the type subspecies, description is given in a comparative form. Sicula in Mielnik-1 specimens is somewhat smaller, attaining a length of 1.76 mm (with the dorsal process, dp) or 1.60 mm (without the dp). Apex of prosicula reaches to the level of the aperture of th_2 or the protheca of th_3. Initial bud is situated at a distance of 0.3–0.2 mm from the aperture of the sicula (Pl. 23: 1–2a).

Thecae and rhabdosome are strikingly similar to those in *N. lochkov. lochkovensis.* Apertures of the proximal and medial thecae are provided with paired lateral lobes, thus representing the bilobate type of apertural accessories (Pl. 23: 2b, 3, 4, Fig. 8D). Length of the apertural lobe in th_1 is 0.56 mm, its free part stretching beyond the thecal tube is 0.28 mm. Rhabdosome is straight, gradually increasing in width and being some 0.4 mm immediately at th_1 and some 0.5 mm, beyond th_4.

Since specimens exceeding the critical length of 15 thecae were not available in the material from the Mielnik-1 borecore, the discrimination between the type subspecies and *N. lochkov. branikensis* is based on thecal characters, namely on the size and shape of the apertural lobes. As observed by JAEGER (1986: p. 326), the apertural lobes in the proximal thecae of *branikensis* "are typically less downcurved than those in *M. lochkovensis*". The form assigned herein to *N. lochkov. branikensis* exhibits apertural lobes which are somewhat smaller and usually end bluntly (in some cases they are pointed). They do not reveal the so-called "beaks" or "hooks", so characteristic of the apertural lobes in higher zonal populations of true *N. lochkovensis.*

Taxonomic position. — Because of a great morphological similarity between the *N. lochkov. branikensis* and the type subspecies, as well as because of a purely quantitative nature of the crucial distinguishing character: the presence *(*true *lochkovensis)* or lack (*branikensis)* of an overlap in distal thecae (beyond 15 thecae), *N. lochkov. branikensis* is ranked in the present paper as a chronosubspecies. If we follow the practice of considering these closely related forms distinct species (as suggested by JAEGER 1986), the bulk of the specimens available in routine works, would remain unidentified. I therefore believe that for practical reasons the concept of *N. lochkovensis* should be maintained in a broad sense. Besides, it is morphologically intermediate between *N. ultimus* and *N. lochkov. lochkovensis*, being much closer to the last named taxon (JAEGER 1986: p. 325). The morphological intergradation is best illustrated on one hand by the resemblance of the most proximal thecae in the advanced morphotypes of *N. ultimus* to *N. lochkov. branikensis,* and on the other, by the resemblance between the juvenile growth stages of *N. lochkov. lochkovensis* and *N. lochkov. branikensis* (Fig. 8B–D). These facts provide a substantiation to JAEGER's (1986: p. 325) opinion that his *branikensis* "could well be a descendant of *M. ultimus* and the ancestor of *M. lochkovensis*". However, because of the gaps separating the vertical ranges of the taxa, both in Barrandian and in the Mielnik-1 section, the immediate intergradations between them cannot be traced in the sequence.

Stratigraphic distribution. — In the Mielnik-1 wellcore *N. lochkovenesis branikensis* makes its FA at a depth of 671.30 m and disappears at a depth of 669.80 m. *N. lochkov. branikensis* stratigraphically precedes the appearance of *N. lochkov. lochkovensis* both in Barrandian (JAEGER 1986) and in the Mielnik-1 section.

Occurrence. — Outside Central Bohemia *N. lochkovensis branikensis* has been found in the Kursala Formation of the Turkestan-Alai Range, Central Asia (KOREN', in press).

Neocolonograptus lochkovensis lochkovensis PŘIBYL, 1940
(Pls 24–26, Figs 49–55, 56A)

1940. *Monograptus (Pristiograptrus) lochkovensis* sp. n. PŘIBYL; PŘIBYL, p. 69, pl. 1: 6.
1964. *Pristiograptus aduncus* n. sp. TELLER; TELLER, p. 42, pl. 1: 4, pl. 2: 1–6, pl. 7: 18, 19, pl. 9: 4–9, text-fig. 5a–d.
1964. *Pristiograptus bugensius* n. sp. TELLER; TELLER, p. 40, pl. 2: 4, 5, 9, pl. 7: 13–15, pl. 9: 1–3, text-fig. 4a–c.
1977. *Monograptus lochkovensis* (PŘIBYL); JAEGER, p. 324, text-fig. 3A–C.
1986. *Monograptus lochkovensis* (PŘIBYL); JAEGER, p. 324, text-fig. 39a, b, pl. 1: 16, pl. 3: 16, 17.

Material. — A few dozens of rhabdosome fragments, mostly proximal parts with growth stages of the sicula and th_1. Distal fragments short and rare. Specimens frequently well-preserved, three-dimensional and flattened to different degrees.

Description. — Sicula (Fig. 49A, B; Pl. 24: 1a, Pl. 25: 2, Pl. 26: 1, 2), straight and rather large, approximately 2.00 mm long when measured with the dorsal process of the metasicula, 1.80 mm, without it. Metasicula distinctly widens towards the aperture attaining a diameter of 0.40 mm. Aperture of the sicula displays a conspicuous dorsal process, shovel-like or angular in shape, sometimes incurved

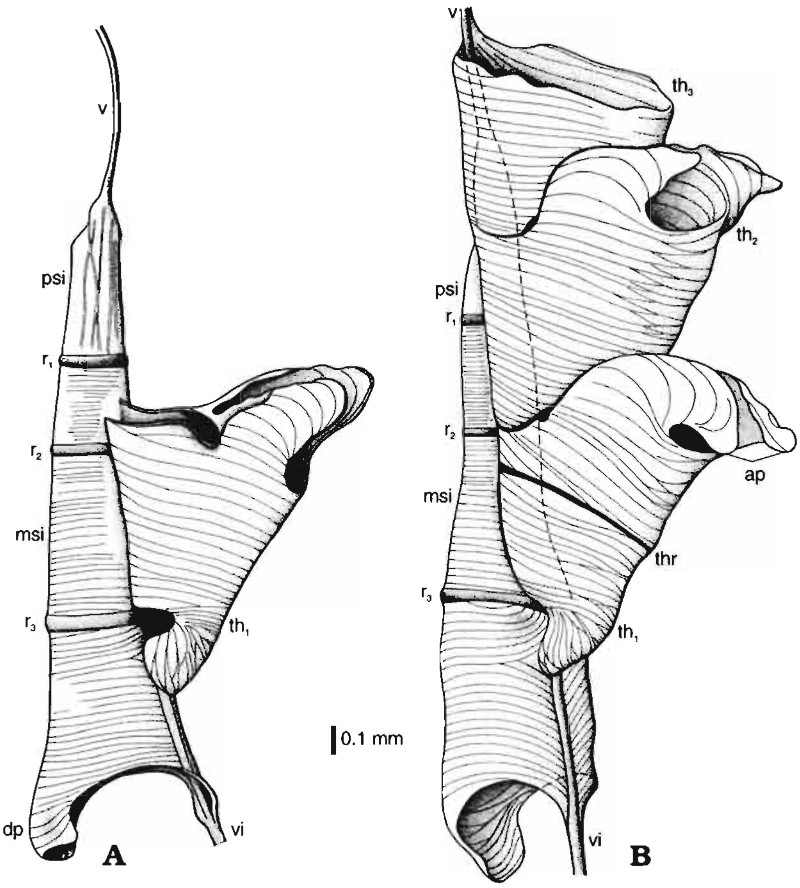

Fig. 49
Neocolonograptus lochkovensis lochkovensis (PŘIBYL). Sicula with the first theca (**A**) and proximal part of the rhabdosome (**B**) seen in reverse aspect. Mielnik, depth 659.30 m, *lochkovensis* Zone.

ventrally. Margins of the aperture are frequently bordered by a thickened rim (Pl. 24: 1a). Apex of the sicula is situated immediately below or at the level of the th$_2$ aperture.

Bleached early growth stages of the sicula reveal a regular monograptid pattern of development. Prosicula, 0.60–0.70 mm long, exhibits numerous longitudinal threads (Fig. 49A, psi) and is provided with a strong apertural ring (r$_1$). During the growth of the metasicula two more rings (r$_2$, r$_3$) appear, the last being situated at the primary notch. The number of rings (3 instead of 2) and especially the position of r$_3$ gives the sicula a "primitive" appearance, reminiscent of Gorstian pristiograptids (p. 117 herein). Budding of the initial bud follows the ordinary stages (*sinus* and *lacuna*), with the first fuselli of th$_1$ being laid down in a standard way (Fig. 50, pn, ib). Metasicula is 1.50–1.60 mm long, with the initial bud situated at a distance of mm from its final aperture which, being 0.60 mm in diameter, exhibits a conspicuous dorsal process, 0.20–0.40 mm long (dp, Fig. 51A), and a strong virgella (vi). Abnormal, trumpet-like apertures were also observed (Fig. 51B).

Thecae are of a pristiograptid appearance but the proximal ones have elaborated paired lateral lobes (the bilobate adaptive type). Th$_1$ subtriangular, rather short (0.86–0.92 mm) and wide (0.54–0.70 mm at the aperture). A thin dark thecal ring may be seen on some bleached specimens (Fig. 49B, thr), being another "primitive" feature inhererited from the Gorstian ancestors. Remaining proximal thecae are tubular, but rather short and wide (Pl. 24: 1a, Pl. 25: 1).

Proximal thecae are provided with strongly developed paired and symmetric apertural lobes (Figs 52–54; Pl. 25: 3–9, l). A study of strongly bleached apertural lobes, detached from the theca with a needle, reveals that at an early growth stage the lobe (l) is made of 1–2 fuselli which are shortened and produce no zig-zag sutures. Instead, ventral and dorsal notches (dn) are formed (Fig. 54A). Further growth occurs by addition of a number (7–9) of fuselli in a characteristic arrangement: they converge towards the base on the ventral margin, ending freely on the dorsal one (Fig. 54B). The lobes of the most proximal thecae

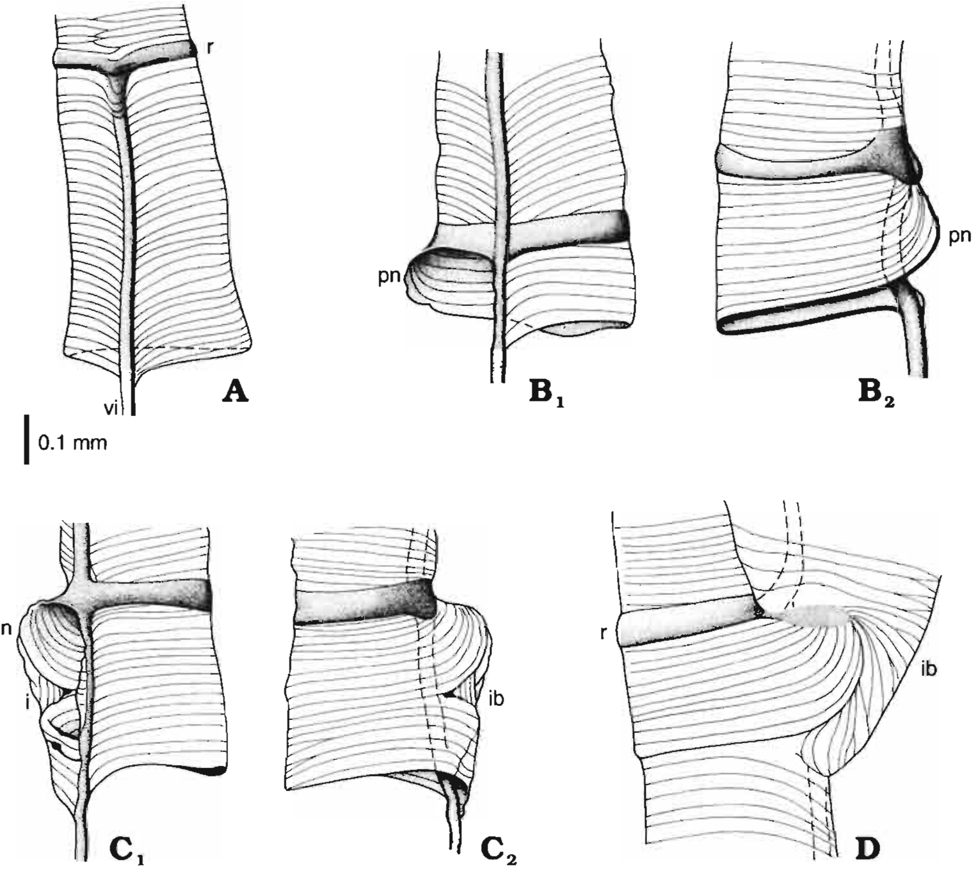

Fig. 50
Neocolonograptus lochkovensis lochkovensis (PŘIBYL). Growth stages of metasicula: onset of virgella (**A**), formation of the open primary notch ("sinus" stage) seen ventrally and laterally (**B**$_1$, **B**$_2$), closed primary notch ("lacuna" stage, **C**$_1$, **C**$_2$), fusellar structure of the initial bud (**D**). Mielnik, depth 665.60–644.00 m, *lochkovensis* Zone.

show an angular bending (Figs 52B, 54B; Pl. 25: 7, 9). This portion of the lobe overhangs the aperture, producing a kind of a roof, while the free margins of the adjacent lobes are separated by a slit. The last two fuselli on each lobe produce a pointed termination (p), which typically is downcurved (Fig. 54B; Pl. 25: 5–8b). The outer surface of the lobes is more or less distinctly concave (Fig. 52B, C, c). It is difficult to judge whether this feature is primary or preservational. JAEGER (1986) does not mention this lobe-feature when describing his isolated material. Most of the anterior margin of the lobes in the proximal part of the rhabdosome is curved upward to form a narrow rim (Fig. 52B, C). Orientation of the long axis of these lobes is ventro-lateral (horizontal).

The dorsal notch (dn) in the apertural lobes is subject to a certain astogenetic variation. It is shallow in juvenile proximal thecae and deeper, somewhat protruding (in the form of a pocket), in medial ones (Fig. 54A–C). Distalwards it undergoes partial infilling by a secondary deposit (Fig. 54D).

Apertural devices of *N. lochkovensis lochkovensis* display a great amount of preservational variation, due to deformations of the lobes. Frequently they change the appearance of the rhabdosome entirely (Fig. 55; Pl. 26: 3a, b).

Distalwards, the apertural lobes gradually decrease in size to attain the form of small undulations (Pl. 24: 4, 5). However, even the most distal fragments reveal thecae with gently undulated borders. Most authors have described the apertures of the most distal thecae in the species as quite simple, truly pristiograptid.

The degree of thecal overlap increases towards the distal end. This feature is especially well seen on long specimens, embedded in the matrix (compare JAEGER 1986: p. 324). The distal portion of the rhabdosome, made of elongated, strongly overlapping thecae is typical for the subspecies.

Rhabdosome straight and fairly large (up to 80 mm long, according to JAEGER 1986), but observed isolated fragments are no longer than 10 mm.

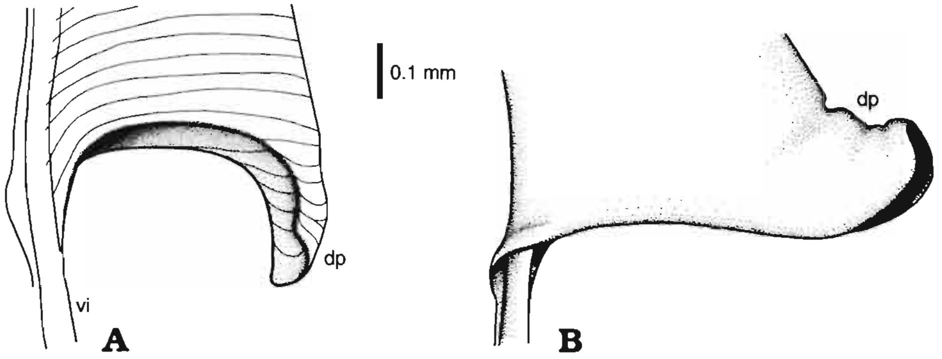

Fig. 51
Neocolonograptus lochkovensis lochkovensis (PŘIBYL). Normal (**A**) and aberrant (**B**) shape of the aperture in metasicula. Mielnik, depth 659.30 m, *lochkovensis* Zone.

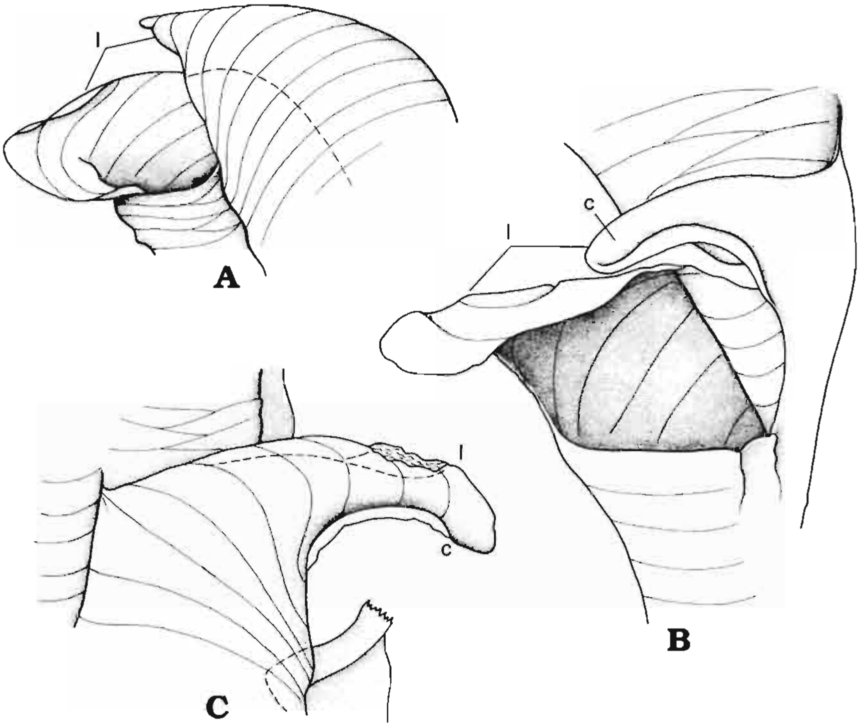

Fig. 52
Neocolonograptus lochkovensis lochkovensis (PŘIBYL). Apertural apparatus examined on bleached specimens: in a proximal theca (**A**) seen laterally, in distal thecae seen ventrally (**B**) and laterally (**C**). Mielnik, depth 659.30 m, *lochkovensis* Zone.

Abnormal development. — The specimen illustrated in Pl. 26: 4, displays a unique morphology: while th_1 and th_3 feature are typically provided with a bilobate aperture (l, arrowed), the aperture of th_2 is hooked (Dl, arrowed). The significance of this teratology is discussed elsewhere (p. 156).

Taxonomic position. — *N. lochkovensis lochkovensis* may best be placed as the terminal link within the *parultimus–ultimus–branikensis* lineage. In my opinion, this view fits best the morphological and stratigraphic record. Although the apertural lobes in the species in question are much more elaborated than those observed in the *parultimus–ultimus* group, this morphological gap is largely bridged by the advanced morphotypes of *N. ultimus* and by *N. lochkovensis branikensis*. The morphological change observed implies an increase of the lobe size by deposition of a greater number of fuselli (a process frequently observed in many groups of monograptids) and a certain alteration in the direction of their growth. The latter was achieved gradually, from the postero-dorsal orientation in the *ultimus* group to the antero-ventral one in the *lochkovensis* group. Advanced morphotypes of *N. ultimus* (such as that figured

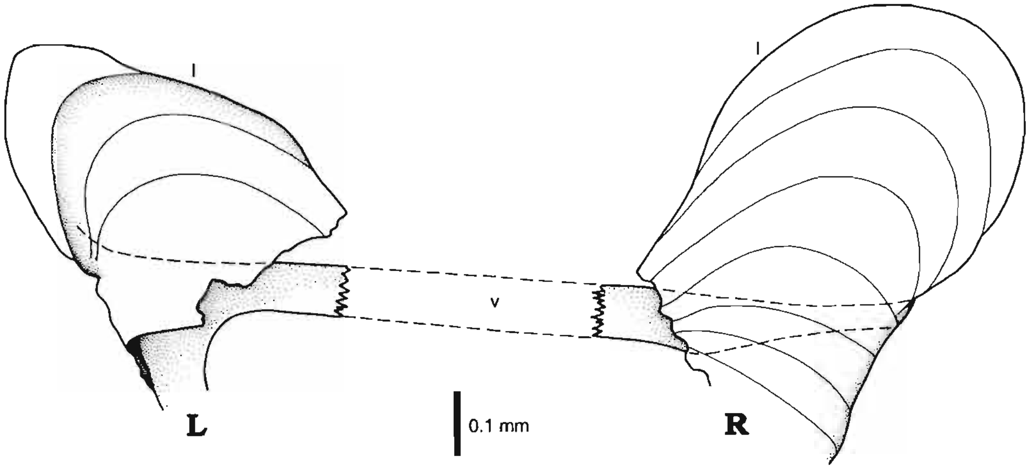

Fig. 53
Neocolonograptus lochkovensis lochkovensis (PŘIBYL). Detached right (**R**) and left (**L**) apertural lobe (l) seen on bleached needle preparation in ventro-distal view. V-thickened ventral apertural margin. Mielnik, depth 659.30 m, *lochkovensis* Zone.

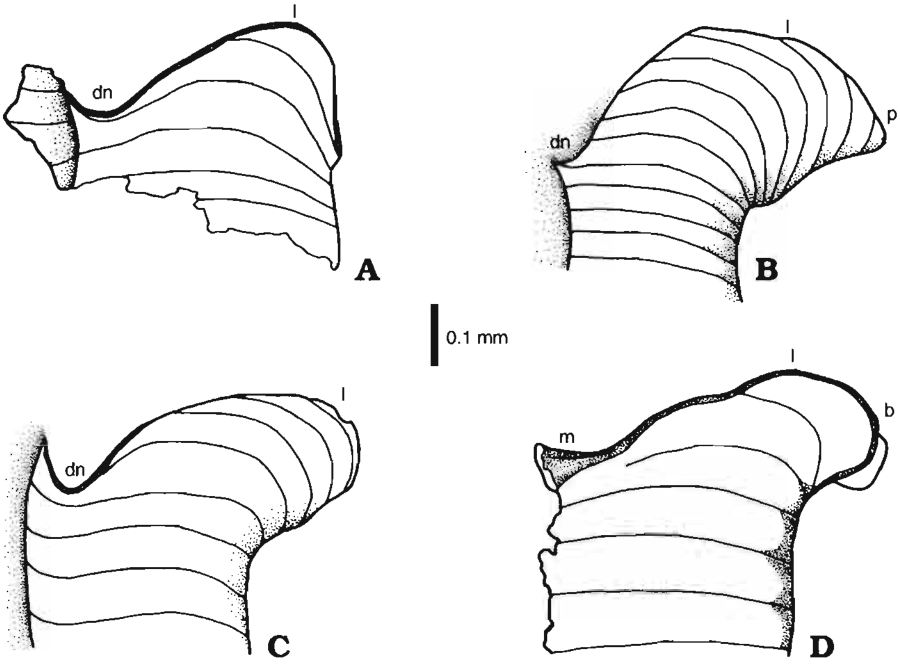

Fig. 54
Neocolonograptus lochkovensis lochkovensis (PŘIBYL). Fusellar structure of apertural lobes (l) seen on strongly bleached specimens: **A**, juvenile growth stage in a proximal theca; **B**, advanced growth stage of th_1; **C**, mature medial theca; **D**, gerontic medial theca. Note the different degree of development of the dorsal notch (dn) and its filling with the secondary material (m) in **D** as well as a pointed (p) or blunt termination of the lobe. Mielnik, depth 659.30 m, *lochkovensis* Zone.

by JAEGER 1986: fig. 37a and c), exhibit an almost *lochkovensis* grade of expression and have th_1, and sometimes th_2, oriented antero-ventrally. Even the standard morphotype of *N. ultimus* displays th_1 resembling *lochkovensis* in the size and orientation of the lobes. Such traits are truly "proterogenetic" as they anticipate the future direction of change. TSEGELNJUK's (1976, 1978) *Skalograptus vetus* may be understood as a morphospecies enveloping phenotypes which are intermediate between *N. ultimus* and *N. lochkovensis*. *N. vetus* is considered conspecific with *N. ultimus* by JAEGER (1986). In any case distinguishing transients as separate species seems a superfluous procedure, because particular sections could contain every possible random sample from the probably continuous, although not necessarily uniform,

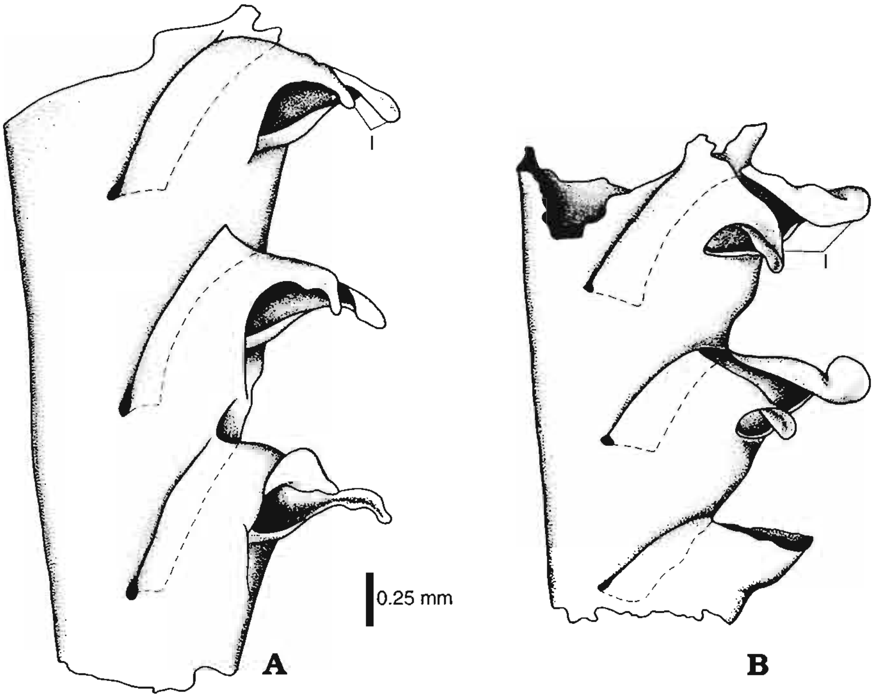

Fig. 55
Neocolonograptus lochkovensis lochkovensis (Přibyl). Distal fragments of the rhabdosome (**A**, **B**) showing different preservational features of apertural apparatus. Mielnik, depth 659.30 m, *lochkovensis* Zone.

phylogenetic progression. The relation of *N. lochkovensis* to the newly erected *Monograptus tumultuosus* (Koren', in press) is unclear and needs further studies (see Teller, this volume, p. 78).

This species may be most safely distinguished from *N. lochkovensis branikensis* by the presence of a considerable overlap in the most distal thecae (Jaeger 1986). However, the proximal thecae also display a species-specific character, namely the presence of downcurved beak-like terminations of the apertural lobes. Original specimens described by Přibyl (1940) from the Marble Quarry locality in Lochkov, as well as other topotypes, all reveal this character. Hence, this particular shape of lobes may be considered a typical character of true *lochkovensis*.

An alternative point of view on the origin of *N. lochkovensis*, as advanced by Tsegelnjuk (1978, 1986), is discussed elsewhere (p. 108). However, a comparison of apertural structures in the standard *lochkovensis* morph (A), in *M. (Dulebograptus) trimorphus* (B), and in the teratological (dulebograptid-like) form (C), as shown in Fig. 56, provides no substantiation for their immediate relations (see p. 156 for an extended discusssion).

Stratigraphic distribution. — In much of the Barrandian area, *N. lochkovensis* marks a distinct zone as recognized for the first time by Přibyl (1940). A recent study by Jaeger (1986) confirmed the full zonal status of this characteristic horizon. According to Jaeger, *N. lochkovensis* is either preceded by beds with *M. pridoliensis*, or the latter species appears somewhat later, within the *lochkovensis* Zone s.l., which results in the subdivision of the zone into the lower and upper subzones (Jaeger 1986: p. 325).

Splitting of *N. lochkovensis* into a number of independent species (Teller 1964, see Teller, in this volume p. 72), has for some time obscured the stratigraphic subdivision and correlation of the Přidoli beds on the EEP. In the present paper, the *lochkovensis* Zone s.l. is subdivided into the lower *N. lochkovensis branikensis* Subzone and the upper *N. lochkovensis lochkovensis* Subzone separated by the *M. (Dulebograptus) trimorphus* horizon (Subzone). This subdivision is roughly homotaxial with the Barrandian sequence (see p. 98). Time will tell whether such a subdivision is tenable for the entire EEP. In the Mielnik-1 borecore, *N. lochkovensis lochkovensis* appears at a depth of 662.75 m and is separated from the range of *N. lochkov. branikensis* by a distinct horizon yielding *M. (Dulebograptus) trimorphus* (Fig. 3). Within its Subzone in the Mielnik section, *N. lochkovensis lochkovensis* occurs abundantly and is associated with rare *Linograptus posthumus* and *Istrograptus* sp. The last specimens were found at a depth of 634.15 m. The species in question is the latest graptolite recognized in the section below the weathered

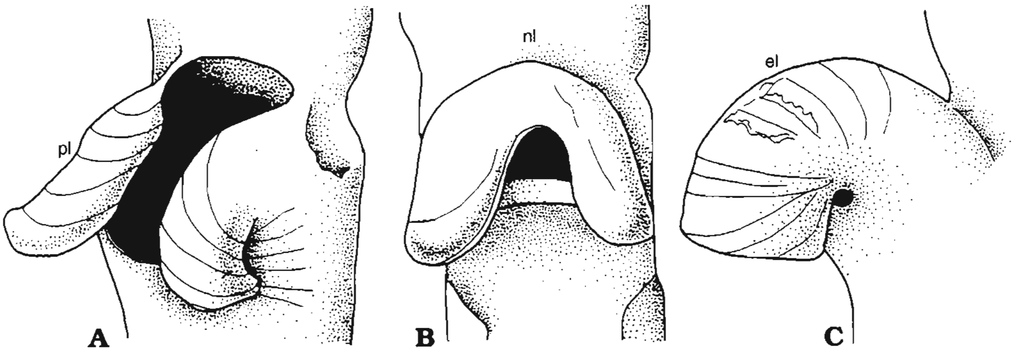

Fig. 56
Diagram showing the apertural structures in standard *N. lochkovensis lochkovensis* (**A**), *M. (Dulebograptus) trimorphus* (**B**) and in *"Dulebograptid"* morph of *N. lochkovensis lochkovensis* (**C**). Note that aperture is provided with paired lateral lobes (pl) in **A**, with notched apertuaral lobe (nl) in **B** and with entire, hooked apertural lobe (el) in **C**. Further explanations in text.

portion of the core. The thickness of the strata with *N. lochkovensis lochkovensis* is some 28.6 m, that of the Subzone was probably even greater.

Occurrence. — Outside Europe (Barrandian: PŘIBYL 1940; JAEGER 1986; EEP, TELLER, this volume, p. 79), *N. lochkovensis lochkovensis* has been recognized in Kazakhstan (Tokrau horizon, N of Lake Balkhash, KOREN 1986a). Specimens from Central Asia as compared with those from Barrandian display a smaller number of thecae provided with apertural lobes and a somewhat greater width of the rhabdosome.

LENZ (1988) emphasizes that so far it has not been found either in N Yukon or in the Canadian Arctic Archipelago.

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LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 1

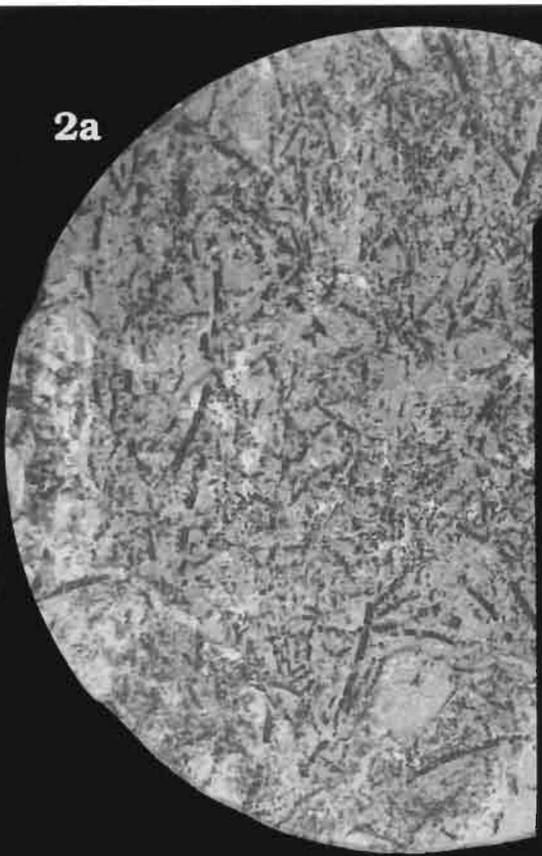
The source of material and its state of preservation:

1. Fragment of the Mielnik-1 wellcore, displaying typical lithology, namely a carbonate nodule (n) within marly sediments (m), Mielnik, approximate depth 915 m, *praecornutus* Zone, Gorstian; × 1.
2. A core sample showing mass occurrence of flattened *M. (F.) formosus* BOUČEK on the bedding plane (2a), Mielnik depth 766.45 m, *acer–spineus* Interval; same species 3-dimensionally preserved in carbonate rich marls (2b), Mielnik, depth 770.50 m, *acer–spineus* Interval, slightly enlarged; × 1.

3–4. Apertural apparatus of an isolated *M. (F.) formosus* BOUČEK, embedded in sediment (3) and cleaned (4) and displaying a preservational fold (pf, 4) due to compaction. Mielnik, depth 766.45 m, *acer–spineus* Interval; × 100.

5–8. Effects of flattening on different monograptid remains, with the inner margin of interthecal septum (arrowed) either seen as a convex body (5) or piercing through lateral thecal walls (6–8). Mielnik, depth 766.45–770.50 m, *acer–spineus* Interval; 5 × 40; 6 × 24; 7, 9 × 120; 8 × 230.

9. Unbleached juvenile th_1 of a *Pseudomonoclimacis* sp. displaying fusellar growth lines. Mielnik, depth 822.40 m, *latilobus/balticus* Zone; × 30.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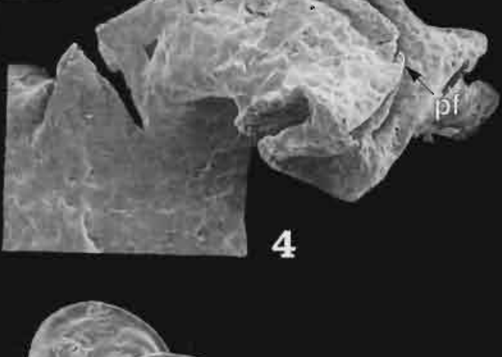
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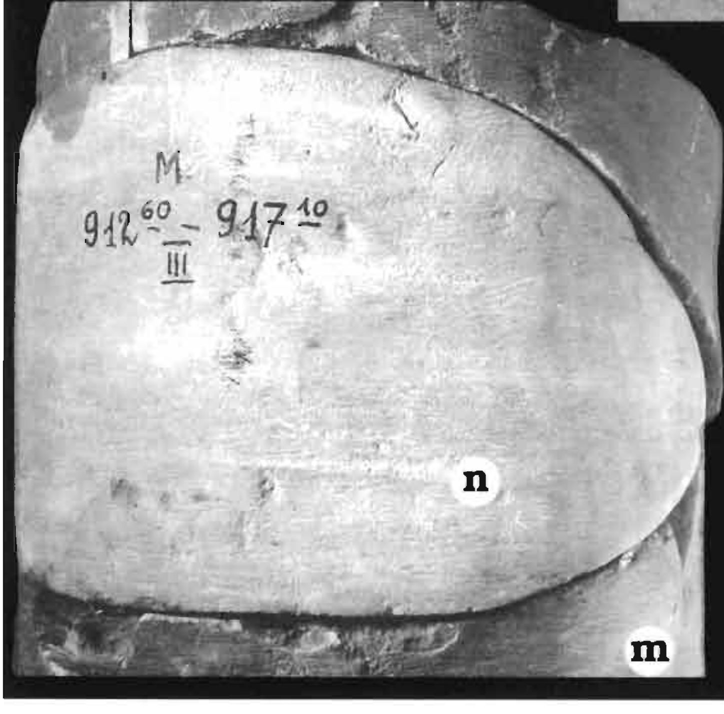
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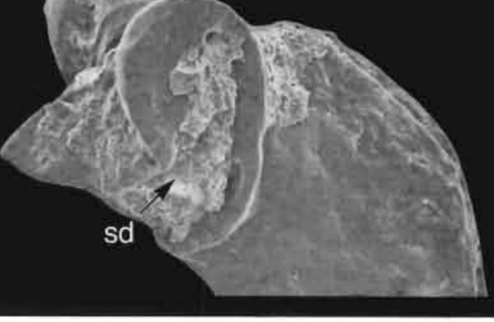
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PLATE 2

Monograptus (Slovinograptus) hamulosus (TSEGELNJUK) 129

1–6. Proximal (1, 2) and distal (3) part of rhabdosome, and the morphology of the thecae (4–6). Note the low position of the initial bud (2) and the cordate outline of the apertural lobe (6). Mielnik, depth 822.90 m, *latilobus/balticus* Zone; 1 × 25; 2 × 21; 3 × 27; 4, 6 × 50; 5 × 100.

Monograptus (Uncinatograptus) uncinatus TULLBERG 105

7–9. Distal (7, 8) and proximal parts of the rhabdosome seen laterally and ventrally. Baltic erratic boulder S.20, Poznań, *nilssoni* Zone; 7 × 50; 8 × 45; 9 × 35.


1


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LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 3

Monograptus (Slovinograptus) balticus TELLER 129

1–12. Proximal (1–7) and distal (8, 9) fragments of rhabdosome as well as morphology of the thecae (10–12). Note the high position of the initial bud (6, 7). Mielnik, depth 814.40 m, *latilobus/balticus* Zone; 1, 2 × 23; 3, 5 × 30; 4 × 13; 6, 8, 9, 11 × 50; 7 × 40; 10, 12 × 130.

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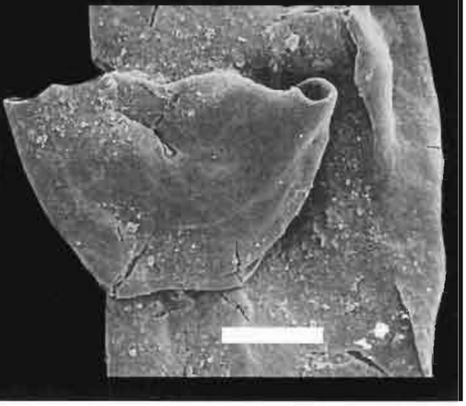
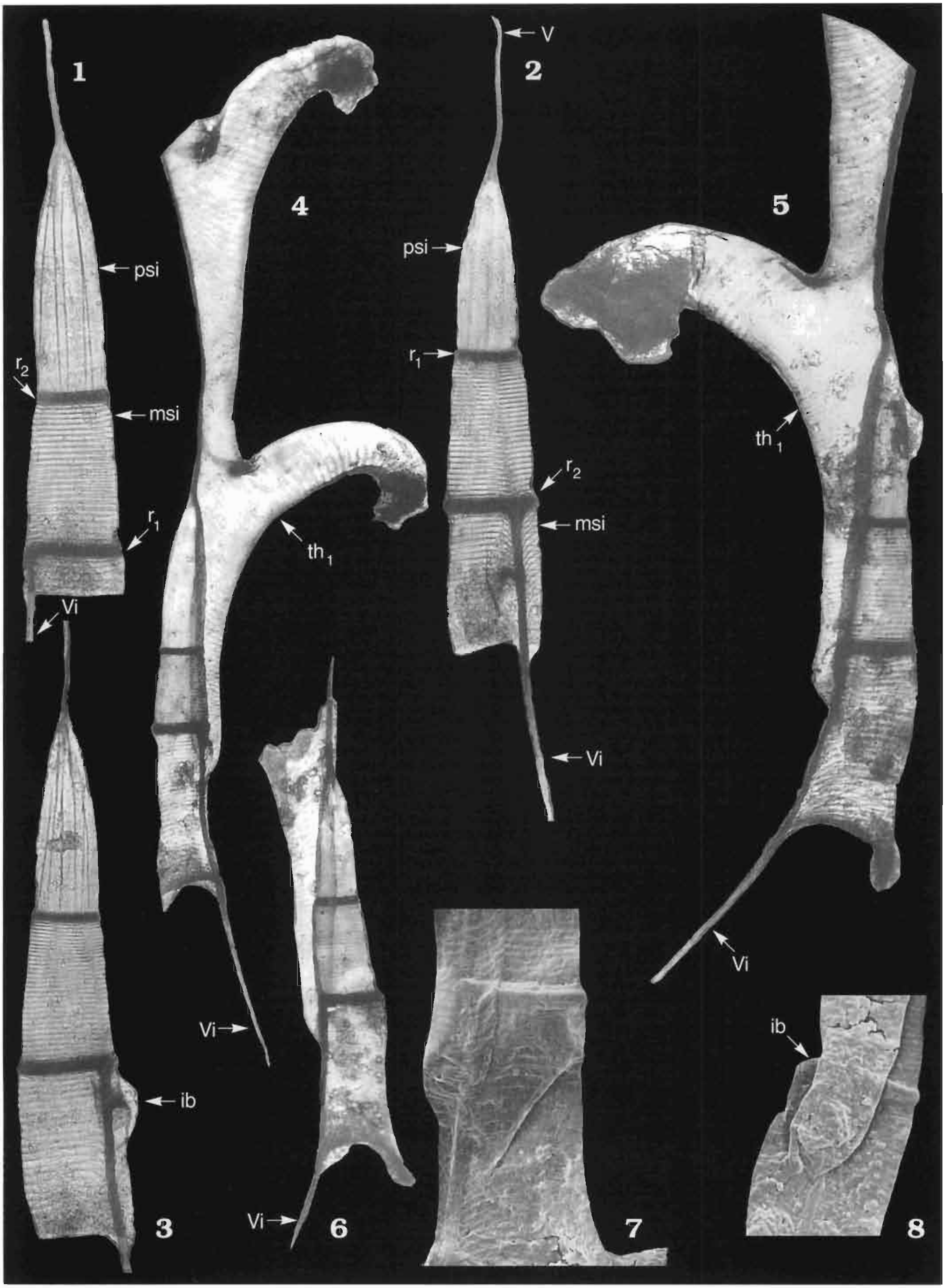

12

PLATE 4

Monograptus (Formosograptus) formosus BOUČEK 134

Early development and proximal parts of rhabdosome as revealed in light (1–6) and SEM (7, 8).
All specimens from Mielnik, depth 766.90 m, *protospineus–spineus* Interval.

1–3. Growth stages seen on bleached specimens; 1 × 94; 2 × 66; 3 × 75.
4–6. Siculae and proximal parts of rhabdosome seen on trasparent specimens; 4 × 56; 5 × 60; 6 × 47.
7–8. Initial bud with visible growth lines seen with SEM; 7 × 160; 8 × 190.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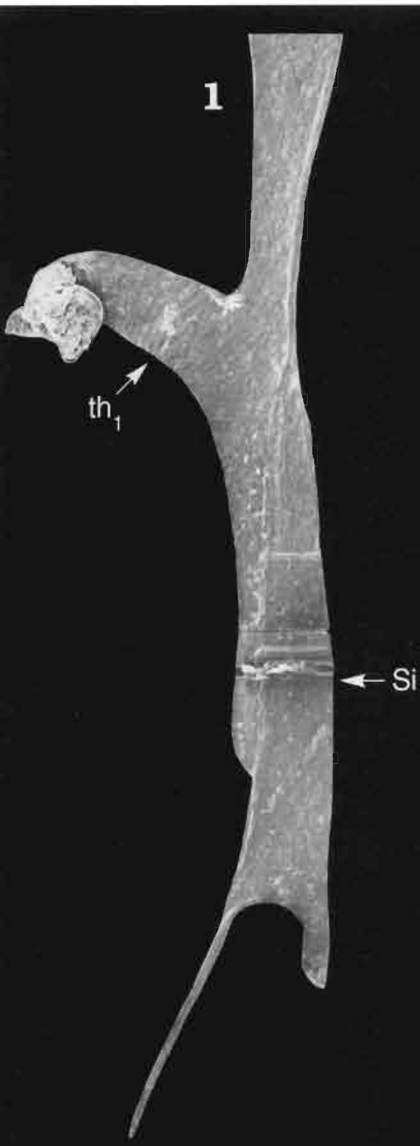
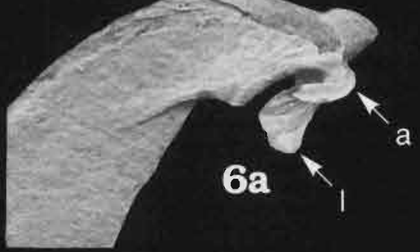
LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 5

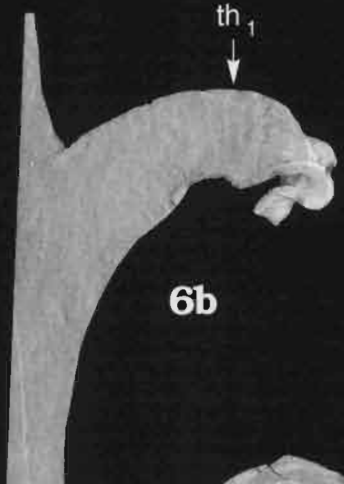
Monograptus (Formosograptus) formosus BOUČEK 134

1–9. Proximal part of rhabdosome (1–2, 5 seen laterally), sicula (3) and its dorsal process (4, dp) as well as morphology of the first theca (6–9). Mielnik, depth 770.40–766.70 m, *formosus* epibole within the *acer–spineus* Interval; 1, 3 × 50; 2 × 30; 4 × 200; 5 × 25; 6 × 75; 6a × 115; 7 × 160; 8 × 300; 9 × 130.


1


6a


2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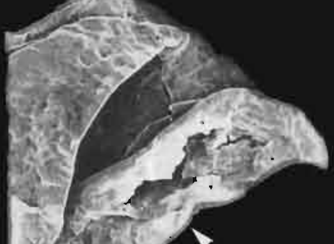
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4

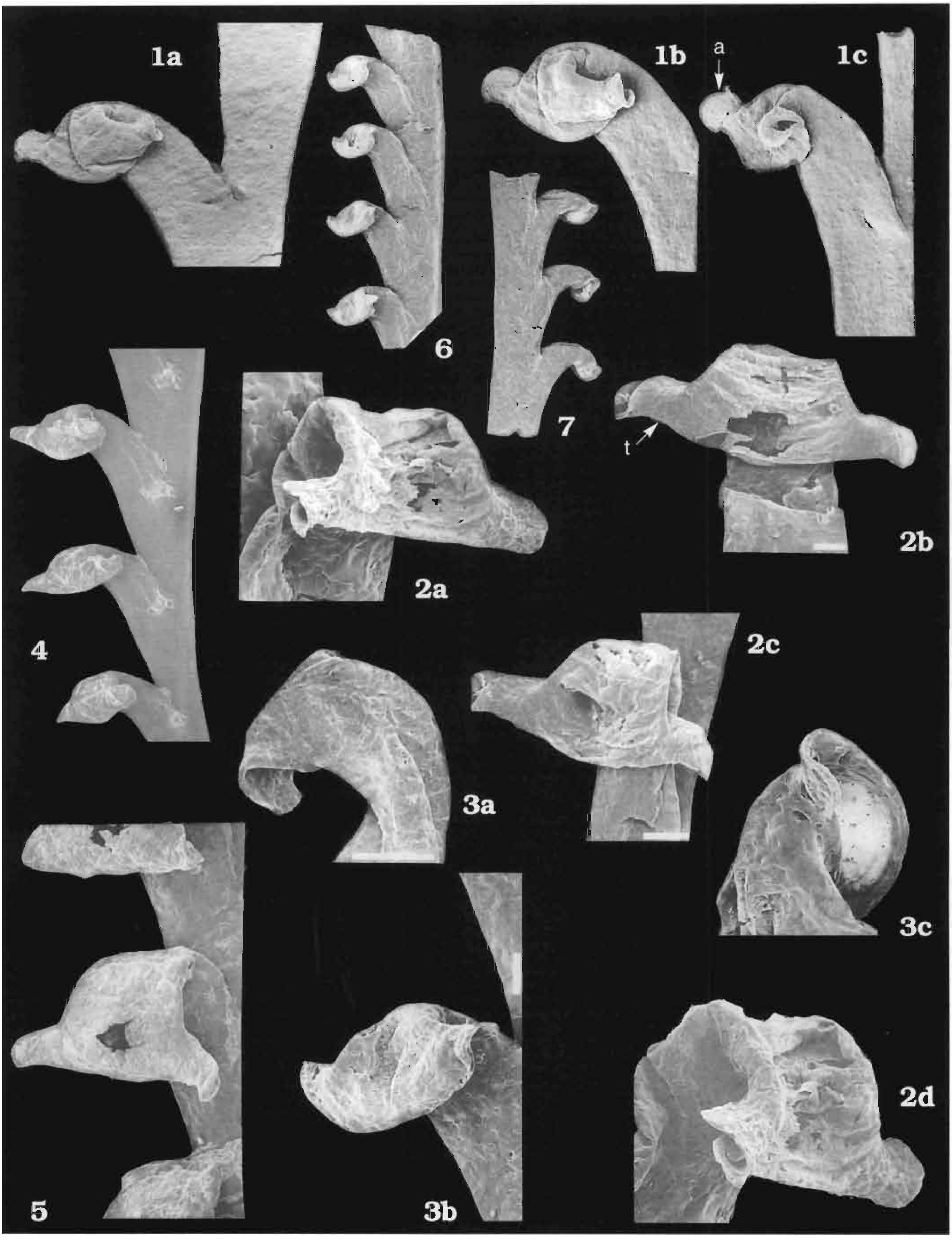

8

LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 6

Monograptus (Formosograptus) formosus BOUČEK 134

1–7. Morphology of proximal thecae (1, 2), first theca (3) as well as the medial thecae of the rhabdosome (4–7). Mielnik, depth 770.70–766.70 m, *formosus* epibole within the *acer–spineus* Interval; 1 × 60; 2a–c × 120; 2d × 160; 3a × 160; 3b × 80; 3c × 120; 4 × 25; 5 × 50; 6, 7 × 23.


1a
6
1b
a
1c
7
4
2a
t
2b
2c
3a
3c
5
3b
2d

LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

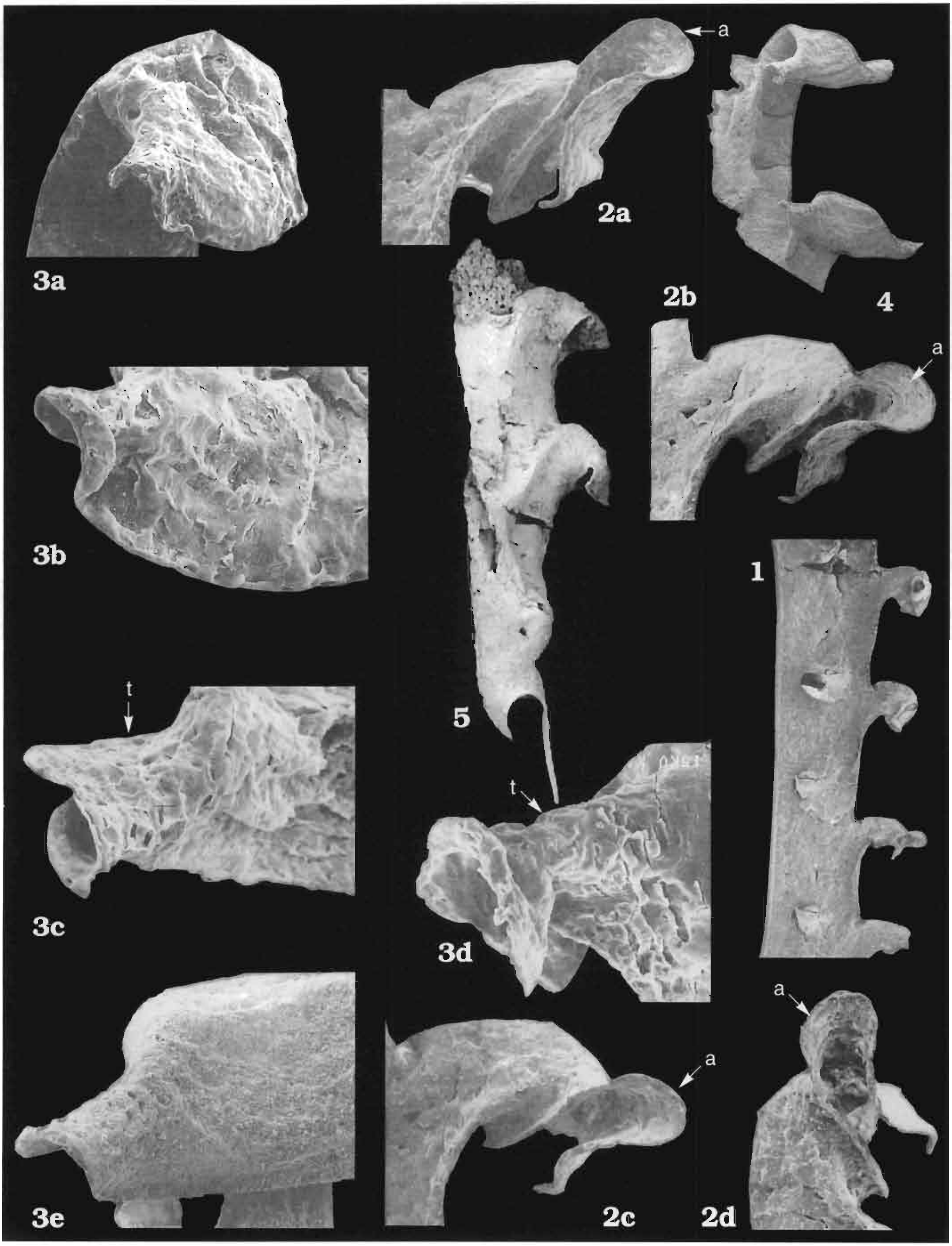
PLATE 7

Monograptus (Formosograpus) formosus BOUČEK 134

1–4. Distal part of rhabdosome (1, 4) and morphology of distal thecae: apertural apparatus (2a–d), tubular outgrowth of the apertural lobe and auriculum (3, 3c, d). Mielnik, depth 770.40–766.70 m, *acer–spineus* Interval; 1 × 30; 2a–d × 120; 3a × 120; 3b × 220; 3d, e × 300; 4 × 60.

Monograptus (Uncinatograptus) uncinatus TULLBERG 156

5. Poximal part of the rhabdosome seen laterally. Baltic erratic boulder S.38, Jarosławiec, *nilssoni* Zone; 5 × 50.


a
2a
3a
4
2b
a
5
3b
1
t
3c
t
3d
a
3e
a
2c
2d

LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 8

Oktavites aff. *spiralis* (GEINITZ) 137

1–8. Thecal morphology (1–6) as compared with those in *Monograptus (Formosograptus) formosus* BOUČEK (7, 8). 1–6 chemically isolated from the nodules of Osmudsberget, Sweden, *turriculatus* Zone, 7, 8 from Mielnik, depth 770.40–766.70 m, interval between *acer–spineus* Zone; 1 × 25; 2, 4–6 × 50; 3 × 100; 7, 8 × 120.

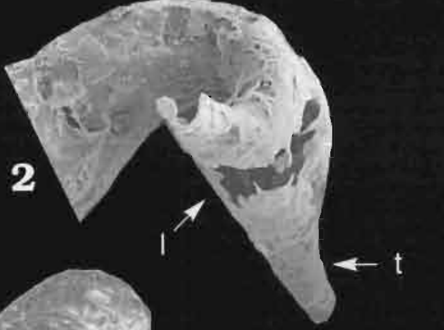
Monograptus (Uncinatograptus) uncinatus TULLBERG 137

9, 10. Shown as a standard hooded Late Silurian monograptid, with apertural lobes seen ventrally (9) and laterally (10). Baltic erratic boulder S. 38, Jarosławiec, *nilssoni* Zone; 9 × 88; 10 × 84.


1


4

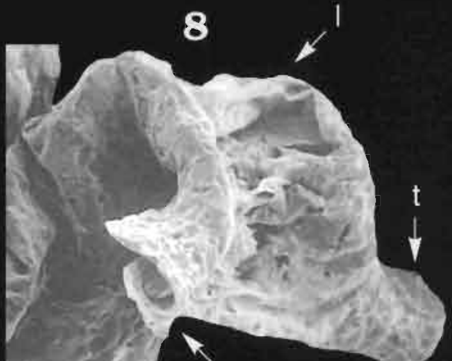
5



2


9

7



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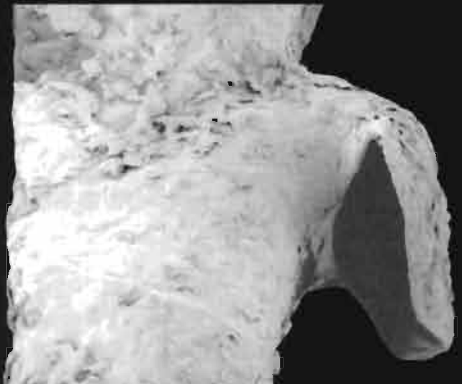
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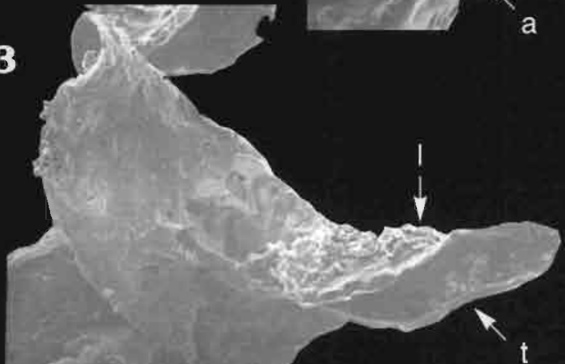

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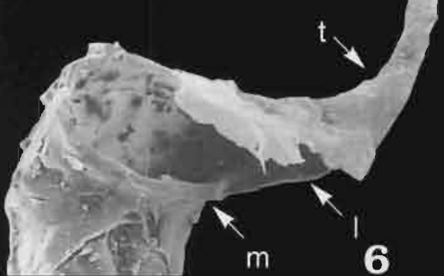

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LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

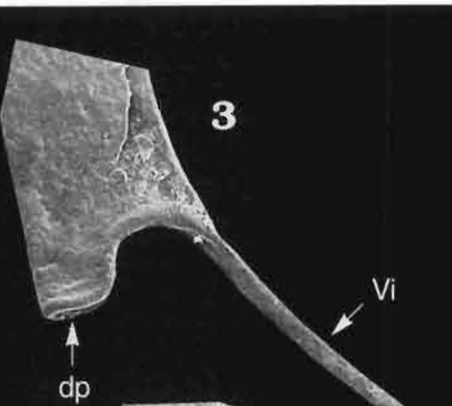
PLATE 9

Monograptus (Uncinatograptus) acer acer (TSEGELNJUK) 140

1–9. Sicula and proximal thecae of rhabdosome (1–7) and some details of thecal morphology (8, 9); 1a, b, 4a aspects of rhabdosome displaying 1/4 turn as compared with rhabdosome in full lateral view (6, 2a); 2b, 3, 4b, 5, 7 details of sicula; 8, 9 thecae seen in two aspects. Mielnik, depth 785.90–789.90 m, *acer* Zone; *acer acer* Subzone; 1a × 20; 1b × 12; 2a × 12; 2b × 24; 3 × 120; 4a × 409; 4b × 120; 5 × 40; 6 × 24; 7 × 130; 8 × 120; 9 × 48.

1a

1b

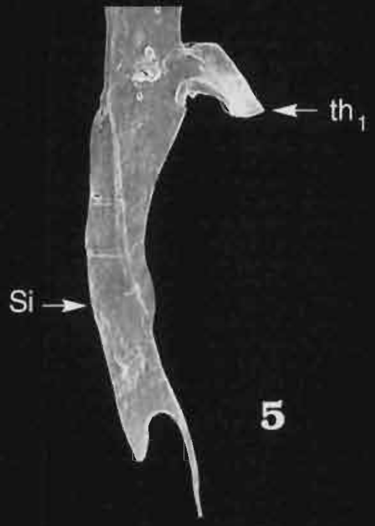


3

2a

2b

6



5

7

8

9

4a

4b

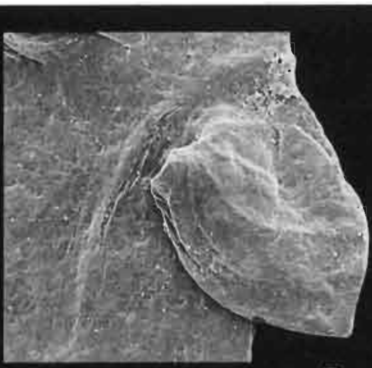
LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 10

Monograptus (Uncinatograptus) acer acer (TSEGELNJUK) 140

1–11. Morphology of apertural apparatus and proximal- to medial part of rhabdosome (5); 1–3 different preservational deformations of apertural region; 4, 6–11 apertural lobe seen in different aspects, m marginal thickening. Note a rapid widening of rhabdosome (5). Mielnik, depth 783.50–785.50 m, *acer* Zone, *acer acer* Subzone; 1, 2 × 130; 3, 7, 9 × 120; 4 × 72; 5 × 12.5; 6 × 60; 8 × 108; 10 × 180; 11 × 216.


1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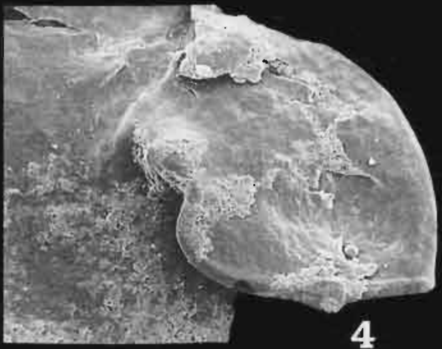
2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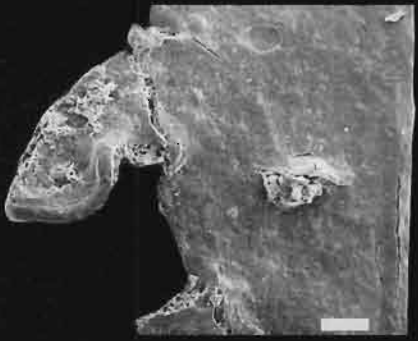
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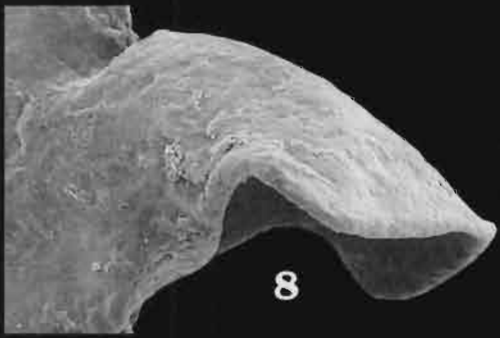
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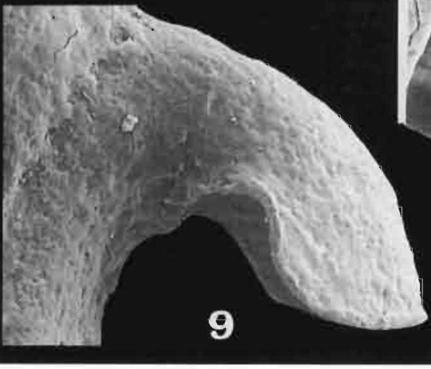
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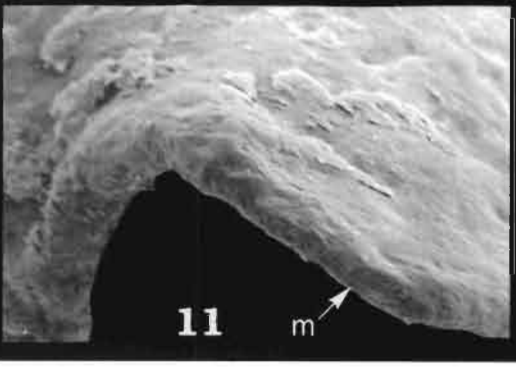
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LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 11

Monograpus (Uncinatograptus) protospineus URBANEK 147

1, 2. Distal fragment of rhabdosome (1) and details of apertural apparatus (2). Mielnik, depth 773.50 m, *protospineus* Zone, ZPAL G.XVII/1; 1 × 25; 2 × 100.

Monograptus (Uncinatograptus) spineus TSEGELNJUK 149

3–6. Apertural lobe (l) and spines (s) in different states of preservational deformation (3–5) as well as promontorium (6, p). Mielnik, depth 760.15 m, *spineus* Zone; 3, 6 × 150; 4 × 200; 5 × 100.


1
2
p
3
s
s
4
f
5
l
s
s
6
p

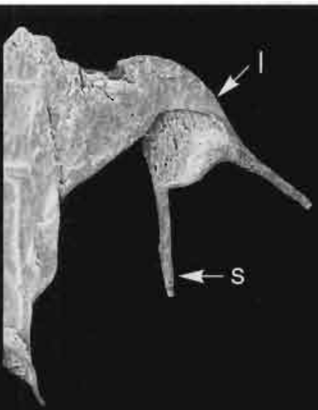
PLATE 12

Monograptus (Uncinatograptus) spineus (TSEGELNJUK) 149

1–11. Proximal part of the rhabdosome (1–4), morphology of the first theca (5–7) and medial thecae (8–11). Note a distinct dorsal curvature of the rhabdosome (1, 4). Mielnik, depth 760.15 m, *spineus* Zone; 1–2, 6–7 × 50; 3 × 40; 4 × 19; 5 × 70; 6 × 50; 7 × 40; 8 × 60; 9 × 70; 10 × 190; 11 × 100.


3


1



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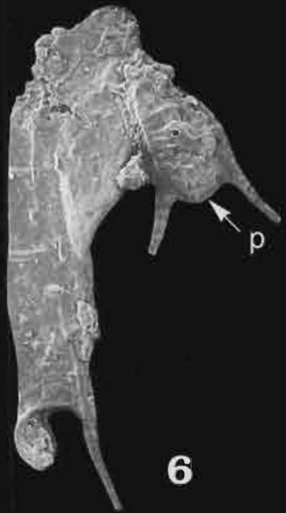
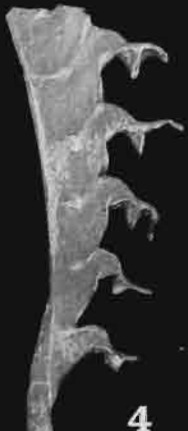


6


2

8


7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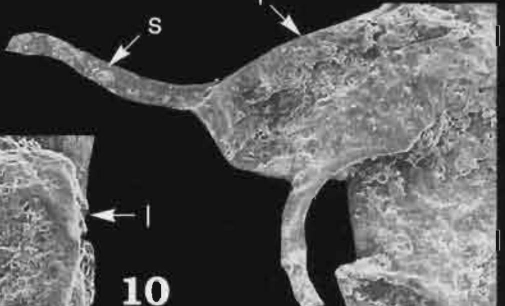

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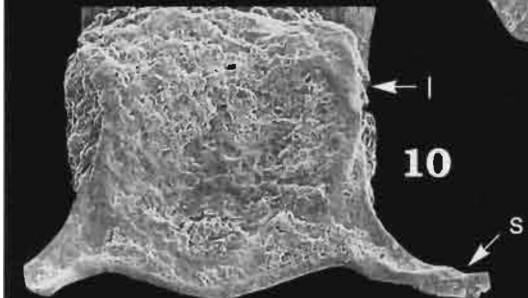

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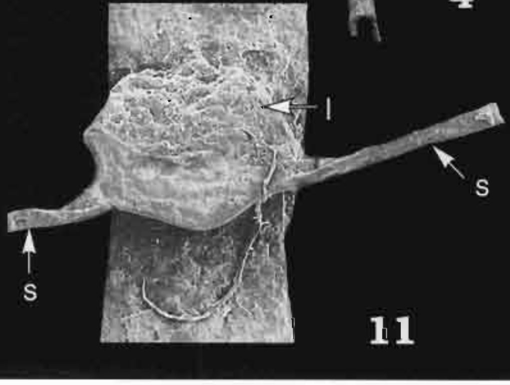

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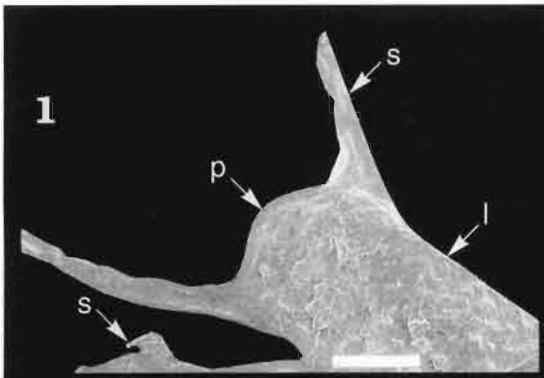
LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 13

Monograptus (Uncinatograptus) spineus (TSEGELNJUK) 149

1–12. Morphology of the apertural apparatus; 1, 2, 6–8 relation of the lobe proper (l) to the apertural spines (s), 4–6 details of the antero-lateral apertural spines (s), 9–11 "telescopic" structure of apertural spines (s) with protruding fusellar heads (f), 12 broken edge of a spine revealing internal cavity (h). Mielnik, depth 760.15 m, *spineus* Zone; 1–3, 5, 9 × 120; 4 × 200; 6 × 120; 7, 8 × 300; 10, 11 × 200; 12 × 1000.

1



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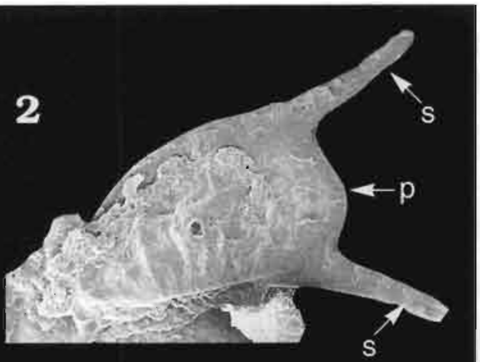

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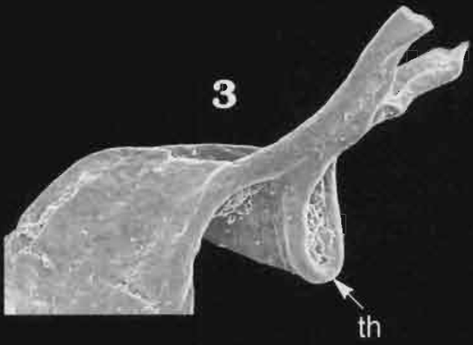

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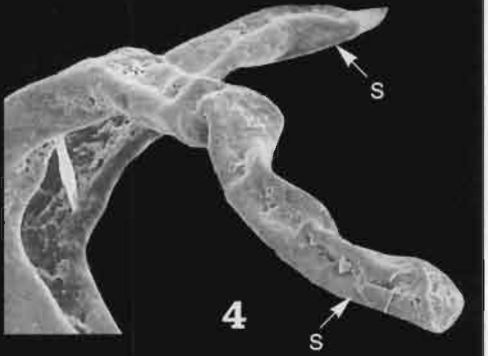

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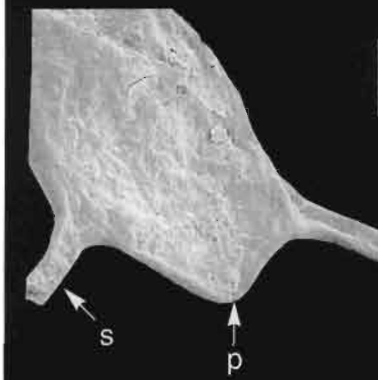

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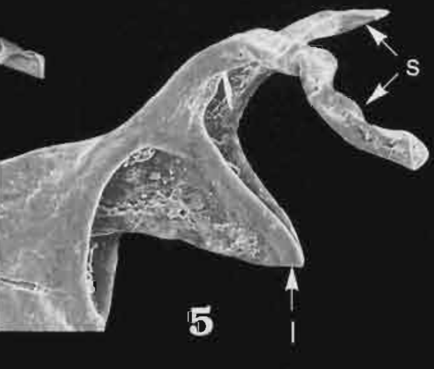

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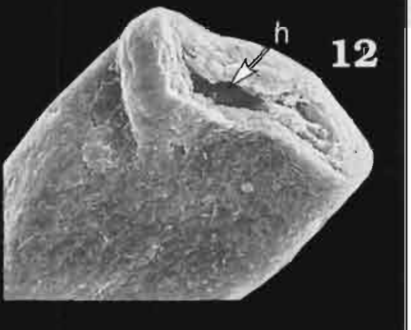

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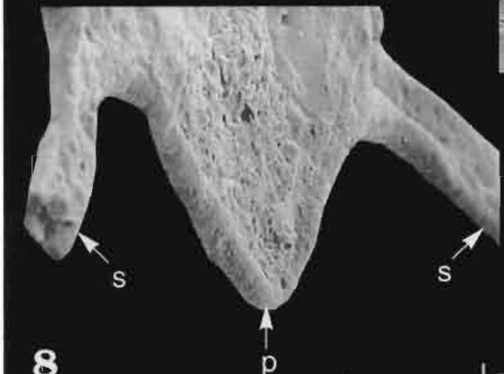

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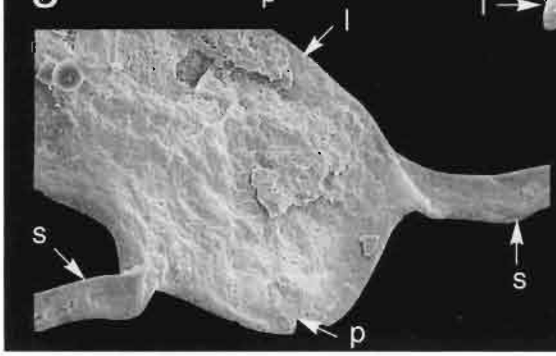

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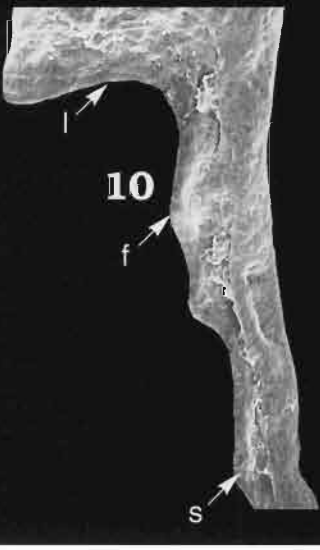

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LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 14

Monograptus (Dulebograptus) trimorphus TSEGELNJUK 154

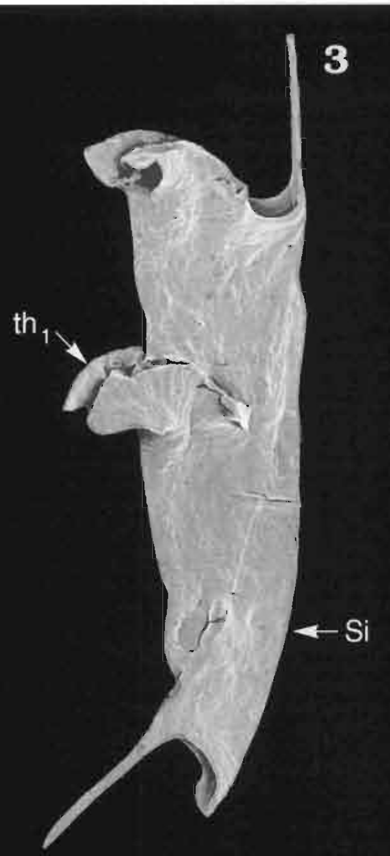
1–6. Morphology of rhabdosome and thecae; proximal part of the rhabdosome (1) in ventral view (note the progressive shortening of the apertural lobe proper (l) and the obliteration of the notched portion) and the details of morphological change in the shape of apertural lobe between th_1 and th_2 (2), as well as the sicular portion of the rhabdosome in lateral view (3) and the distal thecae seen laterally (4) and in ventro-distal aspect (5). Details of th_1 aperture with preservational fold (f) are shown in (6). Mielnik, depth 664.45 m, *lochkovensis* Zone; 1, 3, 5 × 50; 2 × 95; 4 × 40; 6 × 200.


1

th_3
th_1


2

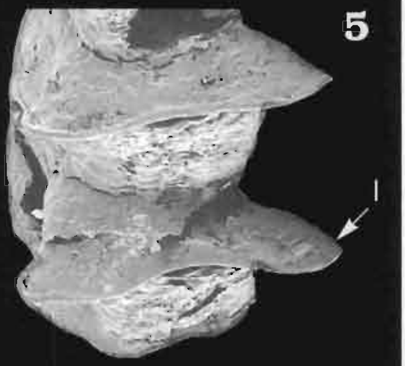
th_3
th_2


3

th_1
Si


4

l


5

l


6

f
l

PLATE 15

Pristiograptus dubius (SUESS) *s.l.* 157

1–4. Proximal (1–2) and distal (3, 4) parts of rhabdosome representing gracile morphotype cf. *frequens* JAEKEL. Mielnik, depth 787.90 m, *acer* Zone, *acer acer* Subzone; 1 × 25; 2, 3 × 15; 4 × 40.

7. Rod-like or tubular virgula, embedded (7a) or free stretching (7b), Mielnik, depth 802.70 m and 815.10 m, *latilobus/balticus* Zone; × 230.

Pristiograptus dubius fragmentalis (BOUČEK) 159

5, 6. Proximal part of the rhabdosome (5–6). Mielnik, depth 5 – 820.50 m, depth 6 – 819.40 m, *latilobus/balticus* Zone; 5 × 15; 6 × 25.

Pseudomonoclimacis latilobus (TSEGELNJUK) 161

8. A natural cross section of distal thecae shoving their distinct excavations (ex). Mielnik depth 819.20 m, *latilobus/balticus* Zone; × 50.


1
7a
7b
V
3
S
5
ex
2
8
4
6

LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 16

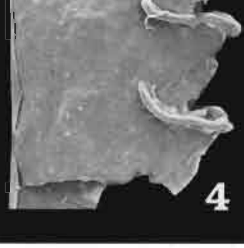
Pristiograptus dubius labiatus subsp. n. 160

1–12. Proximal (1, 2), holotype ZPAL G.XIX/1, medial (3) and distal (4) part of the rhabdosome, as well as the morphology of sicula and thecal apertures (5–11). At 12 apertural margin in *Pristiograptus dubius* cf. *frequens* for comparison with 9. Aperture of sicula (5) and micromorphology of apertural lip on 10 and 11 with coarse cortical fibrils (f) visible. Mielnik, depth 12 – 821.00 m, *latilobus* Zone, all remaining depth 756.50–718.00 m, *protospineus–spineus* Zone and post-*spineus* interval; 1 × 12; 2 × 40; 3, 4 × 19; 5–8 × 90; 9 × 130; 10 × 300; 11 × 3000; 12 × 60.

1

2

3



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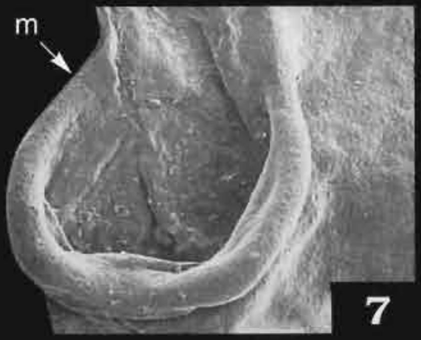
5

6



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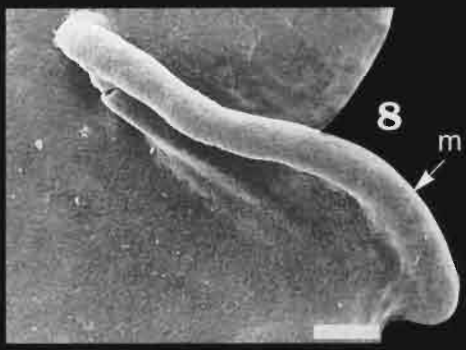

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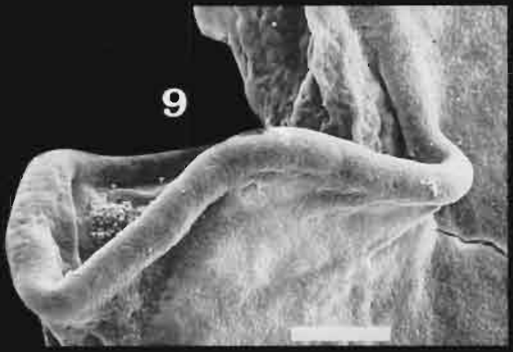

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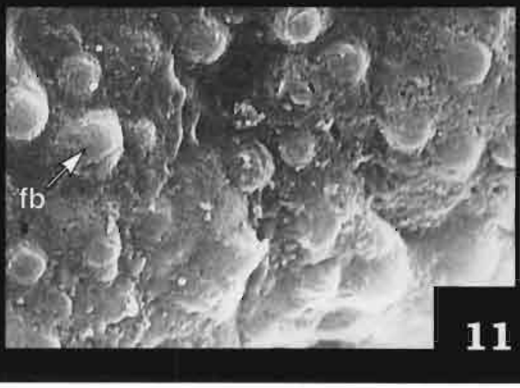

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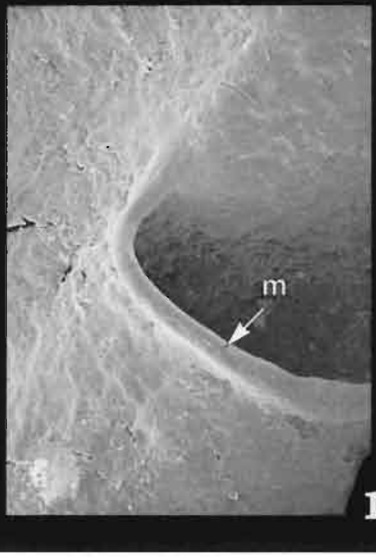

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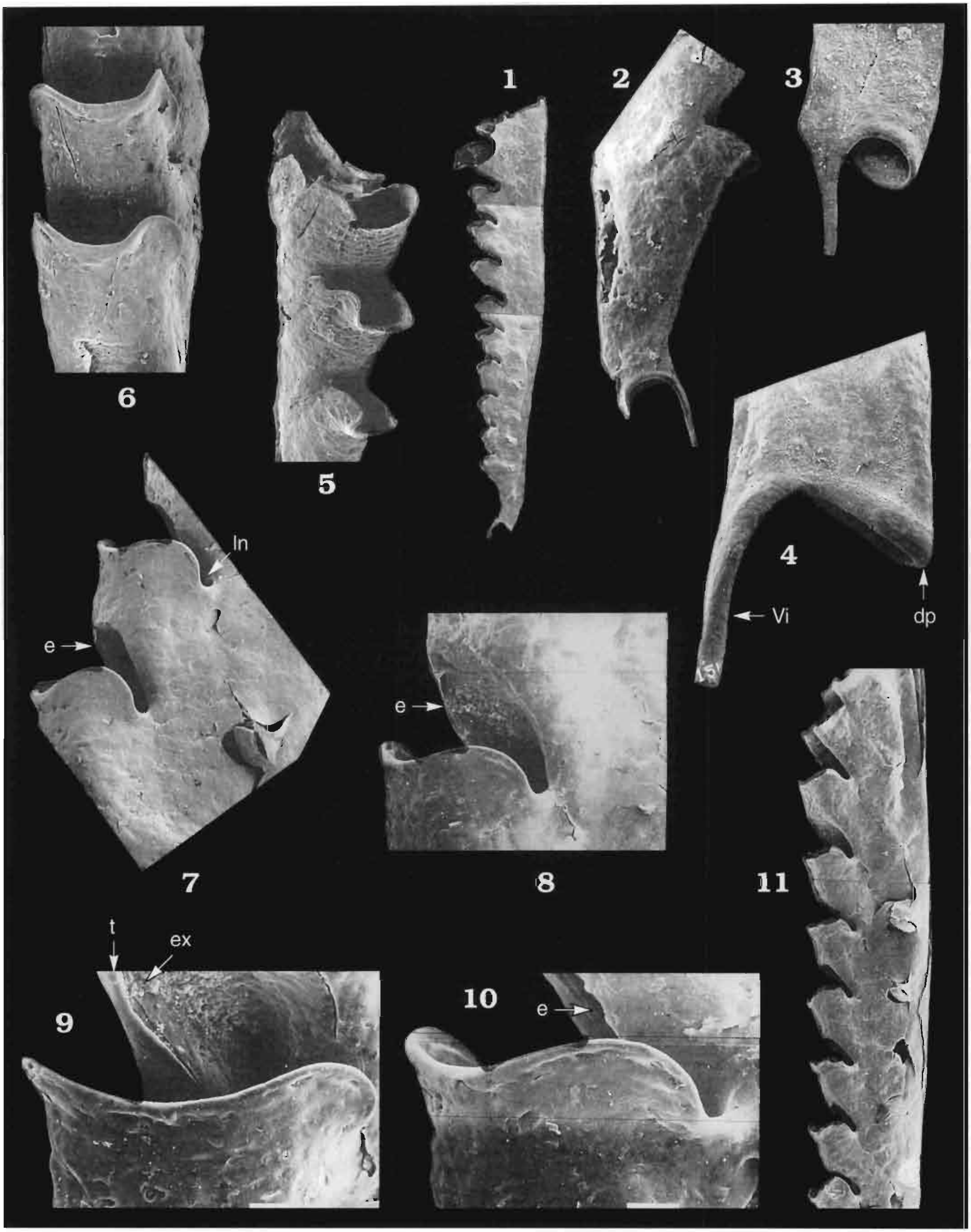
LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 17

Pseudomonoclimacis latilobus (TSEGELNJUK) 161

1–11. Sicula and proximal part of the rhabdosome (1–4) as well as morphology of the thecae (5–11). Note the presence of excavations (e) between thecae and elaborations of the apertural margin, especially a deep lateral notch (ln), bordering the elevation (e). Mielnik, depth 819.40 m, *latilobus/balticus* Zone; 1 × 12; 2 × 54; 3, 4 × 130; 5 × 20; 6, 7 × 25; 8 × 50; 9, 10 × 90, 11 × 20.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3
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4
ln
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11
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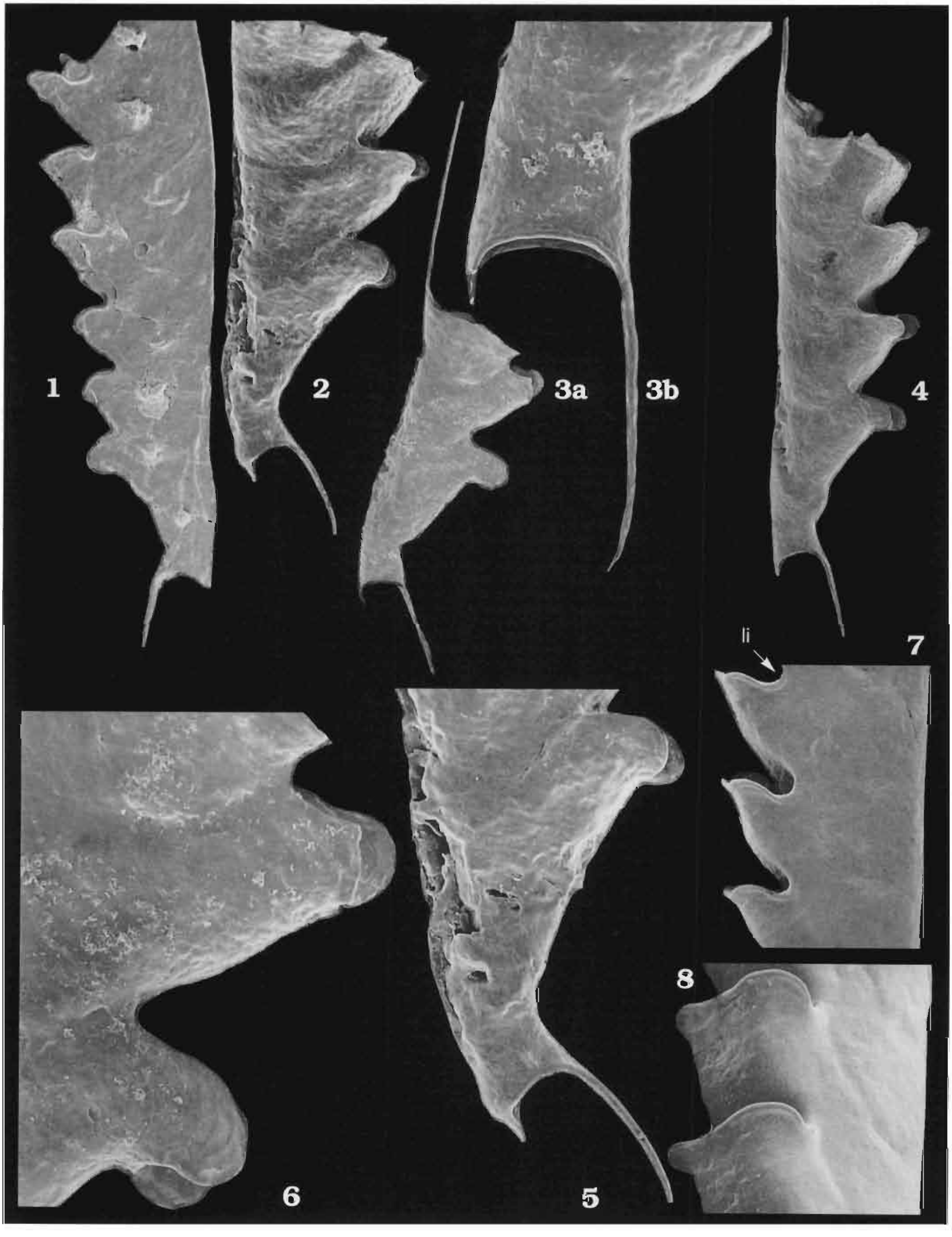
e

PLATE 18

Pseudomonoclimacis latilobus (TSEGELNJUK) 161

1–8. Sicula and proximal thecae (1–5) as well as details of morphology in proximal (6) and medial (7, 8) thecae. Note the strong elaboration of th_1, the distinct excavations in medial thecae and presence of lateral notch (li). Mielnik, 3, 4 depth 822.20 m, remaining 823.20 m, *latilobus/balticus* Zone; 1 × 20; 2a × 30; 2b × 45; 3a, 4 × 25; 3b × 85; 7 × 25; 8 × 35.


1
2
3a
3b
4
li
7
8
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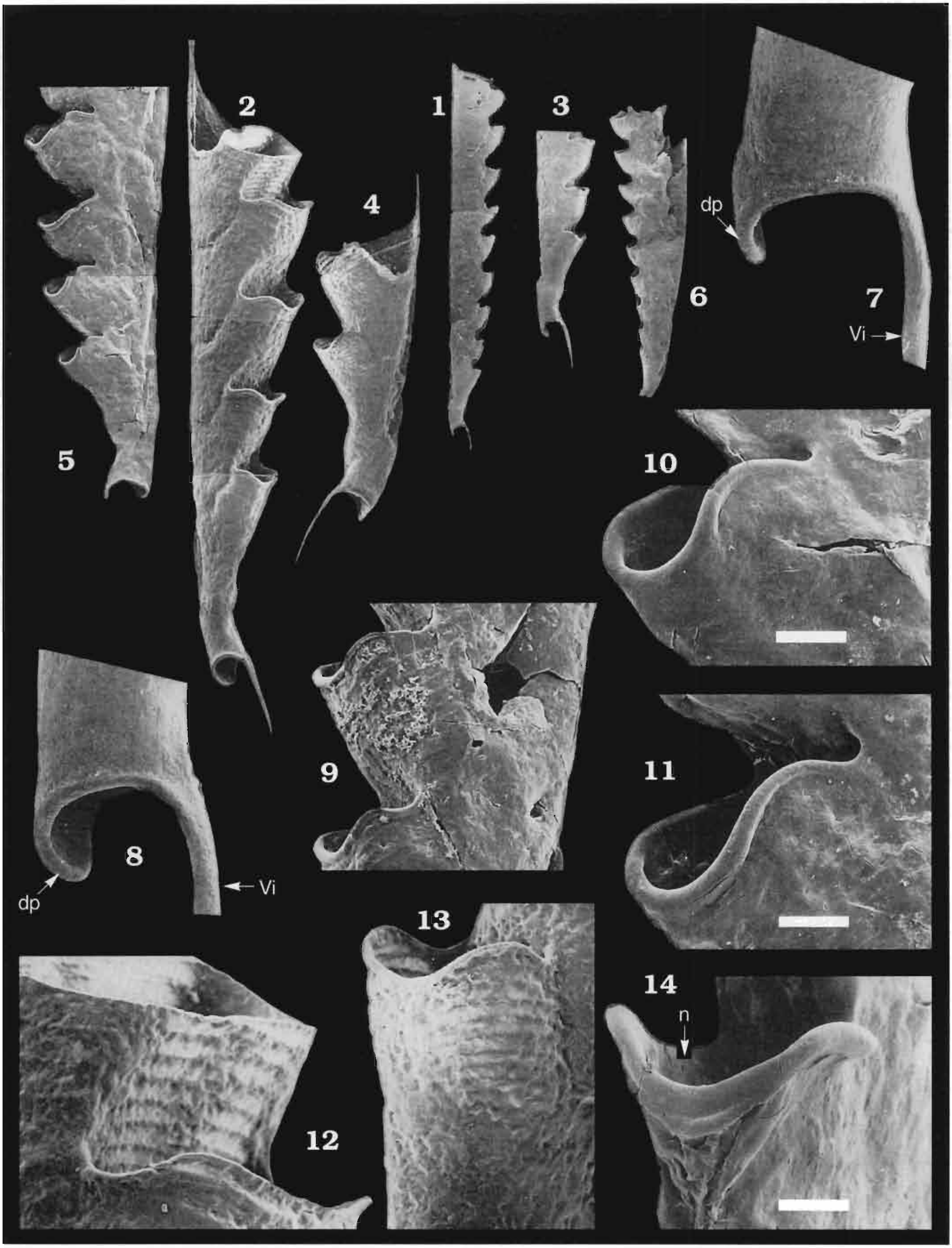
5

LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 19

Pseudomonoclimacis latilobus (TSEGELNJUK) 161

1–14. Morphology of the less advanced morphotype showing proximal part of rhabdosome (1–5) and thecal characters in proximal and medial part of the rhabdosome (9–14). Gerontic proximal part of rhabdosome (6) and details of sicular aperture with more (7) and less strongly (8) developed dorsal process (dp). Mielnik, depth 821.40 m, *latilobus/balticus* Zone; 1 × 13; 2 × 30; 3 × 15; 4 × 30; 5 × 30; 6 × 15; 8 × 120; 9 × 110; 7, 10, 11, 14 × 130; 12, 13 × 100.


2
1
3
4
6
7
dp
Vi
5
10
9
11
8
dp
Vi
13
14
n
12

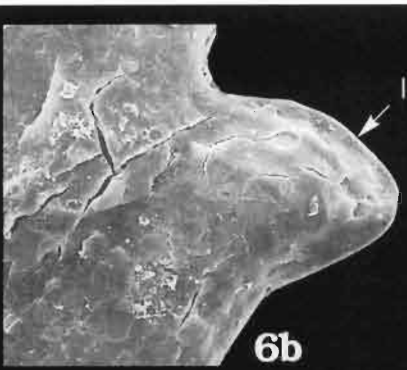
LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 20

Istrograptus trangrediens rarus (TELLER) 165

1–5. Proximal parts of the rhabdosome showing details of sicula and thecae. Note the characteristic *transgrediens* profile of th$_1$ in figs 2, 3. Mielnik, depth 689.55 m, *parultimus* Zone; 1 × 60; 2, 4 × 20; 3, 5 × 40.

6. a–c *Istrograptus trangrediens* aff. *rarus* (TELLER), early growth stage of rhabdosome with strongly developed wing-like lobes (l) in th$_1$, th$_2$. Mielnik, depth 689.55 m, *parultimus* Zone; 6a × 10; 6b, c × 60.



6b

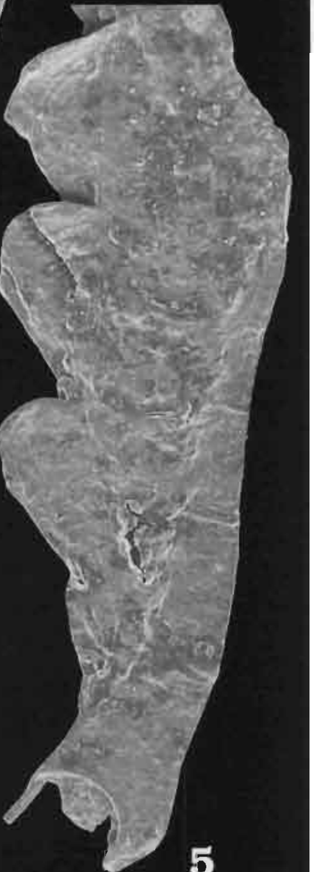
6a

3

4

1

2



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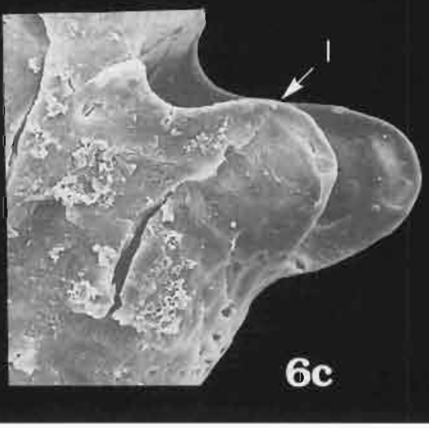


6c

LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 21

Neocolonograptus parultimus (JAEGER) 166

Morphology of the rhabdosome.

1–3. Lower zonal morphotype, proximal parts of rhabdosome seen laterally. Mielnik, depth 690.55 m, *parultimus* Zone; 1, 2 × 24; 3 × 48.

4–7. Proximal (4–6) and distal (7) fragments of rhabdosome, 5–6 seen ventrally. Note a very slight elaboration of apertural undulations. Mielnik, depth 690.30 m, *parultimus* Zone; 4, 5, 7 × 48; 6 × 24.

8. An advanced morphotype. Note a distinct elaboration of the apertural undulations especially in th_1. Mielnik, depth of 675.65 m, *parultimus* Zone; 8 × 48.

4

1

5

8

7

2

6

3

PLATE 22

Neocolonograptus ultimus (PERNER) 167

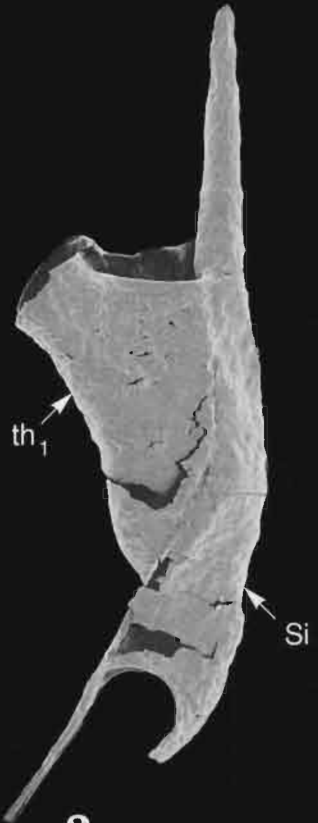
1. Morphology of rhabdosome and thecae: proximal part of rhabdosome seen laterally (1a) and latero-ventrally (1b); 1 × 20.
2. Sicula and juvenile th_1 in lateral view; 2 × 50.

3, 4. Details of thecal morphology in medio-distal thecae; 3, 4 × 50.

5. Top view on th_1 aperture; 5 × 100.

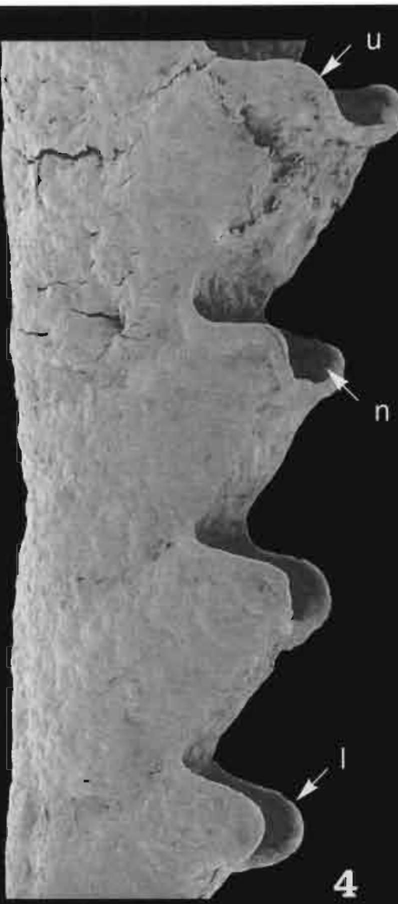
All specimens from Mielnik, depth 675.00 m, *ultimus* Zone.

1a



2

1b



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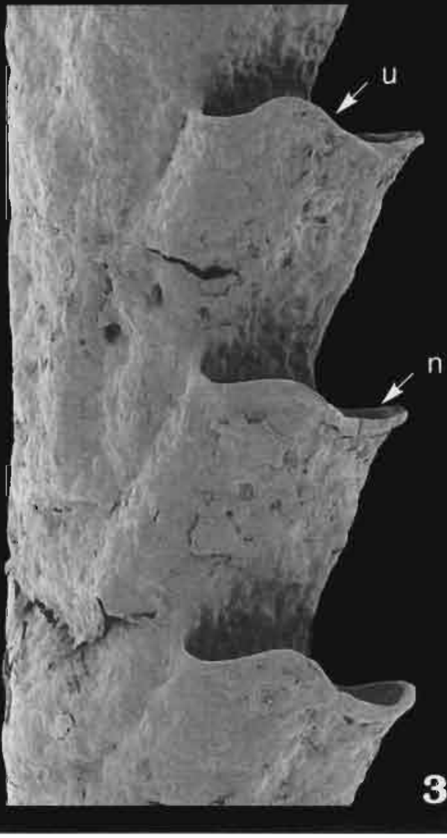

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5

PLATE 23

Neocolonograptus lochkovensis branikensis (JAEGER) 168

1–4. Morphology of the proximal part of rhabdosome (1, 2a) and structural details of thecae and apertural lobes (2b, 3, 4). Mielnik, depth 671.30 m, *lochkovensis* Zone, *branikensis* Subzone; 1, 2b, 3, 4 × 50; 2a × 20.

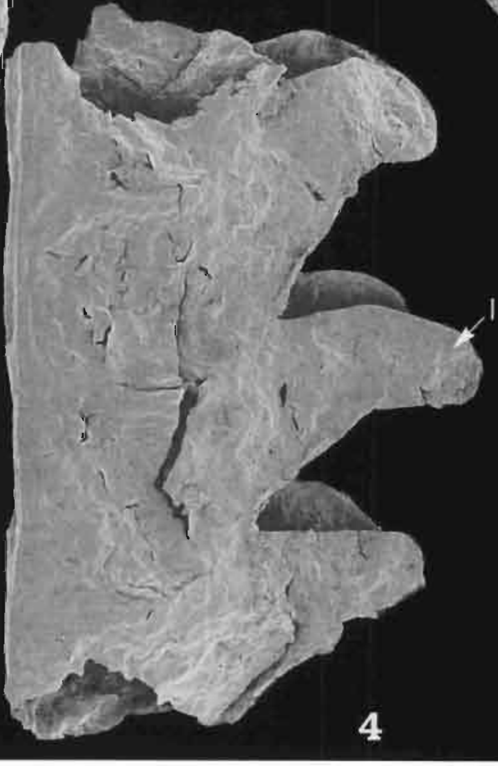
3

1a

2a

1b

2b



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LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 24

Neocolonograptus lochkovensis lochkovensis (PŘIBYL) 169

1–6. Proximal part of the rhabdosome (1–3) and the morphology of the proximal thecae (2–6). Note astrong development of the paired apertural lobes (l) in proximal thecae and their decrease in distal ones (5). Mielnik, depth 661.30 m, *lochkovensis* Zone; 1 × 25; 2 × 12; 3 × 17; 4, 5 × 20; 6 × 25.

1a

2

3b

4

3a

5

1

6

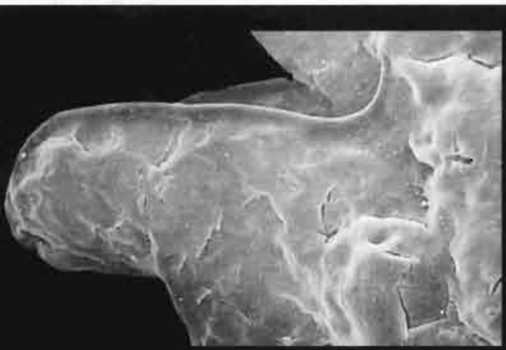
PLATE 25

Neocolonograptus lochkovensis lochkovensis (PŘIBYL) 169

1–9. Proximal parts of the rhabdosome with sicula partly damaged (1) and completely preserved (2) as well as the morphology of apertural apparatus (3–9). Note the variation in the shape of the terminal part of the lobes (1) from blunt to pointed and beak-like (b). Mielnik, depth 644.00 m, 2, 9 – depth 645.00 m, 3–8 — depth 661.30 m; *lochkovensis* Zone, *lochkovensis lochkovensis* Subzone; 1 × 12; 2 × 31; 3–5, 7 × 130; 6 × 140; 8 × 200; 9 × 94.


1


2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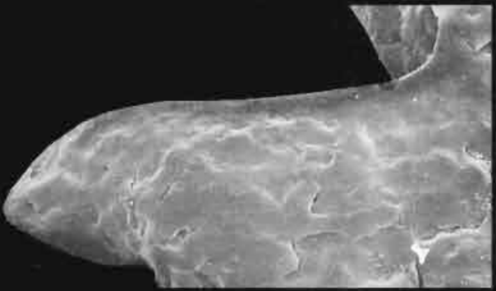
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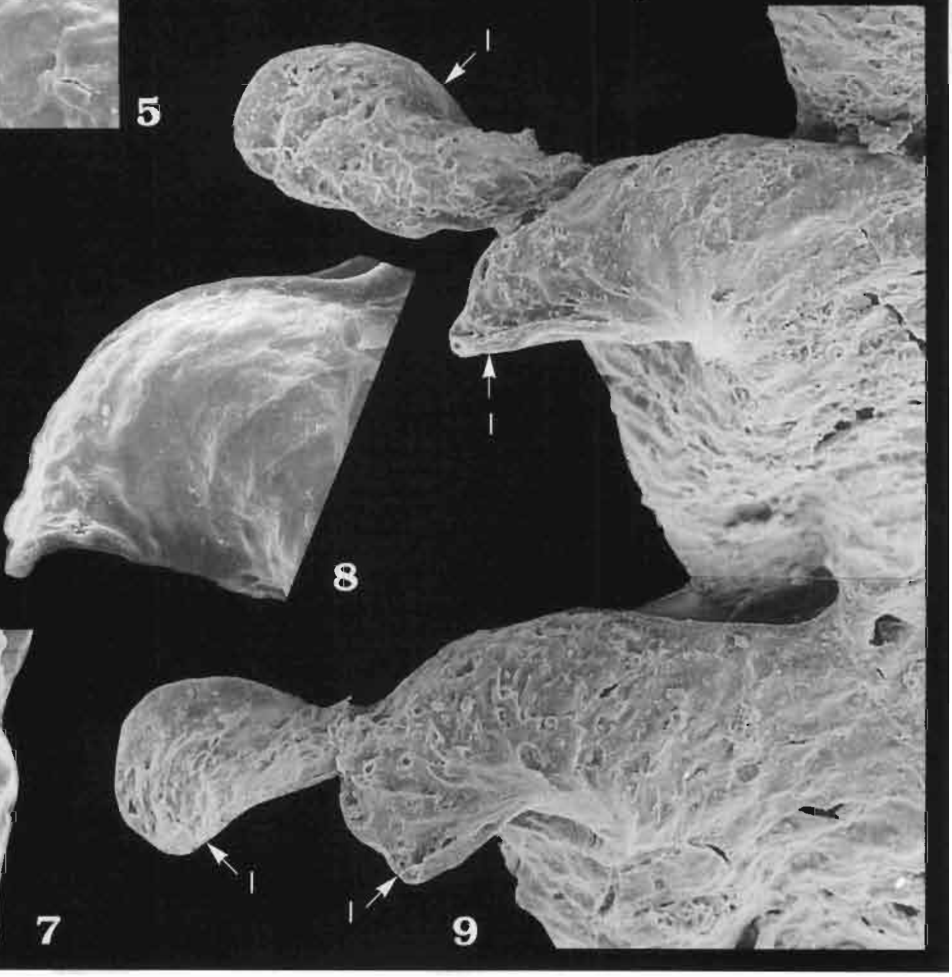
5

6


7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LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 26

Neocolonograptus lochkovensis lochkovensis (PŘIBYL) 169

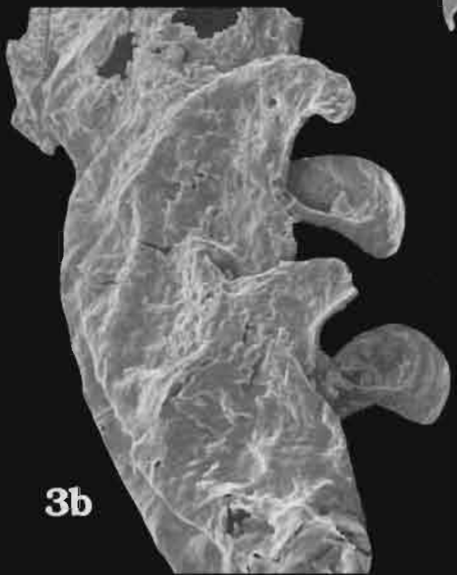
1–5. Standard morphotype with paired apertural lobes preservationally distorted (3) and normally preserved (1, 2, 5) as well as a teratological ("*Dulebograptus*"-like) structure of aperture in th_2, while th_1 and th_3 preserve their standard characters (4). Mielnik, depth 1–5 – 645.60 m, *lochkovensis* Zone, *lochkovensis lochkovensis* Subzone; 1a × 12; 1b, 2, 3a, 4a, b × 25; 3b × 45; 5 × 50.

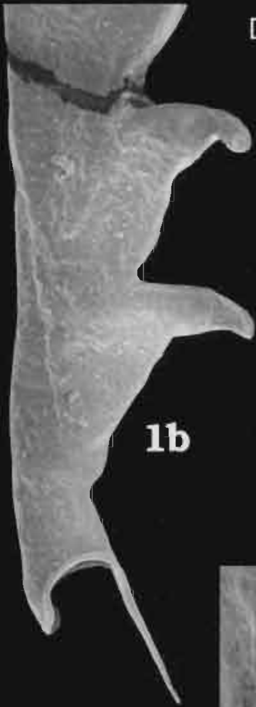

3a


1a

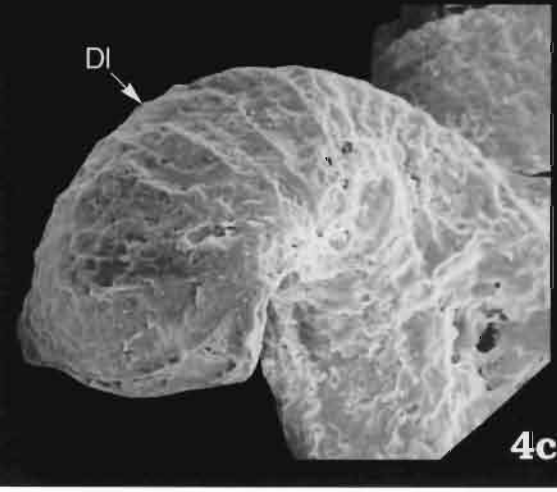

2

4a

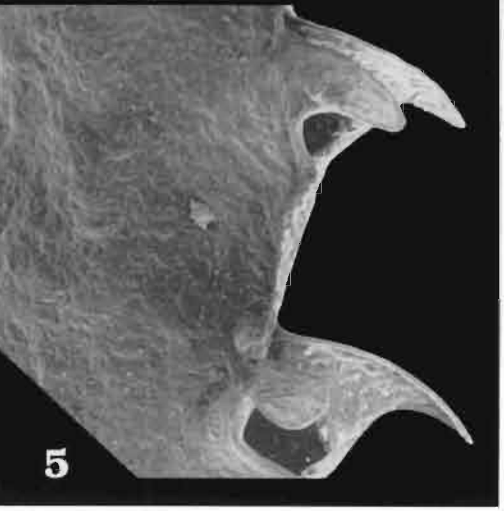

3b


1b

4b



4c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THE EMERGENCE AND EVOLUTION OF LINOGRAPTIDS

ADAM URBANEK

Urbanek, A. 1997. The emergence and evolution of linograptids. *In:* A. Urbanek and L. Teller (eds), Silurian Graptolite Faunas in the East European Platform: Stratigraphy and Evolution. — *Palaeontologica Polonica* **56**, 233–269.

Macroevolutionary effects due to anagenetic changes within a single lineage have been traced in the Linograptinae from Late Wenlock single-stiped *Lobograptus*? *sherrardae*, through bipolar *Neodiversograptus* and multibrachiate *Linograptus*, to Early Devonian compound colonies of *Abiesgraptus*. The ability to generate a number of sicular cladia improved the stability of the rhabdosome, and, in the evolution of *Linograptus*, the resulting geometrical constraints were overcome by diverting their growth. The main lineage is subdivided into four chronospecies displaying periods of fairly high abundance and a distinct morphological norm. These periods were separated by intervals of comparative scarcity, probably related to the bottlenecking of the lineage. The only instance of change in large populations is the *L. posthumus–A. tenuiramosus* phyletic transition. Speciation events (transformations) seem to be governed by the mechanisms of transient polymorphism, whilst periods of relative persistence of the norm were probably related to microevolutionary changes in monomorphic populations. A disparate origin of unit characters within the complex *Abiesgraptus* pattern is suggested. These characters appeared independently and heterochronously within the populations over the entire range of distribution of the ancestral species to be later assembled into a single adaptive syndrome. Cosmopolitan distribution of both the ancestral and the daughter species implies a polycentric or a pantopic emergence of the *Abiesgraptus*.

Key words: Linograptinae, multiramous colonies, phyletic evolution, macroevolution, adaptive syndrome.

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CONTENTS

INTRODUCTION

In the last decades much attention has been paid to macroevolution as opposed to speciation, and especially, to microevolutionary events. Theoretical considerations on the mechanisms involved in macroevolutionary changes can certainly be illuminating, but empirical examination of the instances of macroevolution as represented in the fossil record has always been of crucial importance. It provides a starting point for speculations as well as the criteria for the falsification of the hypotheses and explanations proposed.

The origin of the multiramous graptolite colonies within the subfamily Linograptinae is a graphic example of macroevolution, perfectly suitable for a case study. Moreover, the generation of compound colonies may be regarded as the most conspicuous event in the late history of the Graptoloidea.

Morphologically, the net result was transformation of the one-stiped monograptid rhabdosome into a multiramous one, achieved through the budding of a number of secondary branches radiating from the aperture of the sicula. This structural foundation was further developed by the formation of lateral cladia on some of the stipes. The taxonomic effect was the appearance of three genera (*Neodiversograptus, Linograptus*, and *Abiesgraptus*) forming a separate subfamily, the Linograptinae. The ecological results involved the formation of a novelty – in the form of compound rhabdosomes probably adapted to living in low energy waters. This was a great evolutionary success, and such colonies were flourishing in the Late Silurian–Early Devonian seas.

In every respect, therefore, the emergence of linograptids represented the transspecific level of evolutionary changes. What is more, the case of the Linograptinae illustrating the mesoscale of changes is especially instructive as it enables tracing the relations between sequential speciation and macroevolutionary processes proper. In addition to the analysis of the record, the aim of the present paper is to provide a conceptual framework for understanding of the processes involved.

DEFINITION OF THE PROBLEM

The change from the standard one-stiped monograptid rhabdosome to the multiramous compound colony may be visualized as an instant process. The appearance in a siculozooid of an ability to produce more than just a single daughter zooid by means of simultaneous budding seems morphogenetically a relatively simple event, a possible result of a single mutation with a considerably large phenotypic effect.

A similar mode of budding is represented by some cephalodiscid pterobranchs, e.g. by *Cephalodiscus gracilis*, where an adult zooid is capable of an almost simultaneous budding of a number of daughter individuals. They form a stellate group of buds in different growth stages (HARMER 1905: pl. 1, fig. 4 therein), thus providing a living model of morphogenesis in the *Linograptus* colonies (URBANEK 1963).

However, the emergence of linograptids followed a different pathway, that of stepwise generation of a multiramous condition. The fossil record available indicates that compound *Linograptus* colonies were preceded by pauciramous forms, chiefly represented by two-stiped bipolar colonies of the ancestral species – *Neodiversograptus nilssoni*. It therefore seems safe to stipulate that the "technology" applied in the macroevolutionary processes within the Linograptinae was piecemeal rather than total, stepwise rather than instant, producing a cumulative effect as a result of some partial improvements (see, however, RICKARDS *et al.* 1994 for a different opinion as well as p. 242 herein).

Another important feature of the linograptid phylogeny is its being restricted to a single line of descent. All morphological changes were realized in one lineage, practically without splitting. Almost all species belonging to the Linograptinae were sequential (chronospecies) and, consequently, no real multiplication of species is to be found (see p. 162 for a detailed discussion).

The idea that phyletic evolution in a single lineage may bring about macroevolutionary effects has fallen in disgrace mainly due to the wide acceptance of the punctuational model of phylogeny. As stated by STANLEY (1979: p. 17), "the punctuational model does not deny the existence of phyletic evolution, but relegates this mode of change to a subordinate role". Moreover, there is a strong conviction that "the speciational component of evolution so outweighs the phyletic component, in general, that it accounts for a large majority of transitions between genera. The role of phyletic evolution in the origin of families and orders is even smaller" (STANLEY 1979: p. 19). Recently this view has been strengthened by JACKSON *et al.* (1990), who claim that no anagenetic advances have ever been recorded in the evolution of a single monophyletic lineage. GOULD (1990) approves this conclusion as "a strong point", and similar ideas seem to prevail presently, with the notable exception of HOFFMAN (1988). He did not exclude that macroevolutionary effects may be attained within a single line of descent, quoting as an example my earlier studies on the Linograptinae (URBANEK 1963, see also LEVINTON 1986).

It is difficult to say whether the presently prevailing assessment of the significance of phyletic and speciational changes for transspecific evolution is generally adequate, but it may well be. Unfortunately, there is something in the very nature of scientific ideas that makes them universally accepted in their most extreme form. Punctuationalism is no exception to this rule. Hopefully, the present case study revealing the great role of phyletic evolution in shaping the major features of a large group of fossil animals may provide stimulative evidence for the ongoing debate about the mechanisms and the course of macroevolution.

MATERIAL AND METHODS

The material analyzed herein contains not only the samples previously etched out from the Mielnik IG-1 borecore and described in URBANEK (1963), but also some additional ones obtained from the Přidoli age section of the core.

More material was obtained from newly collected and dissolved erratic boulders coming from the locality Rewal and numbered S.236 in the author's collection, as well as from S.22 boulder (Jarosławiec, the collection of Dr. A. KOZŁOWSKA-DAWIDZIUK, Institute of Palaeobiology PAN, Warszawa), referred to as sample A further on. Whilst S.236 contained typical *Neodiversograptus nilssoni* and its age may be defined as the *N. nilssoni* Zone, the boulder marked S.22 in A. KOZŁOWSKA-DAWIDZIUK collection contained a transient form, *N. nilssoni/N. beklemishevi*, identified herein as *N.* cf. *beklemishevi*. Graptolites from this boulder were described by A. KOZŁOWSKA-DAWIDZIUK in her MSc thesis (unpublished). The associated fauna (*Lobograptus parascanicus*, *Cucullograptus pazdroi*, *Saetograptus chimaera*) is indicative of what is currently defined as the *L. scanicus* band.

Sample B corresponds to linograptid remains etched from the Mielnik borecore at a depth of 934.50 m (the *S. leintwardinensis* Zone) and representing a transient *N. beklemishevi/L. posthumus*.

Thus samples A and B contained transients while the bulk of the material may be assigned to one of the well-defined chronospecies of the Linograptinae.

The methods used may be defined as an inductive approach to the study of phylogeny, which means tracing morphological changes in the sequential series of samples obtained from succeeding horizons. Following a modern wording, it can also be called stratophenetic (GINGERICH 1976). However, the use of morphometric and statistical methods has been strongly restricted by the small numerical size of the samples. This cannot be overlooked as an important limitation of the material presented herein.

Although based on real specimens, all figures are presented diagrammatically in order to illustrate generalized concepts rather than factual data. They are completed by ideograms illustrating the working hypothesis advanced in the present paper.

Scanning electrone micrographs were taken from gold-platinum-coated isolated specimens with a Cambridge Stereoscan at 15 kV.

The material of *Linograptus posthumus* (Rheinhard RICHTER) illustrated on Pl. 1 is housed at the Institute of Palaeobiology of the Polish Academy of Sciences, Warszawa, and designated in the collection as ZPAL. G.XX.

THE FOSSIL RECORD

The recent views on the origin and evolution of linograptids owe much to the penetrating work of JAEGER (1959, 1960, 1969) as well as to papers by TELLER (1962, 1964) and PALMER (1971). I (URBANEK 1963) also contributed in a study based on well-preserved, isolated material from deep boring. It has elucidated a number of open problems concerning the linograptid phylogeny and astogeny. The descent of the linograptid lineage is a difficult problem. The crucial fact for its understanding is a striking resemblance between the early

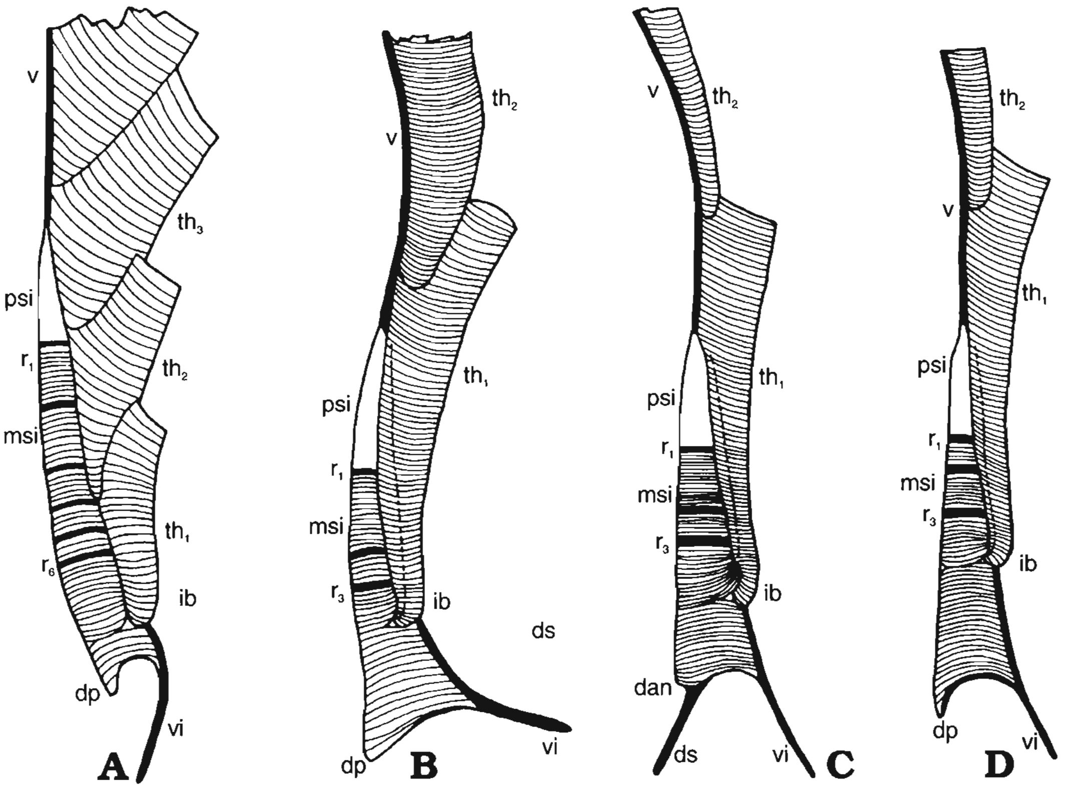

Fig. 1

Resemblance of the sicular part of rhabdosome as evidence of common ancestry. **A**, *Pristiograptus dubius* (SUESS, 1851). **B**, *Lobograptus? sherrardae* (SHERWIN, 1974). **C**, *Neodiversograptus nilssoni* (BARRANDE, 1850). **D**, *Lobograptus progenitor* URBANEK, 1966. All diagrammatical, growth lines in **B** are conjectural (after URBANEK 1966 and KOREN' and URBANEK 1994, modified). Abbreviations: dan – dorsal apertural notch of metasicula, dp – dorsal process of metasicula, ib – initial bud, msi – metasicula, psi – prosicula, r_1–r_6 – sicular rings (annuli), th_1–th_3 – successive thecae, v – virgula, vi – virgella.

representatives of the three major Ludlow lines of evolution – the Linograptinae, the Cucullograptinae, and the Neocucullograptinae (represented by *Bohemograptus).* Though these lines featured quite divergent trends of evolution, the differences between their early representatives were insignificant and did not increase until much later. This might suggest that all three derived immediately from a single ancestral species (URBANEK 1966, 1970). It was argued (URBANEK 1966) that this, still missing link must have resembled, in its essential features, *Lobograptus progenitor* URBANEK, 1966 – an early member of the cucullograptid lineage, and that it must have been devoid of either cucullograptid or linograptid specialization. KOREN' (1991, 1991a, and personal information) has most recently proposed *Lobograptus*? *sherrardae* (SHERWIN, 1974) from the *praedeubeli* Zone as the best candidate for their common ancestor and provided convincing stratigraphical and morphological evidence to corroborate her view. *L.*? *sherrardae,* which may be classified either as an advanced pristiograptid or a primitive linograptid, appeared due to adaptive radiation that followed the *lundgreni* Event, a great biotic crisis in the late Wenlock (KOREN' and URBANEK 1994). The material collected by KOREN' (1992) makes it possible to trace its origin to non-specialized survivors, namely to the *Pristiograptus dubius* stem lineage. In the *praedeubeli* Zone the divergence attained was still rather insignificant and consequently *L.*? *sherrardae* displayed only a slight distinction from its ancestor (cf. Fig. 1A, B). Such minor features as a gracilized and slightly dorsally curved proximal end of the rhabdosome, combined with some increase in the width of the sicular aperture, exhausted the linograptid "specialization" at that stage! Indeed, the crucial feature of the linograptid adaptive type – the ability to form sicular cladia – had not evolved yet, and the scope of future morphological (and ecological) changes remained wholly unpredictable at the *L.*? *sherrardae* stage of the evolution. Nevertheless, its morphology is unique among its collateral relations (described by JAEGER 1991 and KOREN' 1992), placing *L.*? *sherrardae* as an almost perfect candidate for a common ancestor of true linograptids (*Neodiversograptus nilssoni)* and the earliest cucullograptids (*Lobograptus progenitor).* Both the last named species share a number of common features with *L.*? *sherrardae* (as can be seen in Fig. 1A–D), and appear in stratigraphic sequence. *L.*? *sherrardae* represents the prelinograptid stage of evolution. Its obvious relation to the conservative pristiograptids of the *dubius* group makes the earlier views on the cyrtograptid ancestry of linograptids entirely obsolete.

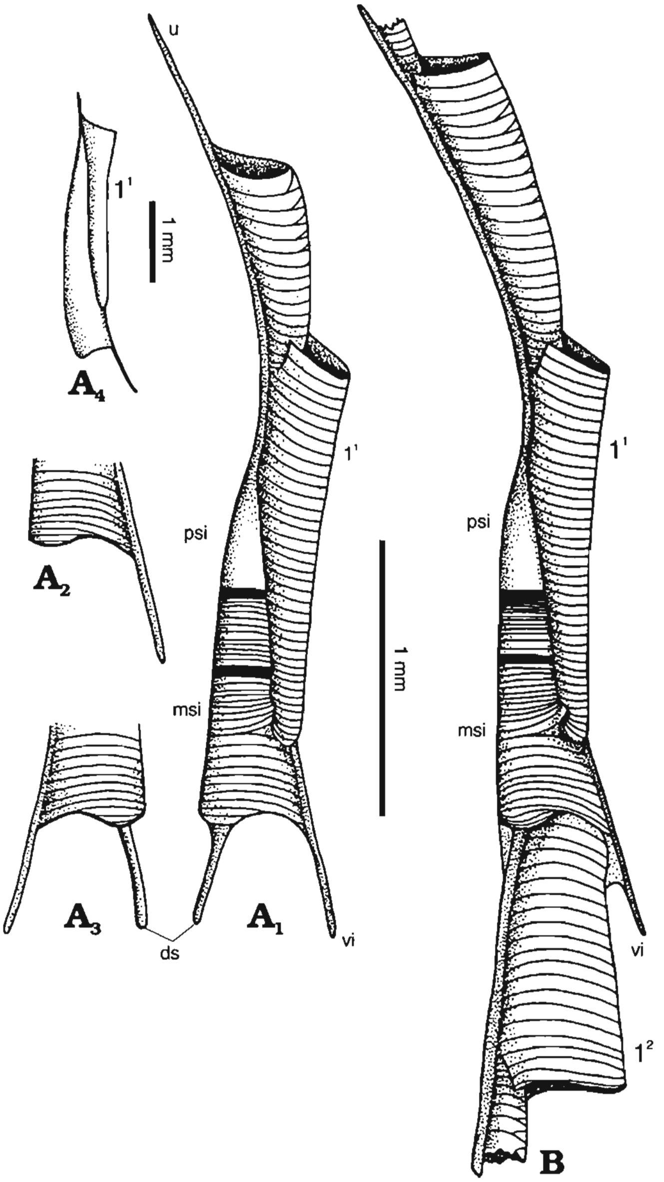

Fig. 2

Neodiversograptus nilssoni (BARRANDE, 1850) from *N. nilssoni* Zone, an example of the early linograptid organization. **A**$_1$, proximal end of a young unipolar colony. **A**$_2$, **A**$_3$, an early and advanced growth stage of bilobate dorsal process seen in both aspects. Note the presence of asymmetric dorsal spine (ds) in **A**$_1$–**A**$_3$ – a crucial linograptid specialization. **A**$_4$, proximal end of the young primary cladium with growing theca 1^1 and sicula lacking any apertural elaborations. **B**, a young bipolar colony.

The prelinograptid stage of evolution is represented by *Neodiversograptus* with its two species recognized. The earlier of the two, *N. nilssoni* (BARRANDE) as defined by me (URBANEK 1954, 1963), occurs

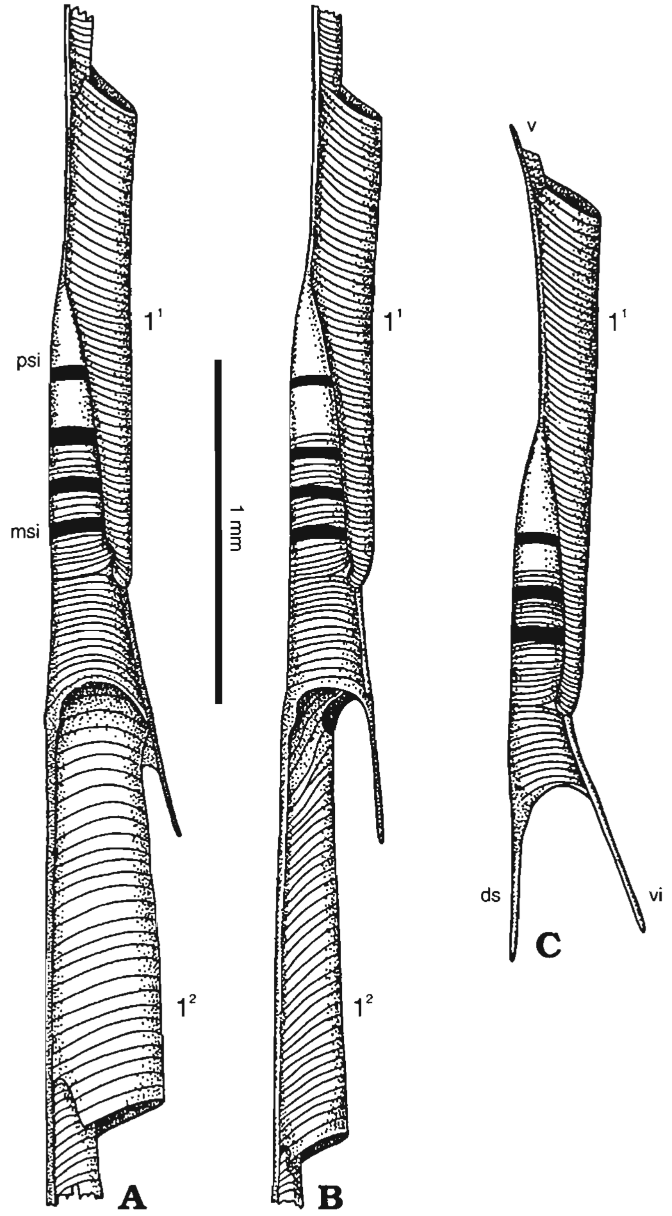

Fig. 3

Advanced linograptid organization as revealed by: **A**, *Neodiversograptus* cf. *beklemishevi* (sample A, *L. parascanicus* Zone) exhibiting transitional features between *N. nilssoni* and *N. beklemishevi*, namely gracilized but holoperipheral theca 1^2. **B**, *Neodiversograptus beklemishevi* URBANEK, 1963 (from *scanicus* Zone), showing meroperipheral theca 1^2 and free virgella. **C**, *Neodiversograptus beklemishevi* (from *leintwardinensis* Zone) displaying slight deviation of virgella (vi) (**B**, **C** after URBANEK 1963, **A** after unpublished drawing by A. KOZŁOWSKA-DAWIDZIUK).

within the eponymous Zone. The sporadic occurrence of bipolar rhabdosomes in the populations of *N. nilssoni*, e.g. rhabdosomes composed of a primary stipe, a procladium and an additional sicular stadium (Fig. 2A, B), may be considered the first distinct manifestation of the linograptid trend of specialization (JAEGER 1959; URBANEK 1963). The sicular cladium is supported by a peculiar asymmetrically placed dorsal apertural spine of the metasicula (URBANEK 1954), which later forms an additional virgula of a kind, the pseudovirgula, of this cladium. This function of the assymmetric dorsal spine was accurately guessed by JAEGER (1959) although he had no direct evidence to support his supposition. The first such evidence was provided somewhat later (URBANEK 1963), and since that time more specimens of this kind have been found. The scarcity of bipolar rhabdosomes is indicative of a morphogenetically non-stabilized nature of the newly acquired trait whilst the robust appearance of the initial thecae in the sicular cladium suggests that there was a considerable lag in the generation of the cladium as compared with that of the primary stipe. Therefore the growth of the sicular cladium coincided with that of the distal thecae of the procladium. It is safe to conclude that those bipolar, "diversograptid" rhabdosomes had low frequency in the *N. nilssoni* populations but cooccurred steadily with the standard "monograptid" morph within the same breeding community.

The second species, *N. beklemishevi* URBANEK, 1963, occurs somewhat higher, namely in the interval between the *L. parascanicus* Zone (= the early part of the *L. scanicus* Zone) and the *S. leintwardinensis* Zone, as currently defined. It represents a more advanced stage of morphological evolution towards *Linograptus*, the pseudovirgula of the first sicular cladium being first formed as a symmetrically placed dorsal apertural spine. Moreover, the material available comprises both the forms which are capable of forming only one sicular cladium (Fig. 3A, unpublished material) and those having a potential ability to generate more such cladia (Fig. 3B). In the latter case, the first theca of the sicular cladium conceals no more than part of the metasicular aperture, leaving considerable space to be used subsequently by additional sicular cladia. But even then the pseudovirgula stretches straight and forward, without producing any divergence (the angle between the dorsal wall of the metasicula and the theca is approximately 180°) (Fig. 3C). It is only in the *S. leintwardinensis* Zone that the first occurrence of forms with a certain divergence was noted (an angle about 150°) (Fig. 4A). Such forms approach *Linograptus* to a great extent, except for the standard structure of their virgella.

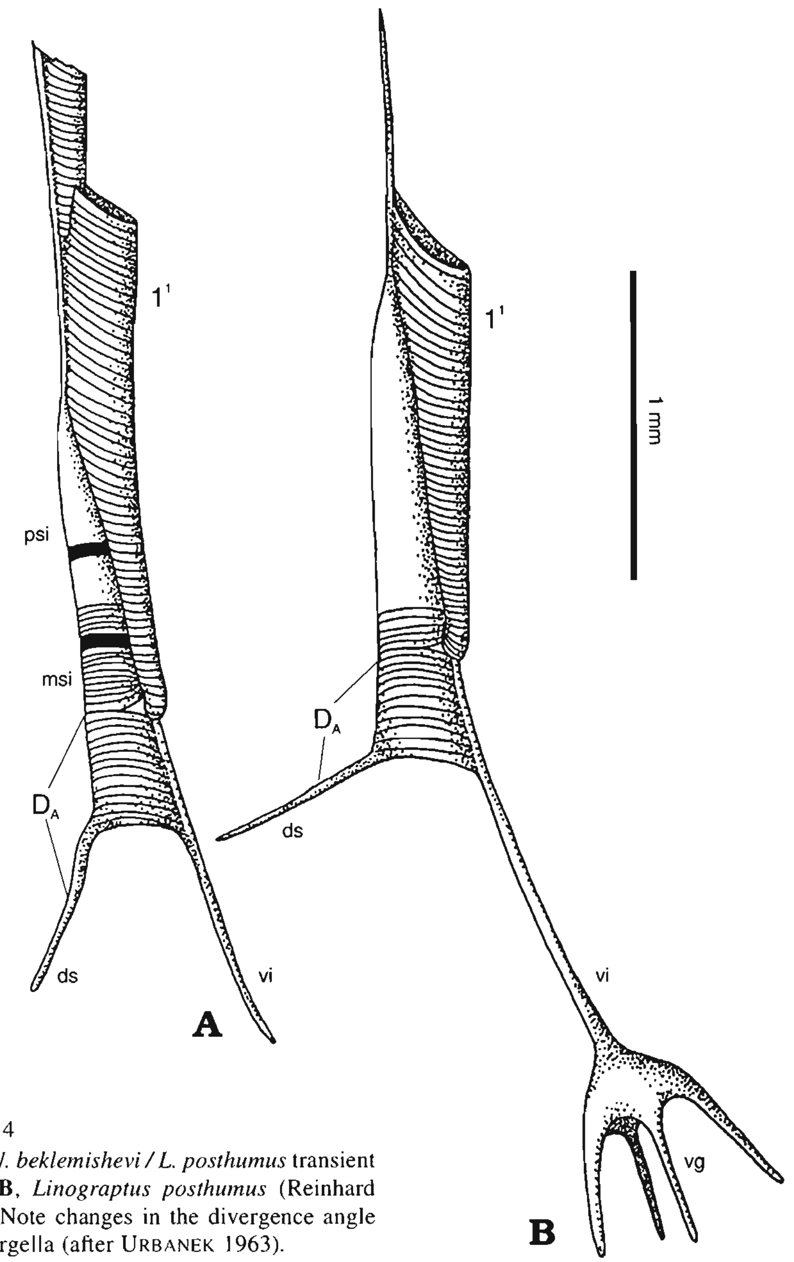

Fig. 4
Restructuring of the sicula as seen in: **A**, *N. beklemishevi / L. posthumus* transient (sample B, *S. leintwardinensis* Zone); **B**, *Linograptus posthumus* (Reinhard RICHTER, 1875) from the *ultimus* Zone. Note changes in the divergence angle (D_A) and modification of the virgella (after URBANEK 1963).

Linograptus with its species *L. posthumus* (Reinhard RICHTER, 1875) attain a truly multiramous condition, all colonies being capable of forming more than one sicular cladium. The dorsal spine of the metasicula and, consequently, the pseudovirgula of the first sicular cladium usually diverges at an almost right angle from the aperture of the metasicula (Fig. 4B), thus leaving more space for the buds of additional sicular cladia which appear in a rapid succession (Fig. 5). They come out as small tubercules on the apertural margin of the metasicula that later extends into the pseudovirgula or the axis of a given sicular cladium. The first sicular cladium appears very early, with only a slight delay in respect of the primary stipe (procladium, Fig. 5). Up to 6 uniserial stipes are usually formed, but in some cases as many as 15 have been observed (JAEGER 1964). The four-stiped (JAEGER 1959, 1969) or six-stiped (TELLER 1964) rhabdosomes were claimed to represent the astogenetic norm (a fully grown typical rhabdosome). Although the data on the numerical prevalence of rhabdosomes consisting of a certain number of stipes at different stratigraphical levels are somewhat confusing (JAEGER 1969), the entirety of the evidence available points to the four-stiped compound rhabdosome as the basic morphological unit in *Linograptus*. Moreover, the intrinsic tetrameric arrangement of the *Linograptus* colonies is indicated by the symmetry

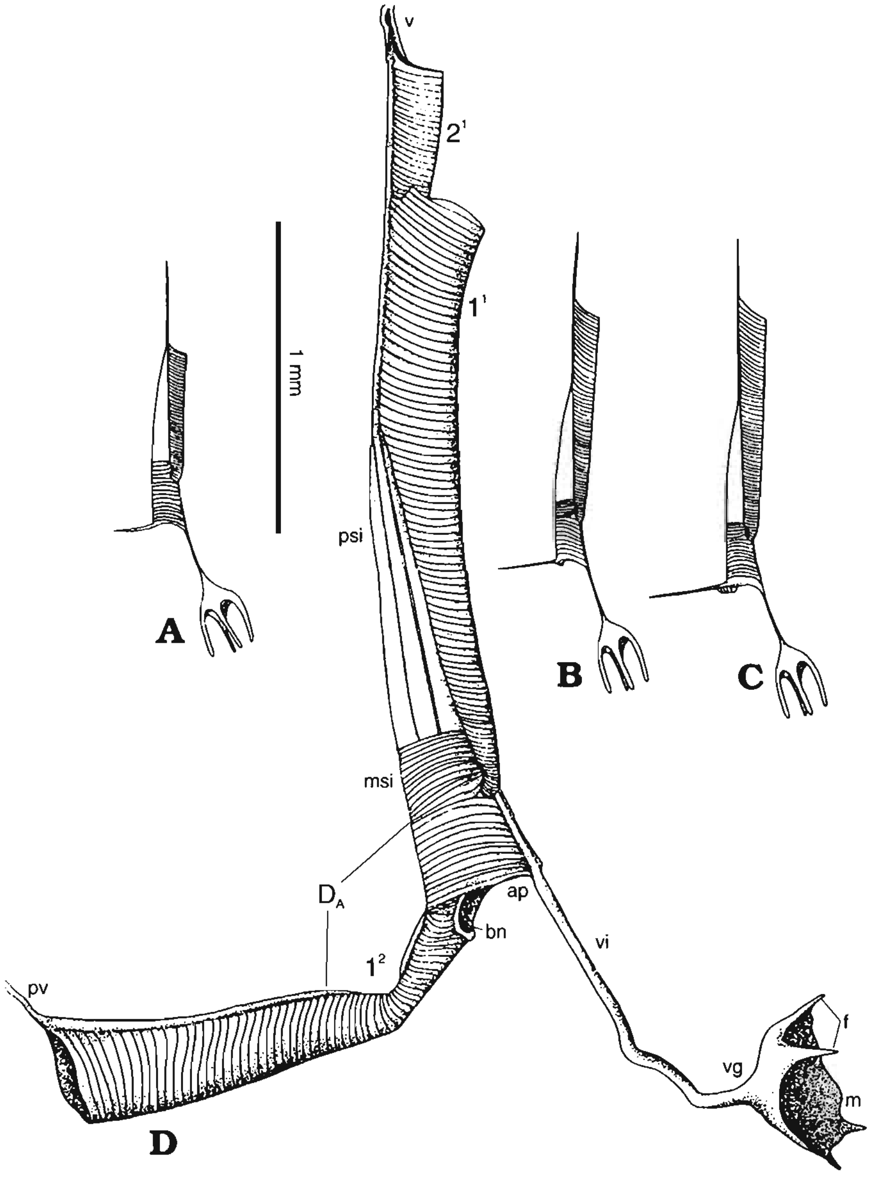

Fig. 5

Growth correlations within sicular part of the rhabdosome in *Linograptus posthumus* (Reinhard RICHTER, 1875). **A–C**, early stages showing concommitant growth of distal part of theca 1^1 and incipient portion of 1^2. **D**, Advanced stage showing that growth of theca 1^1 is completed simultaneously with the formation of prothecal part of theca 1^2 (after URBANEK 1963).

of the virgellarium, the termination of the long and robust virgella. This unique colonial device is composed of a membraneous portion (m) which produces four petals, each ending in a long fingerlike outgrowth (Fig. 5; Pl. 1: 1a, Vg, f).

The time of the appearance of the virgellarium cannot be precisely defined. The earliest finding of this structure, already fully developed, was recorded in the Mielnik borecore at a depth of 823.00 m and may be related to the *latilobus/balticus* Zone (for its definition see URBANEK 1995 and this volume p. 94). But the bulk of the linograptid material was obtained from somewhat earlier strata (837.60–820.00 m), that is from the *N. kozlowskii–Pseud. latilobus* Interzone. These linograptids, hardly differing from the later Přidoli forms, were probably provided with a virgellarium, which, however, has not been preserved. This assumption was recently confirmed by ŠTORCH (1995) who recorded *Linograptus posthumus* with typical virgellaria in the *kozlowskii* Zone of the Barrandian area. According to him these specimens are early representatives of the type subspecies (*L. p. posthumus*), although they reveal some features which fits better the earlier *L. p. tenuis*. Thus the early Ludfordian most probably corresponds to the time of the

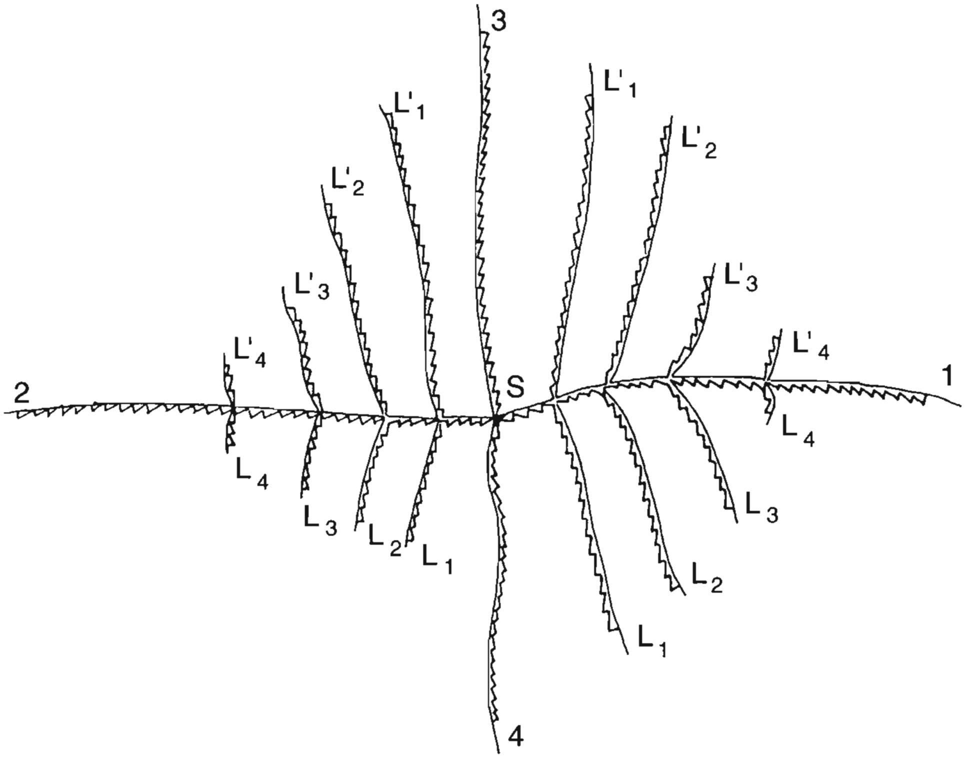

Fig. 6
Pattern of colony organization in *Abiesgraptus* as interpreted by JAEGER (1959). The paired lateral cladia (L'_1–L_1) are produced at rather regular intervals only on the procladium (1) and on the first sicular cladium (2), while remaining two sicular cladia do not display branching (3, 4). S means sicula (after JAEGER 1959, modified).

origin of the virgellarium. The questions whether it could have appeared still earlier (in the *leintwardinensis* Zone) and whether its mode of appearance was rapid or gradual remain open. The appearance of the virgellarium and the multibrachiate nature of the compound rhabdosome are the main evolutionary novelties developed by *Linograptus.* It was capable of producing truly giant rhabdosomes with stipes more than 60 cm long and colonies numbering more than 1500 individuals (JAEGER 1969)! The stratigraphical occurrence of *Linograptus* is largely defined by the conventionally set morphological boundaries. For the purpose of the present analysis, its first appearance may be identified as the top of the *leintwardinensis* Zone whilst its upper limit is the top of *hercynicus* Zone.

In the Lower Devonian (the *M. uniformis–M. praehercynicus* Zone), the linograptids with a tetrameric foundation gave rise to highly symmetric (rhombic) colonies of *Abiesgraptus* (JAEGER 1959, 1969). As interpreted by JAEGER (1959), the *Abiesgraptus* rhabdosome is composed of two main stipes (the procladium and the first sicular cladium) producing , at certain intervals, paired thecal cladia, and of two additional sicular cladia placed normal to the main stipes and devoid of thecal cladia (Fig. 6). During its early astogeny, the *Abiesgraptus* rhabdosome is indistinquishable from the four-stiped *Linograptus.* It is not until later that many paired thecal cladia are produced on the two earliest stipes, which results in a sharp morphological discontinuity between otherwise closely related taxa. Thecal cladia grow bilaterally from the aperture of the parent theca (supra-apertural budding), being supported by a pseudovirgula, a rigid rod which probably emerged as a lateral apertural spine of the parent theca. The generation of paired thecal cladia on the main stipes of the *Abiesgraptus* rhabdosome may have led to an improvement of the colony balance and to a better use of space and food resources (JAEGER 1969). The resulting complex colonies densely covered large areas (approximately 1770 square centimetres), intensively exploited by a great number of zooids (perhaps more than 3000 zooids in a single colony; MÜLLER 1965). The presence of a virgellarium has not been proved in *Abiesgraptus* because of the strong "carbonization" of the central portion of the colony, making structural details quite obscure (JAEGER, personal communication). It is, however, equally possible that a virgellarium was present as a legacy from the linograptid ancestors or that it was already reduced to be replaced by a generally more efficient suspension system thanks to the lateral branching and the extensive area occupied by the colony. The abiesgraptid species constituted the final stage of the *L.*? *sherrardae–N. nilssoni* evolutionary line, representing at the same time, one of the most complex graptoloid colonies ever formed. One can conclude that there are sufficent data allowing the origin, divergence and anagenetic advance in this lineage to be traced over an imposing time span – from the *praedeubeli* Zone (Homerian) to the *hercynicus* Zone (Lochkovian), and possibly even higher up to the *fanicus* Zone of Pragian, where last abiesgraptids were recorded.

While the bulk of the material available is strongly suggestive of a stepwise emergence of multiramous condition, the recent study by RICKARDS *et al.* (1994) on the Ludlow graptolite fauna from New South Wales (Australia), speaks in favour of a rapid origin of multiramous forms, directly from *N. nilssoni.* This is indicated by the occurence of an endemic multiramous form, *Linograptus orangensis*, at the bottom of the *nilssoni* Zone. The form in question is in some respects rather unique and even in opinion of RICKARDS *et al.* (1994: p. 12) "does not help understanding of the relationship of *Neodiversograptus* to *Linograptus*". This is because of the growth direction of sicular cladia in *"L." orangensis* are either reclined or straighforward (and only in one specimen a sicular cladium grows downwards). In my opinion the Australian form represents a stage of evolution comparable with *N. beklemishevi* and probably is of a somewhat later age (boundary of *nilssoni–progenitor* or even bottom of *scanicus* Zone). It is possible that large part of what is considered there the *nilssoni* Zone, should be already assigned to the *scanicus* Band, as it is indicated by the FA's of advanced lobograptids in NSW sections. The precocious origin of this multiramous form might be explained as illusory, an effect of different interpretation of stratigraphic data in Australia and in Europe. More enigmatic is the still earlier occurrence of a single specimen of multiramous *Linograptus* sp. in *ludensis* Zone. However, until more data are available I would prefer a stepwise emergence of *Linograptus*, to RICKARDS' hypothesis of its instantaneous origin from *N. nilssoni.* The latter view fails to explain why in Europe the evolution of multiramous linograptids is stretched over several graptolite Zones.

THE FUNCTIONAL AND ADAPTIVE MEANING OF THE EVOLUTIONARY CHANGES

The life orientation of the standard monograptid uniramous colony in the water column has not been convincingly established, current opinions representing contradictory views summarized in the papers by BATES and KIRK (1984), LENZ and CHEN (1985), and FINNEY and JACOBSON (1985).

In the light of new studies (RIGBY and RICKARDS 1989; RIGBY 1992) on physical models of graptoloid colonies, the characteristic dorso-ventral curvature in the proximal part of the *N. nilssoni* procladium could be regarded as a factor causing the rotation around the long axis and enhancing the feeding efficiency. There is little doubt that the appearance of two-branched, bipolar-growing ("diversogratid") rhabdosomes in *Neodiversograptus nilssoni* had a great impact on the balance and hydrodynamic properties of the colony. The resuling situation, however, can only be described in a hypothetical way.

Accepting the vertical orientation of the uniaxiate monograptid colonies as the most reasonable hypothesis, one could posit a horizontal orientation for the diversograptid bipolar morphs. This may be visualized all the more easily assuming a heterodoxal, "upside down" life orientation of monograptid colonies, with the sicula directed upwards as suggested by KIRK (1969, 1972, 1978). The change of orientation from the standard form to the diversopraptid one may be expressed as follows: $\overline{\mathrm{V}}\rightarrow\mathrm{H}-$, where $\overline{\mathrm{V}}$ is vertical orientation with the sicula directed upwards, whilst H-denotes a horizontal life position with the sicula in the middle (Fig. 7A, B).

Less obvious is the impact of such changes on the balance of the uniaxate colonies oriented vertically with their siculae positioned downwards ($\underline{\mathrm{V}}$, Fig. 7A). It seems probable that in the latter case the bipolar rhabdosome preserved its primary vertical orientation: $\underline{\mathrm{V}}\rightarrow\mathrm{V}-$, rather than changing it to a horizontal position: $\underline{\mathrm{V}}\rightarrow\mathrm{H}-$ (Fig. 7C).

A reversed orientation as proposed by KIRK (1969) would be a kind of prospective adaptation to future changes in the life position of the rhabdosome. Such horizontally oriented bipolar rhabdosomes, both in their rectilinear and bent form, ought to face a number of hydrodynamic problems, even if one assumes fairly great flexibility during life.

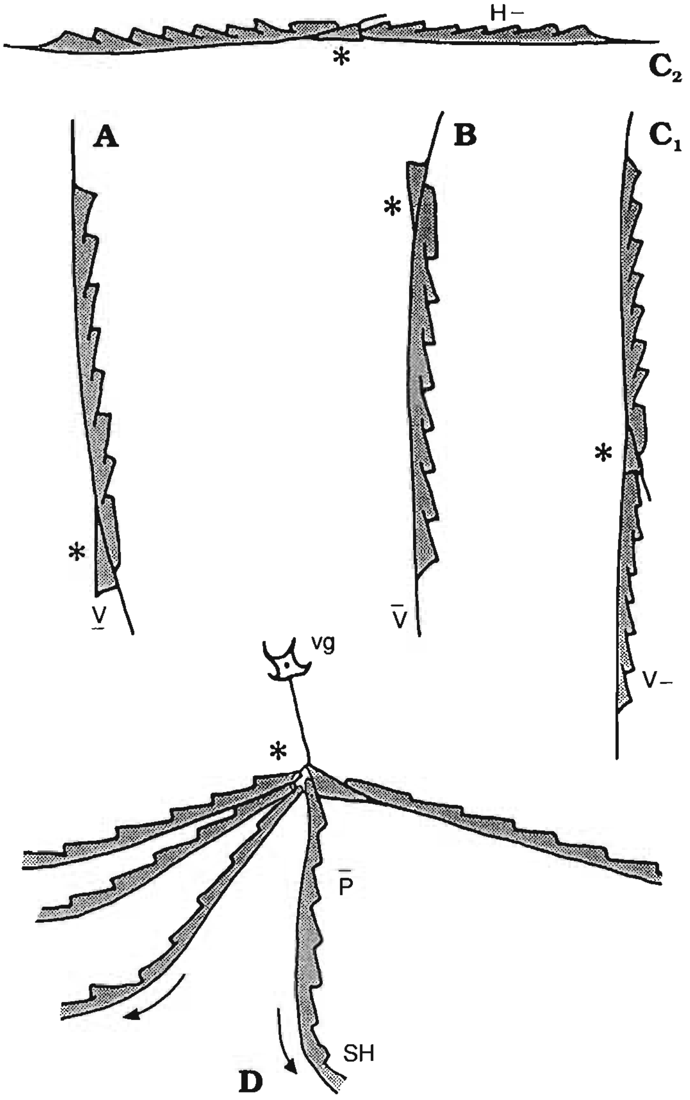

Fig. 7

Diagram showing the possible orientation of linograptid colonies in the water column: **A**, **B**, vertical orientation of unipolar colony with its sicula downwards (**A**) and upwards (**B**); **C**$_1$, **C**$_2$, possible orientations of siculate bipolar colonies, with sicular cladium downwards (**C**$_1$) or both cladia oriented horizontally **C**$_2$); **D**, compound colony of *Linograptus* oriented with virgellarium (vg) and sicula upwards while proximal part of branches are pendent and later bent subhorizontally. Further explanations in text.

The ability to generate a number of sicular cladia in *N. beklemishevi* was a certain improvement in the stability of the rhabdosome and produced a larger working surface which may have prevented sinking. But it was the appearance of a regularly multiramous *Linograptus* rhabdosome that radically improved the balance of the colony, ensuring a far better stability in calm waters. The presence of a divergence angle in the proximal portion of the stipes resulted most probably in a pendent position of the rhabdosome ($\overline{P}$), at least in the early astogenetic stage (URBANEK 1963). This may take the form of: $H^- \rightarrow P$ and is shown in Fig. 7D as seen in the isolated proximal fragments of some such rhabdosomes.

However, the distal portions of the cladia were secondarily reflexed taking again a more horizontal orientation (JAEGER 1959). Thus the orientation of the *Linograptus* colony may be described as changing astogenetically from pendent ($\overline{P}$) in the centre to horizontal (H–) or subhorizontal (SH–) on the periphery. As long as we assume a buoyancy function of virgellarium (vg), a reverse position of rhabdosome (with vg oriented downward) seems very unlikely.

Such distinct differences in the shape of particular growth stages of the colony provide evidence of their obviously different mode of life position in the water column, and general hydrodynamic properties.

According to FINNEY (1986), such growth differences were instrumental in avoiding too severe intraspecific competition thanks to confining the juvenile and the mature growth stages to different habitats. This strategy was surely important for organisms like linograptids which probably frequently lived in huge and densely crowded populations.

A *Linograptus* colony may be visualized as essentially passively suspended in the water column due to a specialized device, the virgellarium (cf. p. 240). Its structure and position within the rhabdosome is strongly suggestive of a buoyancy function (URBANEK 1963; TELLER 1964; JAEGER 1969) although its operation is difficult to understand. The earlier suggestions that the virgellarium was merely part of the skeleton supporting a vesicular structure made of soft tissues (URBANEK 1963) are undermined by more recent views on the mode of secretion of the graptolite colonies. (CROWTHER 1981). They assume a purely pterobranch way of secretion by individual contributions of the zooids, which depositing new skeletal material due to the movements of the cephalic disc were responsible for the secretion of both the fuselli and the cortical bandages (see URBANEK 1986 for an extended discussion of this question). The presence of any extrathecal soft tissue in graptoloid colonies seems therefore doubtful, although FINNEY (1979) presented new and suggestive data in favour of the old idea about the presence in them of vesicular buoyancy organs. Still it is also possible that the petals and the finger-like outgrowth of the virgellarium served as the place of attachment of a gas bubble or a large droplet of a liquid fatty substance capable of reducing the relative density of the colony (Fig. 5). Such a buoyancy material may be imagined as secreted by the siculozooid, and regulation of its amount could result in vertical migration of the colonies. In the Early Přidoli, several branches within a single linograptid colony produced an additional suspension effect (although they mostly served as stabilizers), while geologically younger forms with a reduced number of branches were suspended mainly with the help of an elaborated virgellarium (Fig. 7D, vg).

The generation of lateral thecal cladia in addition to the main stipes of the *Linograptus* rhabdosome finally solved the problem of balance. The resulting *Abiesgraptus* compound colony was strongly stabilized. The potential ability to produce lateral thecal cladia appeared early in the phylogeny of the *Linograptus–Abiesgraptus* line of descent, as shown by the sporadic occurence of rhabdosomes provided with only one pair of thecal cladia (TELLER 1964; the Přidoli, probably the *ultimus* Zone) or even with a single unilateral cladium (JAEGER 1969; the Lochkovian, the *uniformis* Zone). Such trials which instantly offered a certain advantage in the balance were probably favoured by natural selection and followed by a more ordered generation of numerous thecal cladia with a precise morphogenetic control of their formation (see p. 256 herein).

In addition to a high degree of stability, lateral thecal cladia also accounted for an increase of the working surface in *Abiesgraptus*, which prevented sinking and had a suspension effect. Combined with the flattening of the proximal part of the rhabdosome, these features made the *Abiesgraptus* colony leaf-like.

This suggests that advanced linograptids were partly hydrogliders capable of gliding on horizontal currents (BERRY *et al.* 1987). However, in contrast to what BATES and KIRK (1984) say they were not stiffly branching, but highly flexible, yielding to wave motion rather than resisting it.

This rhabdosome type seems to represent extreme adaptation to the near surface dwelling. Thus the entire evolution of linograptids may be interpreted as an escape from the oxygen deficient zones towards better aerated surface waters, with *Abiesgraptus* manifesting the terminal stage of the process. The above interpretation differs from that of BATES and KIRK (1984) who posit that *Linograptus* and *Abiesgraptus* were lower layer colonists (a habitat created, in their opinion, in the Late Silurian–Early Devonian as a result of eustatic changes in the sea level!) and not surface dwellers. The present interpretation seems to offer a better explanation of the foliate shape of the *Abiesgraptus* rhabdosome, agreing well with the most recent model of the hydrochemical regime of the Silurian seas proposed by BERRY *et al.* (1987). Based on the Recent conditions observed in the Pacific Ocean off Peru, this model assumes the presence of a "hanging", shallow (a few hundred meters deep) Oxygen Minimum Zone (OMZ) instead of a massive bottom anaerobic zone as implied by the classical Black Sea model. The upper level of the sea must have constituted the graptoloid habitat while the presence, depth and thickness of the OMZ were probably the main environmental factors controlling their evolution. Moreover, linograptids (and especially *L. posthumus*) were ubiquitous representingg an almost omnipresent element of the various graptoloid assemblages. According to the line of reasoning offered by COOPER *et al.* (1991), such behaviour seems more indicative of an epipelagic depth zone than of any deep water biotope. Therefore, unlike the slender multiramous Ordovician dichograptids and contrary to what was posited by BATES and KIRK (1984), linograptids must have occupied the near surface waters of the ocean, "leaking" from this biotope into the epipelagic zone of the shelf.

The pattern of the *Abiesgraptus* rhabdosome,especially its numerous and regularly spaced lateral cladia, indicates that a certain principle of economy was involved in the formation of such colonies (JAEGER 1959). *Abiesgraptus* evidently represented an instance of a very effective utilization of space and exploitation of the trophic resources. FORTEY and BELL (1987) applied the notion of harvesting array for graptoloid colonies, considering this factor to be responsible for the pattern of the multiramous ones. Linograptids provide a convincing example of the maximization of harvesting efficiency. As calculated by MÜLLER (1965), an *Abiesgraptus* colony covered an area of some 170 square cm exploited by more than 3000 zooids on its branches! Thus a high harvesting efficiency was achieved in *Abiesgraptus* through a mere increase of the number and concentration of zooids (dense packing in a limited area). The solution of the adaptive problem, however, did not involve the elaboration of complex apertural aparatuses allowing an increase in the individual feeding efficency of particular zooids (the trend of recorded evolution encountered in the Cucullograptinae and Neocucullograptinae and a number of other groups). The strategy chosen by the linograptids resulted in the development of simple thecae and complex colonies whereas in the majority of monograptids the thecae were elaborated and the colonies simple.

Thus the flat leaf-like colonies of *Abiesgraptus* featured an adaptive syndrome ensuring the solution of the three main problems at once: a perfect balance of the colony, its almost steady suspension, and a high harvesting efficiency of the colony as a whole.

A MORPHOGENETIC INTERPRETATION OF THE RECORD

The appearance of a bipolar siculate morph in *Neodiversograptus nilssoni*, although *per se* a crucial evolutionary event, was by no means unique. Sporadic occurrences of such bipolar rhabdosomes were recognized by RICKARDS (1973) and RICKARDS *et al.* (1977) in a number of quite unrelated monograptid groups. It may be thought, therefore, that the latent ability to produce sicular cladium in advanced astogenetic stage, was a common feature in most monograptids. Phenotypic expression of this morphogenetic potential in *N. nilssoni* (and in other similar cases), may probably be ascribed to developmental switches, due to mutation or other changes in the genomic background, as it was recognized in epigenetic systems of many extant organisms. In the case of *Diversograptus* and *Neodiversograptus* this new pattern of development was later fixed as a norm, probably due to favourable selection pressure. The nature of the adaptive advantage represented by bipolar morph is obscure and may only be hypothetized (see p. 242, herein), but the evolutionary success of it is clearly demonstrated by the available fossil record.

Moreover, the ability of *Neodiversograptus nilssoni* to generate not only a normal monograptid branch (the procladium), but also an additional one (the sicular cladium) seems to be due to a mechanism similar to the rejuvenation of the siculozooid. The daughter individual (1^2) produced by the siculozooid (si) conceals the entire metasicular aperture, leaving no space for the siculozooid proper (Fig. 2B). Therefore the first zooid of the sicular cladium (1^2) may only be considered a further growth stage of the metasiculozooid, the result of additional growth after a considerable arrest marked by the thickened apertural margin of the metasicula. This may be best explained as a morphogenetic reactivation of the metasiculozooid, a process similar to the cases of rejuvenation or parricidal budding in some corals. After being rejuvenated, 1^2 generated 2^2, the first zooid proper of the sicular cladium.

The asymmetric position of the dorsal apertural spine (ds) of the metasicula, later transformed into the pseudovirgula of the only sicular cladium and shifted secondarily into the plane of symmetry, corroborates the view that the entire construction was relatively imperfect at the early stages of its phylogeny. This asymmetry, in turn, was a direct effect of the bilobate nature of the dorsal process divided by a notch into two lateral lobes (URBANEK 1954; Fig. $2A_2$, A_3 herein). Thus, the above-mentioned relative imperfection resulted from simple topographic or geometrical constraints.

The large size of its thecae suggests that the sicular cladium in *Neodiversograptus nilssoni* was a later formation than the primary branch (the procladium). From the growth correlation control within the graptoloid colonies it follows that isochronous thecae are isomorphic (Thorsteinsson rule, URBANEK 1960, 1963, 1970). Thus, the size and shape of the first thecae of the sicular cladium in *N. nilssoni* are indicative of their being formed simultaneously with the distal portion of the procladium (the primary stipe). The rich material analysed by PALMER (1971) shows that the sicular cladium was usually formed around the theca 16^1 growth stage of the procladium, although a certain lag in the development of theca 1^2 observed in other multiramous monograptids may account for its somewhat earlier initiation (say at the theca 13^1 stage). A considerable variation in the timing of the appearance of the sicular cladium has also been demonstrated.

Because of the large size of theca 1^2, its base filled the entire space of the metasicular aperture, which instance may be termed the holoperipheral budding (Fig. 8A). As a result, the aperture of the sicula was completely sealed; there was no space for more buds initiating additional sicular cladia. This was a new geometrical constraint, allowing the formation of only a single sicular cladium. Moreover, the big size of the growing 1^2 involved the incorporation of the main portion of the virgella into the ventral wall of the growing theca, thus excluding the possibility of a progressive modification of the virgella, so characteristic of the later history of the Linograptinae (Fig. 2B, vi).

The majority of *N. nilssoni* specimens figured by PALMER (1971) display some degree of divergence of the sicular cladium, the result of a similar divergence in the growth of a long (up to 8 mm) and stout dorsal apertural spine of the metasicula, which later transformed into the pseudovirgula of the sicular cladium. This contrasts with the straightforward growth of this spine in *N. beklemishevi*. However in *N. nilssoni*, the generally robust theca 1^2 conceals the entire apertural margin of the metasicula (PALMER 1971; Fig. 4 therein), thus the divergence of branches has no effect on making more space for additional sicular buds. Later, after the gracilization of theca 1^2, such divergence produced a far-reaching result, namely, meroperipheral budding (see p. 248 herein).

A delay in the generation of the sicular cladium in *Neodiversograptus nilssoni* accounts for the fact that not until the 16^1 thecal stage was it able to attain the bipolar, diversograptid organization. Although the presence of the long dorsal apertural spine of the metasicula, a prerequisite for the formation of the sicular cladium, is a species-specific character, only a fraction of the colonies displayed the bipolar phenotype. Was the appearance of the bi-ramous rhabdosome only a function of the age of the colony, or did it also involve some genetic differences? The answer is naturally uncertain (see p. 247 herein). But it is worth mentioning that the genetic factors which control the formation of the cladium were expressed fairly late in the astogeny of the *Neodiversograptus nilssoni* colonies.

The populations from the *parascanicus–scanicus* Zone which may be assigned to *Neodiversograptus* cf. *beklemishevi* are composed of forms invariably provided with a symmetrically placed dorsal apertural spine of the metasicula. In spite of this change, these populations still comprise both forms displaying the holoperipheral budding of theca 1^2 and therefore capable of forming only one sicular cladium (unpublished MSc thesis of A. KOZŁOWSKA-DAWIDZIUK), and much more advanced forms. The latter morph features a much smaller size of theca 1^2, thus leaving part of the sicular aperture uncovered and creating a potential for the formation of more than one sicular cladium. This situation may be termed the meroperipheral budding as only part of the aperture of the mother theca is being used (Fig. 8C). In accordance with the Thorsteinsson rule (see p. 245), the smaller size of theca 1^2 is indicative of its earlier generation, at a time coinciding with the growth of the proximal thecae. It is obvious therefore that the mechanism of astogenetic acceleration was used to avoid the obstacles resulting from the above-mentioned geometrical constraints. At the same time, the virgella was set free from its association with the ventral wall of the bulky holoperipheral 1^2, entering the path of its future modification. These comparative advantages were still combined with certain imperfections, such as the straightforward growth of theca 1^2, a mechanical consequence of the same direction of the symmetrical dorsal apertural spine of the sicula, extending into the pseudovirgula of the cladium (Fig. 3A, B).

Thus the course of phylogenetic events was not quite consistent. An earlier trait – the ability of the dorsal apertural spine of the metasicula to diverge, so frequent in the early *N. nilssoni* populations (PALMER 1971), was somehow lost and replaced by a potentially less adaptive ("inadaptive") character state, namely the straightforward orientation of the above spine in *N. beklemishevi* (URBANEK 1963). The adaptive inconsistencies of the real course of the evolution are demonstrated by (1) the functional ineffectiveness of the divergence of the two stipes because of the bulky size of 1^2 in *N. nilssoni* which, in spite of the divergence, covers the entire metasicular aperture, (2) the dissapearance of the divergence when the gracilized theca 1^2 makes it possible to free a part of the apertural space for the additional buds, and moreover, (3) the later restitution of the divergence in the linograptid stage of evolution, thus producing secondarily the most adaptive combination (small theca 1^2 plus the divergence of the sicular cladium (see p. 247 herein). Such a zig-zag pattern of behaviour of a single character seems not exceptional in the phylogeny.

The meroperipheral mode of budding in the advanced forms of *Neodiversograptus beklemishevi* resulted in the co-existence of a physiologically active metasiculozooid (si) with its daughter individual

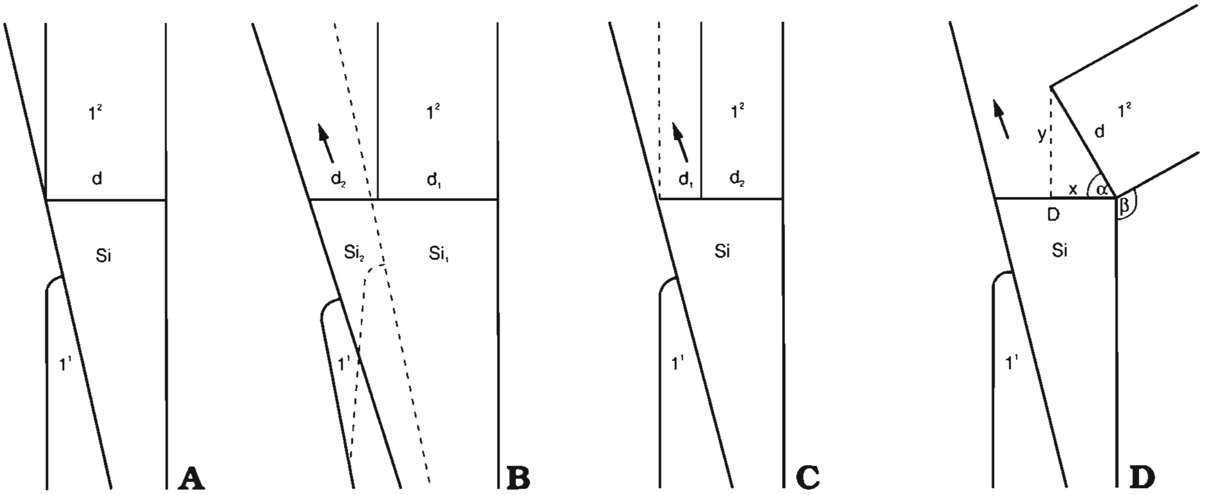

Fig. 8

Geometrical constraints at the aperture of metasicula (si) in Linograptinae: **A**, holoperipheral budding of theca 1^2 in *Neodiversograptus*, occupying the entire diameter (d) of metasicualar aperture and leaving no free space for additional buds. This situation produces an obstacle for generation of more cladia. **B**, more free space (d_2, Si_2) may potentially be gained by simple widening of the aperture from diameter (d_1, Si_1). A free space created in this way could be used by additional cladia. **C**, free space at the sicular aperture (arrow) may also be attained by slimming of theca 1^2 (change from diameter d_1 to d_2), which needs an accelaration in formation of theca 1^2, because of growth correlation within the colony. **D**, more free space at the sicular aperture may be attained with the same width of 1^2, through a deviation in the direction of its growth. Free area is directly related to the angle of deviation, α.

(1^2). The latter is no longer a rejuvenated or parricidal siculozooid, but a normal blastozooid formed due to budding from its parental individual which, correspondingly, behaves as 2^2 in *N. nilssoni.* This effect may also be interpreted as a result of acceleration (see Figs 2B and 3B).

The emergence of *Linograptus* was therefore intimately related to the generation of a number of cladia from the aperture of the parental metasicula, which posed a constructional problem — an elegant and simple instance of constraint. In the case of linograptids, the nature of the constraint is both developmental and physical, as the realization of the multiramous pattern of the colony (a certain phenotype!) is prevented by the physical (geometrical) properties of the metasicula, that is by the limited space of its aperture (Fig. 8A). This hindering of the formation of additional buds imposes quite severe boundary conditions on the development of a multiramous rhabdosome. However, such constraint, arising from the local topographic situation, might be overcome, at least potentially, by a number of simple solutions, e.g. (1) by the expansion (widening) of the aperture of the sicula (Fig. 8B), (2) by the narrowing of the base of the daughter theca 1^2 (Fig. 8C) and leaving in this way some free space, or (3) by the divergence of the primary sicular cladium due to a change in the direction of its growth, thus creating free space for additional buds (Fig. 8D). It is quite obvious that each of these changes (1–3) would have produced some open space at the sicular aperture which could have been used by a number of additional buds, each initiating a new sicular cladium. However, in the real course of evolution, linograptids never used solution 1, although monograptids with a strongly expanded (trumpet-like) sicula occur sporadically in the Upper Silurian and are common in the Lower Devonian. What they used instead was a combination of solutions 2 and 3 (Fig. 8C, D). As a result, theca 1^2 is both slimmer and diverging. The primary requirement – getting slimmer – was in itself quite a complex task because of another developmental constraint – the regulatory mechanism controlling the size and shape of the thecae which are generated simultaneously on the growing tips of the multiramous colonies. Thus a lag in the formation of theca 1^2, the primary cladium, resulted in its concommitant growth with one of the distal thecae (usually 16^1 or even a more distal one) and, correspondingly, determined its robust appearance [the above Thorsteinsson rule (p. 245) stating that isochronous thecae are isomorphic because of their equal morphogenetic potential]. Large-sized 1^2 thus appeared due to holoperipheral budding as defined above. The change to a meroperipheral condition involved the acceleration of the generation time of 1^2 in order to make it grow simultaneously with a much more proximal theca (approximately with 2^1), which automatically dictated its smaller size (Fig. 8C). In other words, formation of 1^2 in *L. posthumus* is accelarated by 15 thecae as compared with *N. nilssoni.*

Thus the processes involved are much more than mere diminution of the thecae of the first sicular cladium – they followed a rigid pattern of colony organization with its system of growth correlation.

The second elementary process, consisting in the divergence of the sicular cladium (change in the growth direction), is of particular importance for it produces more free space for a given diameter of the base of 1^2 (Fig. 8D). As suggested by URBANEK (1989), the problem of the geometrical constraint can be quantified in a simple way. The angle of divergence (marked D or B) is related to the angle of deviation of theca 1^2 according to the formula: $\beta = 180^\circ-\alpha$ and $\alpha = 180^\circ-\beta$.

The free space created by the moving away of theca 1^2 is proportional to D-x, where D is the diameter of the sicular aperture and $x = d \cos \alpha$. Therefore the space (area) which may be operationally used by the additional buds is directly proportional to the angle α, attaining its maximum at $\alpha = 90^\circ$ ($\cos 90^\circ = 0$ and correspondingly $x = 0$ whilst the free area equals that of the entire aperture!), but inversely proportional to the diameter of the base of 1^2. The area accessible to the additional buds is proportional to the free surface of the aperture and may be calculated from the formula given below. The area of the sicular aperture, A, could be aproximately calculated by considering it a circle with a diameter D, which equals that of the aperture, in other words by using the formula: $A = 1/4\ \pi D^2$.

In holoperipheral budding (e.g. in *Neodiversograptus nilssoni),* the diameter d of the circular base of theca 1^2 is equal to the diameter of the sicular aperture, D, ($d = D$). The sicular aperture is completely concealed by the circular base of theca 1^2 (the concealed area $C = A$) and naturally there is no free space F left, thus $F = 0$.

Advanced linograptids with the meroperipheral budding of theca 1^2 display, however, a different relation, $D > d$, and in their case, the base of theca 1^2 conceals only a portion of the apertural area (C), leaving the rest of it (F) free: $A-C = F$, where A and C are the areas of the bigger circle (the sicular aperture) and the smaller one (the base of theca 1^2) as shown in Fig. 9.

Additional free space may be created by the turn of the base of theca 1^2 by an angle α contained between the plane of the sicular aperture and that of the base of theca 1^2 as can be seen in Fig. 8D. The angle α, showing the deviation of theca 1^2 from its horizontal position, is related to the commonly measured angle of divergence of the two main branches of the rhabdosome, β; thus $\beta = 180^\circ-\alpha$. As a rough approximation, one can assume that the recondite area of the sicular aperture corresponds to the orthogonal projection of the base of theca 1^2 on the plane of that aperture. Such a projection represents an ellipse (Fig. 9), whose minor axis b may be calculated from the simple relations shown in Fig. 8D, namely $b = d \cos \alpha$, whilst its major axis, a, remains constant, $a = d$.

Therefore C, the area concealed by the deviating base of theca 1^2, is equal to the area of such an ellipse ($S = \pi ab$) and may be calculated by the formula: $C = \pi d^2 \cos \alpha$. From the above it follows that C depends on the value of $\cos \alpha$ and varies inversely as α increases within the quadrant 0–90°. The greater the angle of the sicular cladium deviation, α, the larger the uncovered area produced within the aperture. At a given angle α, the uncovered area (F) of the sicular aperture equals A–C, where A and C may be calculated by the formulas defined above, and the free area is $F = 1/4\pi D^2-\pi d^2 \cos \alpha$.

The above simplistic approach is valid under the condition that d is considerably smaller than D, $d < D$, which is certainly true in the case of meroperipheral budding, e.g. in *Linograptus*: $d \sim 1/3D$. Only then the entire concealed area fits within the limits of the aperture, A. But when both diameters are close to being equal, $d \sim D$, the recondite area falls largely outside the limits of A, making the calculation of the uncovered area a less trivial task!

This simple case of a single sicular cladium may easily be spread to embrace a multiramous condition involving m sicular cladia under the assumption (and a fairly realistic one) that α and d remain very similar for all branches. Thus a strongly reduced free area, F, will become: $F = 1/4\ \pi D^2-m\ \pi d^2 \cos \alpha$.

In extreme cases where $m = 15$, the bases of the sicular cladia were unbelievably tightly packed, the siculozooid being transformed into a sort of a stolonal node and a bunch of stolons radiating from the aperture of the sicula.

However, standard tetrameric *Linograptus* rhabdosomes offered more space for the continuation of the actvity of the siculozooid along with that of its daughter zooids.

The divergence of the dorsal apertural spine of the metasicula (later transformed into the pseudovirgula of the sicular cladium) may be interpreted also as co-aptation — an instance of regulatory adjustment of different parts of the evolving biosystem in the course of evolutionary changes.

In the real phylogeny, the first process, the acceleration of the formation of 1^2 and its resulting gracilization, occurred earlier (*N.* cf. *beklemishevi*, the *scanicus* Zone) whereas the second one, the change in the direction of the growth of 1^2, was triggered somewhat later (*Neodiversograptus*/*Linograptus*

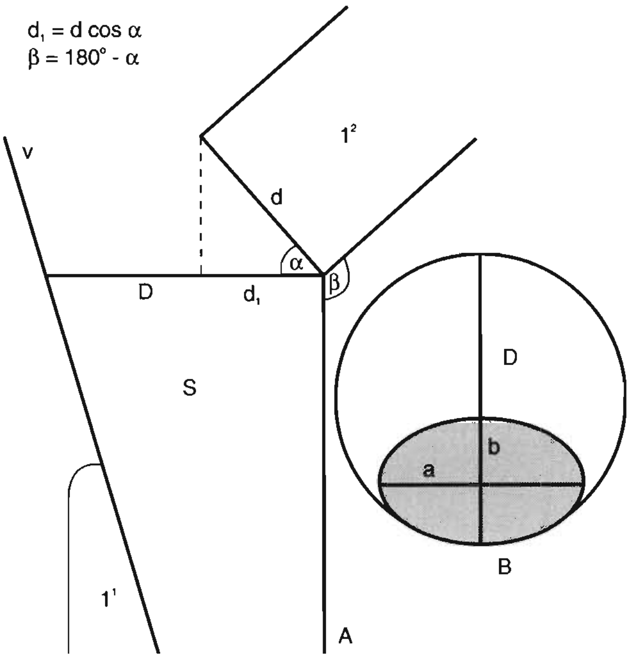

Fig. 9
Relation of coancealed area of metasicular aperture (strippled) from α, the angle of deviation of sicular cladium. Further explanations in text.

transients, the *leintwardinensis* Zone, attaining divergence angle, D_A of some 150° and α 30° as compared with D_A 115° and α 65° in typical *L. posthumus*). Secondarily, however, both features were fused into a single adaptive syndrome.

The *Linograptus* astogeny features a few other changes, which may also be interpreted in the light of the morphogenetic mechanism. The shortening of the metasicula, which is distinctly reduced as compared with that in *Neodiversograptus*, reveals a tendency towards rapid generation of cladia, the metasiculozooid being only a nodal point in the astogeny. A greater share of the prosicula (the larval theca), than that of the metasicula (the theca of a metamorphosed zooid), was interpreted as phoetalization of some kind (URBANEK 1963).

The *Abiesgraptus* rhabdosome appears through the generation of paired thecal cladia on the two primary cladia of the four-branched linograptid foundation. The distance between the mother thecae of the thecal cladia growing distalwards (MÜLLER 1965) is an example of morphological gradients in compound colonies. Each paired thecal cladium which budded from the aperture of a mother theca most probably created a morphogenetic field exerting control over a certain area of the main stipe and inhibiting the formation of other thecal cladia. The areas controlled in this way increased distalwards.

Morphological changes in the evolution of the Linograptinae were focused on the pattern of the rhabdosome, with only negligible effects in the thecal morphology. Whilst the thecae retained their simple structure with only some minor changes, the pattern of the rhabdosome was profoundly transformed. It was the entire colony rather than individual zooids that were the target of natural selection.

A POSSIBLE RECONSTRUCTION OF THE NUMERICAL DYNAMICS IN LINOGRAPTID CHRONODEMES

The temporal species (chronospecies) described within the Linograptinae (*N. nilssoni*, *N. beklemishevi*, *L. posthumus*, *A. tenuiramosus*) were recognized on the basis of a certain distinct morphological norm. One can assume that such norms can easily be traced in large samples, corresponding most probably to the periods of proliferation (acme) of a given lineage. Thus the discrimination of the temporal species is

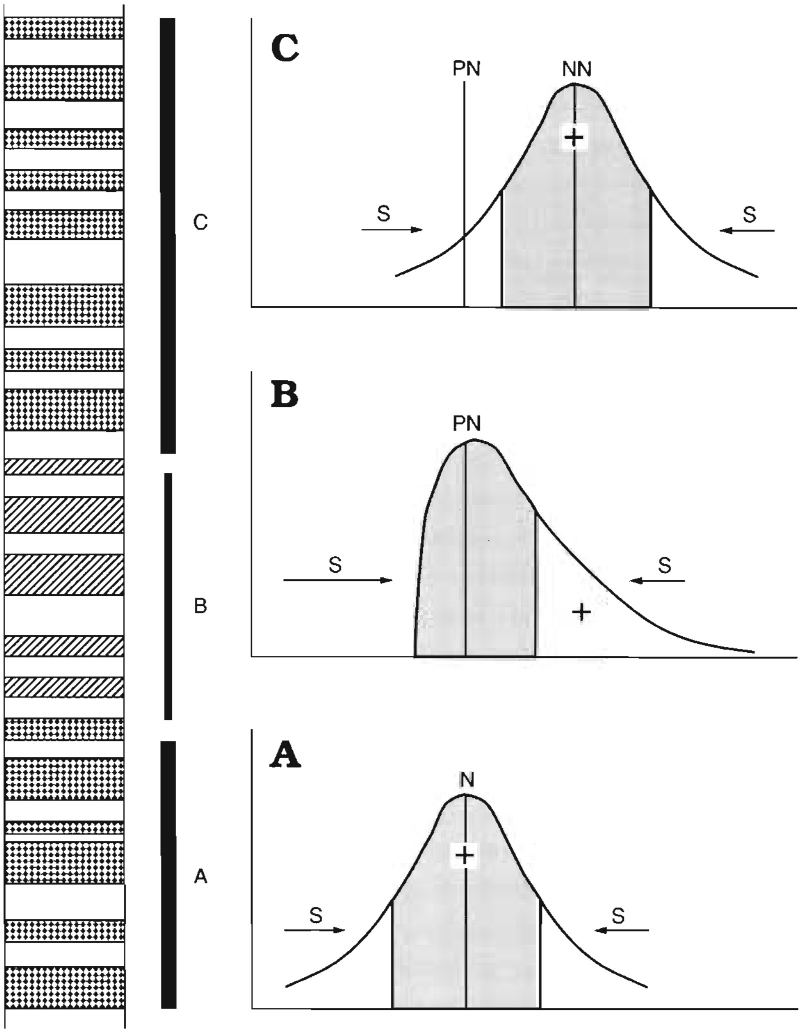

Fig. 10
A diagram showing the alternating pattern of proliferation (**A**, **C**) and scarcity (**B**) of fossil populations (chronodemes) as revealed in the stratigraphic sequence and related to the evolutionary dynamics and variation spectrum of the populations within a lineage. The periods of abundance correspond to adaptive equilibrium when adaptive optimum (+) is situated close to the norm (N) and selection pressure has a stabilizing effect (S with equal arrows in **A**). During the periods of scarcity, primary norm (PN) and adaptive optimum (+) disjunct resulting in a directional selection (S with inequal arrows) and a gradual shift of the mean (**B**). Next adaptive equilibrium is attained when a new norm (NN) reaches the position of actual adaptive optimum (+) and stabilizing selection is restored (**C**). Most chronospecies are defined by populations like **A** and **C**.

to a large extent preconditioned by the very nature of the fossil record displaying episodes when the populations (chronodemes) show high abundance, alternating with intervals of relative scarcity.

Hence prolific populations are commonly discriminated as separate taxa, whilst the taxonomic evaluation of less abundant populations, which occur at the borderline between the adjacent, well-defined chronospecies (*nilssoni–beklemishevi–posthumus*), poses a difficult task. One can hypothesize that during such intervals the population size of successive chronodemes was reduced, thus producing a "bottleneck effect" and creating conditions for a faster transformation. Among such populations a morphological norm is difficult to define because of their scarcity, on the one hand, and considerable changes in the subsequent zonal populations (chronodemes), on the other. Such zonal variation makes any lumping of these populations into a clearly defined species a questionable procedure.

The above pattern of alternating proliferation and scarcity, or of a well-stabilized morphological norm and a changing one, as observed in the history of the Linograptinae, can be interpreted as follows (Fig. 10).

Prolific populations were probably associated with the periods of adaptive equilibrium, when selection pressure having a stabilizing effect was less severe. In terms of punctualism, these periods could be described as stasis, although the application of this term does not imply the entire philosophy of this phenomenon as usually suggested by punctualists. Such periods of relative abundance and stabilized morphology were rather short in the case of *N. nilssoni* and *N. beklemishevi* and fairly long in such species as *L. posthumus* (Fig. 10A, C).

The intervals separating the periods of stasis featured a loss of adaptive equilibrium when there was a shift between the most adaptive condition (favoured by selection) and the previous norm, already fixed in the course of evolution. The resulting directional (dynamic) selection was probably a mover responsible for a relatively fast transformation of the population structure and the phenotypic expression of certain traits (Fig. 10B).

In the Linograptinae, the rate of morphological changes was, however, never particularly high. The presence of transient forms, although insufficient for tracing every change, suggests an essentially continuous pattern, but a succession of rapid shifts cannot be excluded. That is the reason why such scanty and variable populations set an uneasy task to a taxonomist and frequently are simply omitted in identification procedures. In the present paper, they are treated as a borderline between the parental and the daughter temporal species. The processes associated with those periods of relative instability may most probably be regarded as speciation events. As no branching (splitting of the lineage) occurs, such speciation should technically be defined as phyletic speciation or transformation.

The change from *L. posthumus* to *A. tenuiramosus* reveals a somewhat different mechanism – a slow transformation in large populations, without any evidence of bottlenecking in the lineage. Quite to the contrary, the fossil data demonstrate that immediately before the appearance of the descendant species, the ancestral *L. posthumus* displayed (at least in Central Europe) a genuine population explosion (see p. 256 herein).

Thus the periods of relative stability within the sequential species of the linograptid lineage cannot be understood as a complete arrest of morphological change. Such an arrest can be observed in some monophyletic lineages, e.g. *Gryphaea* (Hallam, 1982) or *Metrarabdotos* (Cheetham, 1987). On the contrary, the "zonal evolution" in *Linograptus posthumus* may be used as an example of a series of changes (in the number of the sicular cladia, in the appearance of the thecal cladia or in the direction of the growth of the branches in the proximal end of the rhabdosome), which alone would not be sufficient for the discrimination of a morphospecies as currently defined, but which doubtlessly produce a cumulative effect influencing the course of the phylogeny.

AN ANALYSIS OF THE PERIODS OF STASIS WITHIN THE LINOGRAPTID LINEAGE

The populations (chronodemes) of *Neodiversograptus nilssoni* from the *nilssoni* Zone were composed of two distinct morphotypes: (1) the standard monograptid form with a uniramous rhabdosome and (2) the diversograptid form with a biramous (bipolar) rhabdosome. Although the latter morphotype is rare as compared with the standard one, it seems that the diversograptid form was a steady component of the *N. nilssoni* populations. One may conclude that in spite of the discontinuity of the phenotype, both morphs co-occured within a single breeding community and most probably were capable of intercrossing.

Essentially, the diversograptid morph is merely a more advanced (extended) astogenetic stage of the standard monograptid morph. Therefore its scarcity may be ascribed to the delayed expression of the colony's ability to generate a sicular cladium in the course of the astogeny. Few colonies survive long enough to be able to form one. Thus the age structure of the population and the rare occurrence of old colonies within a given population could be responsible for the scarcity of the bipolar phenotype. Yet it is rather certain that one could regard the monograptid and the diversograptid phenotypes as an instance of genetic polymorphism and their steady co-occurence as a result of balanced polymorphisms.

The relative numerical abundance of *N. beklemishevi* in the *scanicus* Zone most probably means the attaining of another adaptive equilibrium at a new stage of the morphological evolution represented by a novel morphological norm. The earlier formation of the sicular cladium as a result of an astogenetic acceleration (see p. 247 herein) led to an increase in the number of diversograptid morphs within each chronodeme, assuming that the age structure of the populations had not changed since *nilssoni*. The rhabdosomes which at the early stage of astogeny represented the juvenile, monograptid morph were later

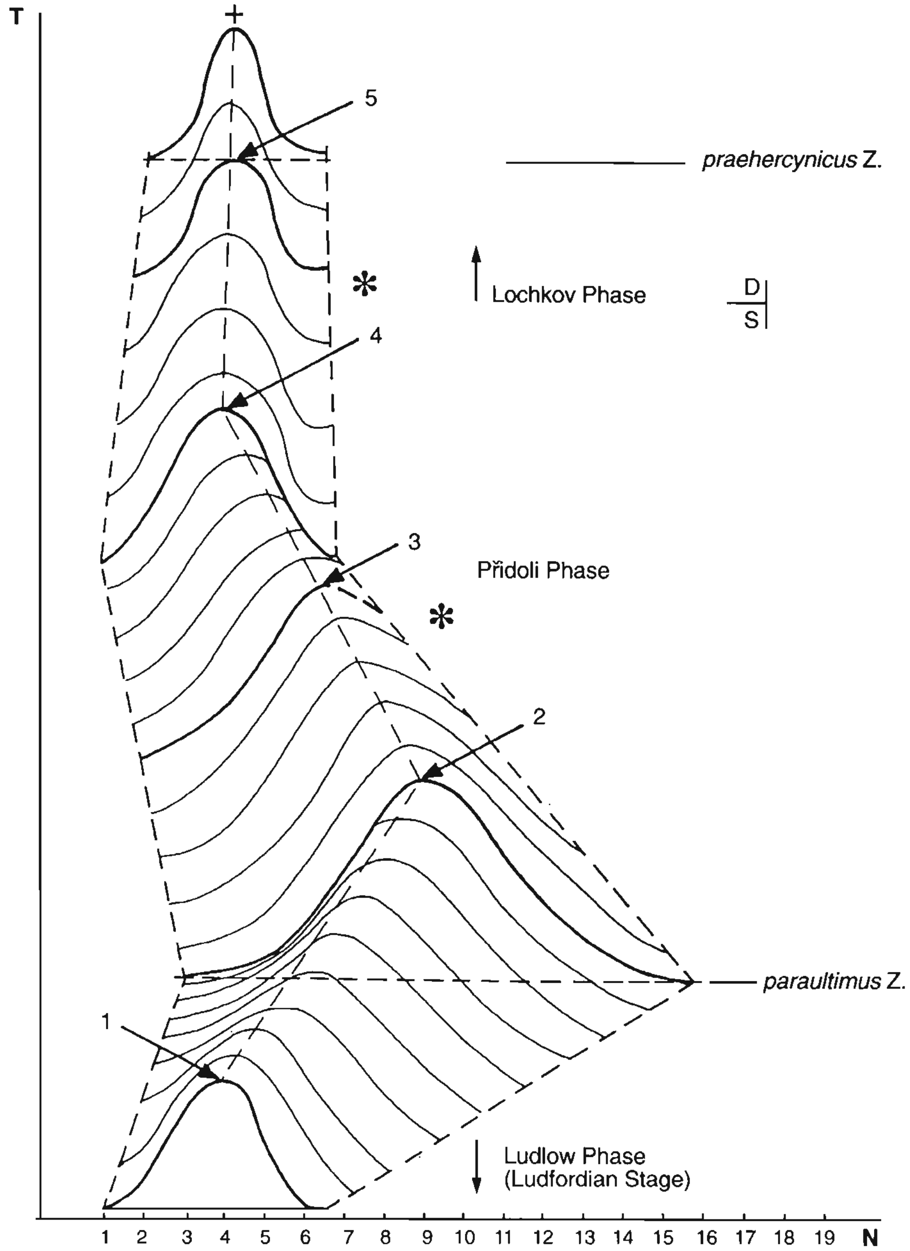

Fig. 11

A tentative scheme showing the range and trends in variation of *Linograptus posthumus* (Reinhard RICHTER, 1875) as revealed by number of cladia (procladium + sicular cladia, N) in populations from sucessive time-levels (T). 1–5 turning points in the phylogeny: 1–2 trend toward polybrachiate condition, 2–3 gradual decrease in the number of cladia until four-branched (tetrameric) condition is attained (3–4), being a structural foundation for compound colonies of *Abiesgraptus* (4–5). Changes in number of sicular cladia are associated with sporadic appearence of lateral (thecal) cladia as noted by asterisks (*).The taxonomic status of Lochkovian *Linograptus* is uncertain as it may represent juvenile colonies of *Abiesgraptus*. Based mainly on data from JAEGER 1959, 1969 and TELLER 1964.

replaced by more advanced diversograptid (bipolar) growth stages. An accelerated realization of the diversograptid rhabdosome may be ascribed to the action of selective forces favouring an earlier expression of the advantageous phenotype.

It is highly probable that some fraction of the *N. beklemishevi* rhabdosomes attained a multiramous stage, thus resembling and foreshadowing the pattern of the *Linograptus* colonies.

Linograptus posthumus, a representative of the genus in the Upper Silurian of Europe characteristically occurs in large populations, frequently displaying mass occurrences (as pointed by JAEGER 1959: p. 153, "In Bereich grösster Häufigkeit werden viele Schichtflächen wie ein Teppich von den langen Zweigen bedeckt...").

This obviously is an indication of a great evolutionary success of the species and doubtless evidence of its adaptive equilibrium. The same is indicated by a wide geographic distribution of *L. posthumus* and the considerable duration of the species.

The occurence in large populations and a high perfection of adaptation resulted in the stabilization of the morphological norm, with only restricted evolutionary changes observed. These were expressed in minor changes of the width of the branches (*L. posthumus posthumus* and the subspecies *tenuis*) and possibly also in the certain zonal evolution of the number of cladia generated. Somewhat contradictory data (JAEGER 1954; TELLER 1964) were later summarized by JAEGER (1969, 1978) who posited directional evolution in a number of the cladia. The earlier populations are marked by a greater variation with a considerable share of multiramous colonies, sometimes exceeding 10 cladia (Ludfordian, Přidoli), whilst the later ones (Lochkovian) display a certain reduction of variation with a distinct predominance of tetraramous forms. The last named morphotype served as a morphological foundation for the origin of *Abiesgraptus* (Fig. 11).

The recognition of linograptid origin of *Abiesgraptus* and the reconstruction of the main stages of its astogeny we owe to the penetrating study by JAEGER (1959). *Abiesgraptus* appears for the first time in the *uniformis* Zone of Thuringia and dissappears in the *praehercynicus* Zone or in the lowermost portion of the *hercynicus* Zone (JAEGER 1954). However, LENZ (1988) found specialized abiesgraptids as high as Pragian of Arctic Canada (p. 261). Its previously restricted geographic distribution has recently been found equal to that in *Linograptus*, while the stratigraphic duration of the genus is much shorter. According to JAEGER (1959), *Abiesgraptus*, from its first appearance, featured a distinct and highly regular morphological pattern of the rhabdosome. Some differences in the width of branches, the size and number of lateral thecal cladia make it possible to distinguish 3 concurrent forms formally recognized as species, but the biological value of the observed differences is obscure.

THE NATURE OF THE SPECIATION EVENTS IN LINOGRAPTIDS

Some of the speciation events (transformations) observed in linograptids seem to involve the mechanism of polymorphism. Their primarily monomorphic populations became polymorphic due to the appearance of discrete morphs co-occurring within a single breeding community. This is especially apparent in the case of *Neodiversograptus nilssoni* and probably also in the *Linograptus/Abiesgraptus* transition (herein, pp. 257–258). As such morphs are kept in a population at more or less stable frequences, and the ensuing situation may be regarded as tantamount to balanced polymorphism, one of the classical microevolutionary mechanisms! In spite of considerable morphological differences between the new (mutant) morph and the primary ("wild") one, they composed a single breeding community. Although variation was represented by discrete classes, their reproduction was probably continuous.

A similar situation is described in JAANUSSON's (1981) model of a dithyrial population, which opens up alternative pathways of further evolution. The linograptids, however, tended to use only one opportunity, that of eliminating one morph and fixing the other through a shift to transient polymorphism. The immediate effect was the lack of splitting of the lineage (bifurcation). Thus the mechanism of transient polymorphism may be largely responsible for the preservation of the cohesion of the sequential linograptid species and for the prevalance of the anagenetic component over the cladogenetic one in their evolution (cf. p. 262 herein). In the case of *N. nilssoni/N. beklemishevi* transition, one could visualize the fixation of diversograptid morph in terms of geological time, as a rather rapid shift. Biologically, however, such change could occur through great number of generations. The resulting monomorphic populations, probably appeared prior to *L. progenitor* Zone, and due to it morphological features should still be assigned to *N. nilssoni.* Hence the shift in polymorphic composition of the ancestral species, had only infraspecific consequences. It was only later evolution, which involved gradual microevolutionary changes ("improvements") of diversograptid morph (Fig. 12A–C), that brought transspecific effects.

One can assume that in spite of their distinct macroevolutionary bearing, speciational events in linograptids were governed by classical microevolutionary mechanisms (balanced and transient polymorphism). At the same time, generation of variation involved sharp morphological discontinuities com-

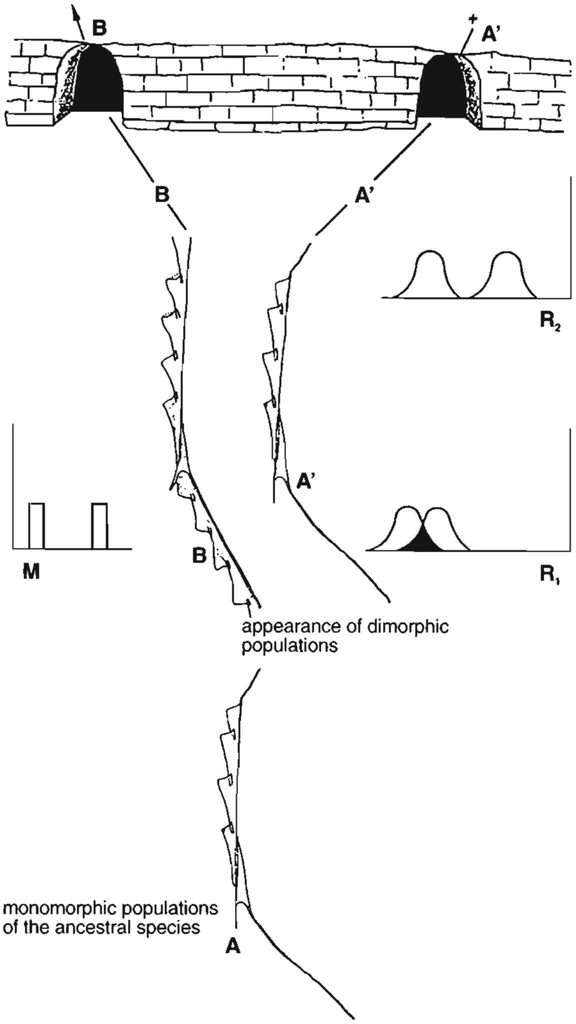

Fig. 12

Early evolution of linograptids explained in terms of genetic polymorphism: A, monomorphic populations of the ancestral species, composed solely of monograptid (unipolar) colonies; A', B, appearance of polimorphism due to origin of diversograptid (B) morph and its co-occurrence with monograptid (A') one. Morphologically both morphs (M) represented discrete phenotypes, but reproductively were interbreeding (R_1). This single breeding community corresponds to balanced polymorphism and may be classified as dithyrial population, as it opens alternative pathways of further evolution (symbolized by the two gates!). The later breaking down of the common breeding system occurred probably due to selection against the heterozygotes (R_2) and implies transient polymorphism. Further evolution included elimination of the monograptid morph (A') as well as the survival and subsequent improvements of diversograptid morph (B).

bined with reproductive continuity within the population. This single process acts as a lens focusing theoretical postulates of both gradualism and punctualism. Moreover, one cannot reasonably insist on the decoupling of micro- and macroevolution. There is also more evidence of the significance of polymorphism and shifts from its balanced forms to the transient ones in the evolution of graptoloids (cf. SKEVINGTON 1967 for *Nicholsonograptus*, and URBANEK 1970 for the appearance of so-called *veliger* morph in *Bohemograptus,* as well as RICKARDS *et al.* 1977, for the origin of an early monograptid, *Monograptus ceryx*, from its biserial glyptograptid ancestor).

The three distinct species recognized within the ancestral-descendant sequence composing the linograptid lineage as defined above (*nilssoni–beklemishevi–posthumus*) are linked by some populations having a less definite taxonomic status. By definition, they coincide with the speciation events, understood herein as periods of relative condensation of phenotypic changes. Thus an intermediate population, (sample A), occurs between *N. nilssoni* and *N. beklemishevi.* This is indicated by its position (a Baltic erratic boulder from the *parascanicus* Zone), that is distinctly above the top of the *nilssoni* Zone, but somewhat lower than the occurences of typical *N. beklemishevi*. As seen in Fig. 3A, specimens from such a population display a combination of characters typical of ancestral *N. nilssoni* (e.g. a single sicular cladium with a holoperipheral 1^2!) as well as of the descendant species *N. beklemishevi* (a symmetric position of the dorsal apertural spine.).

In spite of the incompletness of the record (see p. 250 for the suggested explanation), the occurrence of such intermediate forms is indicative of an essentially gradual course of phenotypic changes between the typical populations of both the species in question.

Although the structure of the sicula is difficult to recognize on flattened forms, the specimens of *N. nilssoni* described by PALMER (1971) from Long Mountain, Welsh Borderland seem to show both an asymmetric dorsal apertural spine (his fig. 4) as well as a symmetric one (shown in his fig. 6). The stratigraphic position of both forms is defined as the *nilssoni* Zone, but the symmetric siculae probably developed somewhat later and might occupy the intermediate position similar to that of population A described above.

Another intermediate population, named B, was recognized in the *leintwardinensis* Zone (the Mielnik deep boring). The rhabdosomes has essentially *beklemishevi*-like siculae, but showes a linograptid divergence of the dorsal spine (D_A) of some 150°. This contrasts with the straight, forward-oriented dorsal apertural spine of the metasicula in the *N. beklemishevi* populations from the underlying *scanicus* Zones.

This structure might have preceded the restructuring of the sicula exhibited by more advanced linograptids. There were two stages in this restructuring, namely the change in the proportion of the sicular segments and a fairly radical transformation of the virgella. The former led to a certain increase in the total length of the sicula, with a greater share of the prosicula and a proportional shortening of the metasicula. Morphologically, these changes are not especially impressive. Biologicaly, however, they may be quite important (see p. 249 herein).

The transformation of the virgella into a robust rod which terminates with a virgellarium – a specialized apparatus of a largely enigmatic function – is a more spectacular event. The starting point of this transformation may be seen in deviation of the virgella in advanced populations of *N. beklemishevi* (Fig. 3C), attaining some 20–22°, equal to that in *L. posthumus* and twice as big as in typical *N. beklemishevi* (10–12°). As traced in the fossil record available, the emergence of the virgellarium seems to be abrupt, since the Lower Přidoli colonies already display a complete apparatus (p. 240 herein). ŠTORCH (1995) has recently found typical virgellaria in *Linograptus posthumus* from the *kozlowskii* Zone (early Ludfordian) of the Barrandian area. However, there is little doubt that the sudden appearance of a "ready-made" complex structure is only an effect of the incompletness of the record, as well as the extreme fragility of the virgellarium, which happens to be preserved only very rarely.

In general, it seems fair to conclude that the differences between *N. beklemishevi* and *L. posthumus* exceed those between *N. nilssoni* and *N. beklemishevi*, and that a certain discontinuity recognized here is only to some extent bridged by intermediate population B (see diagram, Fig. 17 suggesting a change in the direction of the evolution). Ranked taxonomically, these results can be evaluated as the appearance of a new genus.

The scarcity of transient populations between *N. nilssoni* and *N. beklemishevi* as well as between the latter and *L. posthumus* can easily be ascribed to facial changes involving both the palaeoenvironmental and the presevational factors.

However, the entirety of the data are indicative of a probably non-random nature of this scarcity as other graptolite lineages flourished in the epicontinental Ludlow seas of Europe during the *nilssoni–beklemishevi* interval. It seems that temporarily the numerical abundance of the linograptids must have been drastically reduced as they were simply outcompeted by cucullograptids at least in the shelf biota. This does not exclude, however, their greater abundance in the neritic and pelagic realms. Great biotic changes in the *leintwardinensis* Zone (URBANEK 1970) triggered not only the exctinction of cucullograptids, but also, with a certain delay, the reappearance of the linograptids in the shelf waters; it opened new prospects for other survivors as well, namely neocucullograptids. A great abundance of *L. posthumus* after the extinction of the last named group during the *Neocucullograptus kozlowskii* Event, observed in the Mielnik bore core, may also be interpreted as evidence of a competitive replacement.

A close relationship between *Linograptus posthumus* and *Abiesgraptus tenuiramosus* is indicated by the linograptid stage in the astogeny of the latter species. However, from its first appearance, *Abiesgraptus* has all its characteristic features fully developed. They include: a tetrameric (four-branched) foundation of the rhabdosome; an ability to generate, on the main branches of the rhabdosome, paired lateral thecal cladia with a regular spacing between them; and a secondary flattening of the central (sicular) portion of the rhabdosome, i.e. the spreading of the four main cladia in one plane and the obliteration of the divergence angle between the branches at the proximal end, which was characteristic of *Linograptus*. The two first features emerged gradually in the zonal evolution of the *Linograptus* populations. Thus, the four-branched rhabdosome became the predominanting form of the colony within the Lochkovian populations of *L. posthumus*, producing in this way a necessary prerequisite for the origin of *Abiesgraptus* (p. 241).

As was directly observed in the *Linograptus posthumus* specimens from the *uniformis* Zone (Jaeger 1969), the proximal part of the giant tetraramous rhabdosomes produced regular quadrants with the angles between the armpits being nearly orthogonal (measured angles are 80–100° and frequently 90°). These large-sized colonies were "floating crosses", with distal parts of their cladia bending freely due to their natural flexibility. In the vicinity of the sicula, the distances between the zooids situated on the adjacent cladia were small and consequently their depletion zones were overlapping. This probably resulted in a severe competition among the proximally placed zooids. The situation was improving in the course of the growth and expansion of the colony, due to increasing distances between more distally placed zooids. As the growth progressed, the terminal zooids situated on the tips of the expanding colony were in a favourable position, having no competition. However, the total harvesting efficiency of the colony was deteriorating, due to a fairly rapid increase of the area available as compared with the moderate increase of the number of zooids present. More and more area remained underutilized and the terminal zooids more and more "lonely" (a similar conclusion was reached by Jaeger 1969: pp. 493–494). The rotation of the rhabdosome could only partly improve the harvesting efficiency and large-sized tetraramous colonies remained rather inefficient. In terms of the utilization of the resources available, such colonies were probably less effective than their Ludfordian–Přidoli forerunners, with several cladia radiating from the sicula and penetrating more or less uniformly the surrounding space. A radical improvement did not come until the lateral cladia were invented. Situated on the main cladia and oriented normally to them (Fig. 6, L), they penetrated the free space available within the armpits of tetrameric colonies. Such pattern ensured a better use of the resources around the colony (see also Jaeger 1969: p. 494). Therefore, the appearance of the lateral cladia, even sporadic and irregular, presented a distinct adaptive advantage over the tetraramous rhabdosome and was favoured by selection. Hence, I see the origin of *Abiesgraptus* (discussed at some details below) as a process controlled by a strong selection pressure.

From the above considerations one can deduce that the increase of the number of zooids in each cladium should follow the formula: $N = k\,l$, where k is a specific coefficient showing the increase of the number of thecae per 1mm (for *L. posthumus* its value is about 0.7), and l is the distance from the sicula (in mm). Hence, the total number of thecae in a tetraramous colony is 4N. On the other hand the area (a) exploited by a given colony at a certain growth stage is equal to the surface of a circle with a radius l, namely $a = \pi\,l^2$. The harvesting potential of the colony may be estimated using the relation $4N/a$. Some parameters for a growing *L. posthumus* colony are shown on Fig. 13A, B.

One more measure is the degree of "loneliness" of the terminal zooids situated on the growing tips of the colony, namely the calculation of the distance of each zooid from its terminally situated neighbour on an adjacent cladium. With a certain simplification (small differences in the length of cladia being neglected), this distance (d) may be calculated from the formula, $d = \sqrt{2l^2}$. From this it follows that contrasts which develop in a growing *Linograptus* colony are caused by the arithmetic progression of the number of zooids N, and the geometric progression of the area exploited, a.

The ability to form lateral thecal cladia appeared early in the phylogeny of the linograptid lineage. This may be indicated by the sporadic occurencies of such cladia, either paired (Teller 1964, on a three-branched rhabdosome from the early Přidoli) or single asymmetric (Jaeger 1969, from the early Lochkovian on a four-branched rhabdosome). The irregular generation of thecal cladia in *L. posthumus* could be interpreted as an imperfection of the morphogenetic control of this evolutionary novelty, which later was subject to a rigid pattern formation. The horizontal disposition of the three cladia radiating from the sicula probably means the reestablishment of the *N. beklemishevi* condition of growth and *per se* is rather a minor change. Combined, however, these three features brought about the origin of *Abiesgraptus*.

The *Linograptus/Abiesgraptus* transition was in fact rather unconventional, namely it was a transformation in large sympatric populations. Both parameters – the sympatry and the large size of populations involved are in strong opposition to the recent orthodoxy in the field of the origin of species (Mayr 1982). In the latter parameter (large population size), the appearance of *Abiesgraptus* also differs from two other instances of species transformation in the linograptid lineage, suggesting a certain reduction of the

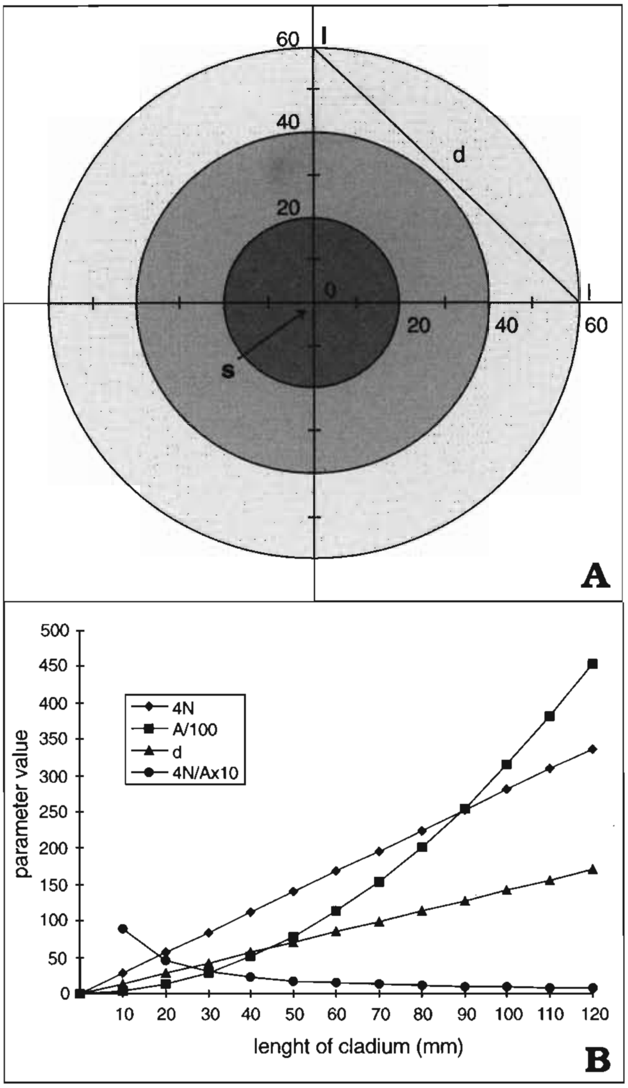

Fig. 13

Stages in the development of cladia (**A**) and main parameters (**B**) in a growing tetraramous *Linograptus* colony. Rapid expansion of the colony due to budding of new zooids on the growing tips of four cladia led to an increase of their total number (4N) and to elongation of each cladium (l, in mm). Increase of distances (d) between zooids reduces the competition between individual zooids, thus improving their feeding conditions. At the same time the geometric progression of the area (a) of the potential exploitation (shown for the convenience in cm^2) and the relation 4N/a (shown for the convenience × 10) are indicative of an increasing underutilization of the resources potentailly available as the colony expands. For further explanations see text.

population size at least in the epicontinental seas and the bottlenecking of the lineage (see p. 250). A fairly rapid morphological evolution as observed in the *Linograptus/Abiesgraptus* transition, suggests that graptolites, possibly hermaphroditic clonal organisms, were capable of using some "non-conventional" mechanisms, e.g. self-fertilization followed by instant homozygotization (cf. URBANEK 1990). Although purely hypothetical, such mechanisms shed some light on this otherwise paradoxical pattern of species transformation.

The record available does not permit a safe recognition of the mode of speciation in *A. tenuiramosus*. JAEGER (1959) was convinced that in the *praehercynicus* time *Linograptus posthumus* and *Abiesgraptus tenuiramosus* had been two morphological forms of the same breeding community, and at that time they could have been assigned to a single species. This still leaves room for different interpretations. Were these forms two morphs (namely, the *linograptid* morph which was not capable of attaining the abiesgraptid growth stage and the *abiesgraptid* morph proper which passed through an earlier linograptid

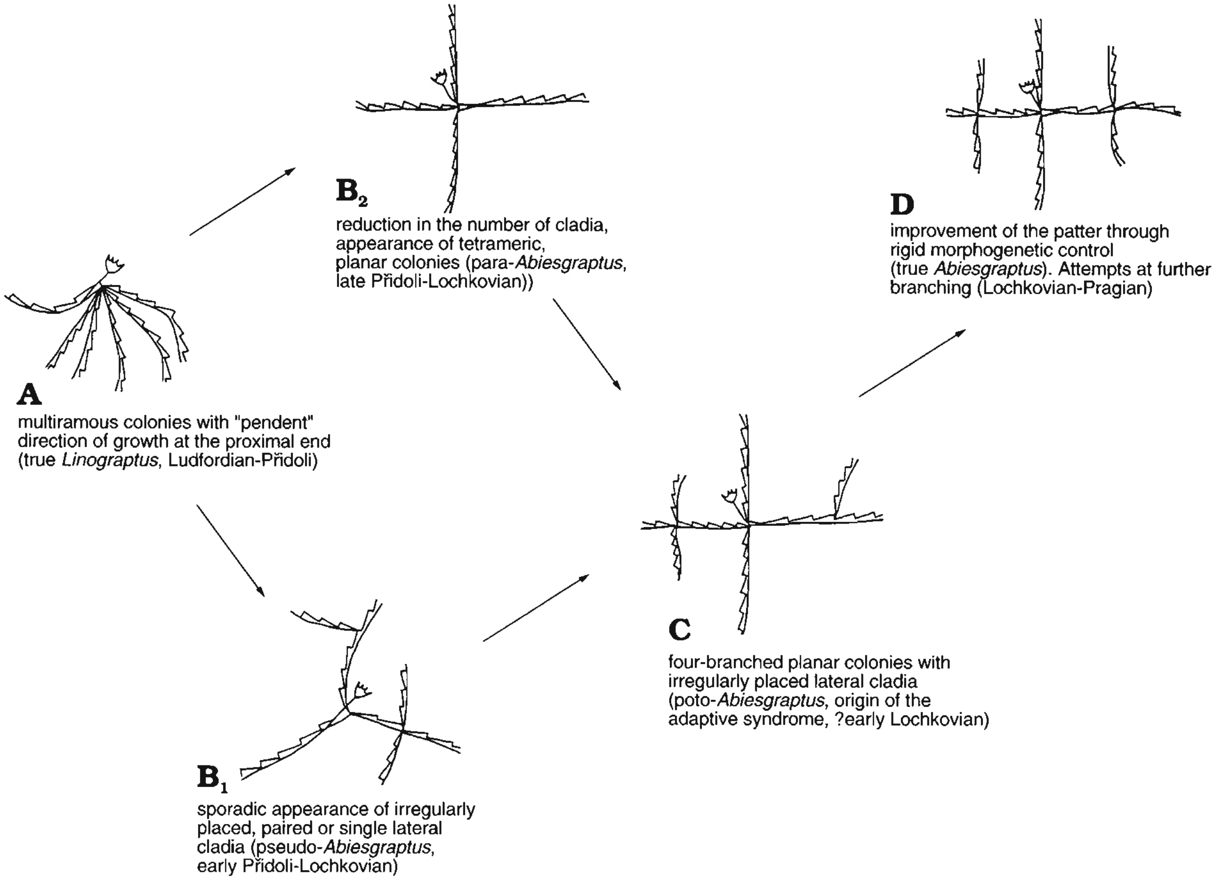

Fig. 14

Conceptual diagram showing the main events in the emergence of *Abiesgraptus* pattern of colony organization. Two independent directions of changes leading to $\mathbf{B}_1$ and $\mathbf{B}_2$ may be derived from ancestral type of *Linograptus*, represented by **A**. The crucial event is represented by **C**, where disparate features, acquired within these two lines, were combined into an adaptive syndrome, later improved and transformed into the perfect, compound colony of *Abiesgraptus* (**D**). Further explanations in text.

growth stage), coexisting within a single population (polymorphism) or was every colony potentially capable of attaining the abiesgraptid characters at some stage of the astogeny? In the first case, the later speciation resulted most probably from transient polymorphism with the elimination of the less advanced morph. The second possibility implies a gradual increase in frequency, expressivity and penetrance of genetic factors responsible for the formation of lateral cladia in tetraramous rhabdosomes, hence, a shift of the mean towards a greater frequency of lateral branches, which started to appear at earlier stages of astogeny (acceleration).

But was the story as simple as that? I would argue for a different scenario of the *Linograptus/Abiesgraptus* transition in view of a gradual and heterochronic appearance of disparate abiesgraptid features within the early linograptid populations. On one hand, some large-sized and four-branched *Linograptus* colonies from the *uniformis* Zone are still deprived of thecal cladia (JAEGER 1969), on the other, lateral branches may occur as early as the lower Přidoli and be situated on three-branched colonies (TELLER 1964). It is clear, therefore, that the potential for generation of lateral cladia appeared early in the phylogeny and obviously was not correlated with the simultaneous formation of tetraramous conditions. The interpretation which, in my opinion best fits the record seems that which claims that the morphotypes shown on Fig. 14 B_1 and B_2, and tentatively named pseudo-*Abiesgraptus* and para-*Abiesgraptus,* evolved within two different semispecies. Each of them showed a distinct trend in variation, directed towards the formation of either a tetrameric foundation of the rhabdosome (*tetra*) or lateral branches (*lat*). This may explain the disparate origin of both features, which was followed by a secondary integration of the species genetic system by means of hybrydization or introgression (Fig. 14C). As a result the two

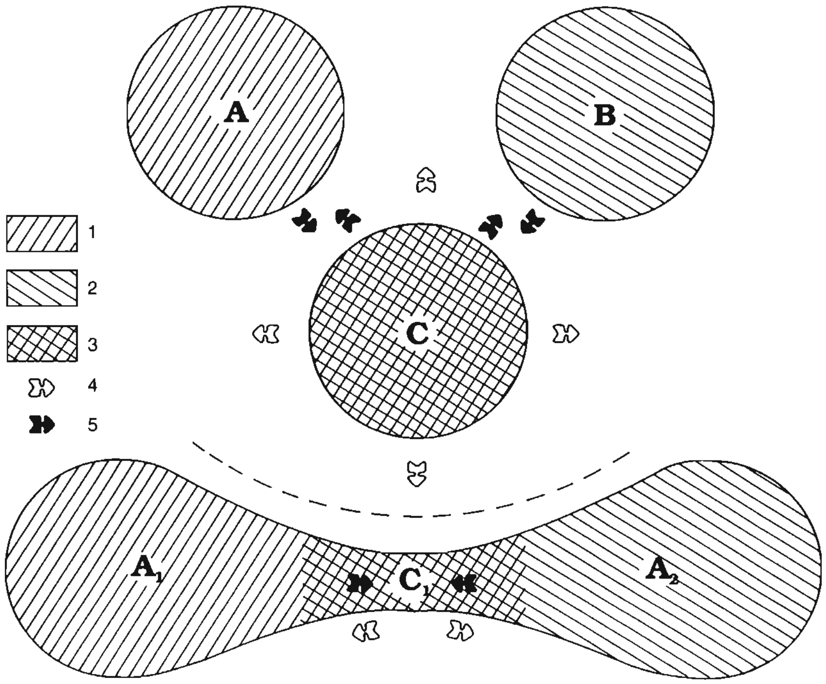

Fig. 15
Ideogram showing the significance of presumed patchiness in linograptid distribution for the disparate origin of evolutionary novelties. Upper part of the figure: the occasional gene flow due to migration (black arrows, 5) between individual patches **A**, **B**, **C**, with different genetic structure (1–3), ensures the appearance of a compound genotype in **C**, which subsequently may spread (white arrows, 4) due to its high fitness. Lower part of the figure: a similar effect due to the merging of the patches $\mathbf{A}_1$ and $\mathbf{A}_2$, followed by an introgression ($\mathbf{C}_1$) and the appearance of a compound genotype. Fit genotype may later spread rapidly (white arrows, 4).

independently acquired unit characters *tetra* and *lat*, became components of a single synthetic morphotype, represented by proto-*Abiesgraptus* (*tetra-lat* morphotype). The above considerations may be tabulated as follows:

morphotypes/ populations	*tetra*	*lat*
B_1	–	+
B_2	+	–
C	+	+

Note: B_1, B_2 and C refer to Fig. 14.

The resulting compound rhabdosome displayed an irregular branching pattern (inherited from pseudo-*Abiesgraptus*), later subject to selection pressure and an increased morphogenetic control (Fig. 14D). The attaining of the abiesgraptus stage in the morphological organization of the colony is clearly a transspecific event. As correctly emphasized by JAEGER (1959), the origin of *Abiesgraptus* means the beginning of a new direction of evolution with a new evolutionary prospect – the emergence of a new genus seen *in statu nascendi*.

It seems almost certain, that in the area of their distribution, planktic linograptids formed a system of semi-isolated populations (patches). Patchiness is a remarkable feature of plankton biology recognized by modern studies (BOXSHALL 1981; BARRY and DAYTON 1991) and used in order to explain a number of phenomena (such as sympatry of a great number of rather similar taxa or the "paradox of plankton" as defined by HUTCHINSON 1959, 1961). Each individual patch is in fact a huge deme of a certain duration in time, the longevity of a given patch being largely proportional to its size. Linograptids as the dominating group of Late Silurian macrozooplankton were surely subdivided into numerous and relatively large patches. Such spatial organization is considered by some authors (e.g., GRANT 1977) to be most favourable

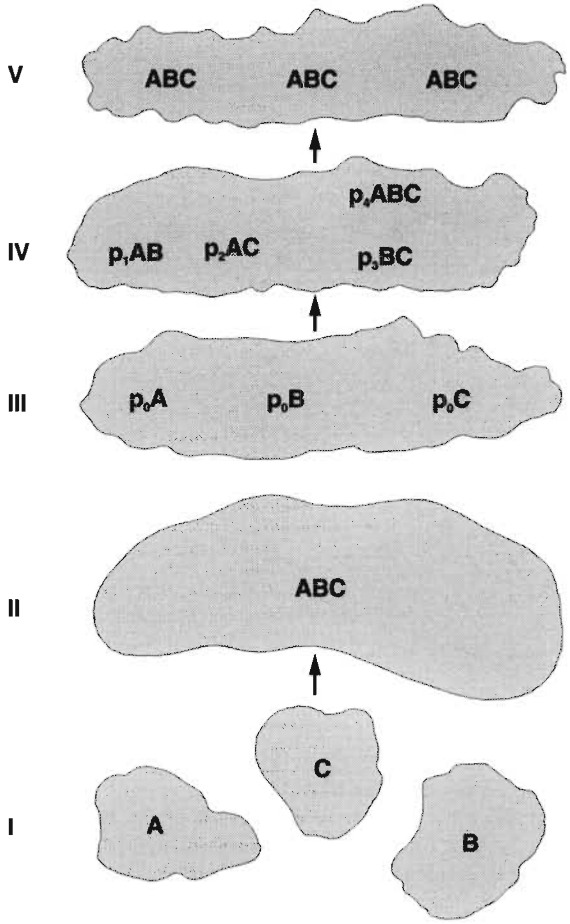

Fig. 16
Possible genetic mechanisms involved in the emergence of an adaptive syndrome. I – patches A, B, C comprising disparate unit characters merge into a common megapopulation (II – ABC) enabling further recombination due to crossing. III–V successive changes in the genetic structure of population from initial frequencies (p_o) of genes responsible for corresponding unit characters (III), through their combinations (only some shown) displaying frequencies p_1–p_4 controled by selection, until superior genotype ABC appears (IV), and is fixed as an adaptive syndrome.

for macroevolutionary changes. Some of recent models advanced to explain genetic polymorphism in krill populations assume that pelagic plankton species are partitioned into numerous patches and that selection is sensitive to differences between the patches (AYALA and VALENTINE 1979; BUCKLIN 1986). I will proceed from a similar assumption.

Each patch probably behaved as a partly autonomous unit ("a floating island") where variation, either generated *in situ* or introduced by an occasional gene flow between the patches, accounted for more or less unique genotypic combinations (Fig. 15A, B, A_1, A_2). One could believe that patchiness was involved in producing the disparate *Abiesgraptus* features and then bringing them together into a characteristic compound or an adaptive syndrome (Fig. 15C, C_1). The patchiness was probably responsible for the origin and maintenance of distinct trends in variation, interpreted above as semispecies. Some events were taking place in semi-isolated systems, producing distinct morphotypes. The cohesion of species' genetic system was, nevertheless, preserved as the evolving populations eventually reunite due to hybridization or introgression, before attaining the reproductive isolation.

The disparate origin of the adaptive characters may be due to a heterochronous and independent appearance of the component parts ("unit characters" as *tetra* and *lat*, see above). Each of them was advantageous under certain circumstances, but when combined into a syndrome (a coordinated complex structure, as *tetra-lat*), they produced the highest fitness, probably as a result of a synergetic effect. In the instance represented by the *Linograptus/Abiesgraptus* transition, particular elements of the future adaptive syndrome must have appeared successively in local populations (patches) to be later assembled by means of a sexual process into a syndrome (Fig. 16, I–II). The genetic and selective mechanisms that were most likely involved in the syndrome formation are shown in Fig. 16, III–V. It is assumed that simple combinations (AB, BC, AC) had a selective advantage over single characters (A, B, C) and, in turn, the compound genotype (ABC) was superior to all the remaining combinations. Such a piecemeal pattern of the emergence of a complex adaptive structure seems not only more probable than its instant origin, but is, at least partly, supported by the fossil record. Another remarkable feature of the *Linograptus/Abiesgraptus* phyletic transition is world-wide distribution (probably warm-water cosmopolitism) of both ancestral and descendant species. This may imply a polycentric or even pantopic appearance of the new species, over large areas within the range of the parental taxon, instead of its local, sympatric or allopatric origin as usually presumed. It seems unlikely that such a wide geographical distribution could have been attained due to migration within so limited a time.

The above disparate mode of the appearance of new characters in the linograptids is only a special case of the mosaic course of evolution. This classic palaeontological rule (also known as the Watson Rule) has recently been elevated by STEBBINS (1983) to the rank of "an integrating principle for the modern synthesis".

EVIDENCE FOR PHYLETIC EVOLUTION IN THE LINOGRAPTID LINEAGE

The evidence available indicates that throughout almost all its history the linograptid lineage was represented, at any given time-level, by a single morphospecies. This is certainly true for the sequence: *Neodiversograptus nilssoni–N. beklemishevi–Linograptus posthumus.* The subspecies of the latter, namely *L. posthumuus tenuis* (JAEGER, 1959), is in every respect identical with the type species, except for smaller size, and may rather represent a zonal variety. Less certain is the nature of *Linograptus phillipsi* described by DECKER (1935, 1939) from North America. Its remains need a modern revision, but for the time being it can be treated as a geographical variety of the European species, whilst var. *multiramosus* is simply an astogenetic variant. Numerous subspecies or species of *Linograptus* erected by Hundt are all of preservational or astogenetic nature (see JAEGER 1959: pp. 143–144).

The *Linograptus/Abiesgraptus* transition as well as the later *Abiesgraptus* diversity need, however, additional comments. The overlap in the vertical range of *L. posthumus* and *A. tenuiramosus* as observed by JAEGER (1959) in the *praehercynicus* Zone may be more apparent than real, since juvenile rhabdosomes of *Abiesgraptus* cannot be distinguished from the *Linograptus* colonies. This occurs because, in its astogeny, *Abiesgraptus* possesses the *Linograptus* growth stage (compare p. 241 herein) which can be identified taxonomically as *Linograptus.* Thus, this overlap is most probably illusory and does not mean a real co-occurrence of the two species in question. As mentioned above, it is more probable that *A. tenuiramosus* originated from *L. posthumus* by means of sympatric transformation and replaced it as a new chronospecies, after its disparate characters were united into a syndrome.

The next case to be explained in the context of the phyletic nature of the evolutionary changes in linograptids is the "terminal variation" of *Abiesgraptus* expressed in relatively small differences in the width and the size of the branches. This variation was used to discriminate formally valid species, such as *A. multiramosus* and *A. longiramosus*, both accompanying the standard form of *A. tenuiramosus.* This may imply multiplication of species and branching of the lineage. However, even if these differences were sufficient to distinguish separate species (which is not perfectly clear), the diversification, immediately preceding the extinction of the lineage, occurred too late to change the general sequential nature of the speciation events within linograptids (diagram Fig. 17). Another instance of increased morphological diversification in phylogenetically late stages of *Abiesgraptus* lineage was described by LENZ (1988). His fragmentary specimens from *fanicus* Zone (Pragian) of northern Yukon (Canada), exhibit first and second order cladia, arising in pairs or singly from the primary stipe. Such features were never seen in earlier representatives of the genus and the Yukon species marks the latest occurrence of the lineage. Most likely it produced a short offshoot of the abiesgraptid stock, being the last attempt at a progressive development of the compound rhabdosome. This attempt failed after a short success in a probably restricted area. Hence, the latest representatives of Linograptinae display an increased amount of variation and a tendency towards splitting of the lineage just before its final exinction. These phenomena may be best explained assuming

SIMPSON's (1944) idea that extinction in many cases is preceded by an increased splitting of the endangered groups or lineages, trying to find out an adequate adaptive response to the changes of the environment.

The application of the morphological species concept to the evolution of lineages is in general charged with danger of treating morphotypes as separate species. Thus common co-existence of two morphotypes, A and B, might be interpreted as their co-occurrence, whilst in fact they represent a polymorphic population (a polymorphic chronodeme) rather than anything else. The same holds for the growth stages in compound colonies, as is the case with the unipolar and bipolar stages of *Neodiversograptus nilssoni* (or *Linograptus/Abiesgraptus* as discussed above) where astogenetic variants may be ranked systematically and treated as apparent instances of cȯ-occurrence.

As demonstrated by linograptids, a long-lasting phyletic evolution in a single lineage implies an unusual cohesion of the genetic (and epigenetic) system of the species. In spite of their world-wide distribution, *Linograptus posthumus* and *Abiesgraptus* spp. preserve a remarkably uniform morphology over vast areas. They exhibit the phenomenon of warm-water cosmopolitism, a common feature of recent plankton. The genetic and phenetic cohesion allowing such species, both extant and fossil, to avoid the consequences of isolation by distance, presents one of the unresolved "paradoxes of plankton".

The evaluation of the entire picture of the linograptid evolution is an uneasy task. Following the reasoning presented by HALLAM (1982) for Jurassic *Gryphaea*, the periods with an increased rate of morphological changes observed in the phylogeny of the linograptid monophyletic lineage may formally be interpreted as punctualism. This is, however, an extrapolation of the primary meaning of the notion directly related to the multiplication of species and branching of a lineage (ELDREDGE and GOULD 1972).

Neither the *Gryphaea* nor the Linograptinae provide convincing evidence for branching events (bifurcation) and consequently there is no stratigraphic overlap between the ancestral and the descendant species. Members of the lineage are in both cases sequential species (chronospecies), displaying, however, an increased rate of morphological changes during the periods coinciding with transformation (phyletic speciation). The term *punctualism* can safely be applied to describe the changes observed in the lineage of *Metrarabdotos*, a Neogene bryozoan, where each speciation is associated with the branching of the lineage and the co-occurrence of the parental and the daughter species (CHEETHAM 1987). In linograptids, the morphological changes are not so strongly punctuated (in *Metrarabdotos*, morphological changes within the confines of the species are practically equal to zero, and the entire morphological change is due to speciation; in the *Gryphaea*, the situation is largely similar), and the stasis does not mean an almost complete arrest of change. Taking into account the sequential nature of the linograptid species and the above-mentioned characteristic of the speciational events in their lineage, one could perhaps define this mode of evolution as *quasi*-punctuated. A number of technical terms were suggested to describe this situation, which only partly correponds to the punctuated model of speciation (condensation of morphological change in time but no splitting and prevalence of anagenesis), to mention only punctuated gradualism (FENSTER *et al.* 1989) or punctuated stasis (SPRINGER and MURPHY 1994).

LINOGRAPTID PHYLOGENY AS AN INSTANCE OF MACROEVOLUTION

As compared with a number of classical examples of macroevolution, frequently quoted in the neontological (e.g. Darwin's finches of the Galapagos Islands and the Hawaiian honey creepers) and current palaeontological literature (ELDREDGE 1989), linograptids possess some unique features. First of all they represent a single lineage, almost devoid of any offshoots, that is an unbroken chain of the ancestral-descendant succession of populations. The pattern of linograptid evolution is therefore characterized by a strong anagenetic component and a very weak cladogenetic component (as defined by HUXLEY 1958 and applied to graptolites by BULMAN 1963).

The predominance of anagenesis in the linograptid evolution is most probably the result of long-lasting directional selection leading to the stepwise improvements of the adaptive type through distinct structural changes of the colony organization. The absence of a pronounced tendency toward multiplication of the species speaks for a great cohesion of the population genetic pool at any particular time, most probably due to a strong action of stabilizing selection associated with the directional vector of selective forces. Stabilizing selection counteracted any disruptive effects or splitting the genetic system of the species. As a result, the linograptid evolutionary changes were strongly canalized, and the main "trials" concentrated along the pathways leading towards multiramous compound colonies.

Within this single line of descent the Linograptinae realized large-scale evolutionary changes, producing new patterns of colony organization and at least three distinct adaptive types. In consequence, the entire evolutionary potential of evolving populations was profoundly changed. The appearance of new transspecific taxa (3 genera, 1 subfamily), new structural types, and great adaptive (ecogenetic) consequences are *prima facies* characteristics of macroevolution. Ample speciation may logically be considered only a side-effect of macroevolution, but not a primary feature of the process. Such commonly cited examples of macroevolution as the Hawaiian honey creepers or the Galapagos finches display a distinct prevalence of speciation over morphological changes, with the key structural type remaining little affected by evolutionary change. They are more representative as illustrations of adaptive radiation than as exponents of macroevolution. Such instances were used for punctualistic generalizations concerning the predominance of the speciational component in macroevolution over the phyletic one. The history of the Linograptinae offers a different logic and corroborates the opposite view (see Fig. 17).

The case of the Linograptinae undermines the common belief based on a punctualistic approach that an increase in the rate of morphological changes, following a period of stasis, necessarily or almost universally means branching of the lineage (splitting or multiplication). It may equally represent an accelerated phyletic transformation, that is sequential replacement of one chronospecies by the other (cf. p. 253). The stasis as observed in linograptids means a slowdown of the morphological rate of evolution, rather than a complete arrest of change. During the stasis the microevolutionary mechanisms might accumulate variation of great significance for the prospective evolution. The phenotypic expression of these newly appeared variants exhibits a low degree of morphogenetic control which is manifested by the changing localization of the gene action and an imperfect symmetry of the phenodeviants (cf. p. 256 herein).

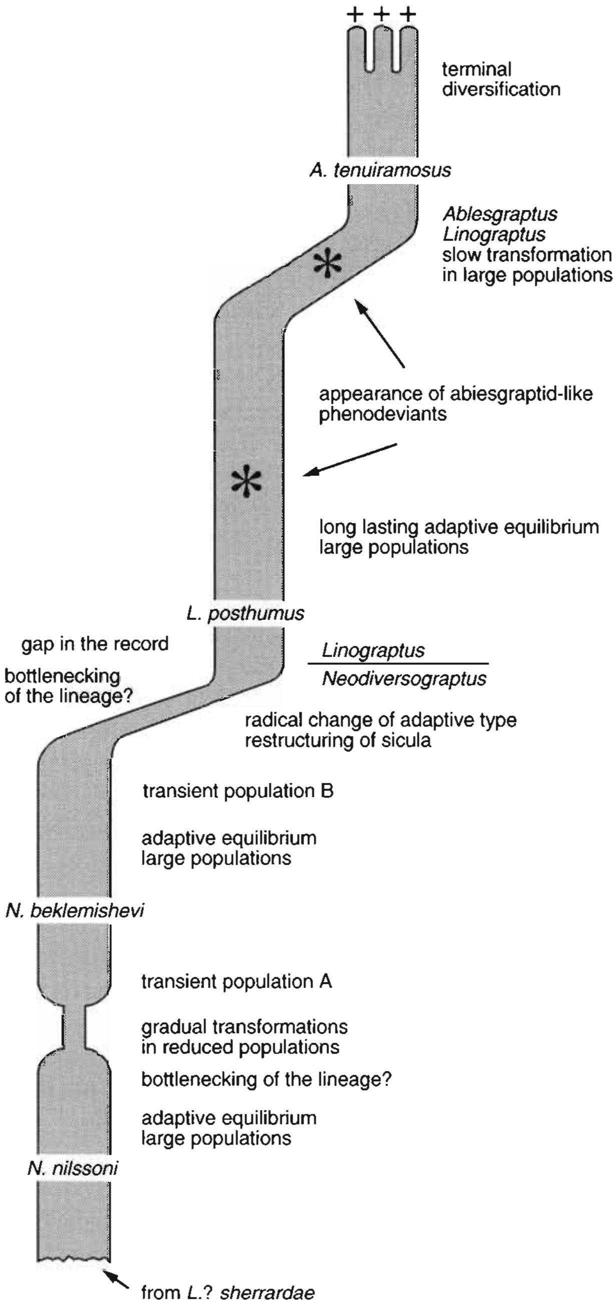

Fig. 17

Diagram showing the main features of evolution in Linograptinae. Note the posible bottleneckings of the lineage, the position of transitional populations A and B, as well as the transformation in large populations and the terminal splitting of the lineage, before the final extinction. Further explanations in text.

Theoretical models of macroevolution are usually based on generalizations of large bodies of empirical data combined with some deductions from the accepted theories in different fields of biological sciences. A single case can hardly be used in their falsification since they could only be tested against a larger class of empirical data. Nevertheless, it is always important to see to what extent the parameters of the phenomena observed fall within the range of values or predictions compatible with the current hypotheses or models.

In this review I will consider only some conclusions which can be drawn from the linograptid case against a wider theoretical background.

The evolution of linograptids offers no evidence in support of saltationary concepts of macroevolution. There are no data indicative of a sudden appearance of new structural types which could have been ascribed to large mutational events. Though the generation of a new cladium does produce an abrupt phenotypic effect, the discontinuity here is secondary, due to a meristic nature of the character involved (an increase in the number of morphological units, a sort of polymerization). However, it is clear that the new patterns were fixed in a stepwise manner, the entire picture suggesting an additive piecemeal "technology" rather than great evolutionary leaps. The presence of well-defined, but intergrading chronospecies, whose phenotypical traits are gradually modified, may be better explained within a neo-Darwinian paradigm.

The pattern of the linograptid evolution only partly corresponds to the punctuational model. Thus phenomenologically, the stasis observed in the linograptid species equals that distinguished by punctualism, but it should probably be ascribed to a certain mode of action of natural selection. There is no substantiation for the essential decoupling of micro- and macroevolution, and frequently the microevolutionary changes have a great bearing on the phylogenetic future of the species (see also URBANEK 1970). The bottlenecking without the splitting of the lineage, as observed in the *nilssoni*/*beklemishevi* and *beklemishevi*/*posthumus* transitions, does not fully correspond to the model of rapid speciation as suggested by the concept in question. Such events as gradual transformation in large populations (*L. posthumus*/*A. tenuiramosus*) or major morphological transitions within a single lineage should be considered by punctualism as practically impossible or quite exceptional. It is also very difficult to make inferences about the causes of past processes from the information available presently on speciation. Opinion is still strongly divided into the adherents of founder-induced speciation, which ascribe great role to the bottlenecking as a precondition for genetic revolution (CARSON and TEMPLETON 1984), and the followers of a quite opposite view that speciation may proceed in moderate or even large size populations by gradual divergence of gene pools (BARTON and CHARLESWORTH 1984). The linograptid case offers some support for the view that both modes of speciation may be involved in the evolution of a single lineage (Fig. 17).

The abiesgraptid growth pattern of the colony seems to be adaptively superior to that represented by the majority of Lower Ordovician multiramous colonies (the Anisograptidae and Dichograptidae). Branching in the last named groups was based on planar bifurcation at a certain angle, and the continuing growth of the rhabdosome (elongation and dichotomy) was constrained by the mutual impinging of the stipes. Such conditions imposed important limitations on the branch configuration in the Ordovician multiramous groups. Abiesgraptids solve this problem in a more satisfactory way, because their lateral branches, although planar, are parallel and situated on the two opposite main branches, thus excluding any impinging (Fig. 6). It is obvious that the appearance of this improved pattern was preceded by less fit "trials", some of which were eliminated by natural selection.

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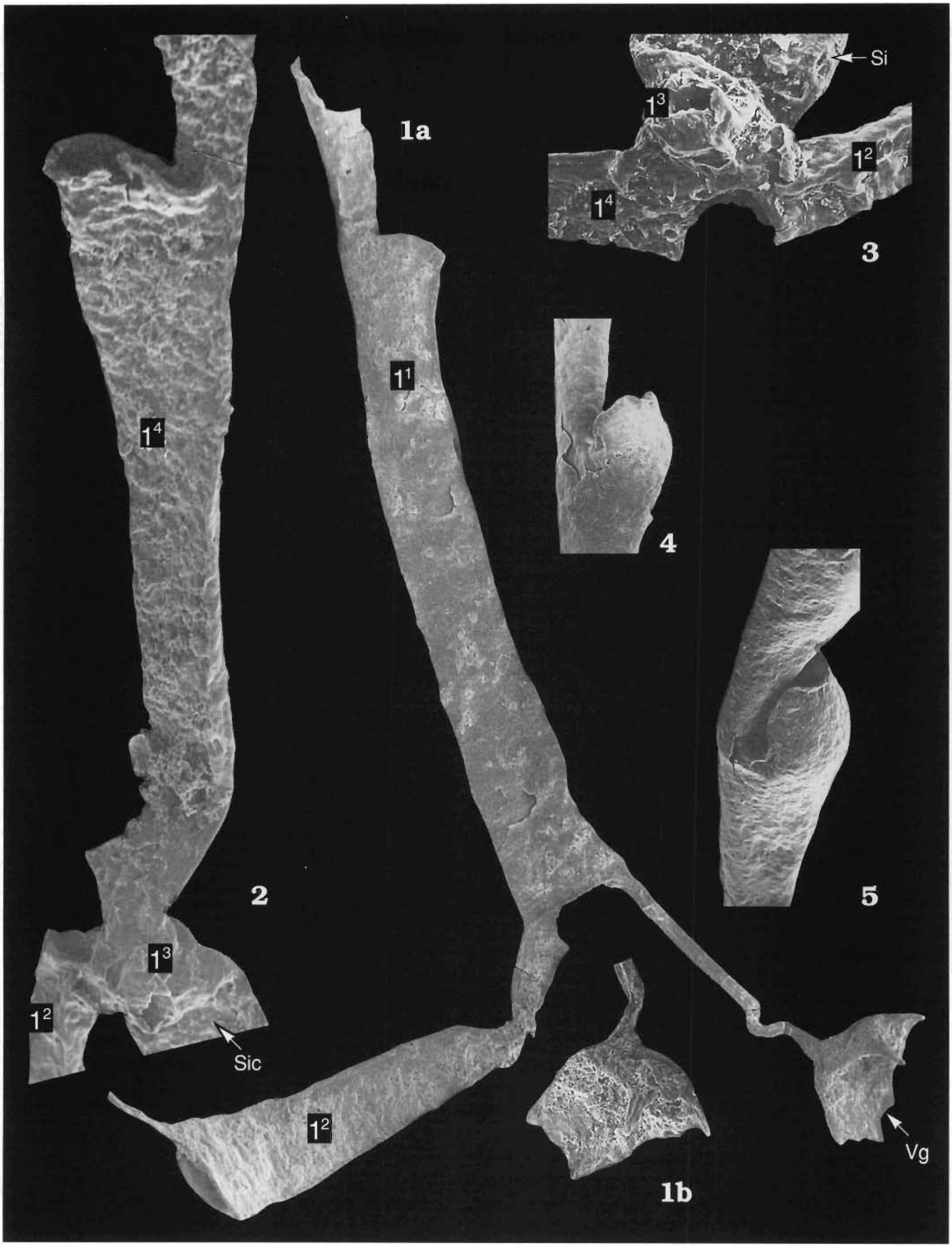
THE EMERGENCE AND EVOLUTION OF LINOGRAPTIDS

PLATE 1

1–5. Early stages of cladial generation (1a, 2, 3), details of virgellarium (1b) and thecal characters (4, 5) in *Linograptus posthumus* (Reinhard RICHTER, 1875); 1a sicula with theca 1^1 of the procladium and theca 1^2 of the first sicular cladium. Note the presence of virgellarium (Vg) preserved in its relation to the sicula and shown in an additional aspect (1b); 2, 3 slightly deformed apertures of metasicula (Si) with sicular cladia radiating from it; 4, 5 apertural parts of distal thecae with genicular ventral wall and apertural lip somewhat introverted. Mielnik-1 borehole; 1 depth 792.25 m, early Ludfordian, *acer* Zone, × 75; 2, 3 depth 764.15 m, late Ludfordian, *protospineus* Zone, 2 × 100; 3 × 175; 4, 5 depth 873.60 m, early Ludfordian *inexspectatus-kozlowskii* Interzone. Si – sicula, Vg – virgellarium, 1^1–1^3 – first thecae of respective cladia.


1a
1¹
2
1⁴
1³
1²
Sic
1²
1b
Vg
1³
Si
1²
1⁴
3
4
5

INDEX OF GENERIC AND SPECIFIC NAMES

PREFACE

Although the study of erratic boulders derived from the classical Silurian succession of the Baltic region, had provided, even earlier, a certain insight into the subsurface Silurian of the Northern part the Polish Lowland, a real breakthrough was made due to a large scale drilling programme initiated in 1957 by the Polish Geological Institute. Within the Early Palaeozoic rocks graptolites were among the most priviledged groups, as their remains were most common and best preserved. They offered a rich material suitable for etching and further morphological scrutiny. Some especially carefully measured and studied wellcores provided crucial information concerning the development of graptoloid faunas and Silurian stratigraphy in the Polish part of the East European Platform (EEP).

The first part of the book discusses the major features of the platformian Silurian in Poland and the adjacent areas, while the second one summarizes and updates the earlier results concerning the development, trends and patterns of graptoloid faunas from Wenlock and Ludlow Series. The following chapters contain up-to-date taxonomic and biostratigraphic studies on the late Ludfordian and Přidoli divisions of the Silurian. The last chapter goes beyond the empirical evidence and shows the emergence of linograptids against a wider background of evolutionary biology.

We thank Mrs Irina Bagajewa-Urbanek (Warsaw) for her inspiring co-operation when translating the text into English and finally we express our gratitude to Professor Alfred C. Lenz (London, Ontario, Canada) from whose comments and remarks our book has benefited enormously.

The Editors