

LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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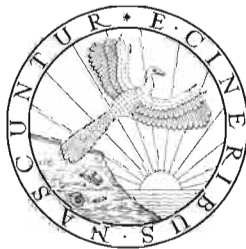
Graptolites etched from the Mielnik-1 wellcore (E Poland) reveal the main features of the development of monograptid faunas within the late Ludfordian–early Přidoli interval. Fifteen species and subspecies are described and *Monograptus* (*Slovinograptus*) subgen. n. as well as *Neocolonograptus* gen. 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 *kozłowskii* 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* Tsegel'nyuk). 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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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 nongraptoliferous 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 inter-

calations 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 rhabdosome, 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 Syncline, 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 Syncline 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 organodetrital 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 Thuszcz), 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 organodetrital (sometimes dolomitic) limestones, and claystones, both

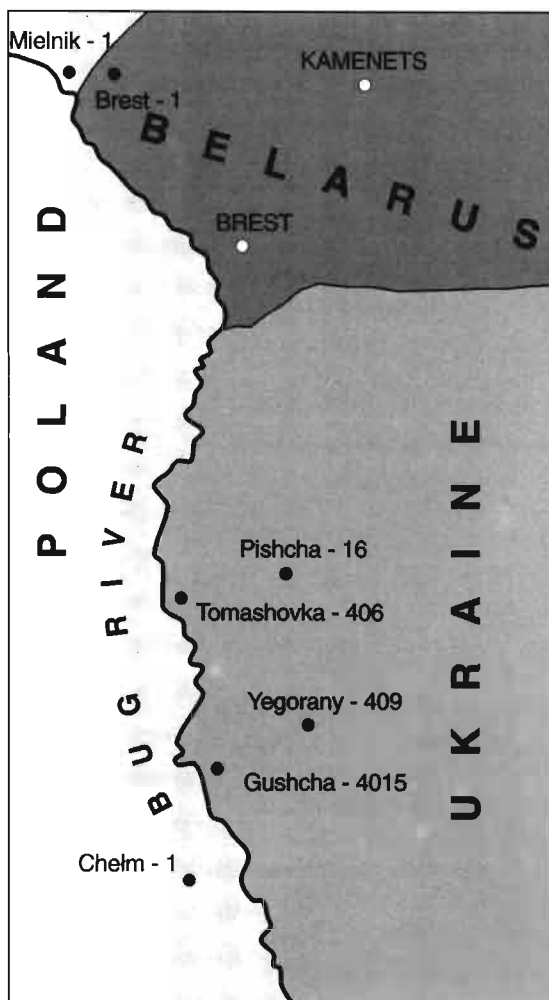


Fig. 1

Location of the Mielenik IG-1 (Mielenik-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 pelitic 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 Mielenik section by LANGIER-KUŹNIAROWA (1979, 1981).

In the Podlasie Formation, claystones, marls and pelitic limestones comprise the main lithology. Limestones are slightly dolomitic, sometimes laminated and bituminous. The top of the Silurian beds in the Mielenik 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, Mielenik displays a rather high carbonate, as well as a relatively high pyroclastic, content even in the rocks classified 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 Mielenik 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, *vide* 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 Mielenik 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 Mielenik.

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).

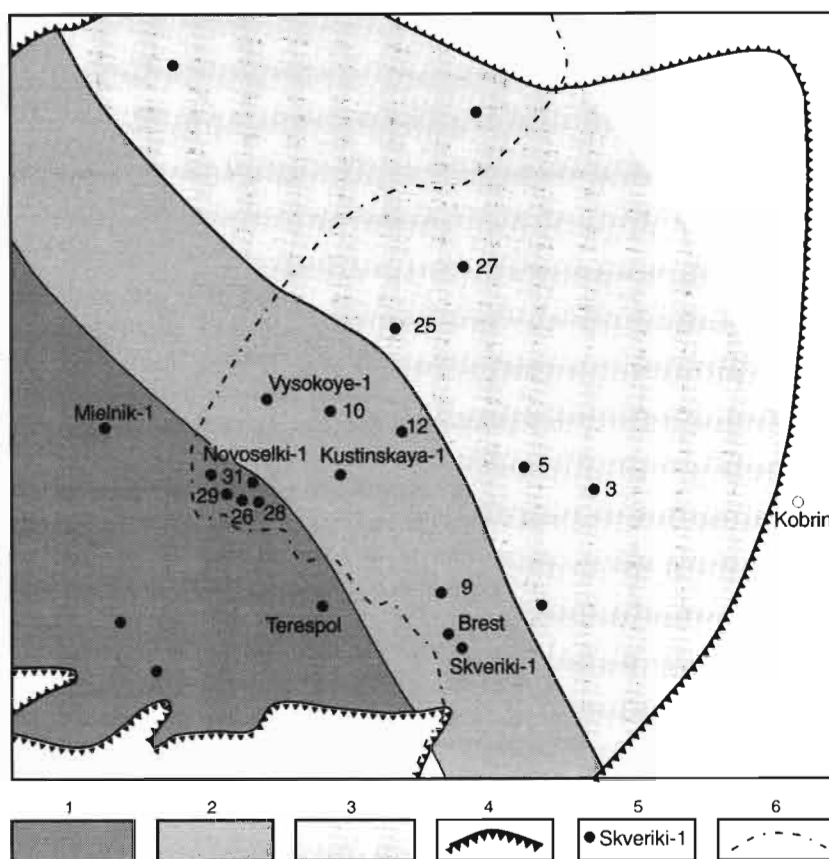


Fig. 2

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 DŽIK’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. (Uncinograptus) 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 (Uncinograptus) 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 ingression of the first *dubius* fauna (see the discussion below).

The frequent occurrence of *Monograptus (Uncinograptus) 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 (Uncinograptus) 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 (Uncinograptus) 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 approximately 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

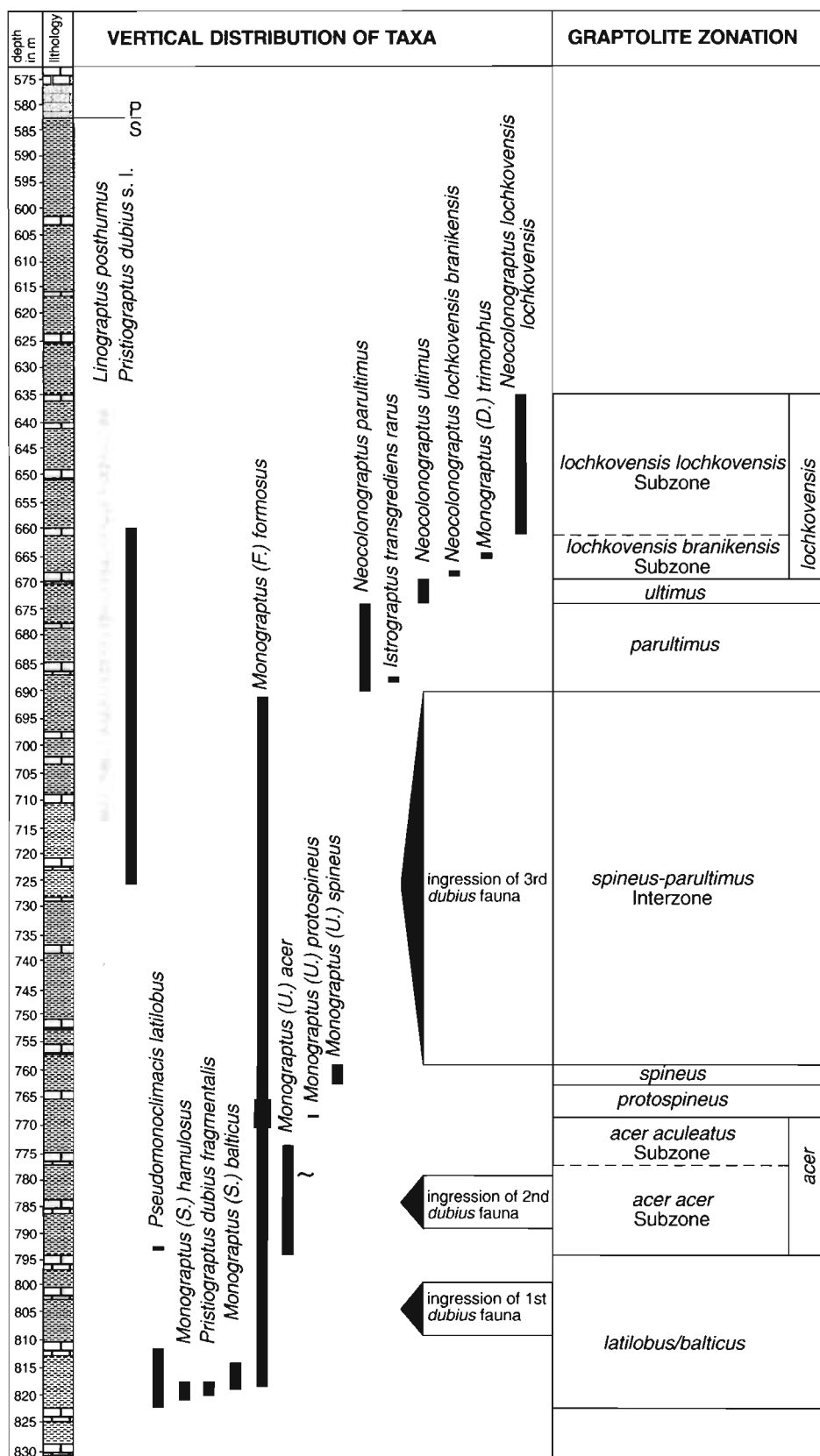


Fig. 3

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*.

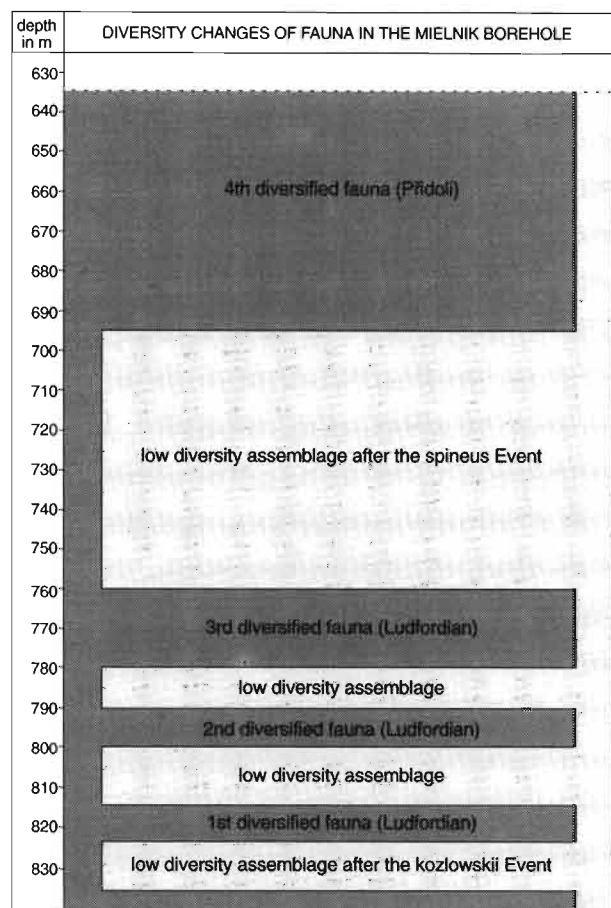


Fig. 4

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.

ous 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).

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 Leba-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 assemblage 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 discontinu-

The first ingress of the *dubius* fauna is recorded at a depth of 814–800 m. Being basically monospecific 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 ingress of the *dubius* fauna (at a depth of 790–780 m) is represented, as above, by pristiograptids 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 ingress 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 ingresses 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 ingress 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 ingresses 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 ingress 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. lochkovens* *lochkovens* is the last index graptolite encountered in the Mielnik section, its last occurrence 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), *Uncinograptus caudatus* TSEGELNJUK, *U. rectus* TSEGELNJUK, *Dulebograptus bresticus* TSEGELNJUK, *Pseudomonoclimacis haupti* (KÜHNE), *P. medius* TSEGELNJUK, *Bugograptus spineus* (TSEGELNJUK), *B. aculeatus* (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* (*Uncinograptus*) *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 *Neocucullograptus* URBANEK, see TSEGELNJUK 1981: fig. 9) were proved to be erroneous and based on a misinter-

pretation 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 (Uncinograptus) 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 (Uncinograptus) acer* (TSEGELNJUK)], are co-eval and occur roughly between bentonite 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_1 " 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 synchronicity. 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, *Dulebograptus trimorphus* TSEGELNJUK, *Tamplograptus formosus* (BOUČEK), *Uncinograptus similis* (PŘIBYL), *U. bouceki* (PŘIBYL), *U. perneri* (BOUČEK), *U. angustidens* (PŘIBYL), *Heisograptus difficilis* TSEGELNJUK, *H. canaliculatus* (TSEGELNJUK), *Ludensograptus parulimus* (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 (Uncinograptus) 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 (KÜHNE 1955; URBANEK 1958). Therefore the lower boundary of the *P. "tauragensis"* (= *dalejensis*) Zone may only be delimited by the disappearance of the lobograptid 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 syncline 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 syncline; 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 syncline (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 *kozłowski* 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). *Neocullograptus kozłowski* 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 flowering of bohémograptids (the "*Bohémograptus* 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 comparison with Volhynia or Eastern Poland. In the post-*kozłowski* 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* (*Wolynograptus*) *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 *Monograptus* (*Uncinograptus*) *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 popula-

tions; 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 kozłowski* 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 kazakhstanensis*), 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 [*Cucullograptus 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-*kozłowskii* part of the Ludfordian (late Ludfordian in the understanding 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 Subcommittee 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 Subcommittee 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 Llandoveryan, 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 approved 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 Homeric 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 Homeric 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 exceedingly 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 occurrence 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 exceedingly 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 pristio-graptid-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 *kozłowski* 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 *kozłowski* Event, or C₃ 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 kozłowski*, and the late bohémograptids 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 independently 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. POREBSKA (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 reappearance 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 reappearance of *uncinatus*-type monograptids is that of *Monograptus ceratus*, recognized in the *leintwardinensis* 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, POREBSKA 1984), but also some earlier groups [e.g. *M. (Dulebograptus)* TSEGELNJUK] display specializations, sufficient to make any immediate derivation from *M. (U.) uncinatus* impossible. Nevertheless, 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 heterogeneous 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 *kozłowskii* Event, namely *Pristiograptus dubius* s.l. and *Linograptus posthumus* (Reinhard RICHTER). The stem-species represented 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 multi-ramous 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-horny*i lineage traced in the type Přidoli by JAEGER (1986),

3b, the *parultimus-lochkovens*is 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 certain 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 “blindlers” (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 *kozłowskii* 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. 7B₁, B₂). 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–C₃). 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. (Uncinograptus) 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.) flmingi* 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. 5B₁, B₂, 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. 5C₁, C₂, 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. 5A₁, A₂).

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

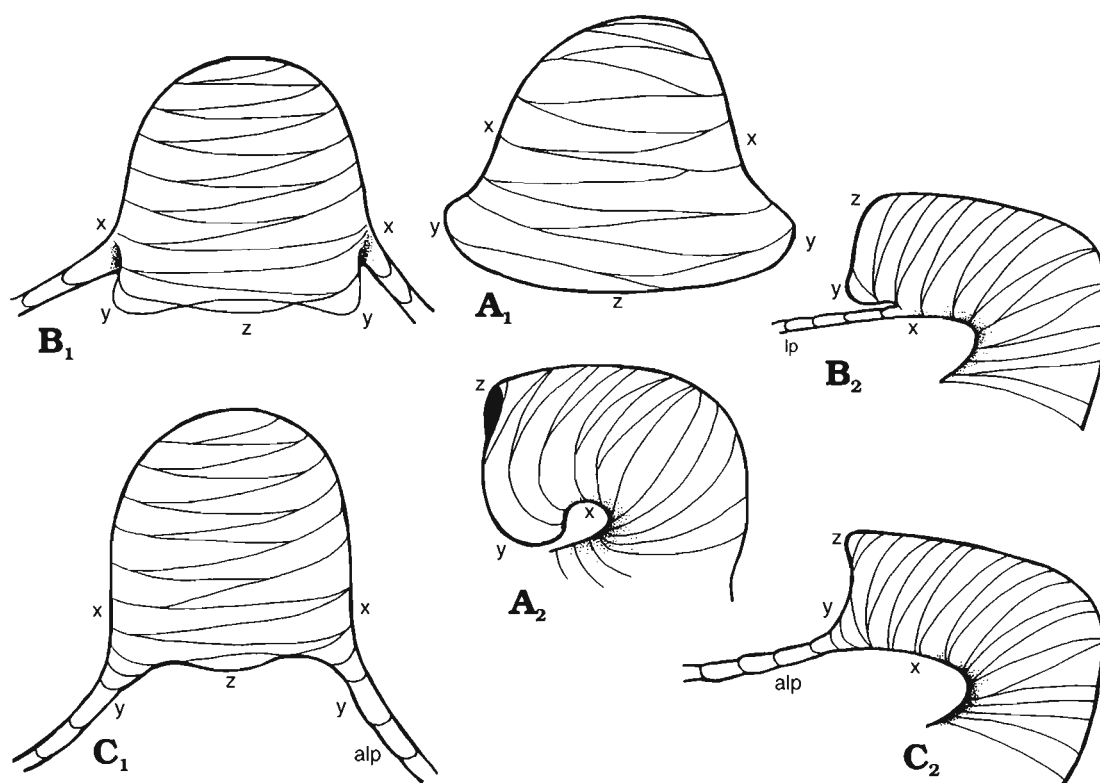


Fig. 5

Comparison of apertural apparatus (A_1 , A_2) in *Monograptus uncinatus* TULLBERG from the *nilssoni* Zone (Ludlow, Gorstian) representing a nonspecialized, ancestral type of structure, 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 homologous 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 placed 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 estimations in 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 exceedingly 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 hypothesize 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 was 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 preserved *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 assignment 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 modern 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 *leitwardinensis*

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 *kozłowski* Event eliminated the last bohemograptids and neocucullograptids. Operculate monograptids were never recreated, their place being taken by quite different morpho-ecological 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. 7C₁–C₃). 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. 7B₁, B₂). 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. 5A₁, A₂). 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. 5C₁, C₂) and not on the lateral margins as is the case with the Wenlockian forms. (Fig. 5B₁, B₂). 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

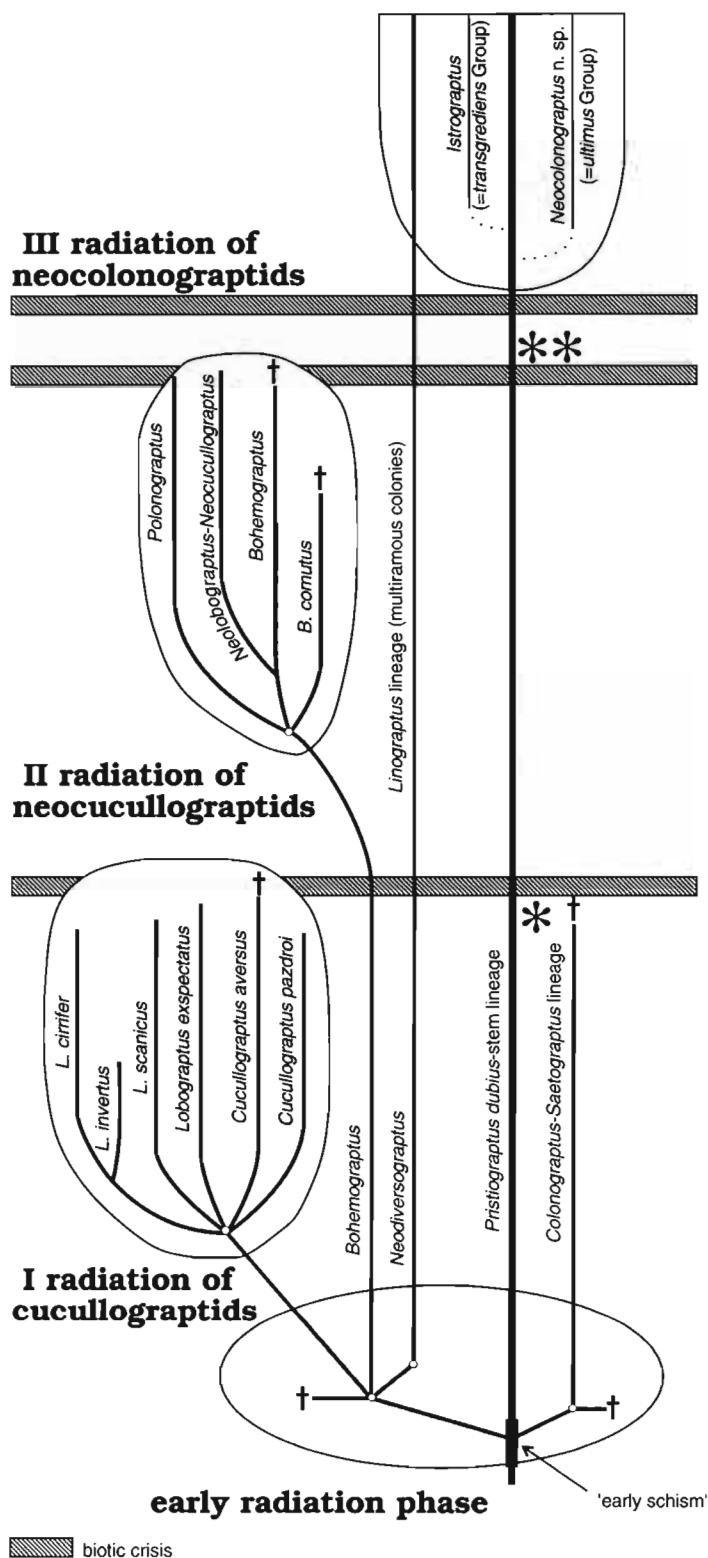


Fig. 6

Simplified history of *Pristiograptus dubius* (SUESS) and related lineages in the Late Silurian. Subject to adaptive radiation in the late Homeric, *P. dubius* stem lineage remains conservative until early Přídolí, 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.

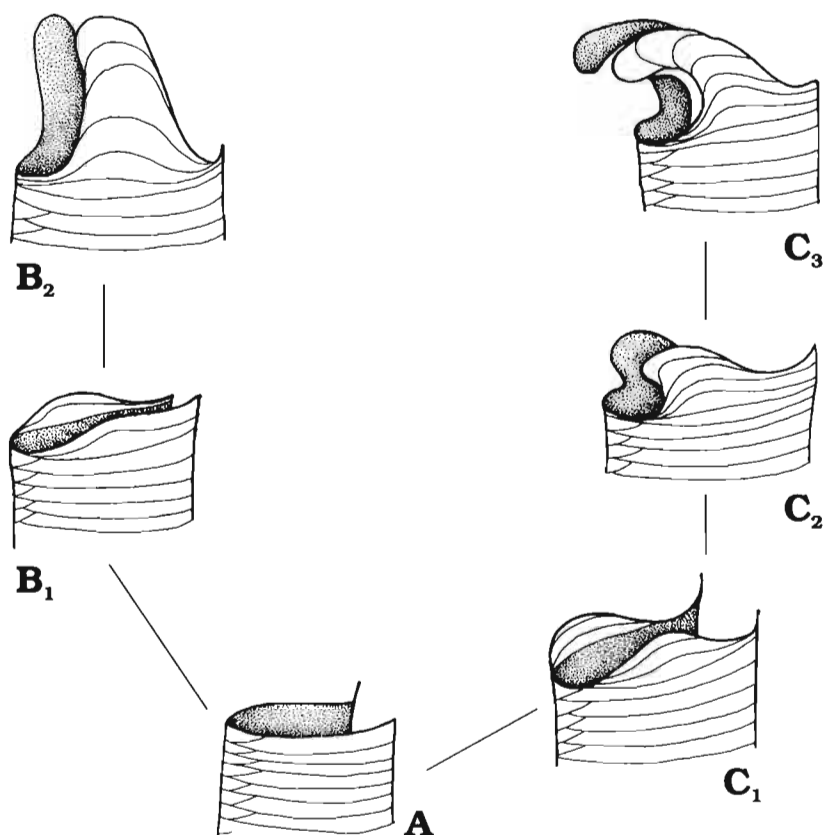


Fig. 7

Comparison of the morphological evolution of bilateral apertural lobes in the proximal thecae of Ludlow colonograptids, as illustrated by *Colonograptus praedeubeli* (JAEGER) (**B₁**, *praedeubeli* Zone) and *Colonograptus colonus* (BARRANDE) (**B₂**, *nilssoni* Zone), with Přidoli neocolonograptids represented by *Neocolonograptus parultimus* (JAEGER) (**C₁**, *parultimus* Zone), *N. ultimus* (PERNER) (**C₂**, *ultimus* Zone) as well as with *N. lochkovenski* (PŘIBYL) (**C₃**, *lochkovenski* 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 prefix *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 “blindlers”, see p. 112), were acquired by pristio-

graptid-like ancestors in the Homerician (*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 resemblence 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 pristiograptid 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, whereas 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 significance 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-

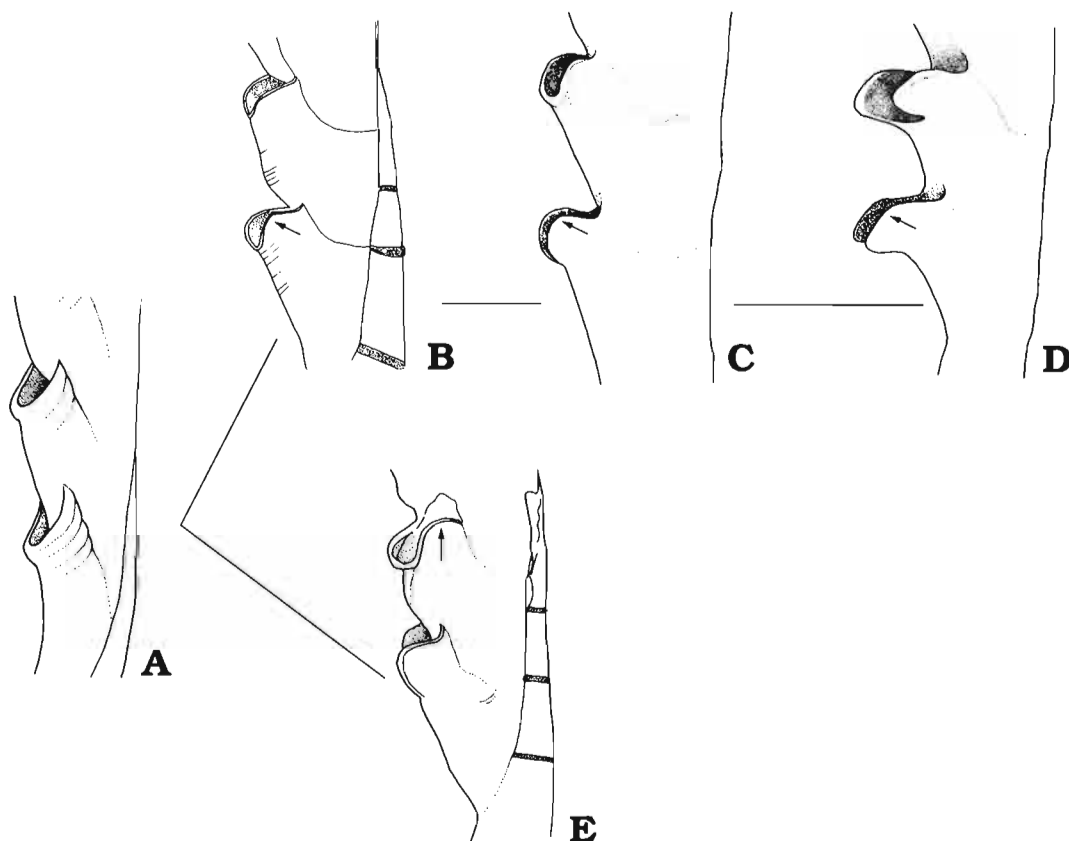


Fig. 8

Morphological change in proximal thecae of Pridoli bilobate pristiograptids, representing *Neocolonograptus* gen. n. (B–D) and *Istrograptus* TSEGELNIUK (E): A, *Pristiograptus dubius* cf. *frequens*, a presumable common ancestor; B, *Neocolonograptus parultimus*; C, *Neocolonograptus ultimus*; D, *Neocolonograptus lochkovenski 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*–*lochkovenski* 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 Homeric (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 blastozoid in the colony, the timing of its budding and the behaviour of both the parental siculozoid 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 demonstrated 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 metasacula. 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

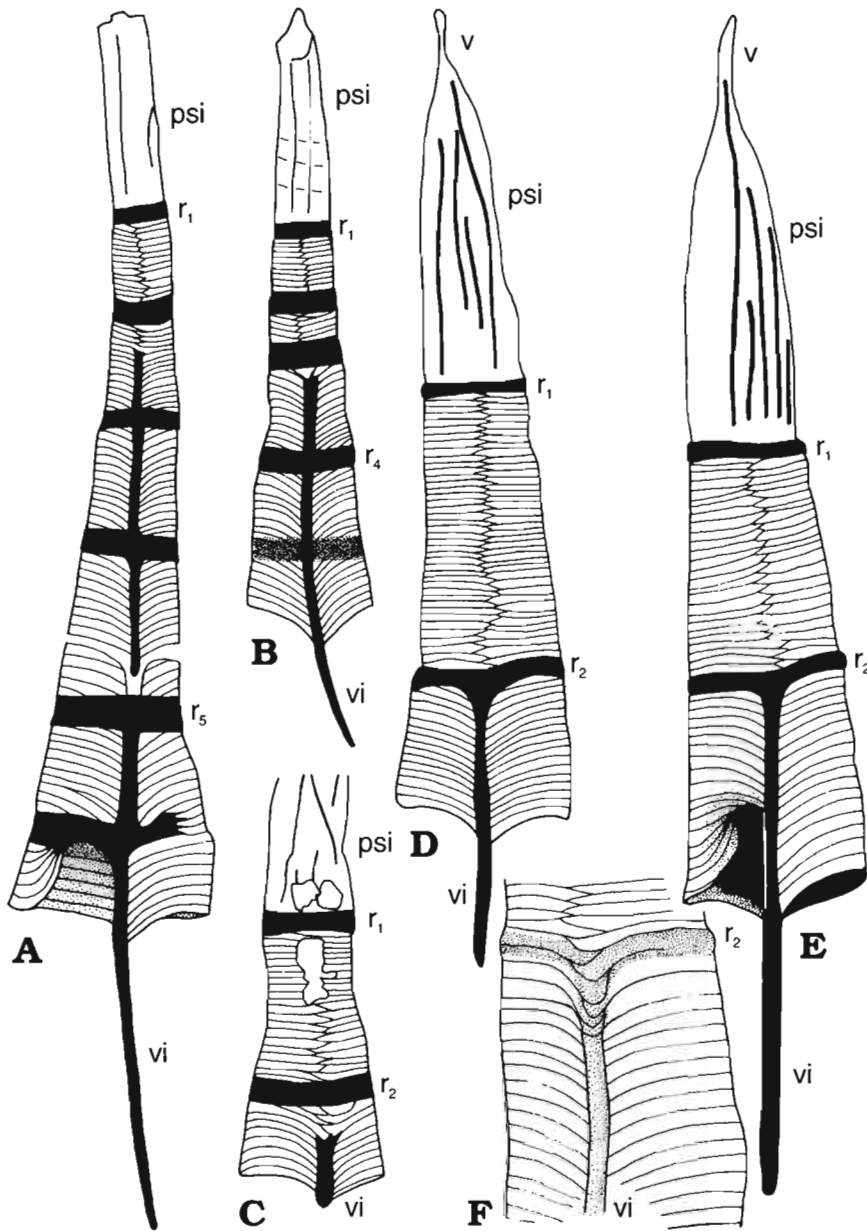


Fig. 9

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. lochkovenski lochkovenski* (PRIBYL). 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 *kozlowski* 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-lochkovenski* lineage). Such conditions can also be encountered in the late Ludfordian *Pseudomonoclimacis latilobus* (POREBSKA 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 crypto-genetic 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 monograptids, 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. 20B₂) or *M. (U.) acer* (Fig. 26B) as well as in the Přidoli *N. lochkovens* (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 hypothesize 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 "pauciannular" version of the sicula was more efficient in the late Silurian pelagic environment than the "multiannular" 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

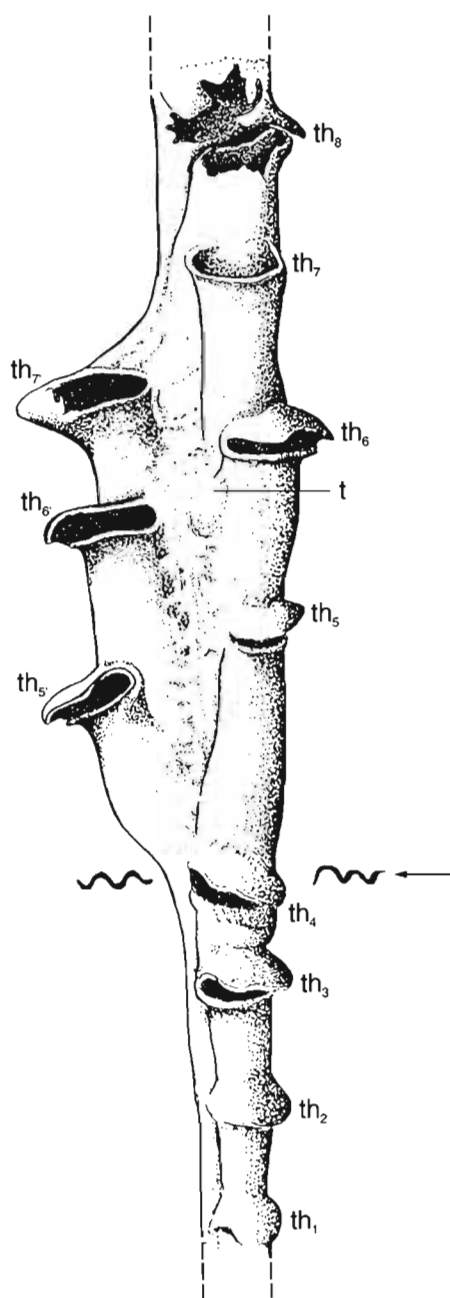


Fig. 10

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.

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.

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

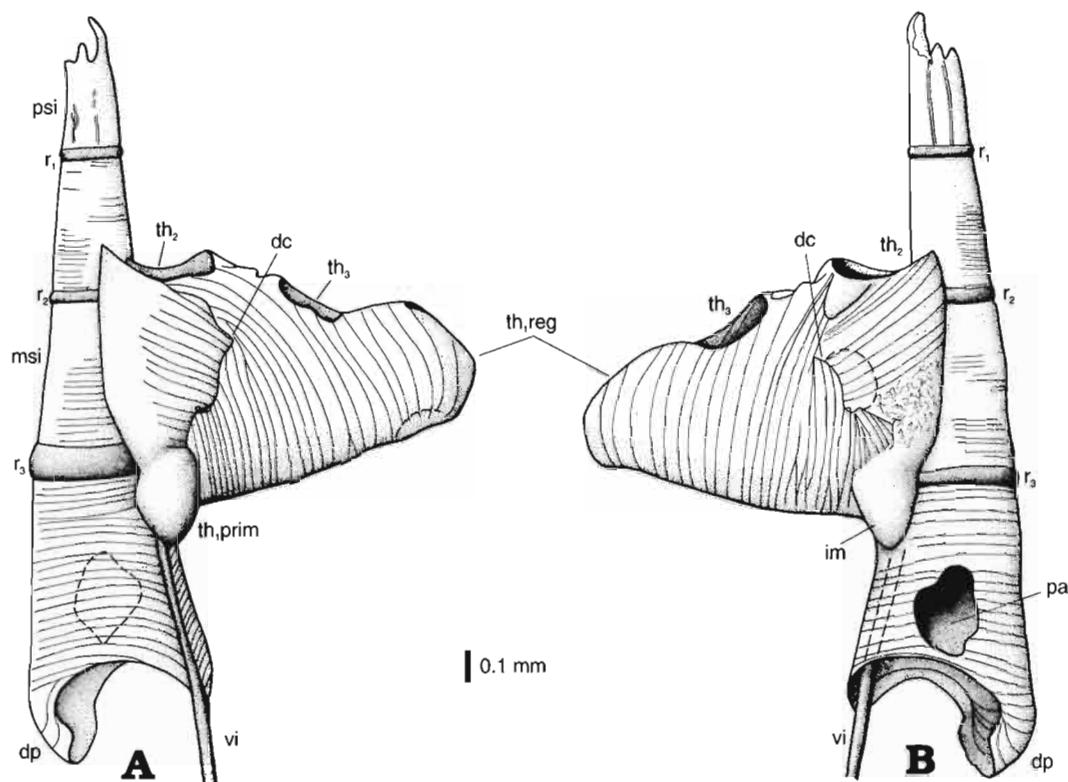


Fig. 11

Abnormal proximal end development in *Neocolonograptus lochkovensisi* (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, *lochkovensisi* 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 lochkovensisi* (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 ($th_{1,prim}$, im) as well as of a newly formed, regenerative portion ($th_{1,reg}$). 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-

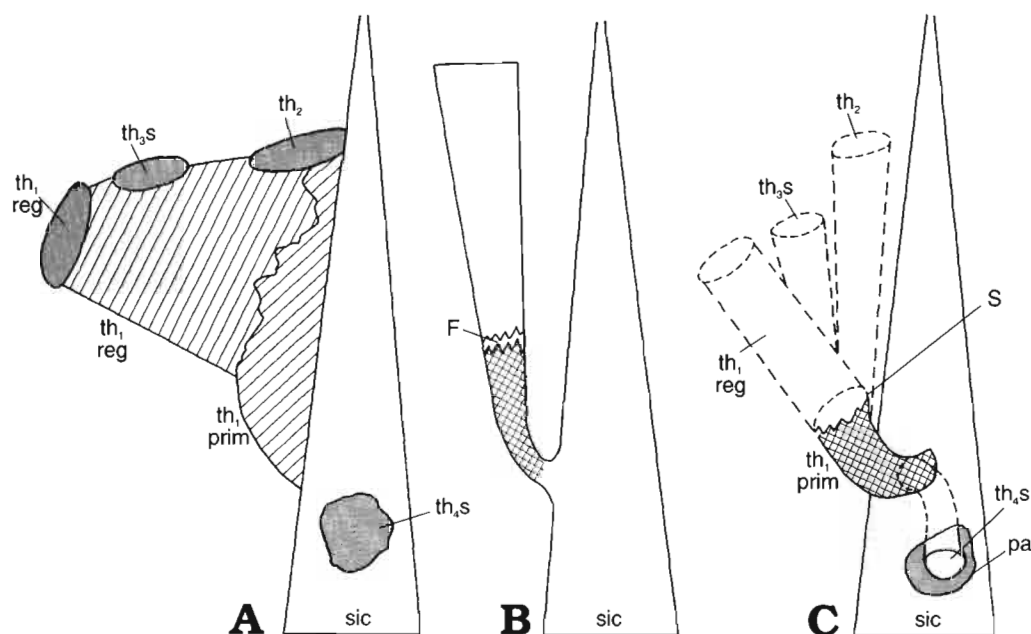


Fig. 12

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 (th₁prim) and regenerative (th₁reg) portion of the first theca, the presence of supernumerary openings (th₃s, th₄s) in addition to normal prothecal opening (th₂) and thecal aperture (th₁); **B**, possible interpretation of the injury (wavy line) resulting in fracturing (F) of the primary th₁; **C**, reconstruction of the regeneration process involving the production of four zooidal buds (th₁reg, th₃s, th₂ as well as th₄s). 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 th₁ are visible as a scar (s).

sicula, close to its aperture, and formed by perforation or rather resorption 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 th₁ was stimulated to intense regeneration (Fig. 12C) and produced a regenerated zooid within th₁reg, the normal bud for the successive th₂ and also two supernumerary buds – one growing up (th₃, s) and one making its way out through perforation (th₄, 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 th₂. 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” appearance 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 lochkovenski* (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 *kozłowskii* 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-*

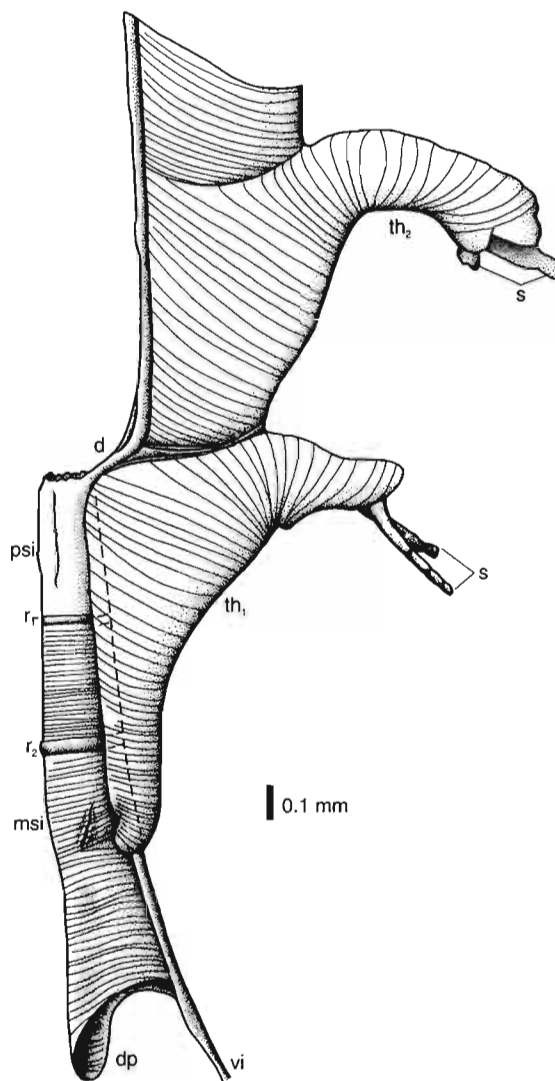


Fig. 13

Monograptus (Uncinatograptus) spineus TSEGELNIUK. 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, $\times 80$.

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 POREBSKA (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 incompleteness 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 heterogeneous 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 al.* 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 conservative 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 attitude 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 assignment 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. lochkovens* lineage. Present in early members (*N. parultimus*–*N. ultimus*), this trait was later lost (*N. lochkovens*). 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. lochkovens*). 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 flattened 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 bifurcate and spinose *priodon-flemingi* group [with *M. (M.) priodon* as the type species]. Further revision will probably expose Wenlock ancestors of *M. (Uncinatograptus)* thus clearing the infrageneric taxonomy of hooked monograptids in general. 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 valleculeus* 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* VESELI-NOVIĆ, 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 Late Silurian and Early Devonian fauna. It is represented by the following subgenera: *Mono-*

graptus (*Uncinograptus*), *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. (Uncinograptus)*] 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 lochkovensensis* PŘIBYL, 1940. TSEGELNJUK's (1988) last proposals to consider *M. parultimus* JAEGER a late survivor of *Ludensograptus*, without any relation to *Pristiograptus lochkovensensis* PŘIBYL, being in his opinion a direct descendant of *Dulebograptus* (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 Homeric–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 assignment 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
<i>Monograptus</i> (<i>Uncinograptus</i>) TSEGELNJUK, 1976	<i>Monograptus uncinatus</i> TULLBERG, 1883
<i>Monograptus</i> (<i>Slovinograptus</i>) subgen. n.	<i>Monograptus balticus</i> TELLER, 1966
<i>Monograptus</i> (<i>Formosograptus</i>) BOUČEK, MIHAJLOVIĆ et VESELINOVIĆ, 1976	<i>Monograptus formosus</i> BOUČEK, 1931
<i>Pristiograptus</i> JAEKEL, 1889	<i>Pristiograptus frequens</i> JAEKEL, 1889
<i>Pseudomonoclimacis</i> MIKHAJLOVA, 1975	<i>Pseudomonoclimacis elegans</i> MIKHAJLOVA, 1975
<i>Istrograptus</i> TSEGELNJUK, 1988	<i>Monograptus transgrediens</i> PERNER, 1899
<i>Neocolonograptus</i> gen. n.	<i>Monograptus lochkovensensis</i> PŘIBYL, 1940

SYSTEMATIC PART

Family **Monograptidae** LAPWORTH, 1873Genus *Monograptus* GEINITZ, 1852Subgenus *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 Slovincians, an ancient Slavic tribe inhabiting Pomerania.

Monograptus (*Slovinograptus*) *hamulosus* (TSEGELNJUK, 1976)

(Pl. 2: 1–6, Fig. 14A, C₁, C₂)

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 th₁ 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. 14A₁, A₂).

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. 14C₁, C₂). 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).

Theca₁ 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, C₃, C₄, 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 *kozłowski* 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 th₁.

Prosicula (psi) with 4–5 indistinct longitudinal threads visible on some specimens is 0.46–0.52 mm long and possesses an apertural ring (r₁). Metasicula (msi) has a length of 1.15–1.30 mm. Its single ring

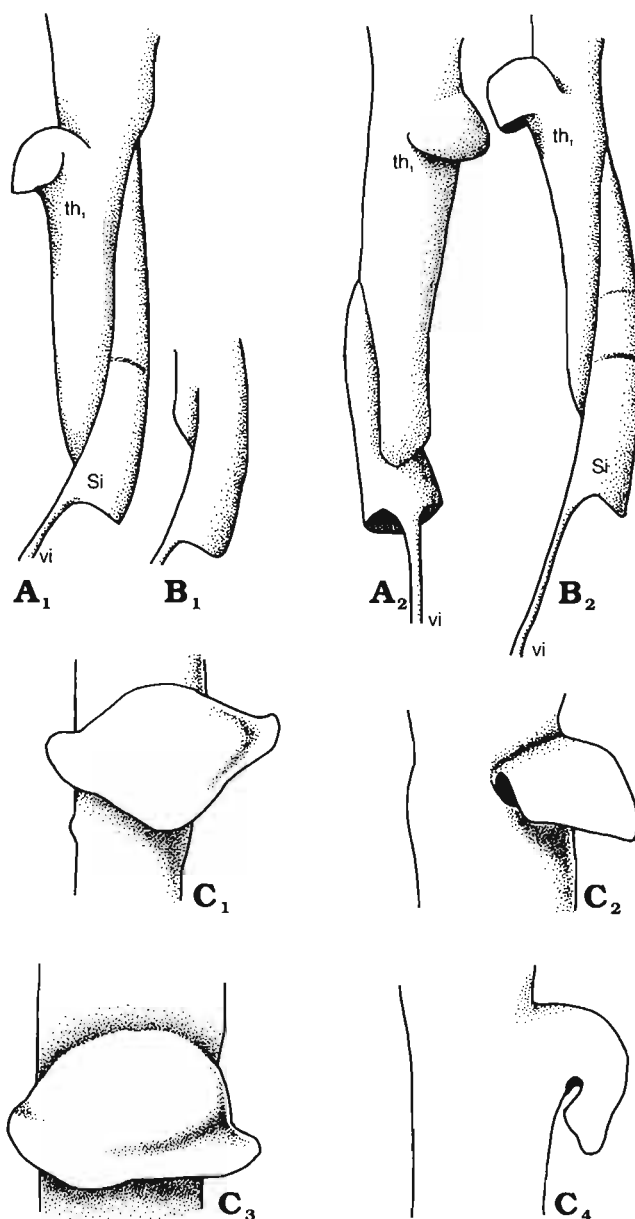


Fig. 14

Diagnostic features of *Monograptus (Slovinograptus) hamulosus* TSEGELNJK (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. 14B₁, B₂). 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 (th₁) 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.

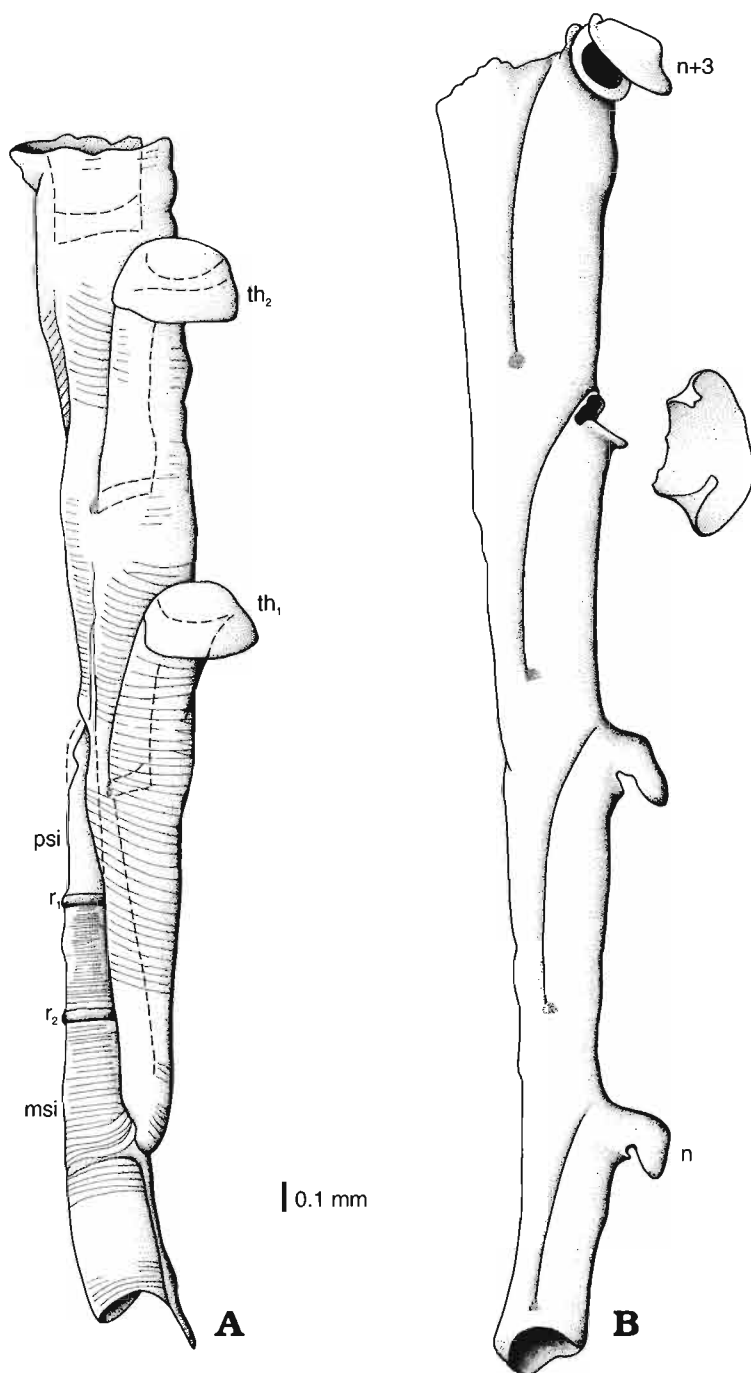


Fig. 15

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, $\times 80$.

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.

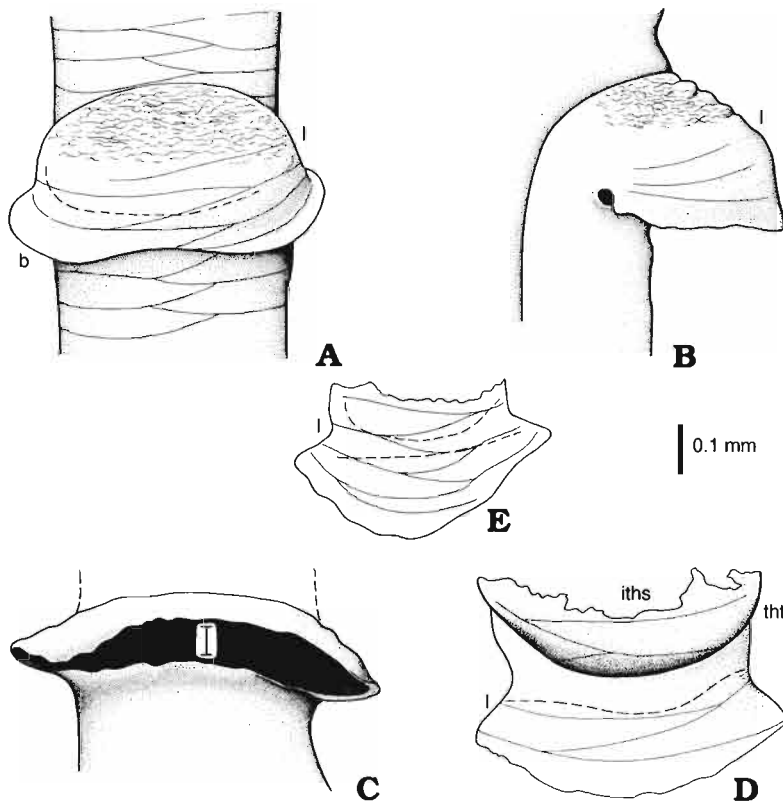


Fig. 16

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

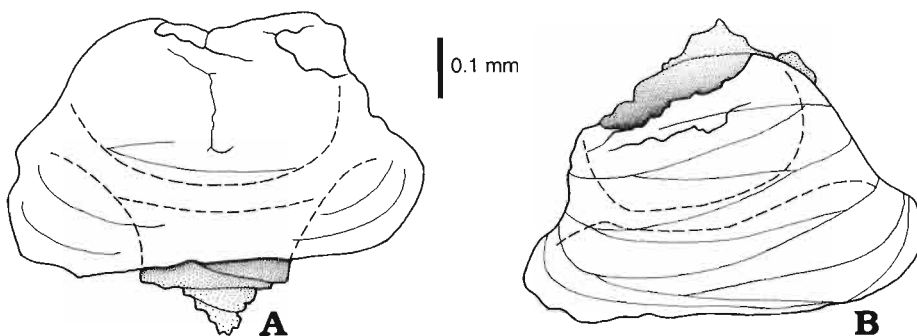


Fig. 17

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.

Stratigraphic distribution. — *M. (S.) balticus* was described by TELLER (1966) from the beds with a poorly characterized assemblage (*Linograptus posthumus*, *Pristiograptus dubius*) in the Ľeba-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 Pageiai 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, Kyrgyzstan (KOREN' unpublished).

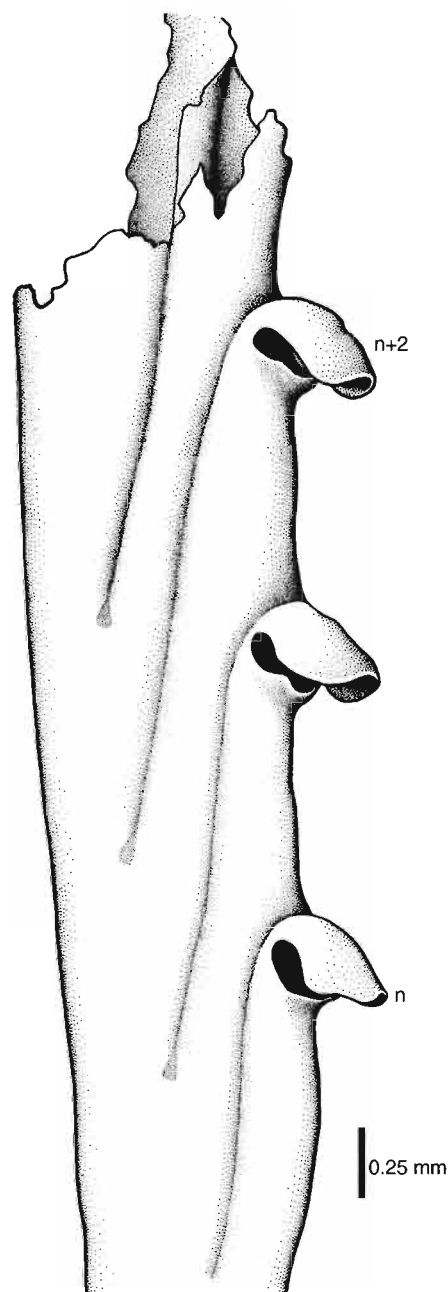


Fig. 18

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

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; PAŠKEVICIUS, 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); TSEGELNIUK, 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, B₁, C). The aperture of the young prosicula without an apertural ring (Fig. 20A₁) which appears at later growth stages (Fig. 20A₂). 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. 20D₂, D₃). 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. 20B₂, D₁, C).

The *th cae*, 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

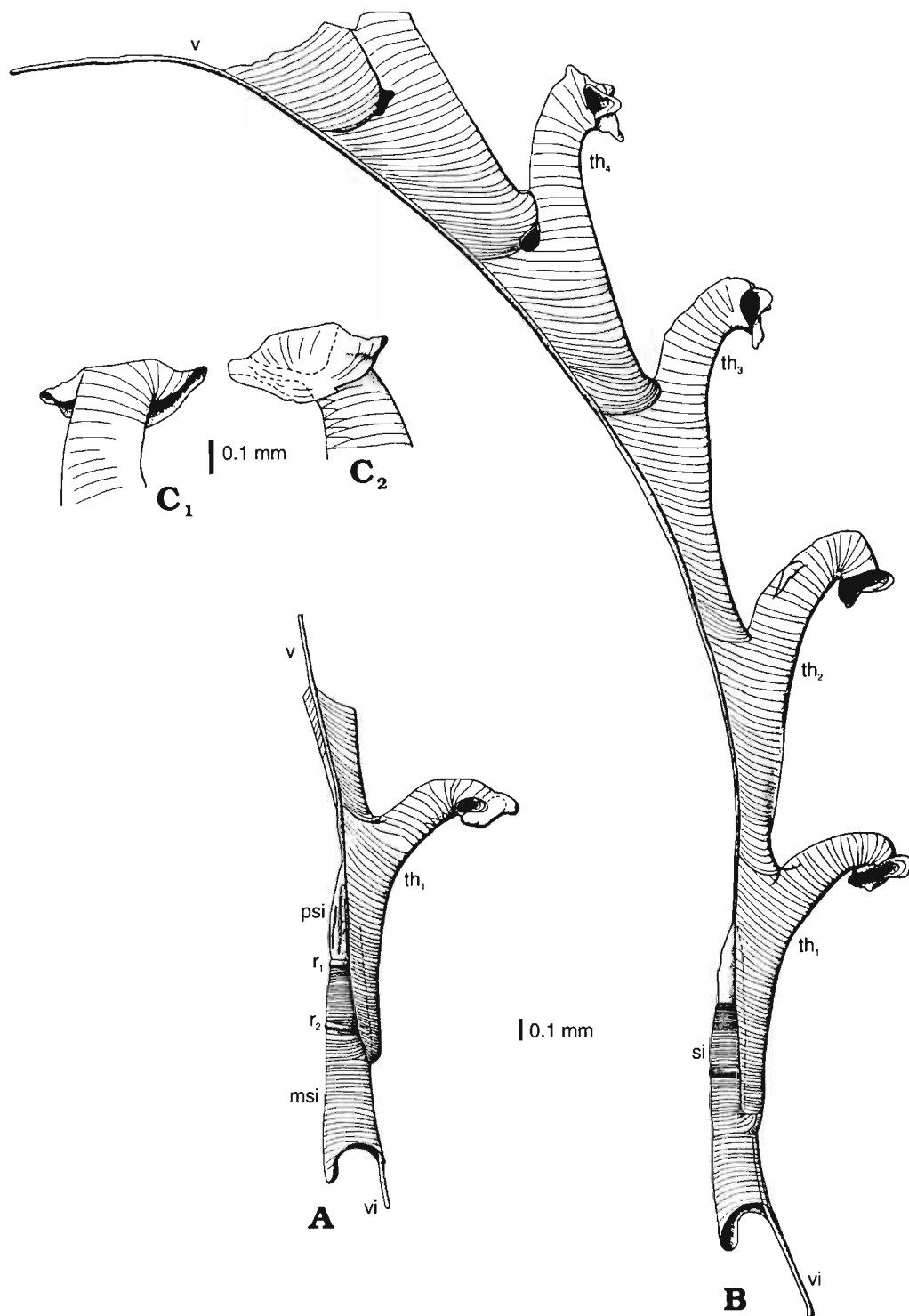


Fig. 19

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 (C₁) and ventrally (C₂). 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

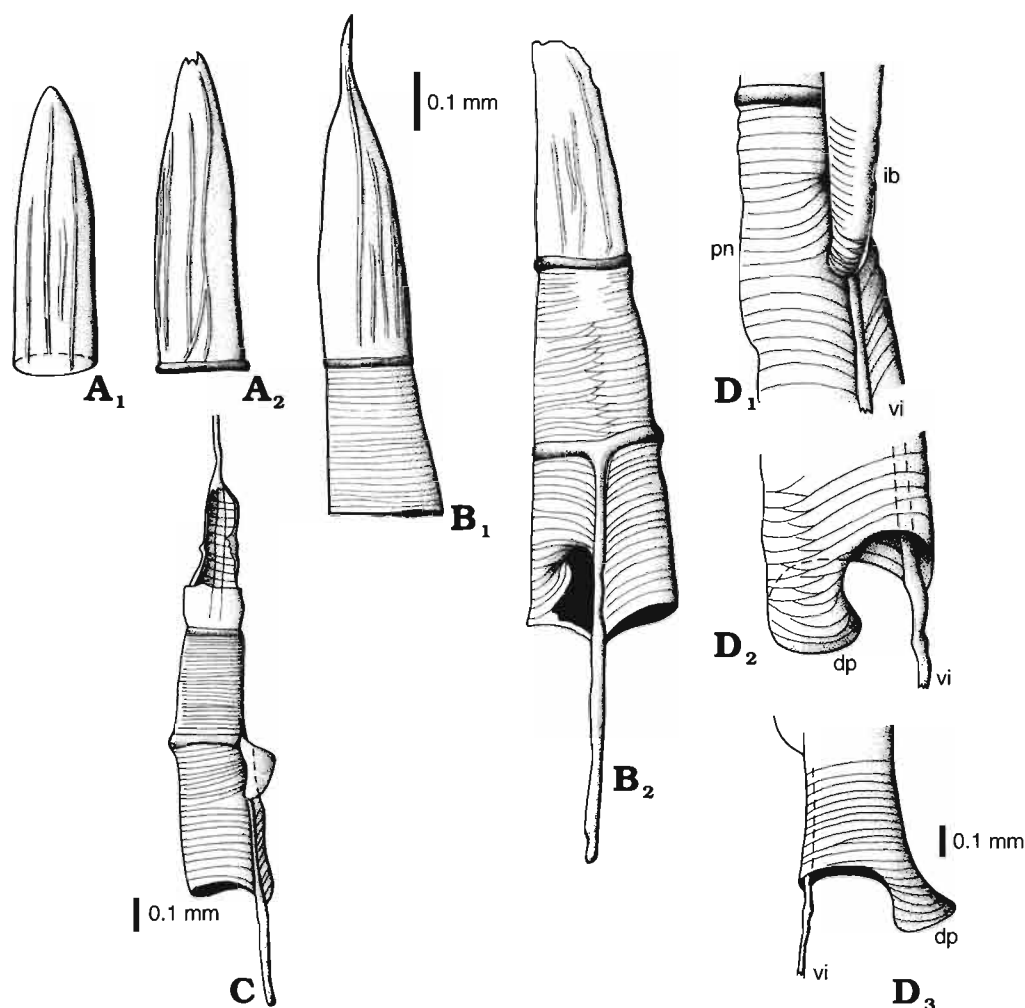


Fig. 20

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 advanced metasicalae; **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 “*formosus* Group” was based on the overall appearance of the rhabdosome of certain forms, defined by the dorsal curvature and hooded thecae (p. 94).

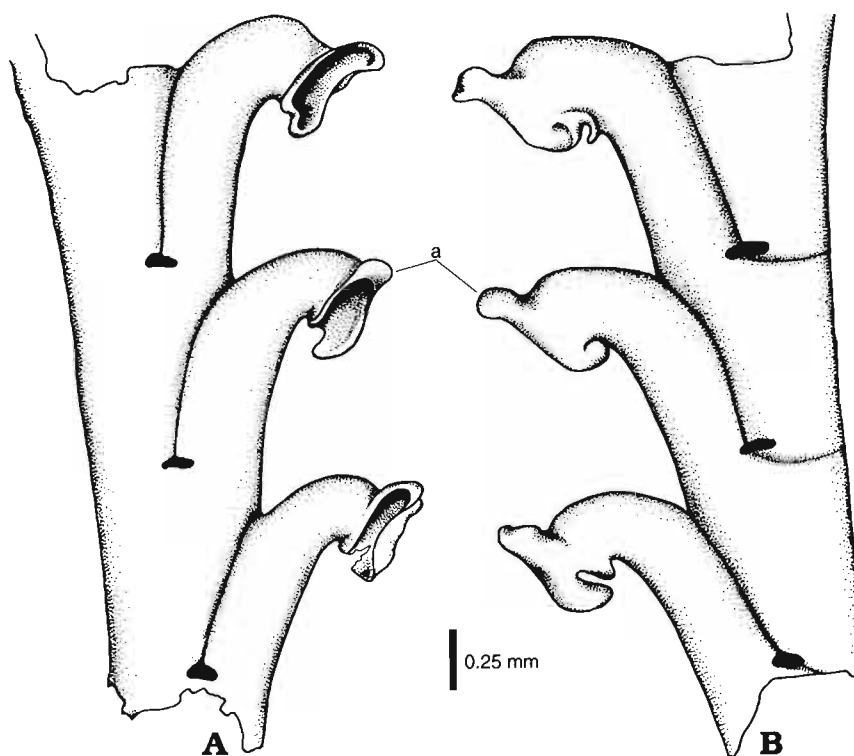


Fig. 21

Monograptus (Formosograptus) formosus (BOUČEK). Distal fragment of the rhabdosome, 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 metascula 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 difficult to interpret. 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).

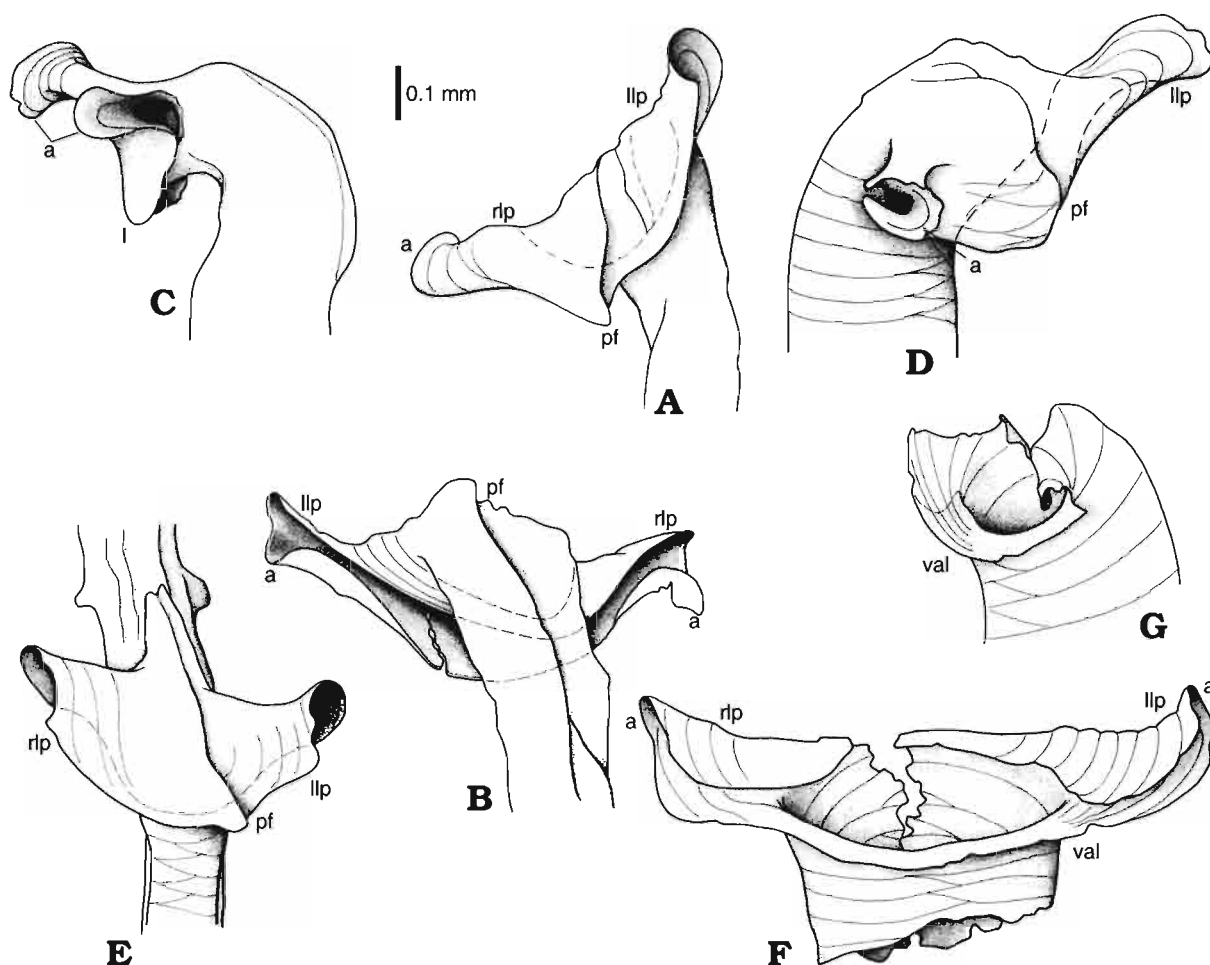


Fig. 22

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 *kozłowskii* 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

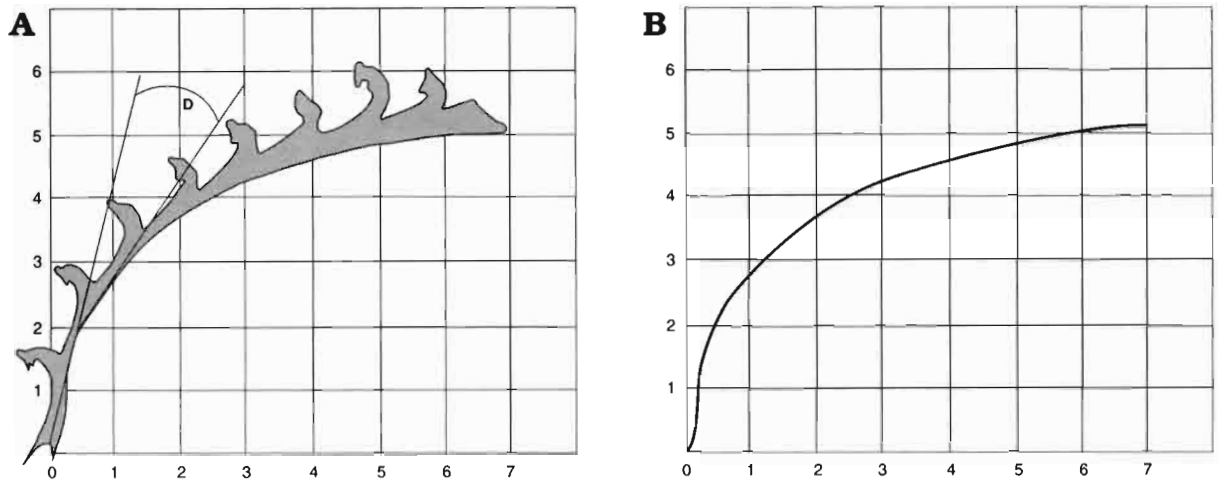


Fig. 23

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.

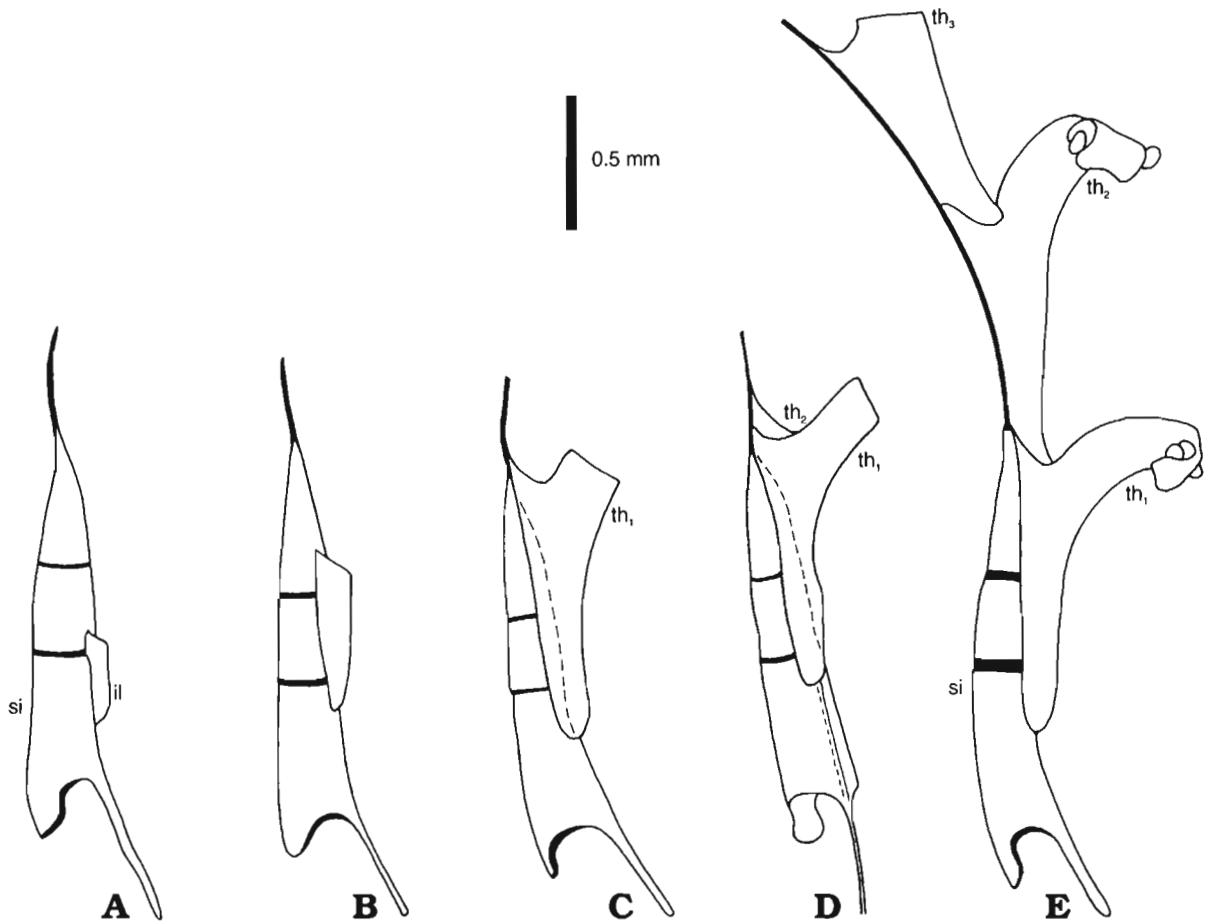


Fig. 24

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.) acer* (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 observed 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 assignment 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

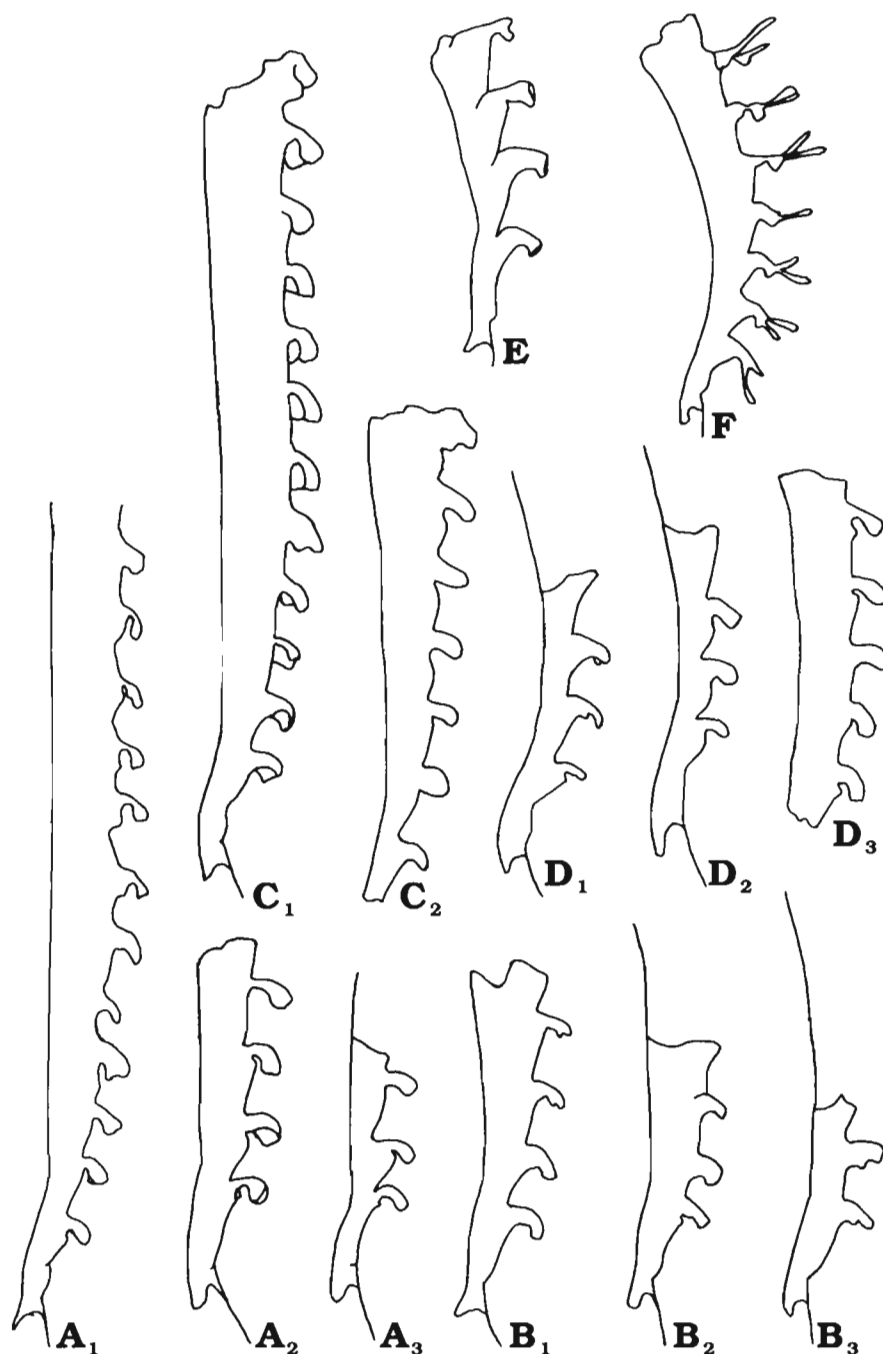


Fig. 25

Change in the degree of the dorsal curvature of the rhabdosome within the *acer-spineus* lineage: **A–C**, *M. (U.) acer acer* (TSEGELNJK), representative specimens from the depth of 792.70 m, 790.90 m and 790.55 m respectively; **D**, *M. (U.) acer aculeatus* (TSEGELNJK), specimens from the depth of 774.50 m; **E**, *M. (U.) protospineus* URBANEK, specimen from depth of 773.50 m; **F**, *M. (U.) spineus* (TSEGELNJK) from the depth of 760.15 m. All specimens from Mielnik-I 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 0.30–0.49 mm long, the total length being

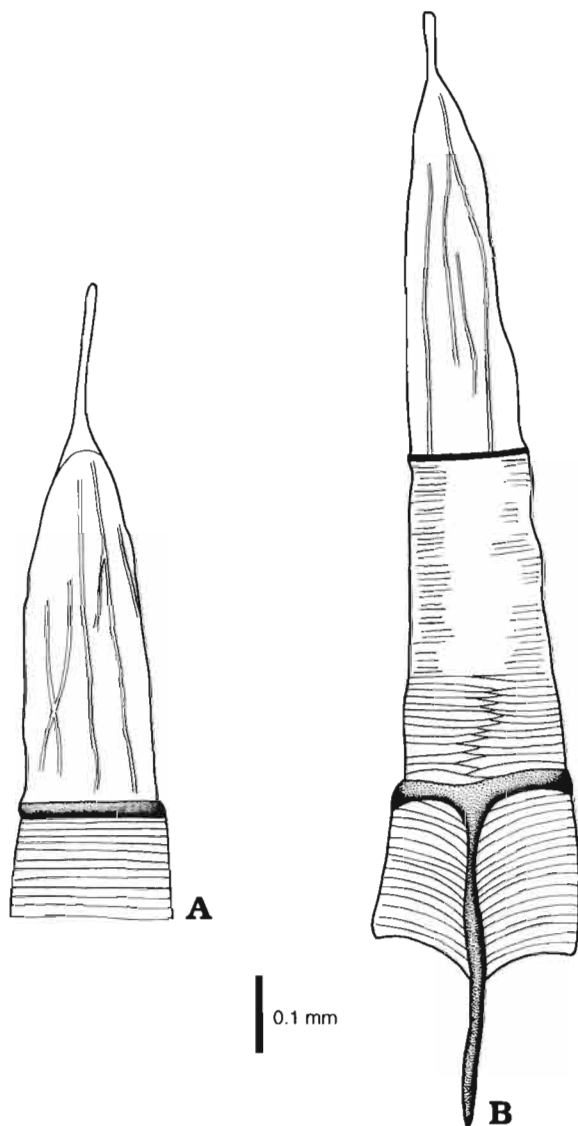


Fig. 26

Monograptus (Uncinatograptus) acer TSEGELNJUK.
Early growth stages of sicle (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 metathaeal 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 forward 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 species-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.

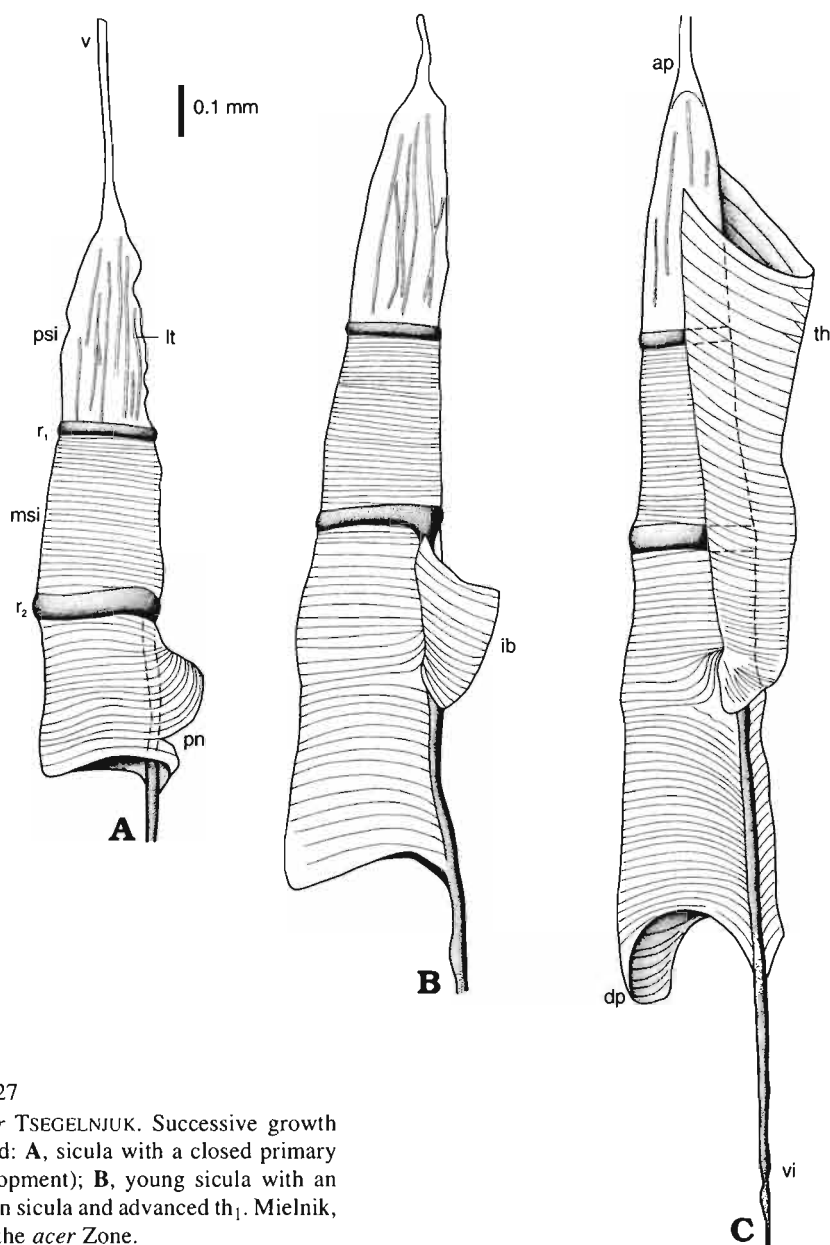


Fig. 27

Monograptus (Uncinatograptus) acer TSEGELNJUK. Successive growth stages of the sical and the initial bud: **A**, sical with a closed primary notch (pn, the lacuna stage of development); **B**, young sical with an incipient initial bud (ib); **C**, fully grown sical 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, C₂), 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 (A₂, C₁).

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).

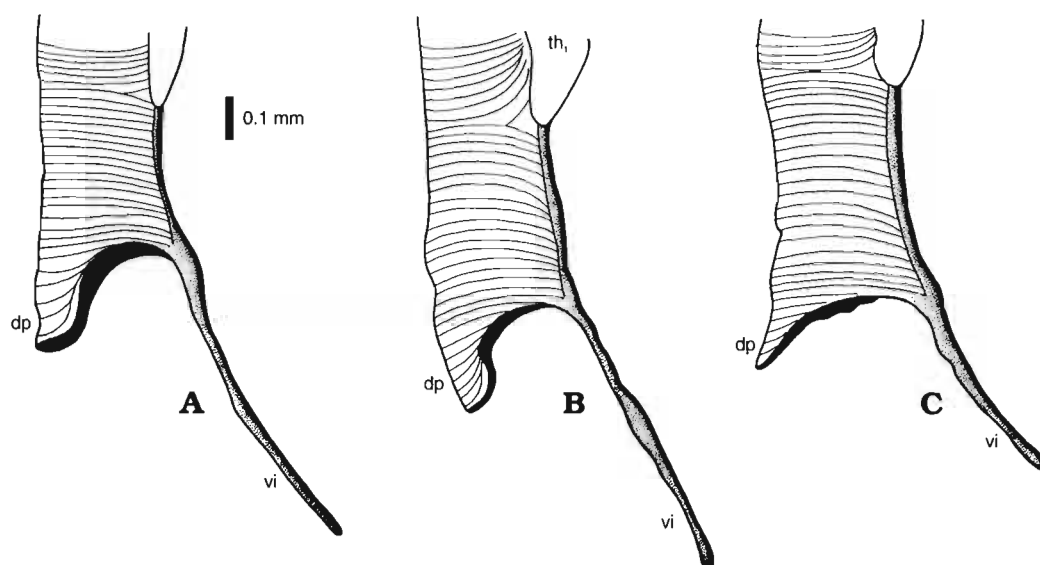


Fig. 28

Monograptus (Uncinatraptus) 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 initiated 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 Pridoli 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. 25A₁–A₃, 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. 25D₁–D₃). 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

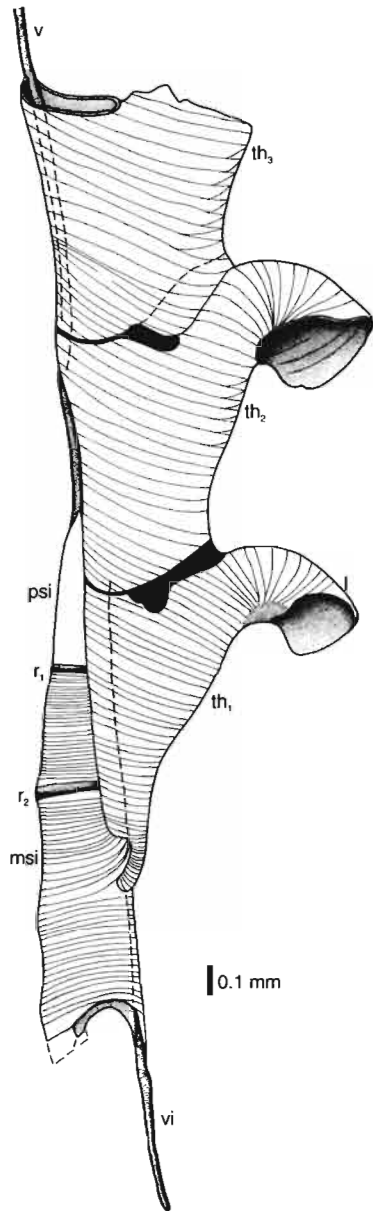


Fig. 29

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

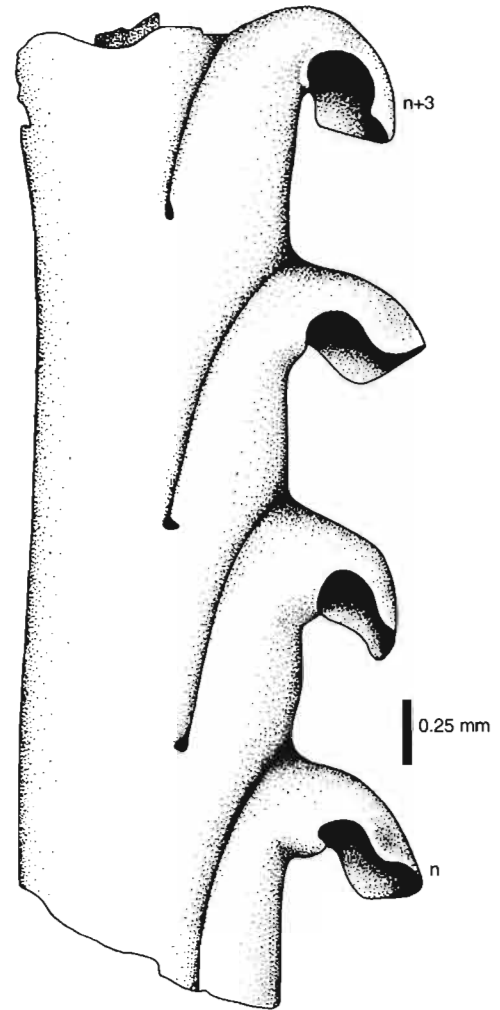


Fig. 30

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 earlier *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, $D < 7^\circ$, (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, $D > 7^\circ$.

In view of a purely quantitative nature of the differences between these subspecies and the presence of numerous transients, the assignment 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

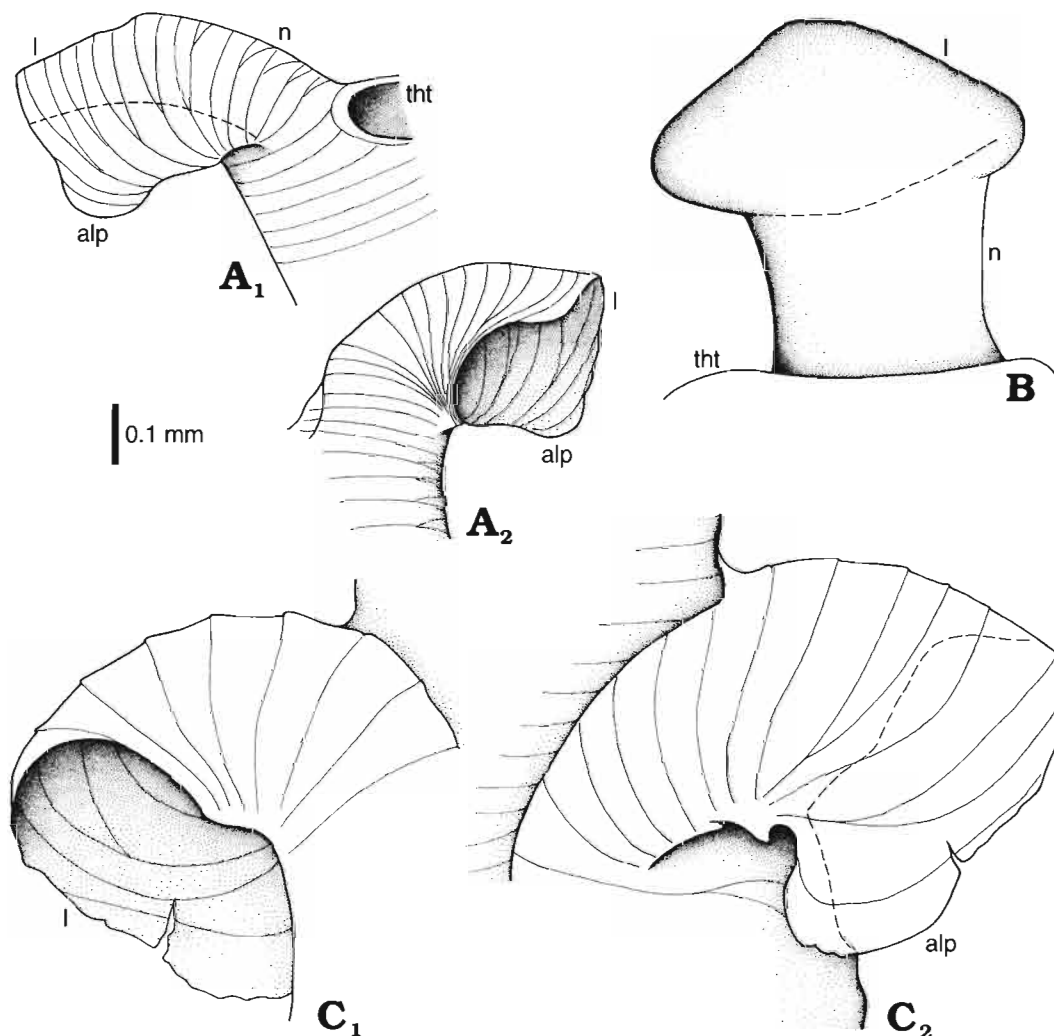


Fig. 31

Monograptus (Uncinatograptus) acer TSEGELNJUK. Thecal morphology and fusellar structure. **A₁**, **A₂**, slightly distorted aperture of *th₁* 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 disappearance 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-occurring 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).

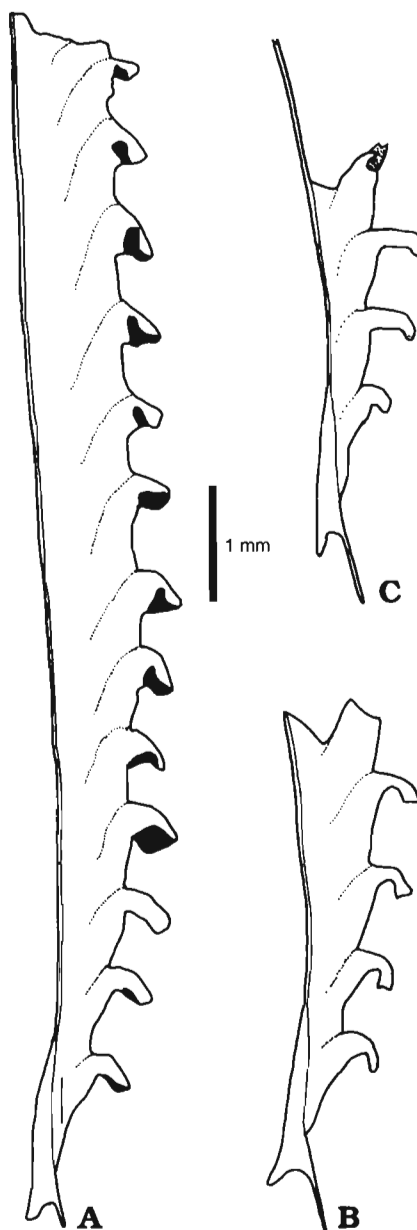


Fig. 32

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

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

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

1995. *Monograptus (Uncinograptus) 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.

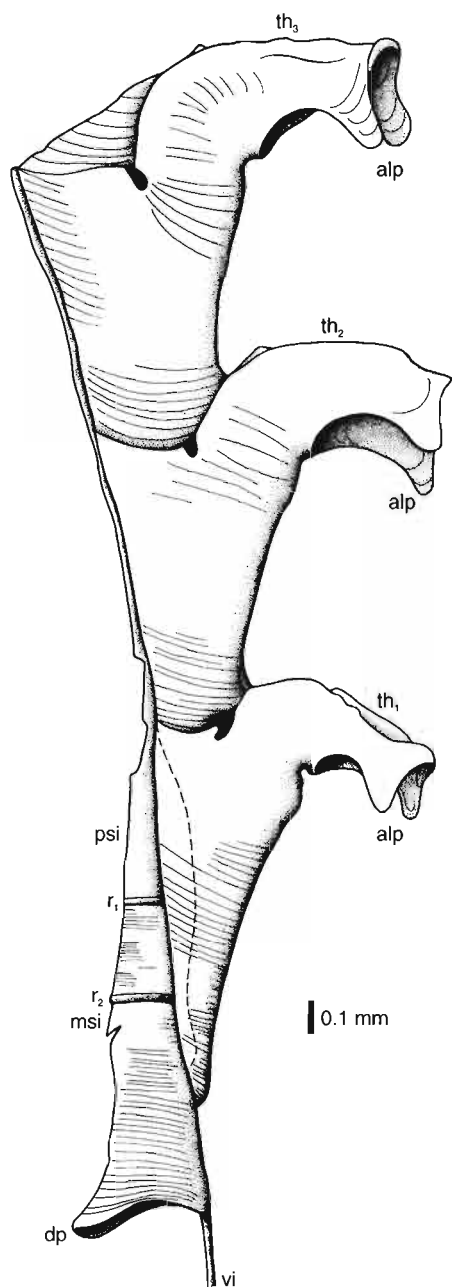


Fig. 33

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. 34B₂). 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 $D=12^\circ$. 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 occurrence 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 occurrence (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.

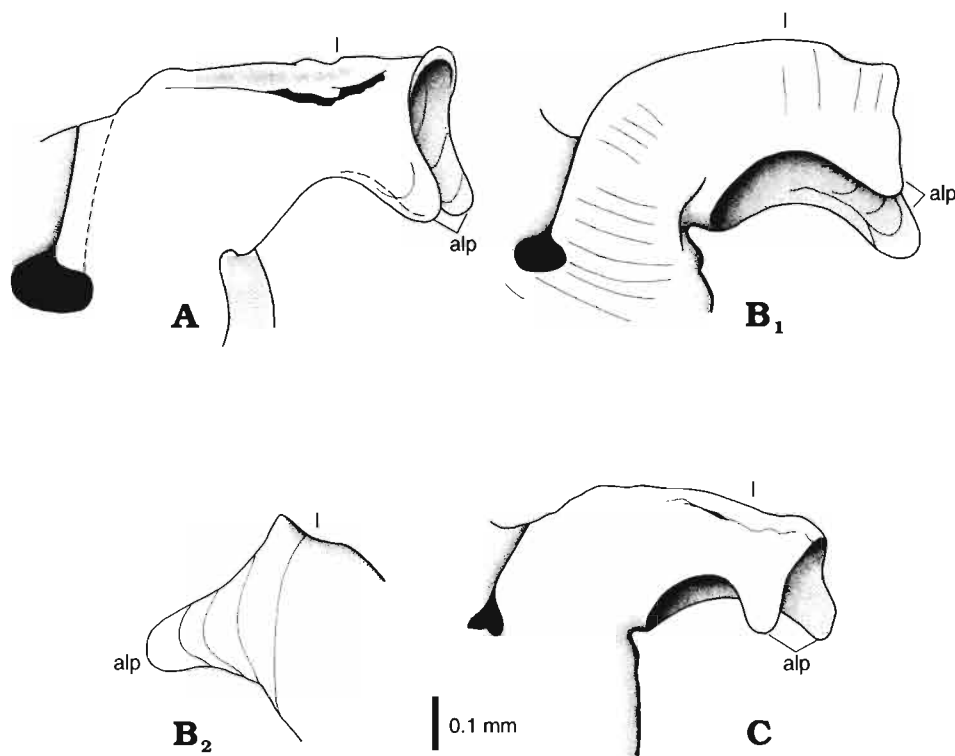


Fig. 34

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.

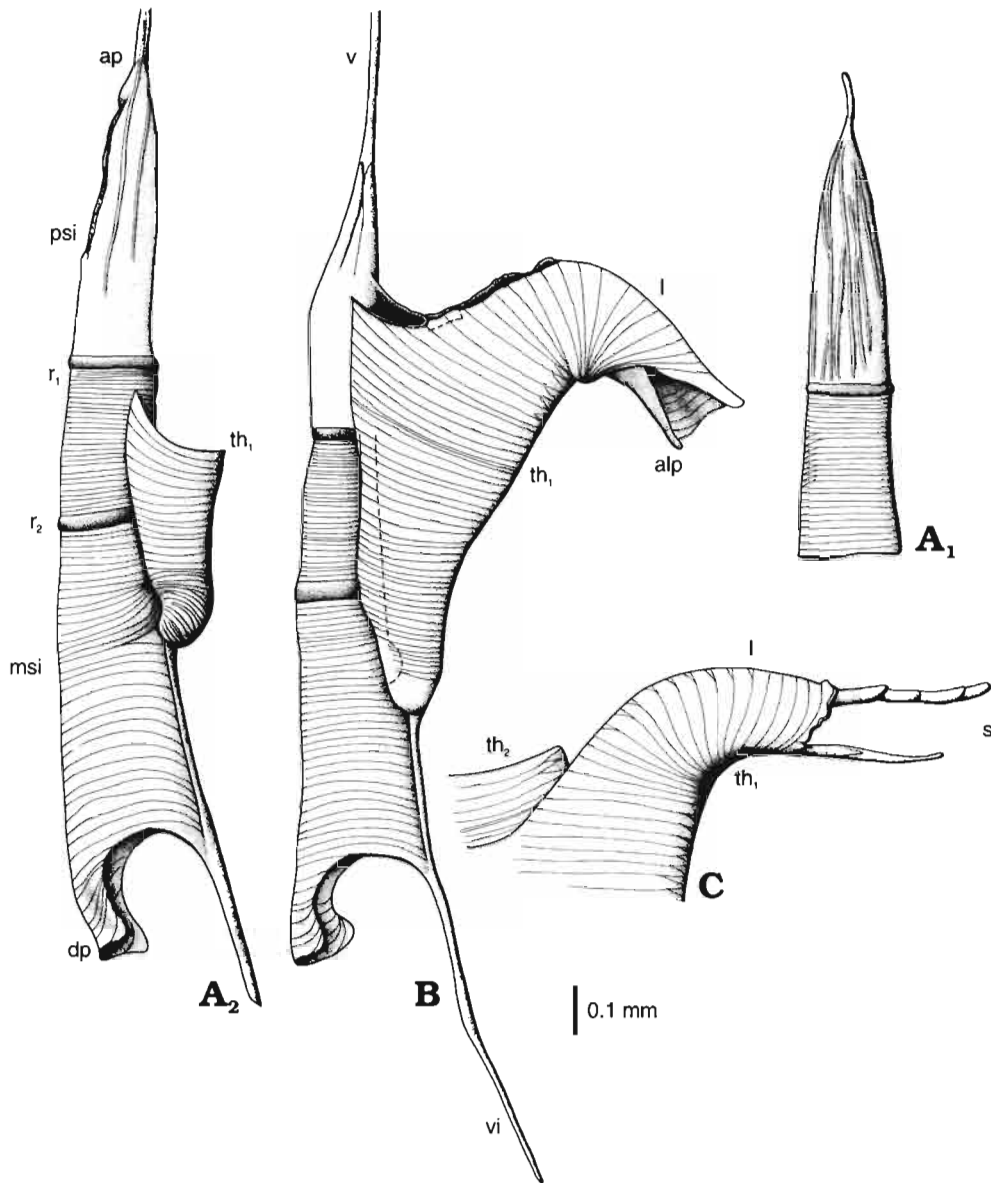


Fig. 35

Monograptus (Uncinatograptus) spineus TSEGELNIUK. 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: 1, 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. 38C₁, p) or angular and pointed (Fig. 38C₂, 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).

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 homologous 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 magnificent 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 Přídolí. Therefore the concept of a conventional *spineus* Zone is preferred in this paper.

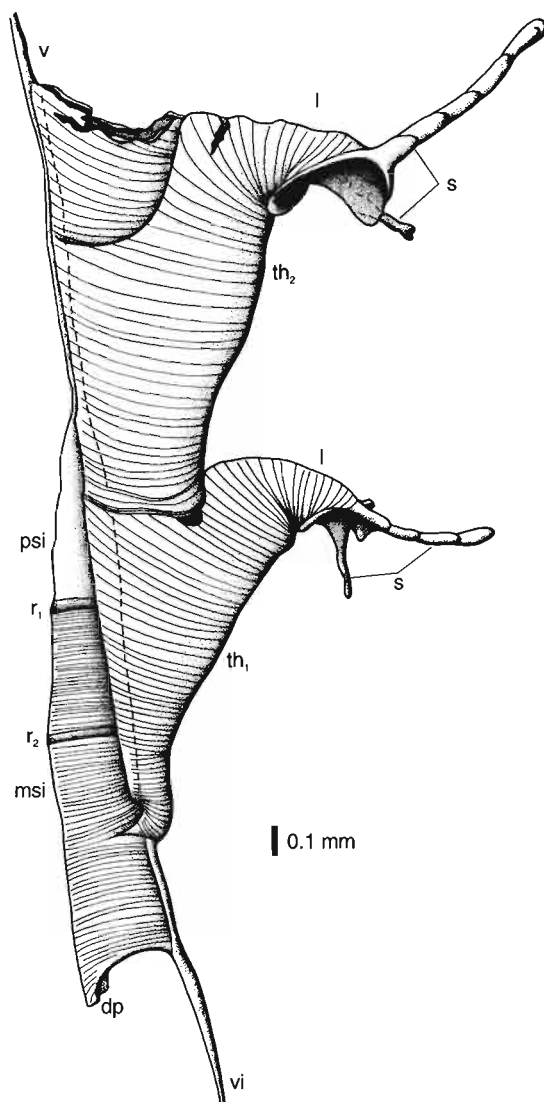


Fig. 36

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

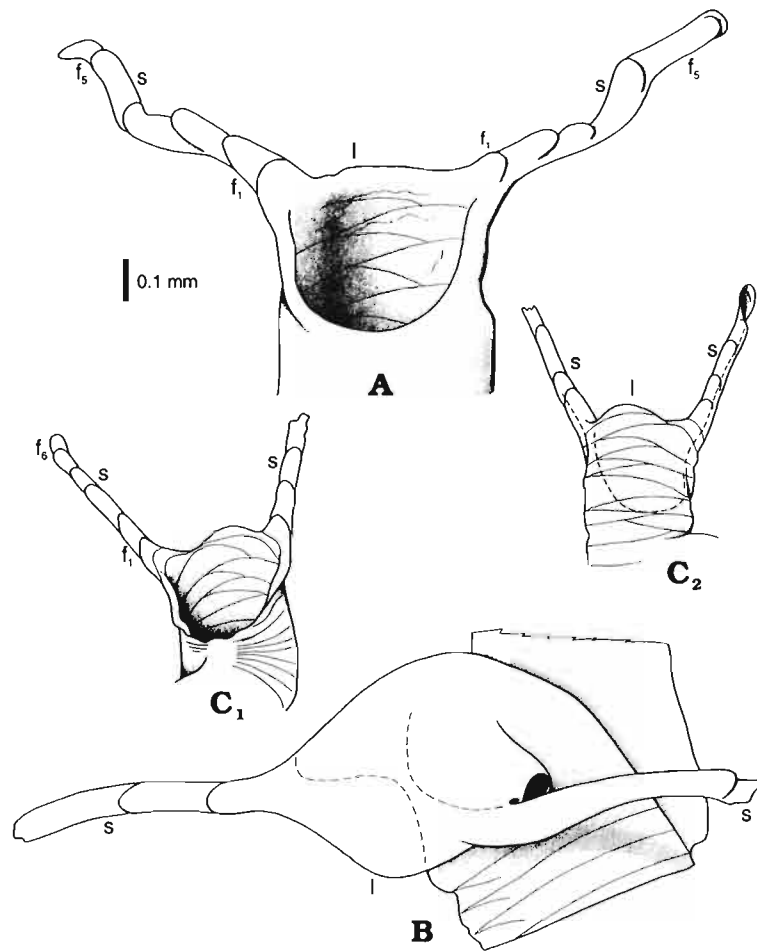


Fig. 37

Monograptus (Uncinatograptus) spineus (TSEGELNIUK). 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; **C₁**, **C₂**, apertural lobe of a proximal theca, ventral and dorsal views. Mielnik, depth 760.15 m, the *spineus* Zone.

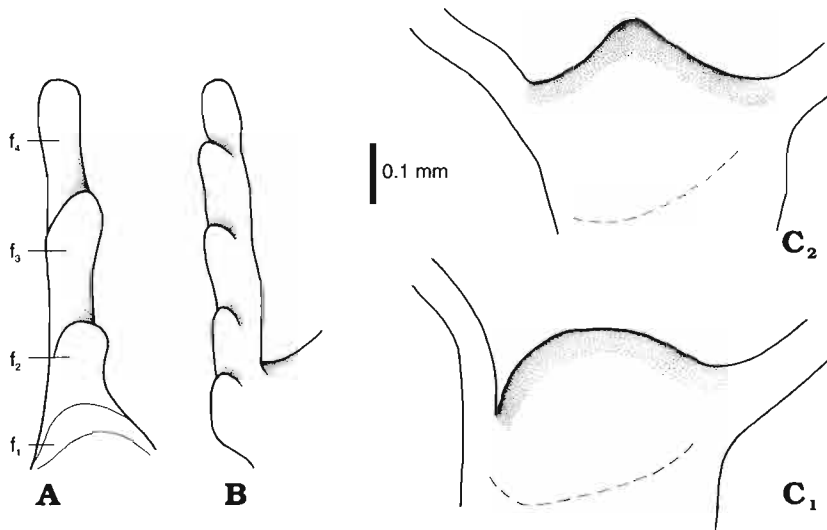


Fig. 38

Monograptus (Uncinatograptus) spineus (TSEGELNIUK). Fusellar structure of the apertural spine (**A**, **B**) and variation in the shape of the promontorium (**C₁**, **C₂**) in two adjacent thecae (n , $n+1$). Mielnik, depth 760.15 m, the *spineus* Zone.

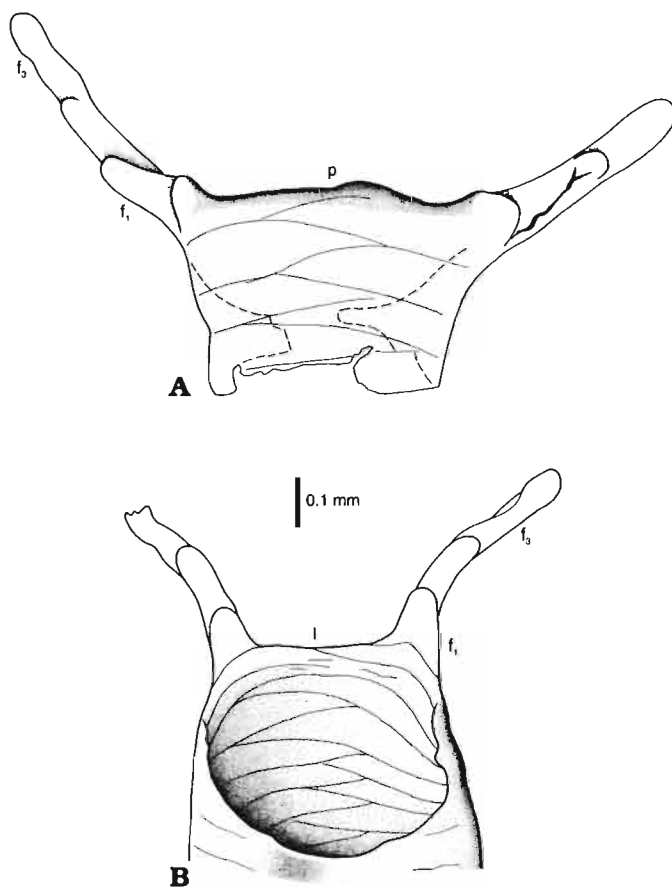


Fig. 39

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.

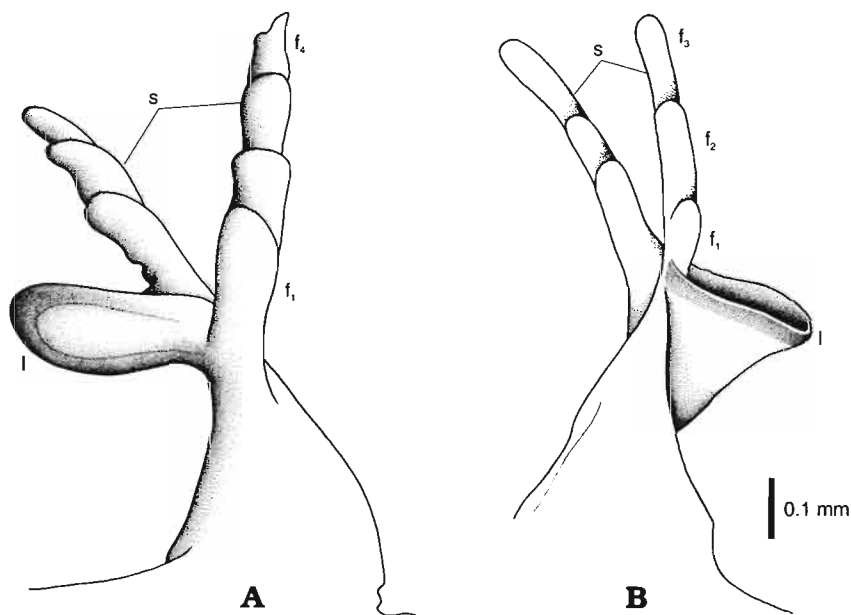


Fig. 40

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.

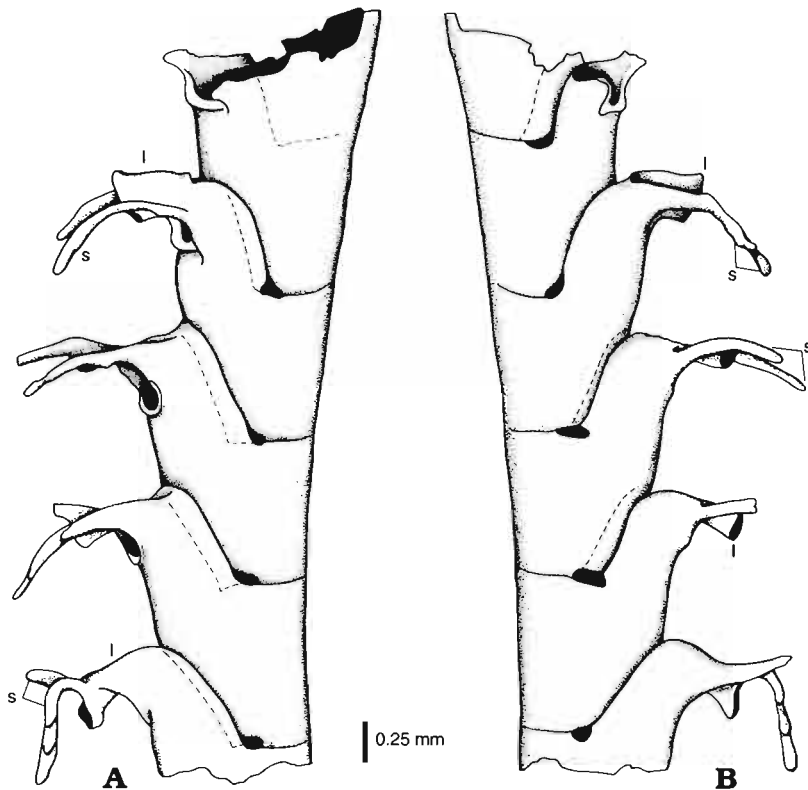


Fig. 41

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). Remaining 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

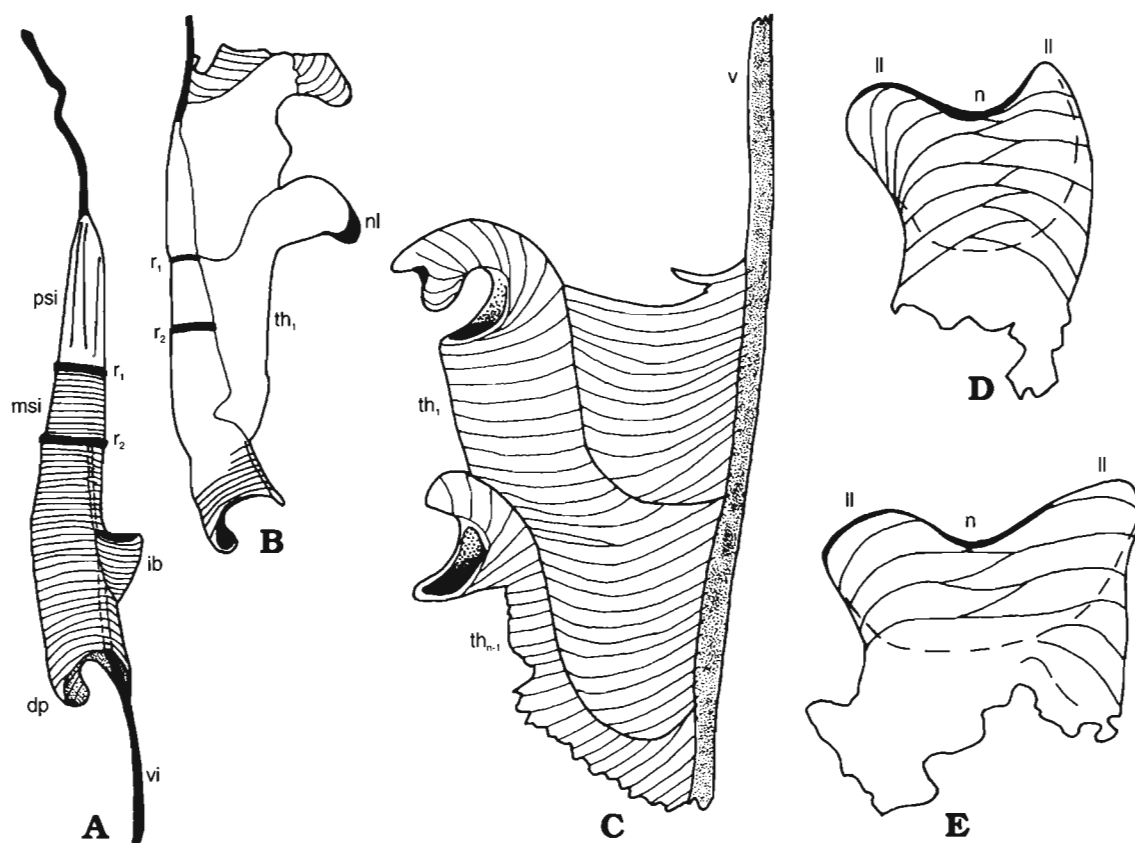


Fig. 42

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) trimorphus* 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 apertural 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 lochkovens* 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 uncinograptids 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 *Dulebograptus*-like phenodeviants in *N. lochkovens* 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. lochkovens*. The former also exhibits the presence of two black rings on the sicula, whereas the porus ring characteristic of the siculae in *N. lochkovens* 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*–*lochkovens* lineage.

Also KOREN' and LYTOCHKIN (1992) interpreted these species as a single evolutionary line. In view of this evidence, TSEGELNJUK's idea on separating *lochkovens* 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. lochkovens* 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 tentatively as cf. *frequens*.

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

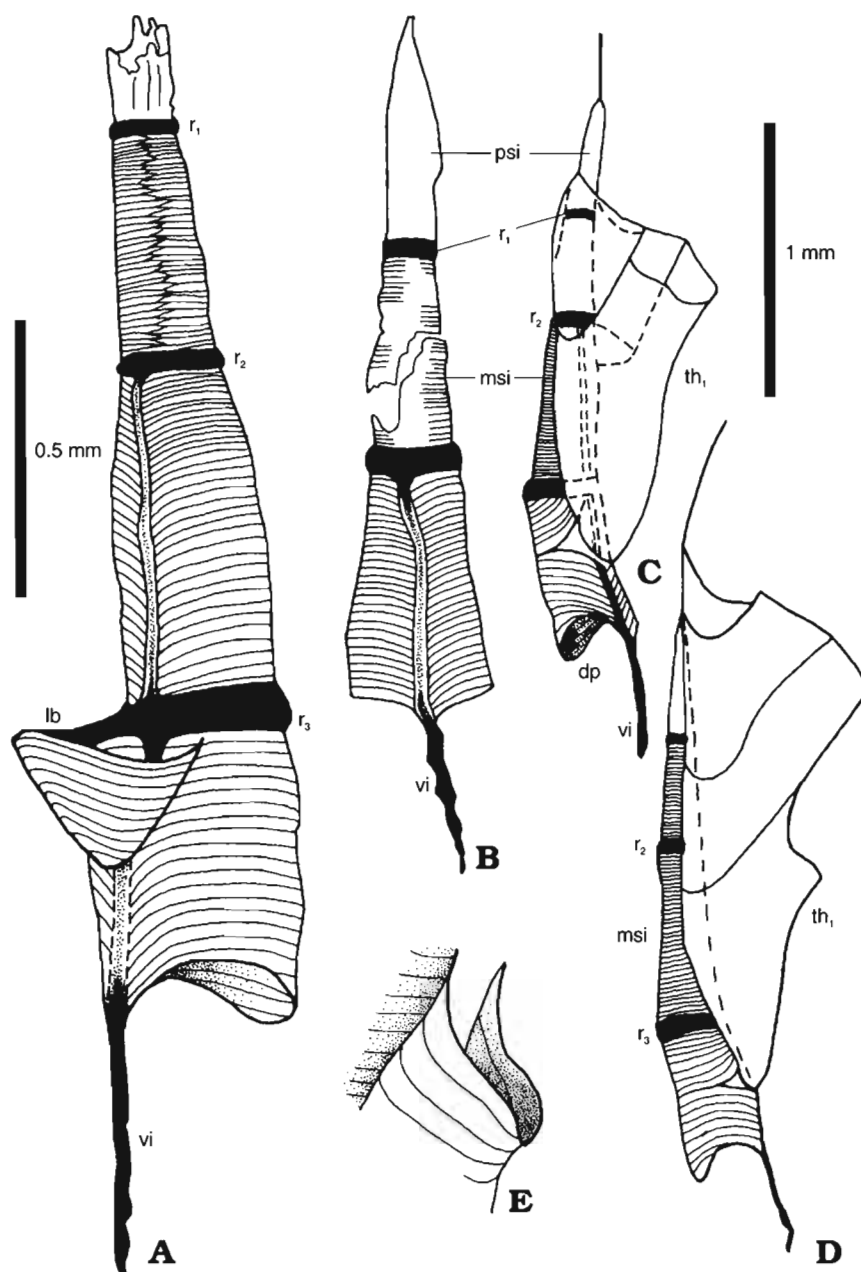


Fig. 43

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, ingresson 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 substantiation 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 *kozłowskii* 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 metasacula, and r_3 placed close to the primary notch area (Fig. 43A, C, D). The significance of this condition is discussed 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. 11–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.

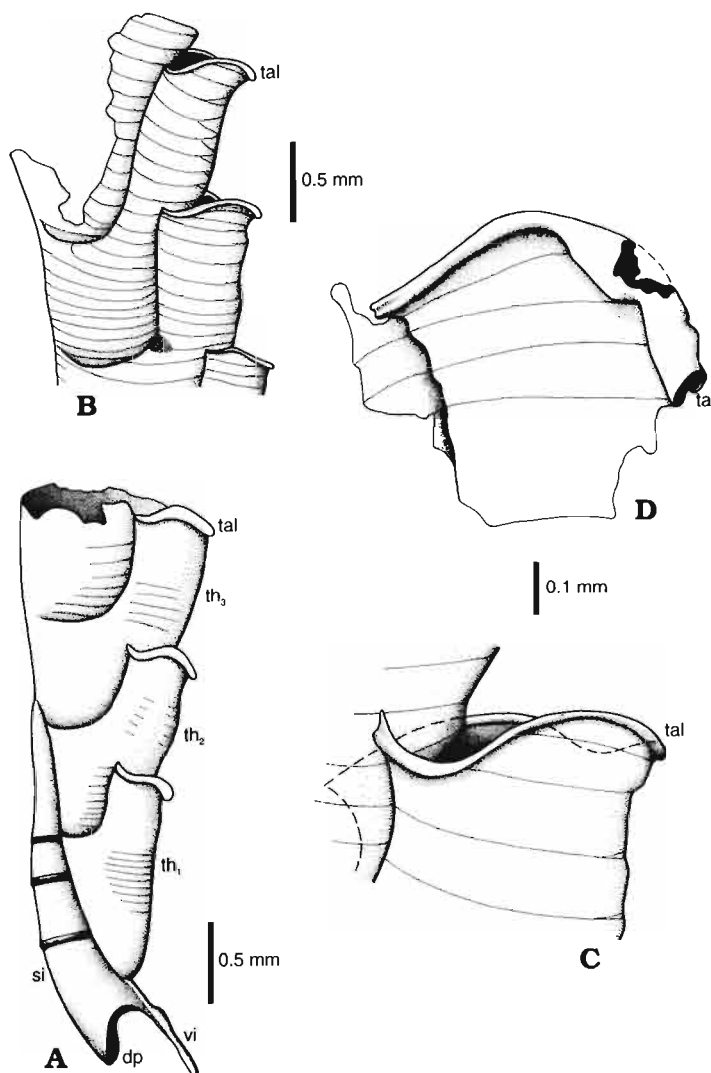


Fig. 44

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 metasacula (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 ingress 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 their upper parts,

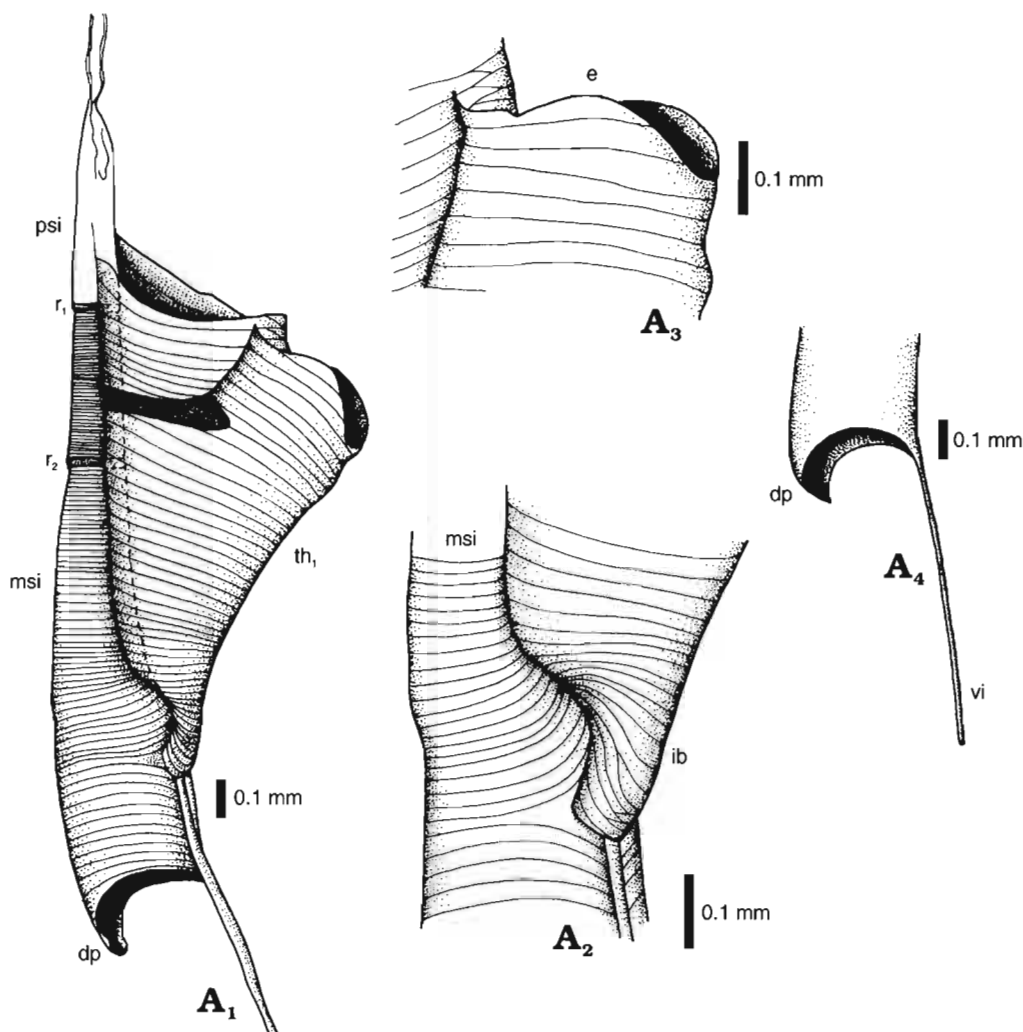


Fig. 45

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 Velký vrch Hill near Koneprusy (Barrandian, Central Bohemia) as well as on some additional material from this locality made available 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 Kopani-na Formation by PŘIBYL (1983: p. 154) is an equivalent of the *latilobus/balticus* Zone as defined above.

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 incompleteness 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.

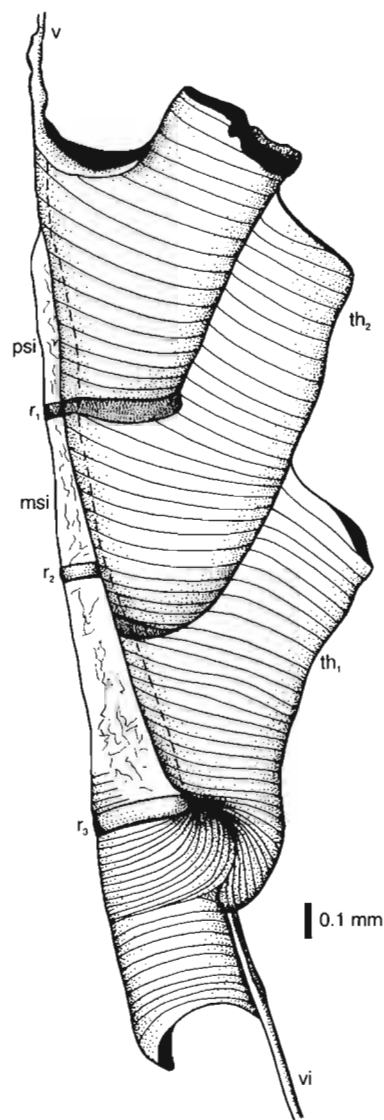


Fig. 46

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

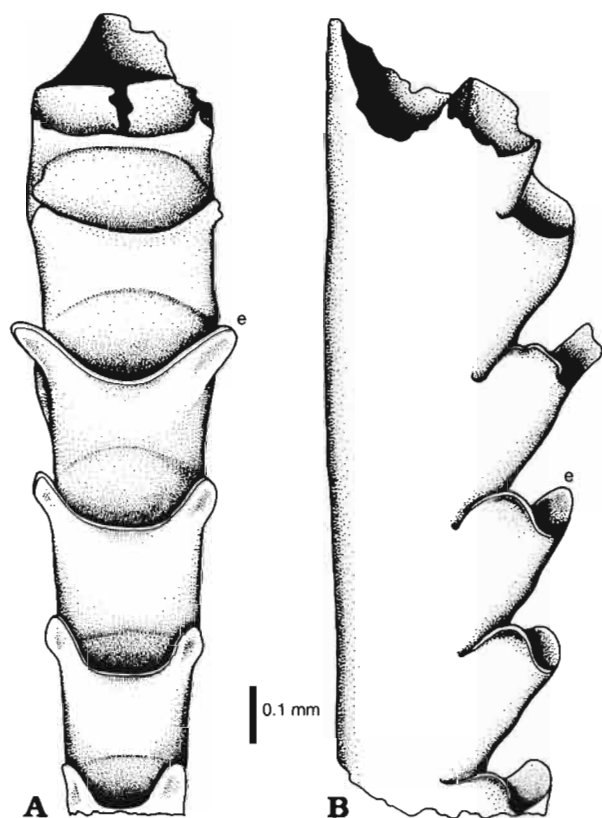


Fig. 47

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 assignment of *Pseud. latilobus* to TSEGELNJUK's (1978) genus *Ludensograptus* unjustified. Also PŘIBYL's (1983) assignment of this species to *Colono-graptus* 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 ingress of a new, late Ludfordian graptoloid fauna, after the *kozłowskii* 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 (Colono-graptus) 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 the 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 distance of 0.25–0.30 mm from the apertural margin of the metasicula.

The *theca* 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 morphotype 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 *transgrediens* 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 = *Neocolonograptus 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 assignment 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 hypothesize 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 hypothesize 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*

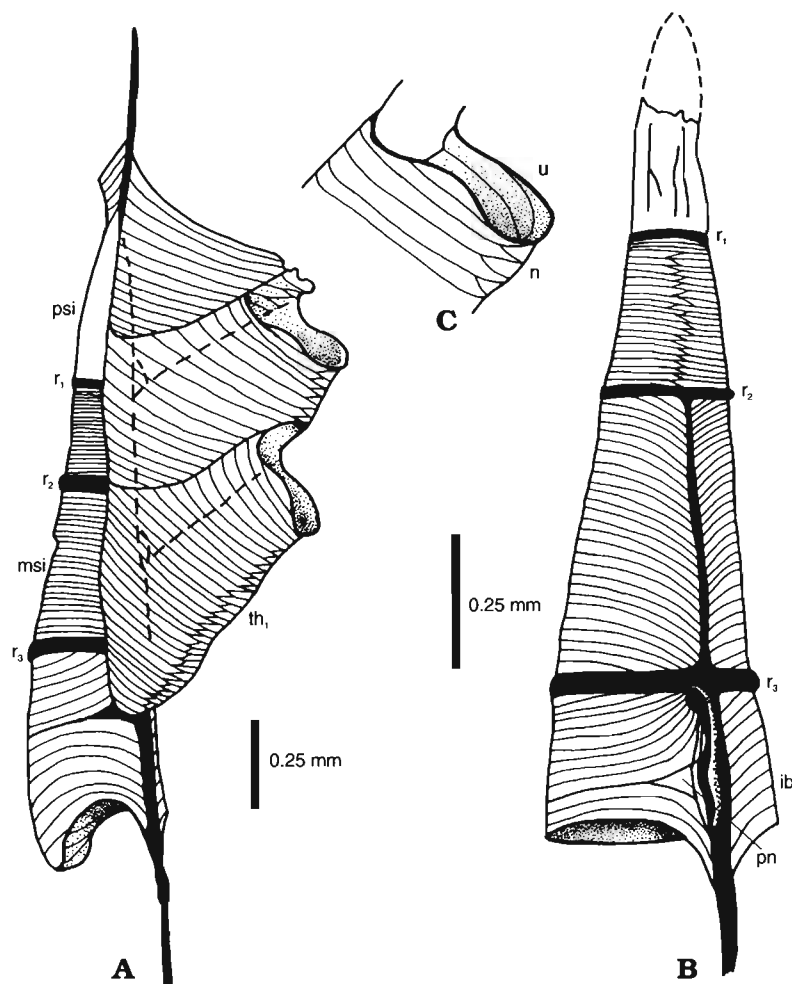


Fig. 48

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 pronounced 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 (assignment 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, TSEGELNJK's (1978, 1988) suggestion to identify the advanced morphotypes found by JAEGER (1986: e.g. fig. 37a) within the *ultimus* populations as a separate morphospecies (*Skalograptus vetus*), intermediate in characteristics between the centrotypes of *ultimus* and true *lochkovensis*, seems unnecessary. It misinterprets 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. lochkovenssis*. 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. lochkovenssis*". 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. lochkovenssis*.

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 *lochkovenssis*) 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. lochkovenssis* should be maintained in a broad sense. Besides, it is morphologically intermediate between *N. ultimus* and *N. lochkov. lochkovenssis*, 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. lochkovenssis* 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. lochkovenssis*". 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. lochkovenssis 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. lochkovenssis* both in Barrandian (JAEGER 1986) and in the Mielnik-1 section.

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

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

1940. *Monograptus (Pristiograptus) lochkovenssis* 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 lochkovenssis* (PŘIBYL); JAEGER, p. 324, text-fig. 3A–C.

1986. *Monograptus lochkovenssis* (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 metasaccula, 1.80 mm, without it. *Metasaccula* 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

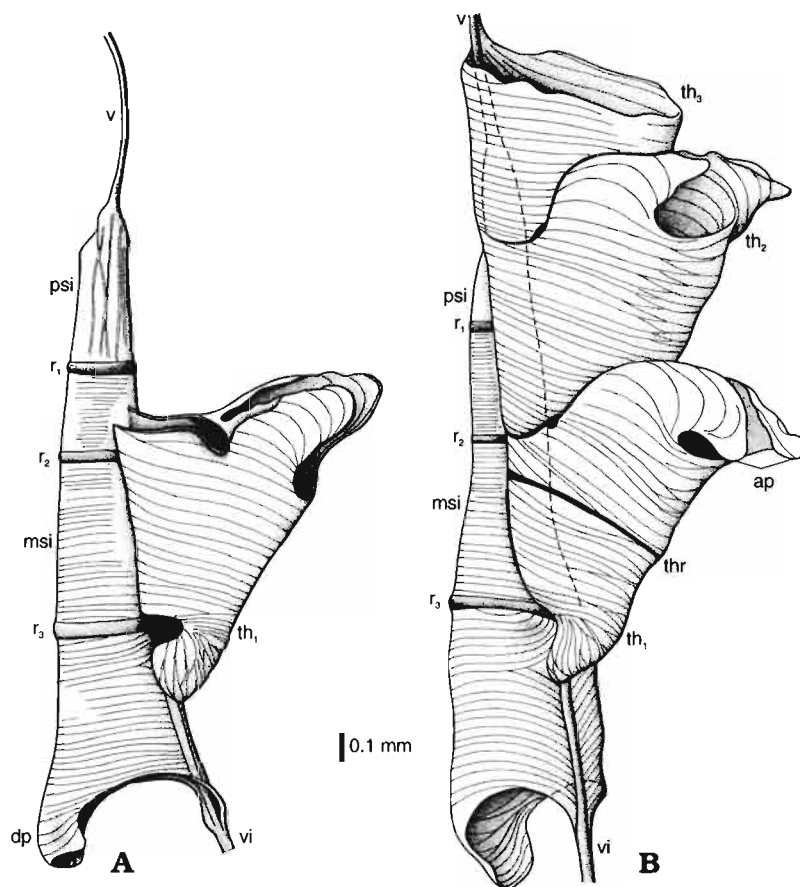


Fig. 49

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

ventrally. Margins of the aperture are frequently bordered by a thickened rim (Pl. 24: 1a). Apex of the sical is situated immediately below or at the level of the th_2 aperture.

Bleached early growth stages of the sical reveal a regular monograptid pattern of development. Pro-sical, 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 meta-sical 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 sical 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). Metasical 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 inherited 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

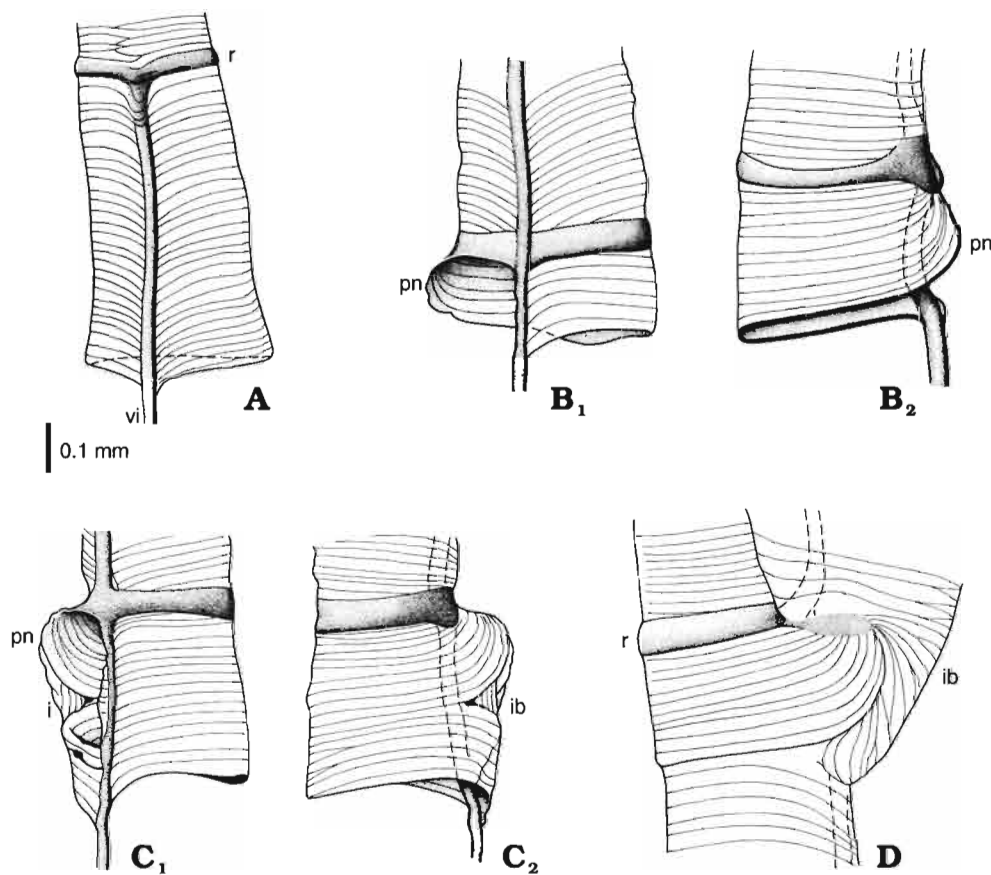


Fig. 50

Neocolonograptus lochkovensensis lochkovensensis (PŘIBYL). Growth stages of metasicula: onset of virgella (A), formation of the open primary notch ("sinus" stage) seen ventrally and laterally (B₁, B₂), closed primary notch ("lacuna" stage, C₁, C₂), fusellar structure of the initial bud (D). Mielnik, depth 665.60–644.00 m, *lochkovensensis* 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. lochkovensensis lochkovensensis* 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.

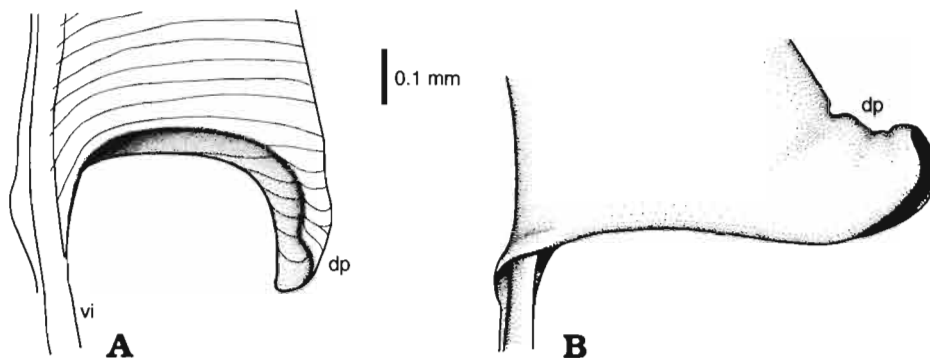


Fig. 51

Neocolonograptus lochkovensii lochkovensii (PŘIBYL). Normal (A) and aberrant (B) shape of the aperture in metasicula. Mielnik, depth 659.30 m, *lochkovensii* Zone.

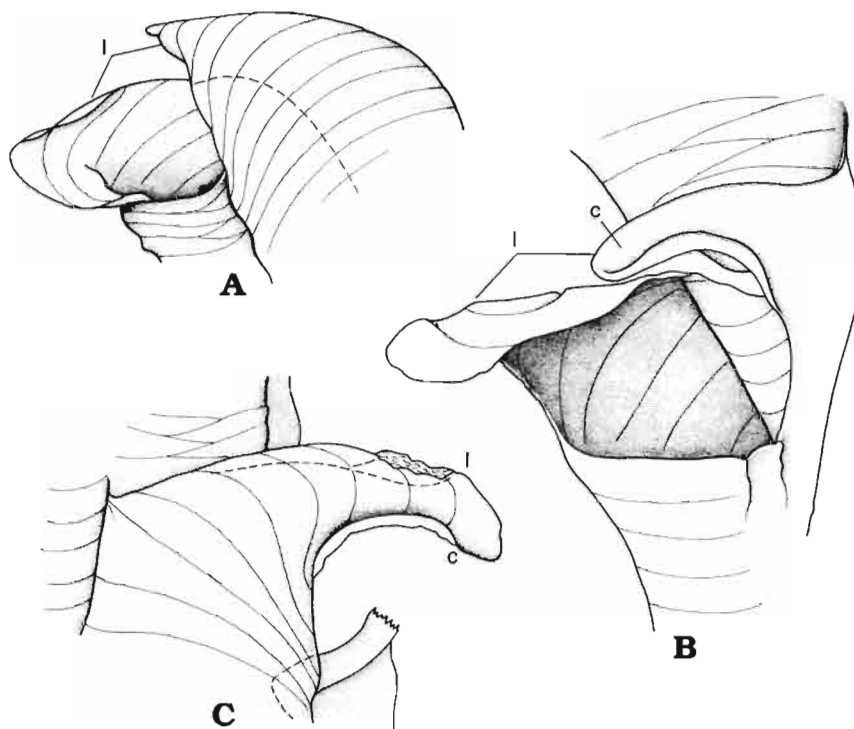


Fig. 52

Neocolonograptus lochkovensii lochkovensii (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, *lochkovensii* 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. lochkovensii lochkovensii* 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. lochkovensii 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 *lochkovensii* group. Advanced morphotypes of *N. ultimus* (such as that figured

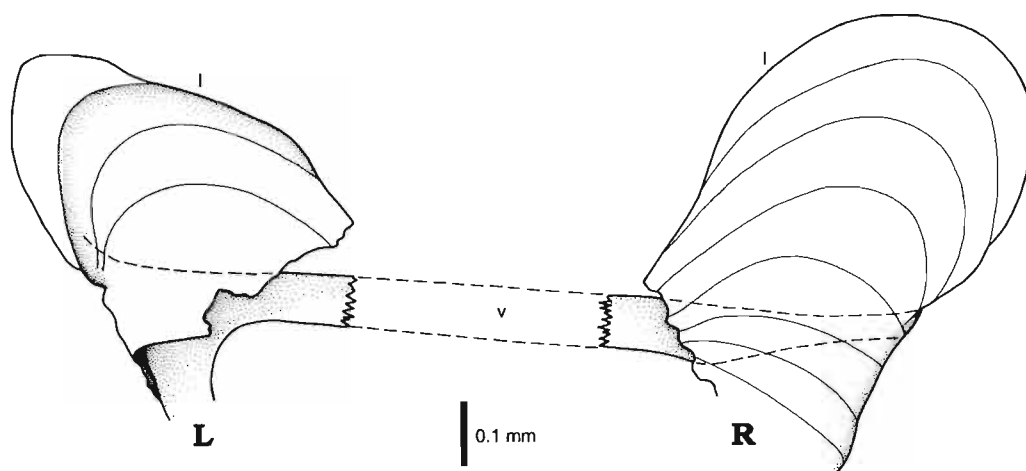


Fig. 53

Neocolonograptus lochkovensisi lochkovensisi (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, *lochkovensisi* Zone.

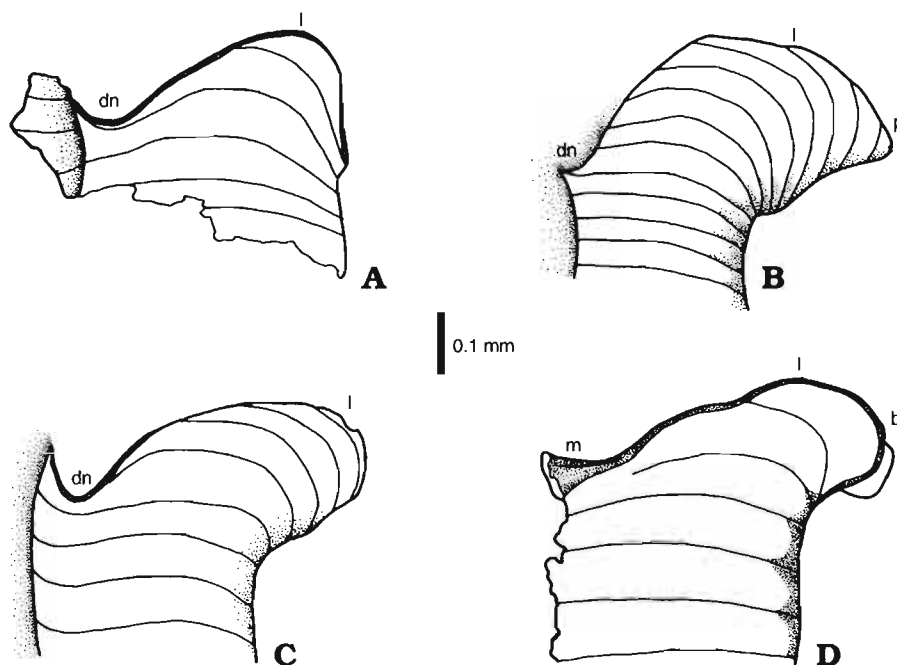


Fig. 54

Neocolonograptus lochkovensisi lochkovensisi (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, *lochkovensisi* Zone.

by JAEGER 1986: fig. 37a and c), exhibit an almost *lochkovensisi* 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 *lochkovensisi* in the size and orientation of the lobes. Such traits are truly “proterogenetic” as they anticipate the future direction of change. TSEGELNJK’s (1976, 1978) *Skalograptus vetus* may be understood as a morphospecies enveloping phenotypes which are intermediate between *N. ultimus* and *N. lochkovensisi*. *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,

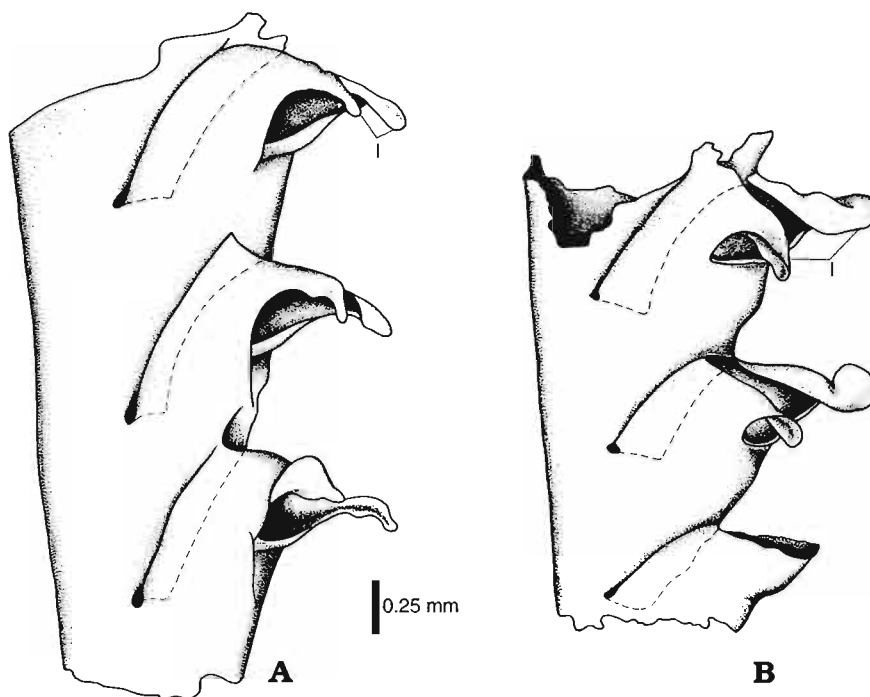


Fig. 55

Neocolonograptus lochkovenski lochkovenski (PŘIBYL). Distal fragments of the rhabdosome (A, B) showing different preservational features of apertural apparatus. Mielnik, depth 659.30 m. *lochkovenski* Zone.

phylogenetic progression. The relation of *N. lochkovenski* 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. lochkovenski 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 *lochkovenski*.

An alternative point of view on the origin of *N. lochkovenski*, as advanced by TSEGELNJUK (1978, 1986), is discussed elsewhere (p. 108). However, a comparison of apertural structures in the standard *lochkovenski* 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 discussion).

Stratigraphic distribution. — In much of the Barrandian area, *N. lochkovenski* 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. lochkovenski* is either preceded by beds with *M. pridoliensis*, or the latter species appears somewhat later, within the *lochkovenski* Zone s.l., which results in the subdivision of the zone into the lower and upper subzones (JAEGER 1986: p. 325).

Splitting of *N. lochkovenski* 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 *lochkovenski* Zone s.l. is subdivided into the lower *N. lochkovenski branikensis* Subzone and the upper *N. lochkovenski lochkovenski* 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. lochkovenski lochkovenski* 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. lochkovenski lochkovenski* 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

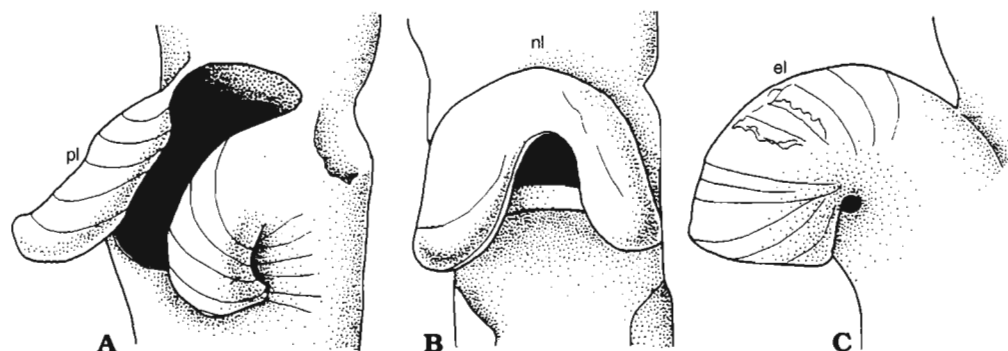


Fig. 56

Diagram showing the apertural structures in standard *N. lochkovensisi lochkovensisi* (A), *M. (Dulebograptus) trimorphus* (B) and in “*Dulebograptid*” morph of *N. lochkovensisi lochkovensisi* (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. lochkovensisi lochkovensisi* 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. lochkovensisi lochkovensisi* 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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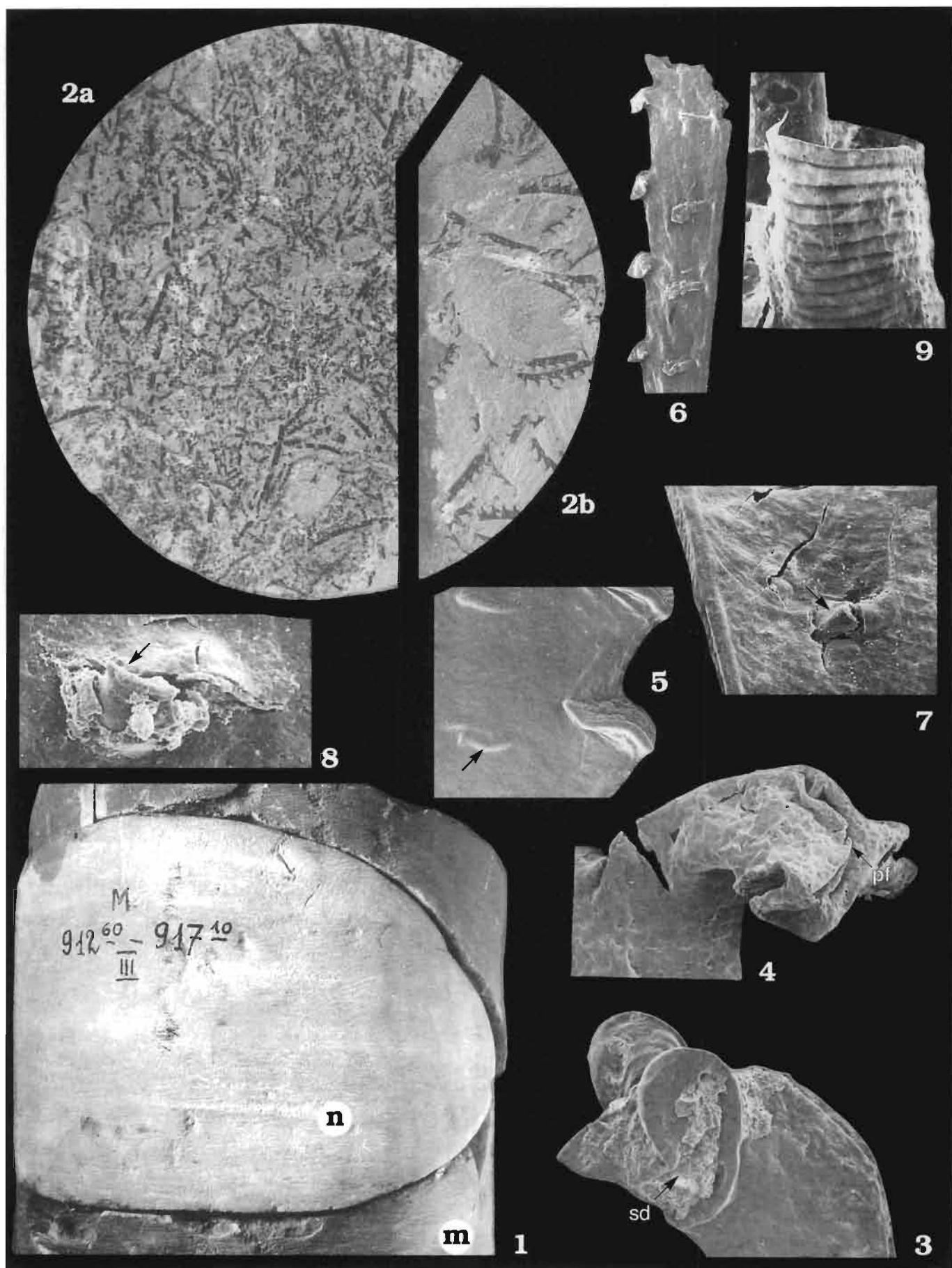
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LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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; $\times 1$.
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; $\times 1$.
- 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; $\times 100$.
- 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 $\times 40$; 6 $\times 24$; 7, 9 $\times 120$; 8 $\times 230$.
9. Unbleached juvenile th_1 of a *Pseudomonoclimacis* sp. displaying fusellar growth lines. Mielnik, depth 822.40 m, *latilobus/balticus* Zone; $\times 30$.



LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

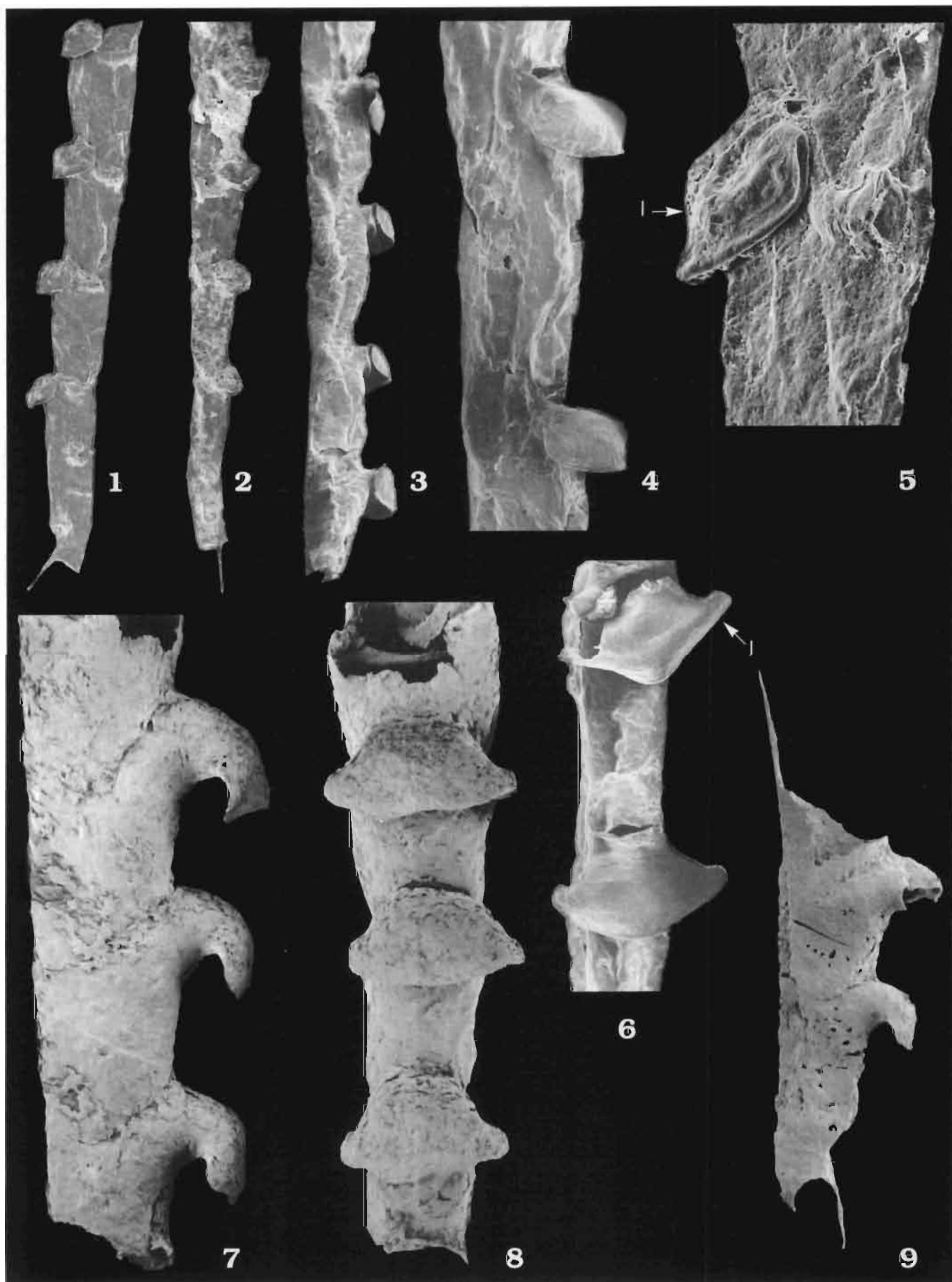
PLATE 2

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.

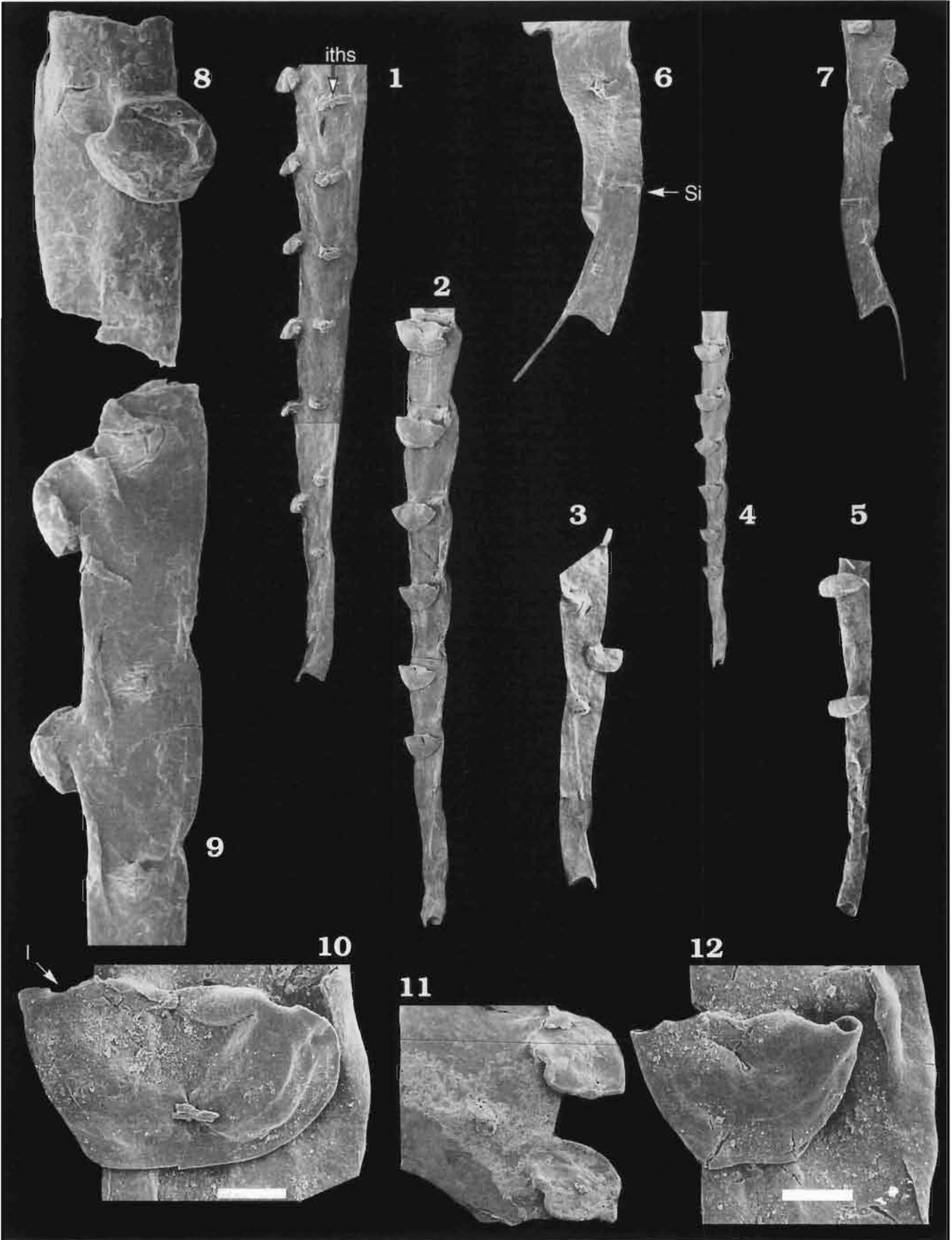


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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.



LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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 transparent specimens; 4 × 56; 5 × 60; 6 × 47.

7–8. Initial bud with visible growth lines seen with SEM; 7 × 160; 8 × 190.

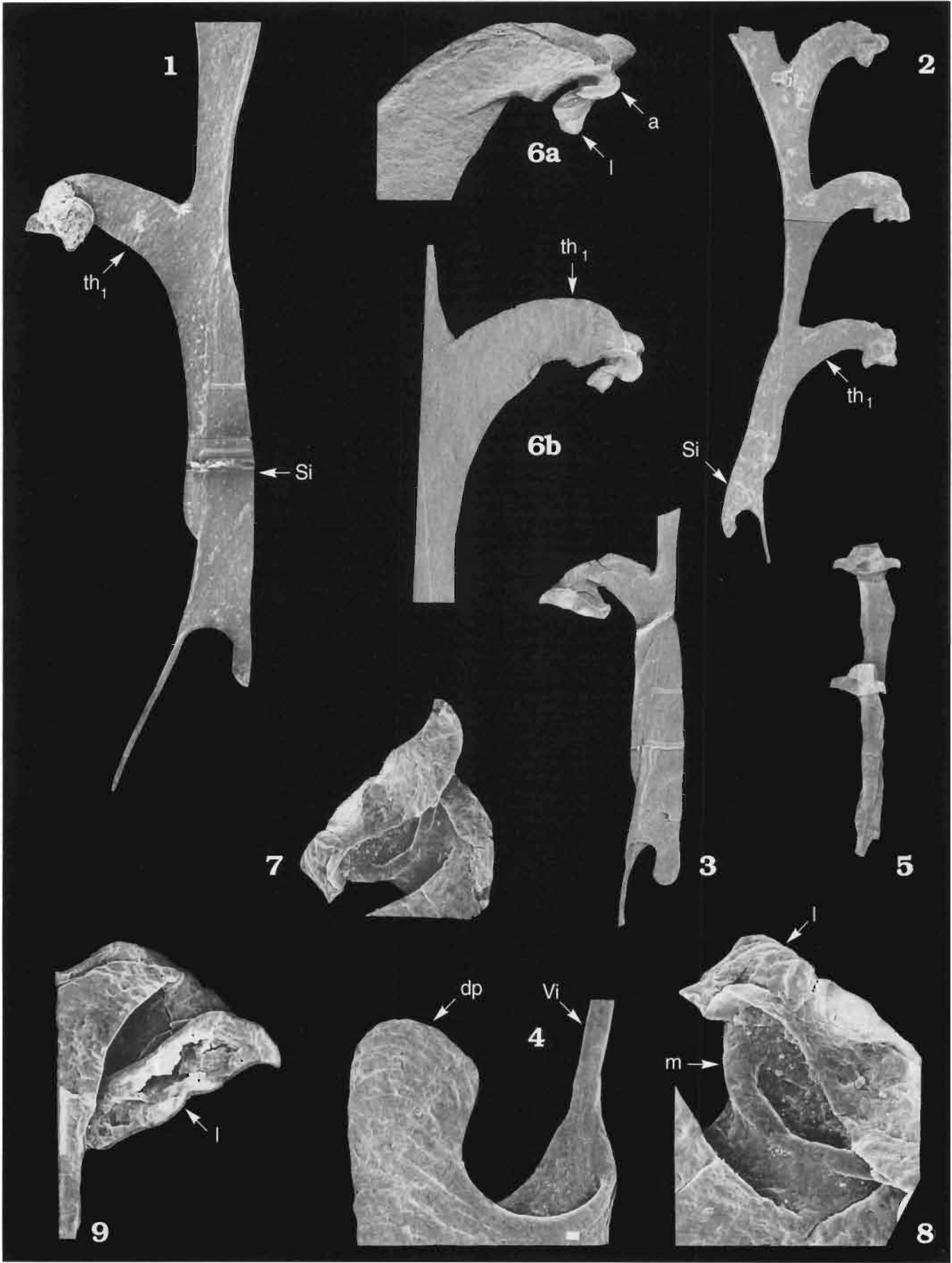


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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.

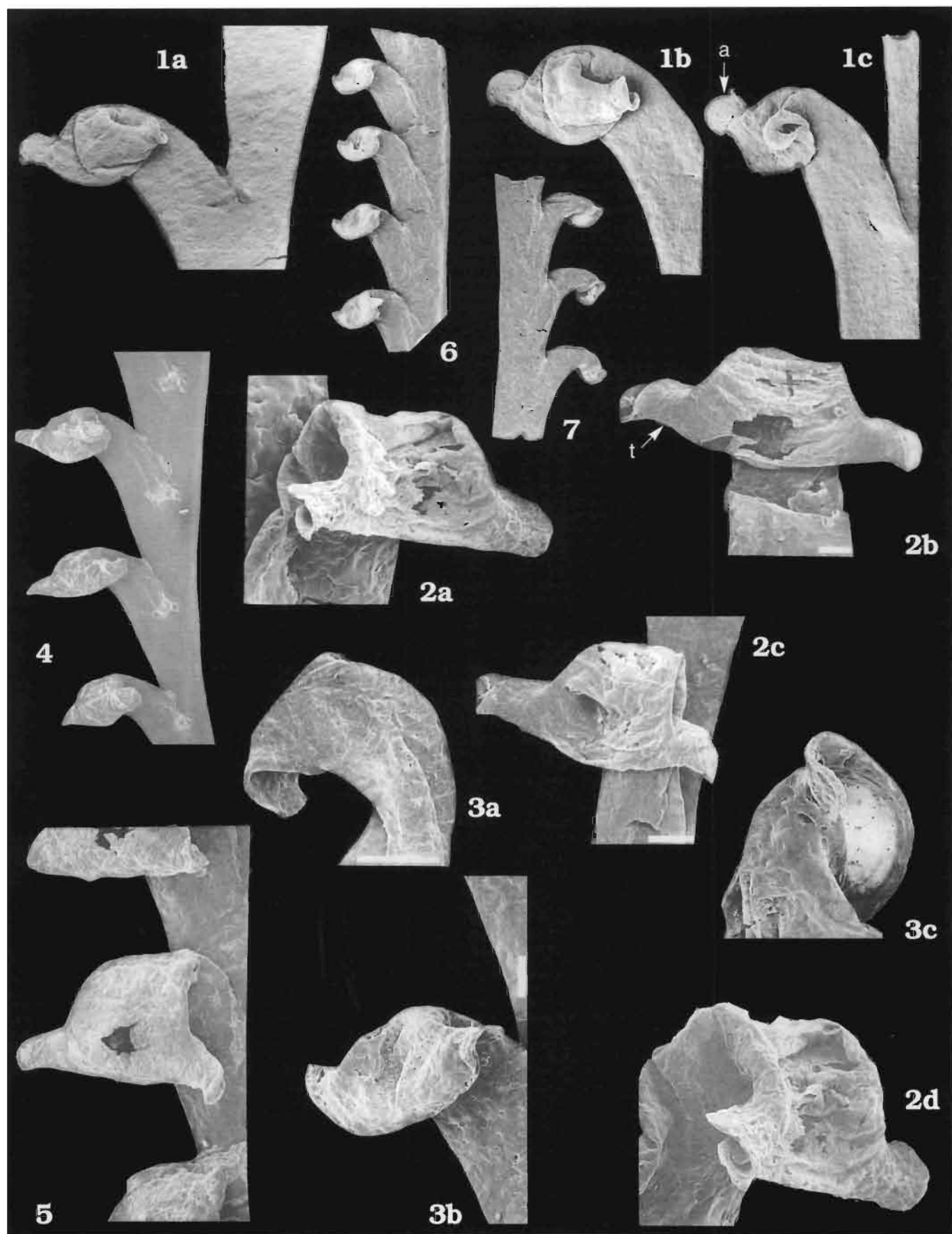


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 6

Monograptus (Formosograptus) formosus BOUČEK 134

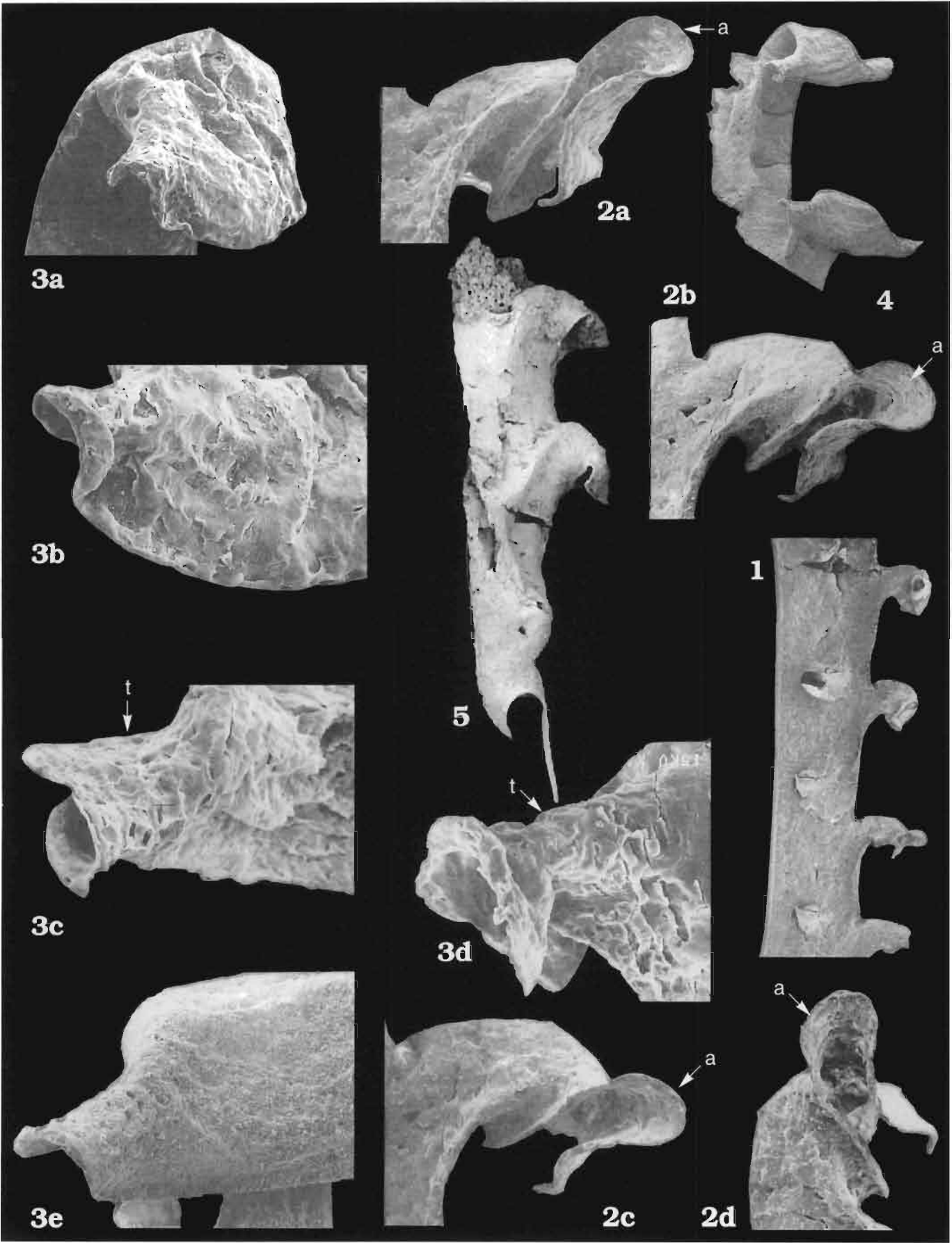
- 1–7. Morphology of proximal thecae (1, 2), first theca (3) as well as the medial thecae of the rhabdosome (4–7).
 Mielnik, depth 770.70–766.70 m, *formosus* epibole within the *acer–spineus* Interval; 1 \times 60; 2a–c \times 120; 2d
 \times 160; 3a \times 160; 3b \times 80; 3c \times 120; 4 \times 25; 5 \times 50; 6, 7 \times 23.



LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 7

	<i>Monograptus (Formosograptus) formosus</i> 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, <i>acer–spineus</i> Interval; 1 × 30; 2a–d × 120; 3a × 120; 3b × 220; 3d, e × 300; 4 × 60.	
	<i>Monograptus (Uncinatograptus) uncinatus</i> TULLBERG	156
5.	Poximal part of the rhabdosome seen laterally. Baltic erratic boulder S.38, Jarosławiec, <i>nilssoni</i> Zone; 5 × 50.	



LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

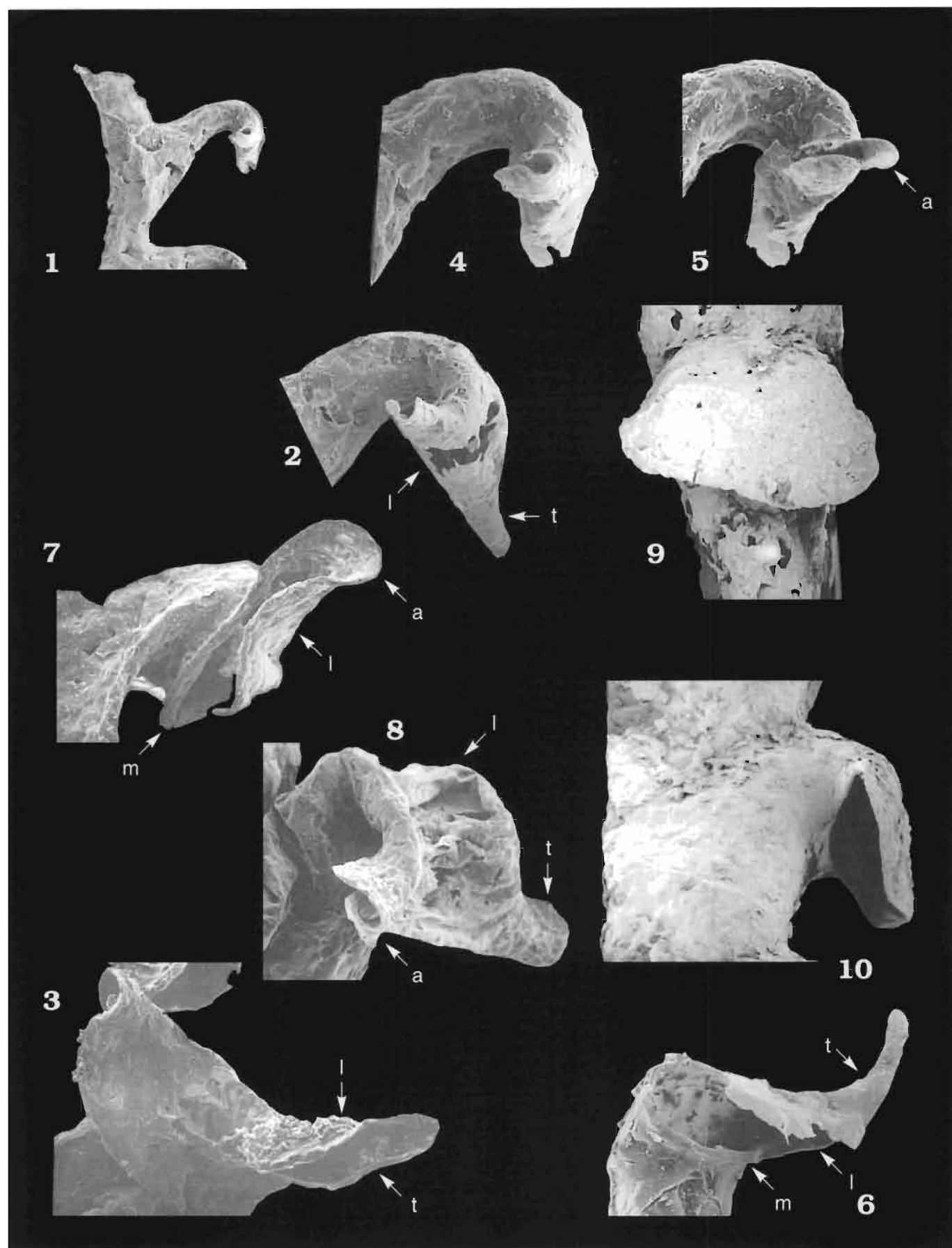
PLATE 8

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.



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.

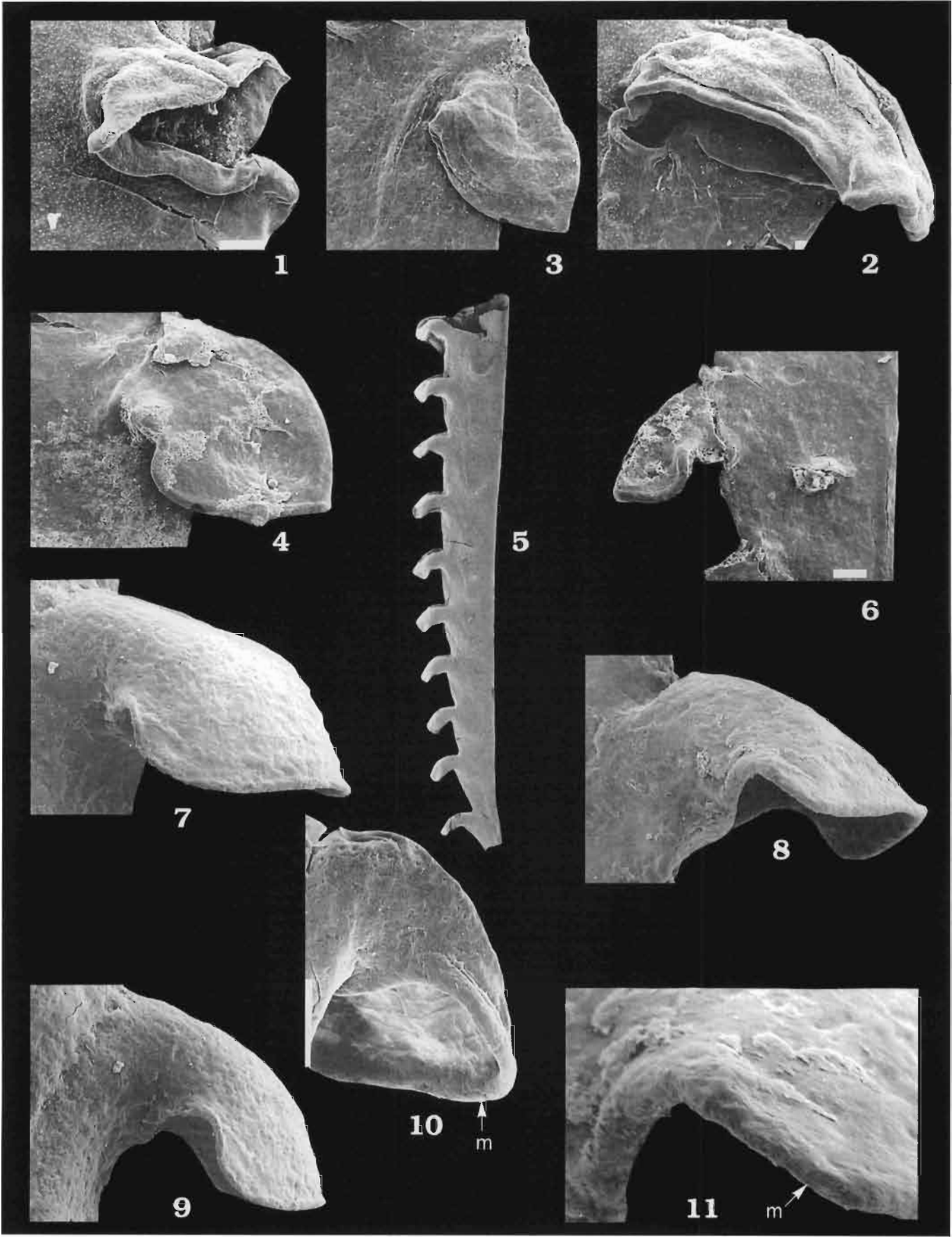


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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.



LATE LUDFORDIAN AND EARLY PRIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 11

Monograpus (Uncinograptus) 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 \times 25; 2 \times 100.

Monograptus (Uncinograptus) 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 \times 150; 4 \times 200; 5 \times 100.

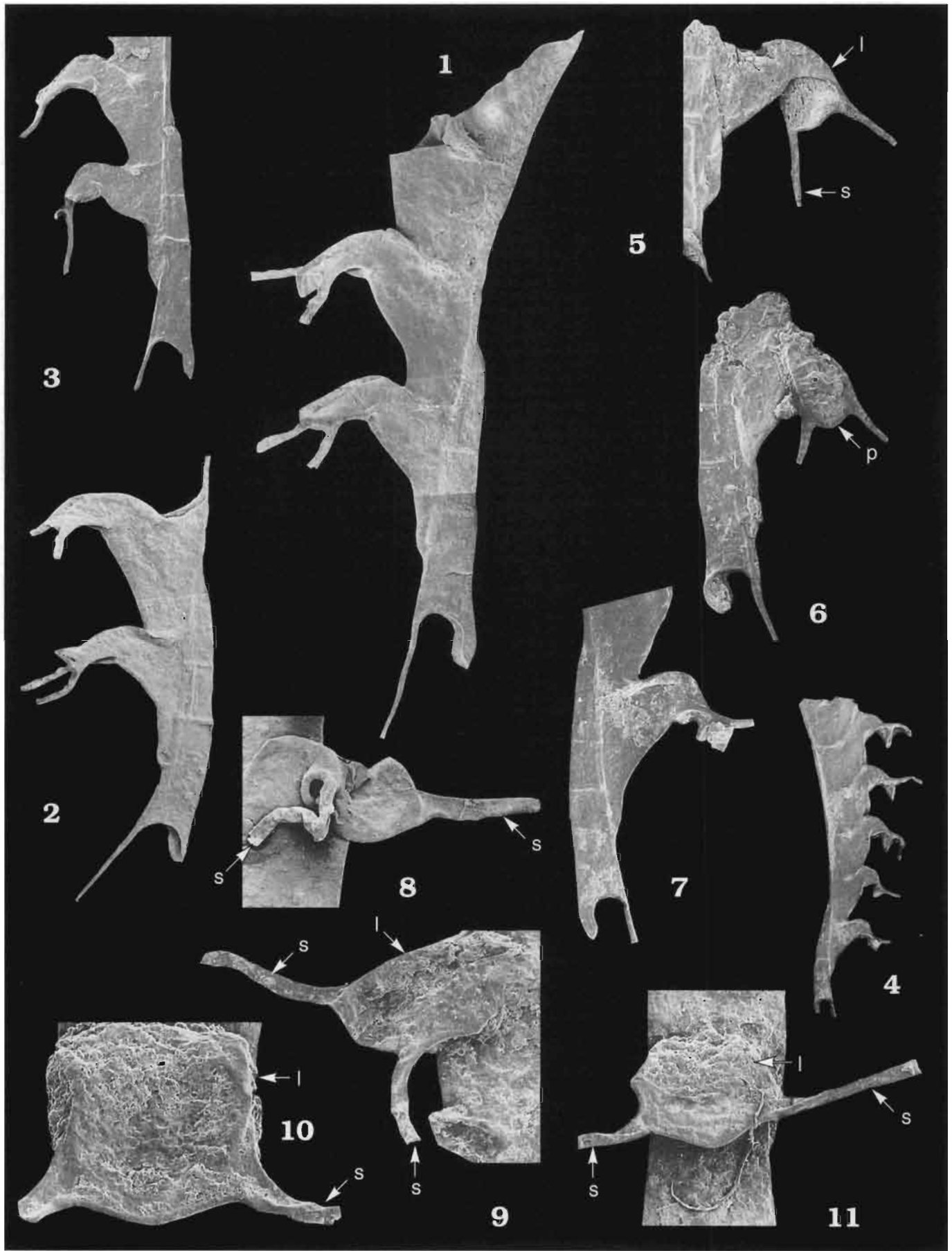


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 12

Monograptus (Uncinograptus) 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.

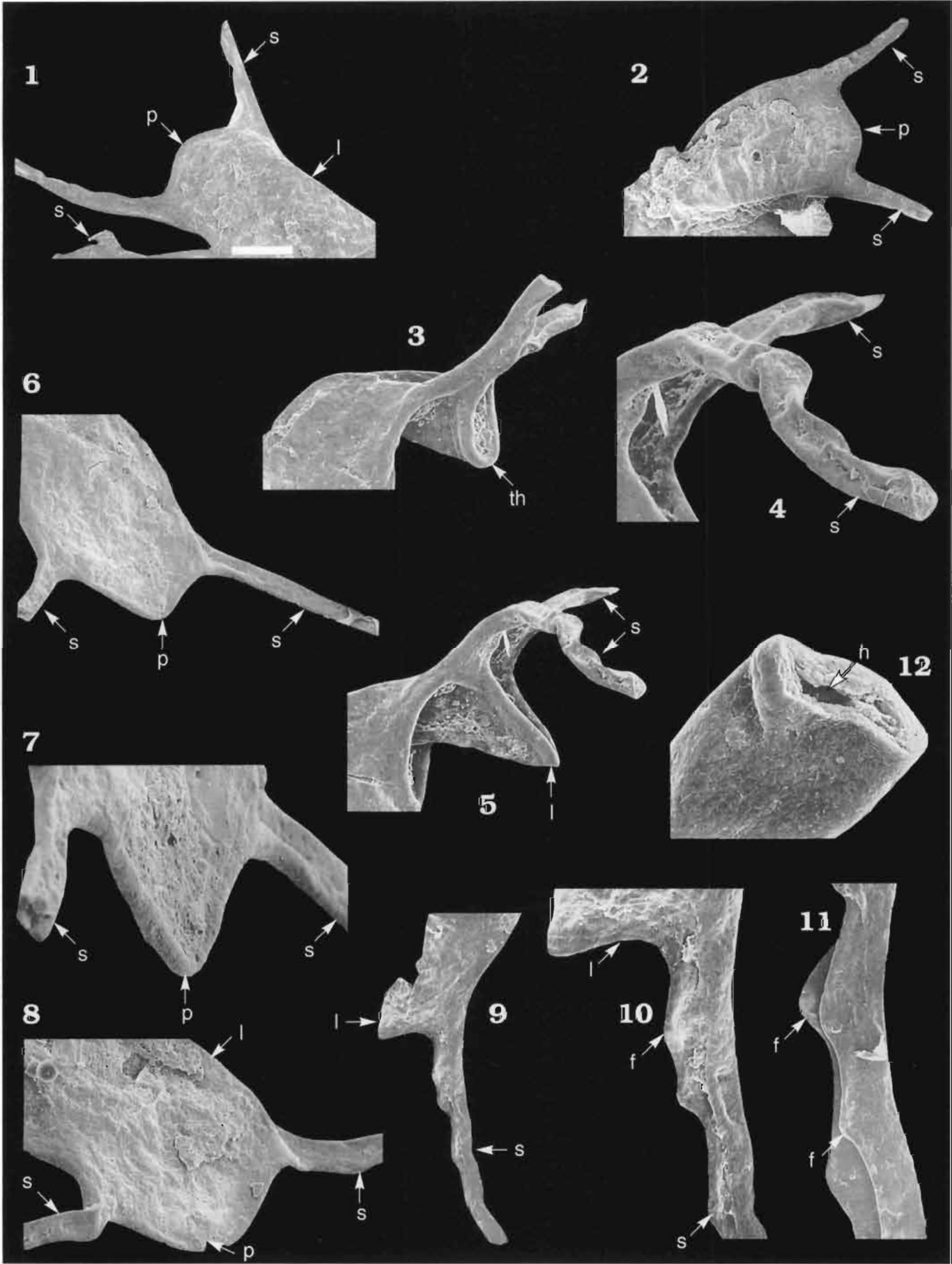


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 13

Monograptus (Uncinograptus) 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.



LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 14

Monograptus (Dulebograptus) trimorphus TSEGELNJUK 154

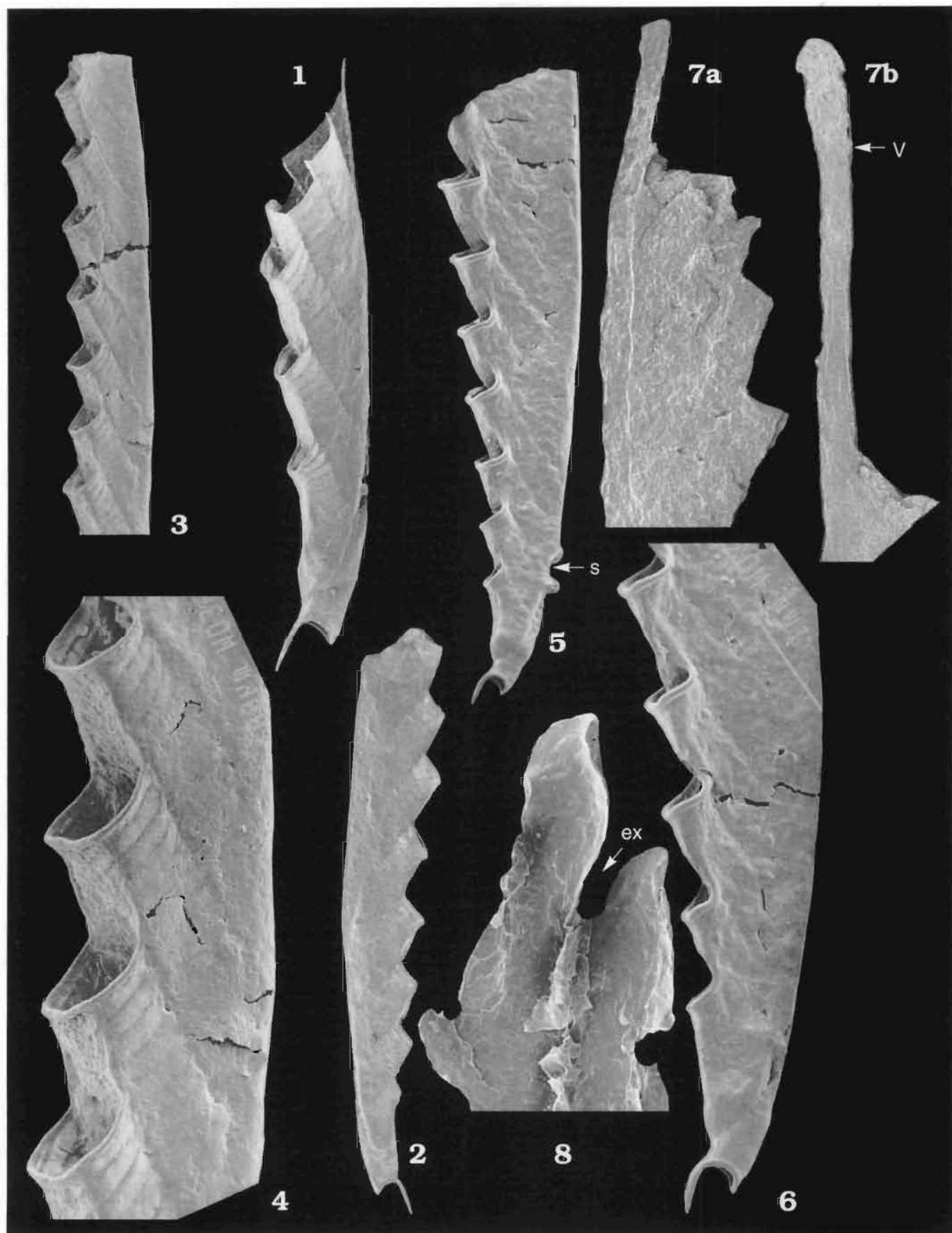
- 1–6. Morphology of rhabdosome and thecae; proximal part of the rhabdosome (1) in ventral view (note the progressive shortening of the apertural lobe proper (l) and the obliteration of the notched portion) and the details of morphological change in the shape of apertural lobe between th_1 and th_2 (2), 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 \times 50; 2 \times 95; 4 \times 40; 6 \times 200.



LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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 showing their distinct excavations (ex). Mielnik depth 819.20 m, *latilobus/balticus* Zone; × 50.

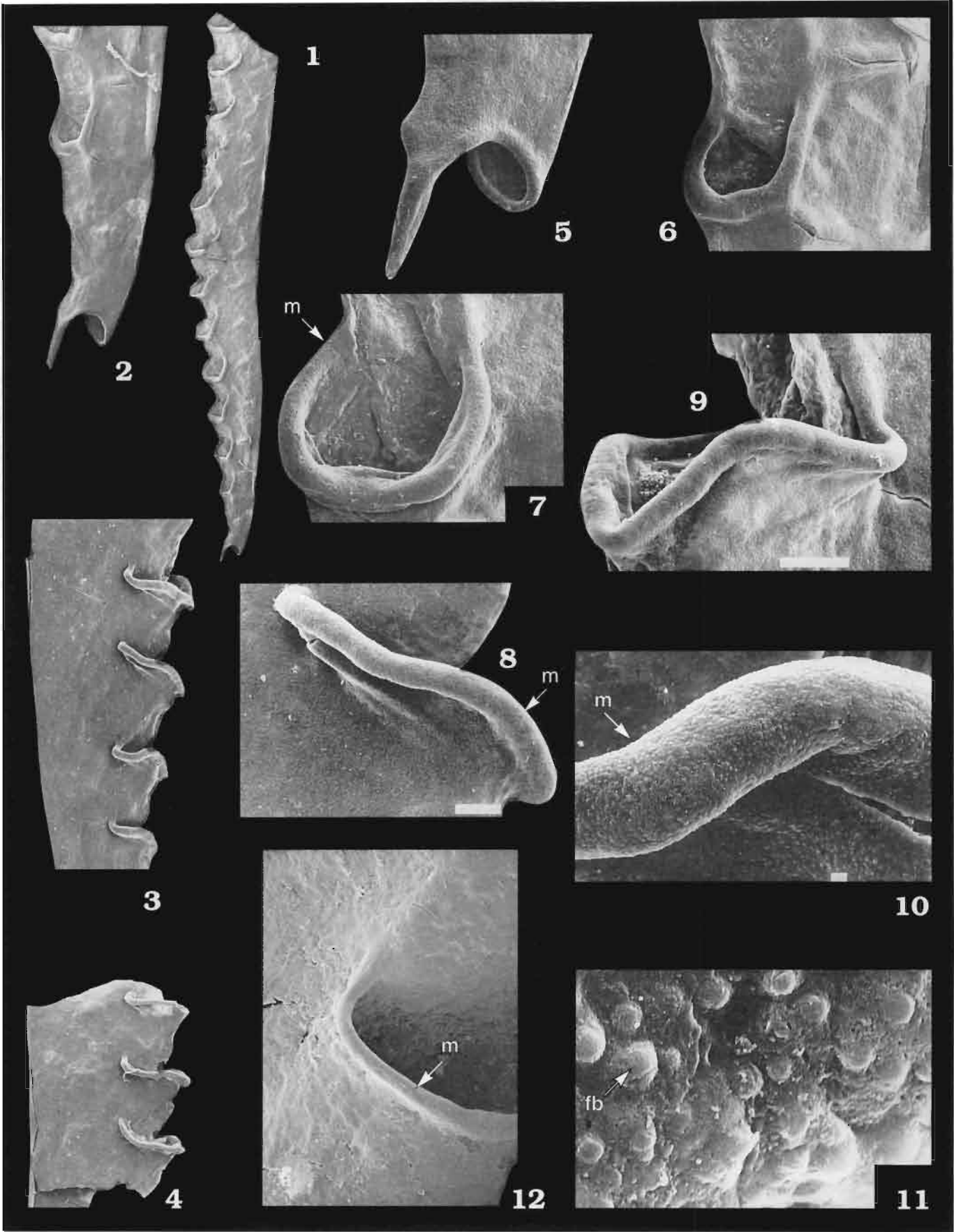


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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.

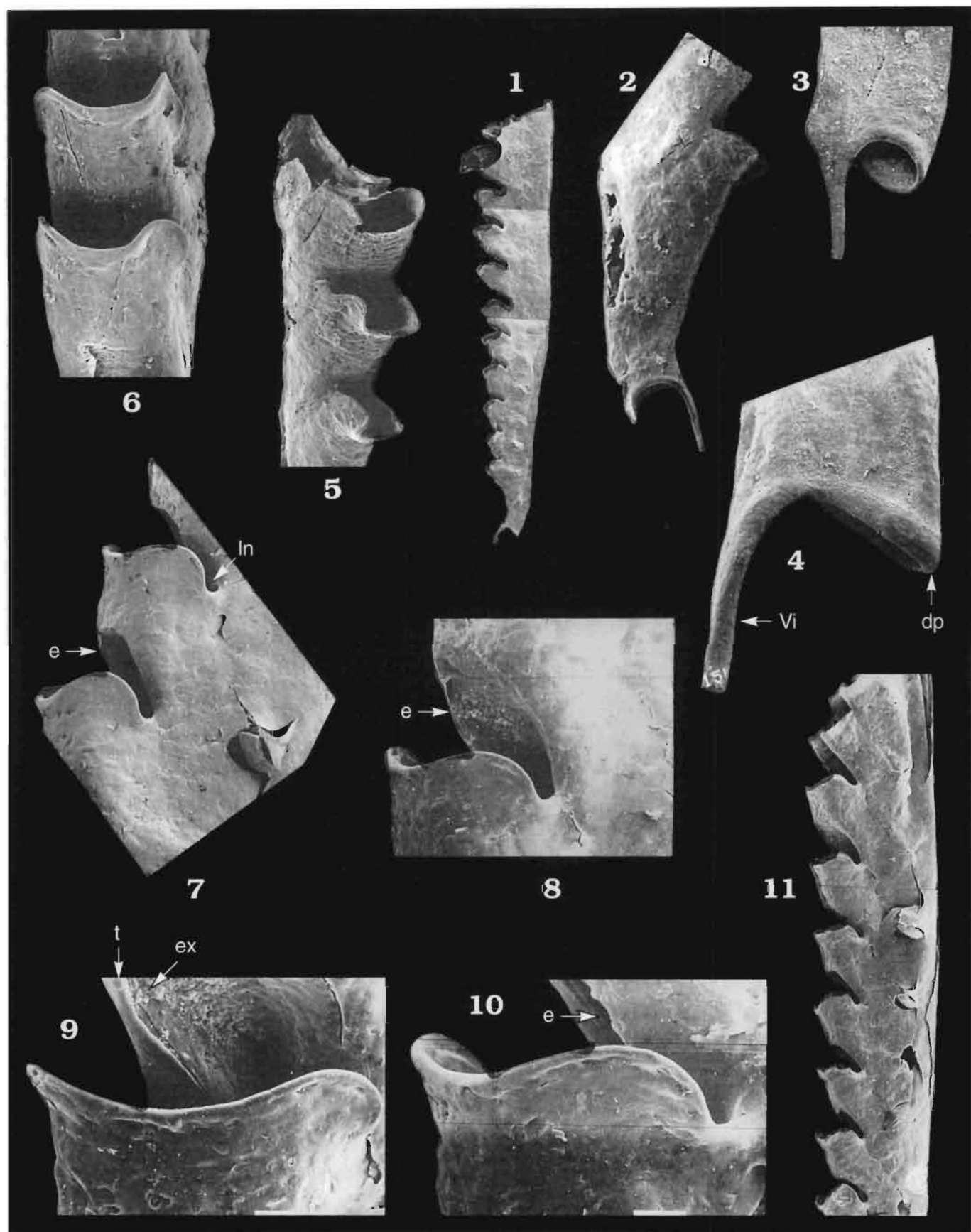


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 17

Pseudomonoclimacis latilobus (TSEGELNJUK) 161

- 1–11. Sicular 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.

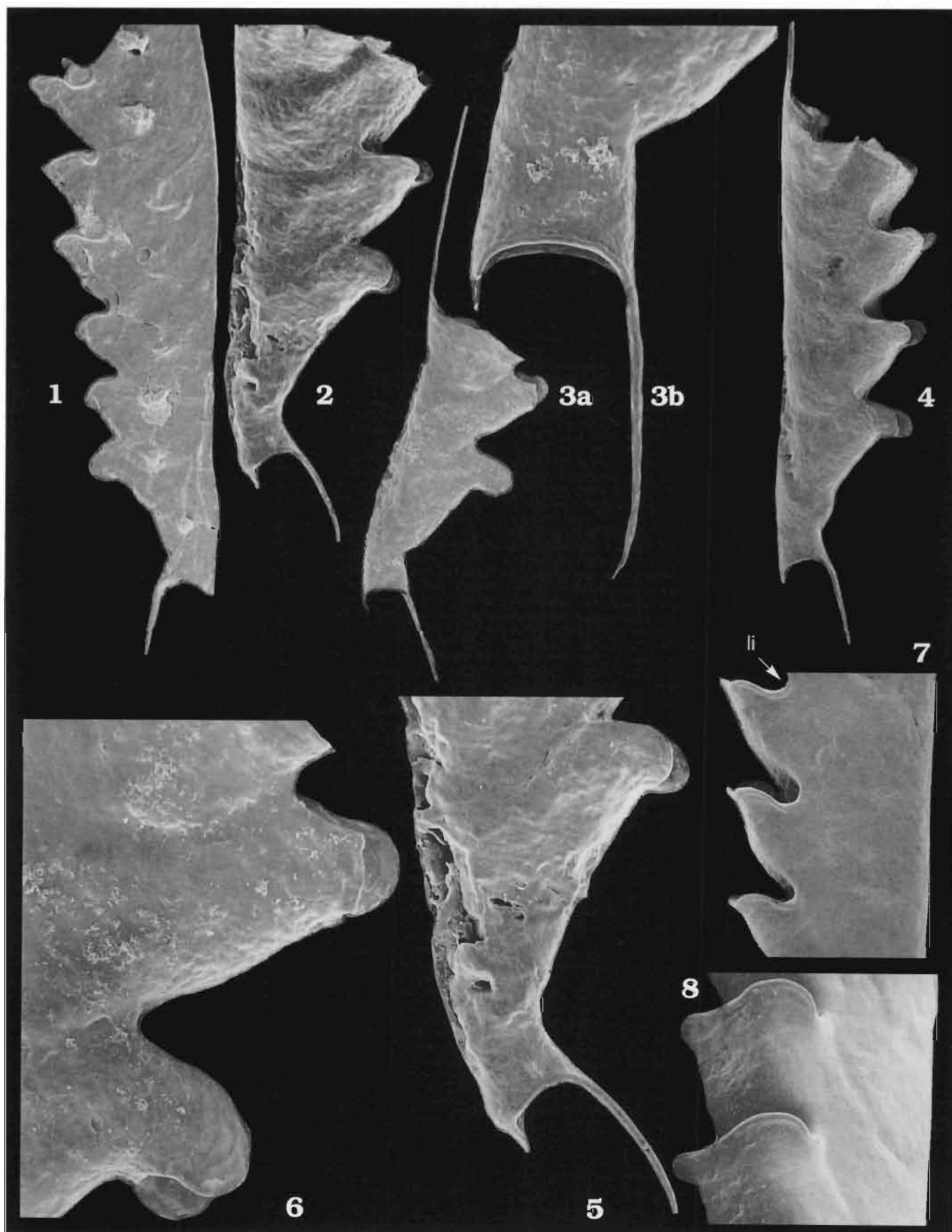


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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 \times 20; 2a \times 30; 2b \times 45; 3a, 4 \times 25; 3b \times 85; 7 \times 25; 8 \times 35.

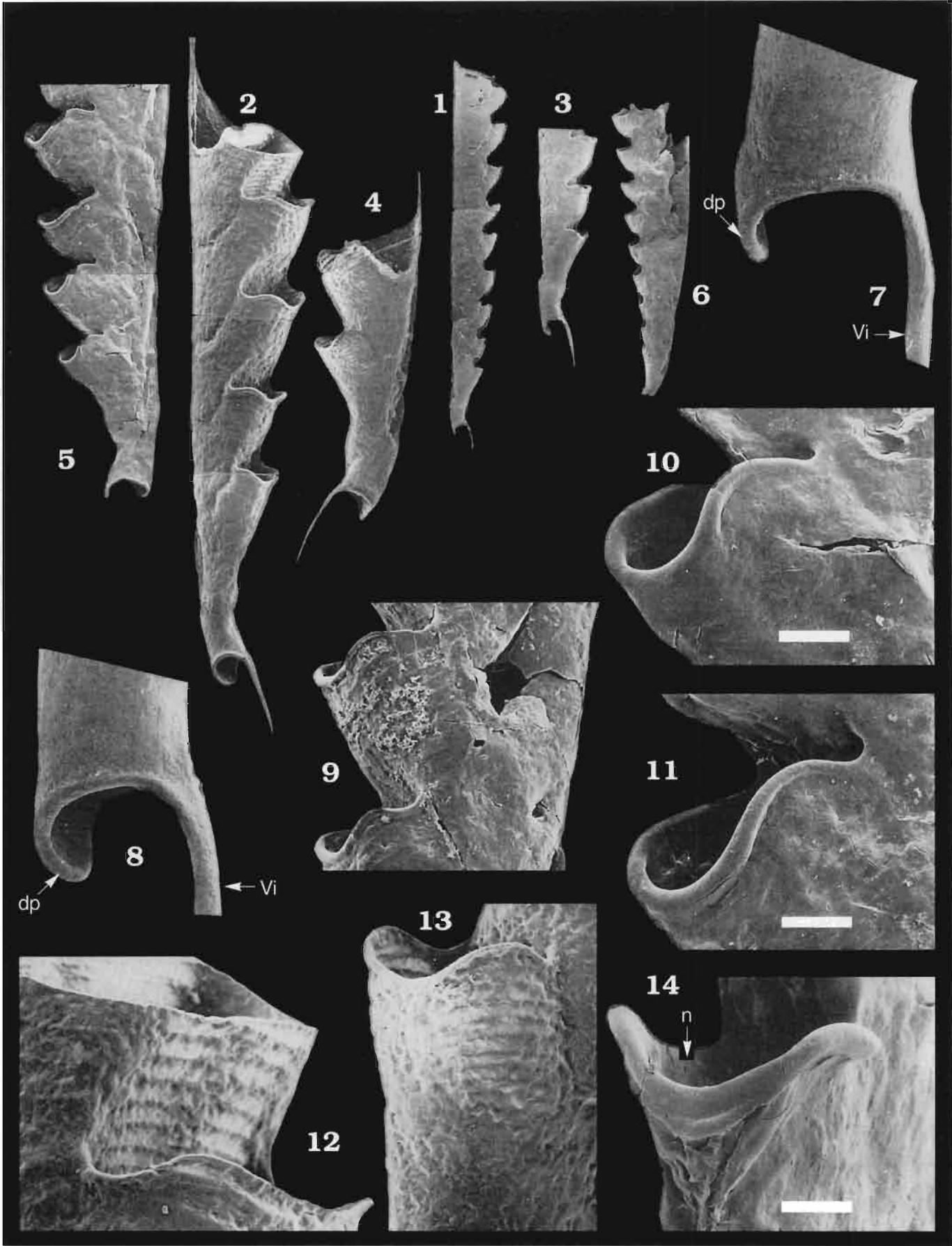


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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.

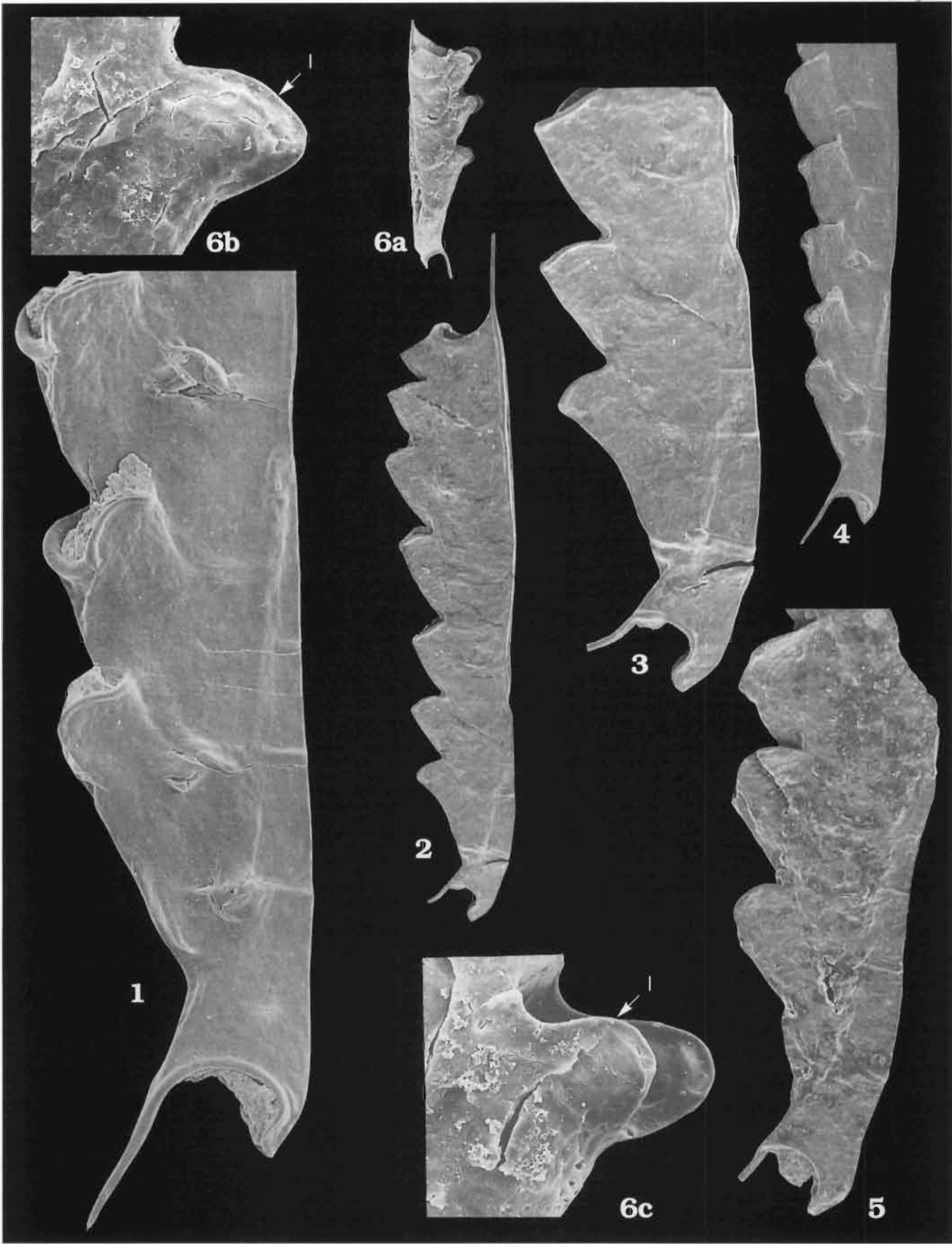


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 20

Istrograptus trangrediens rarus (TELLER) 165

- 1–5. Proximal parts of the rhabdosome showing details of sicula and thecae. Note the characteristic *trangrediens* profile of th_1 in figs 2, 3. Mielnik, depth 689.55 m, *parultimus* Zone; 1 \times 60; 2, 4 \times 20; 3, 5 \times 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 \times 10; 6b, c \times 60.



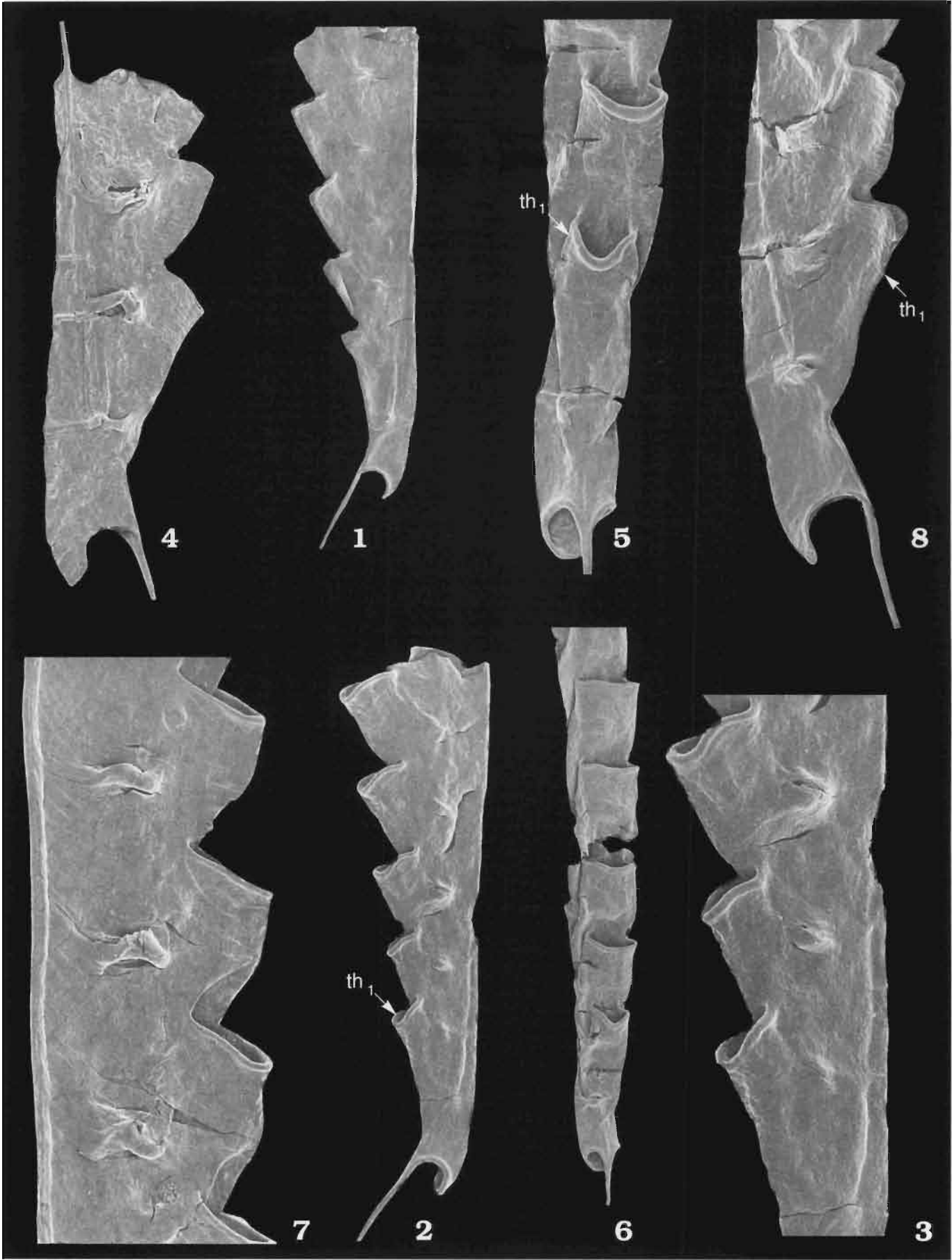
LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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.



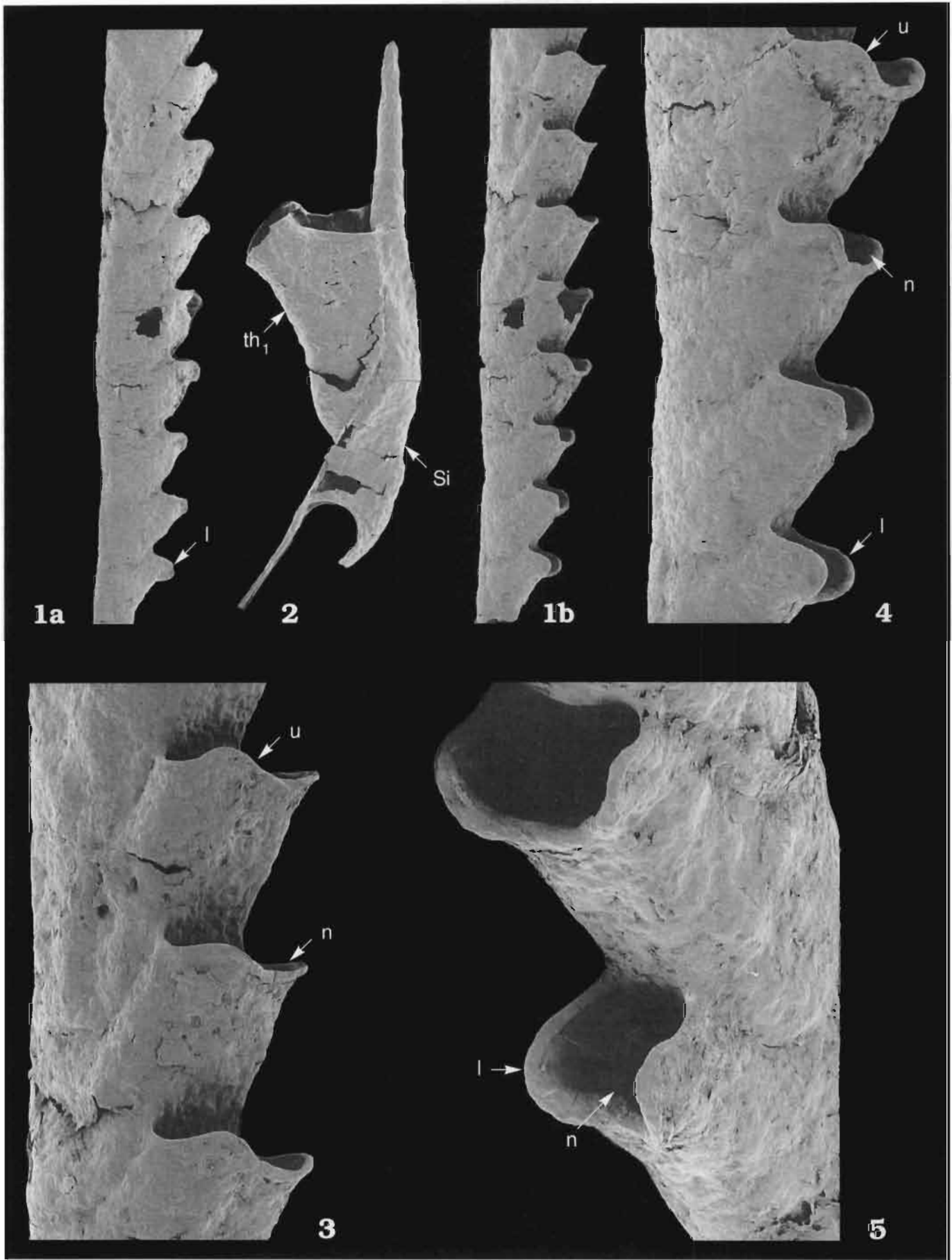
LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

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.

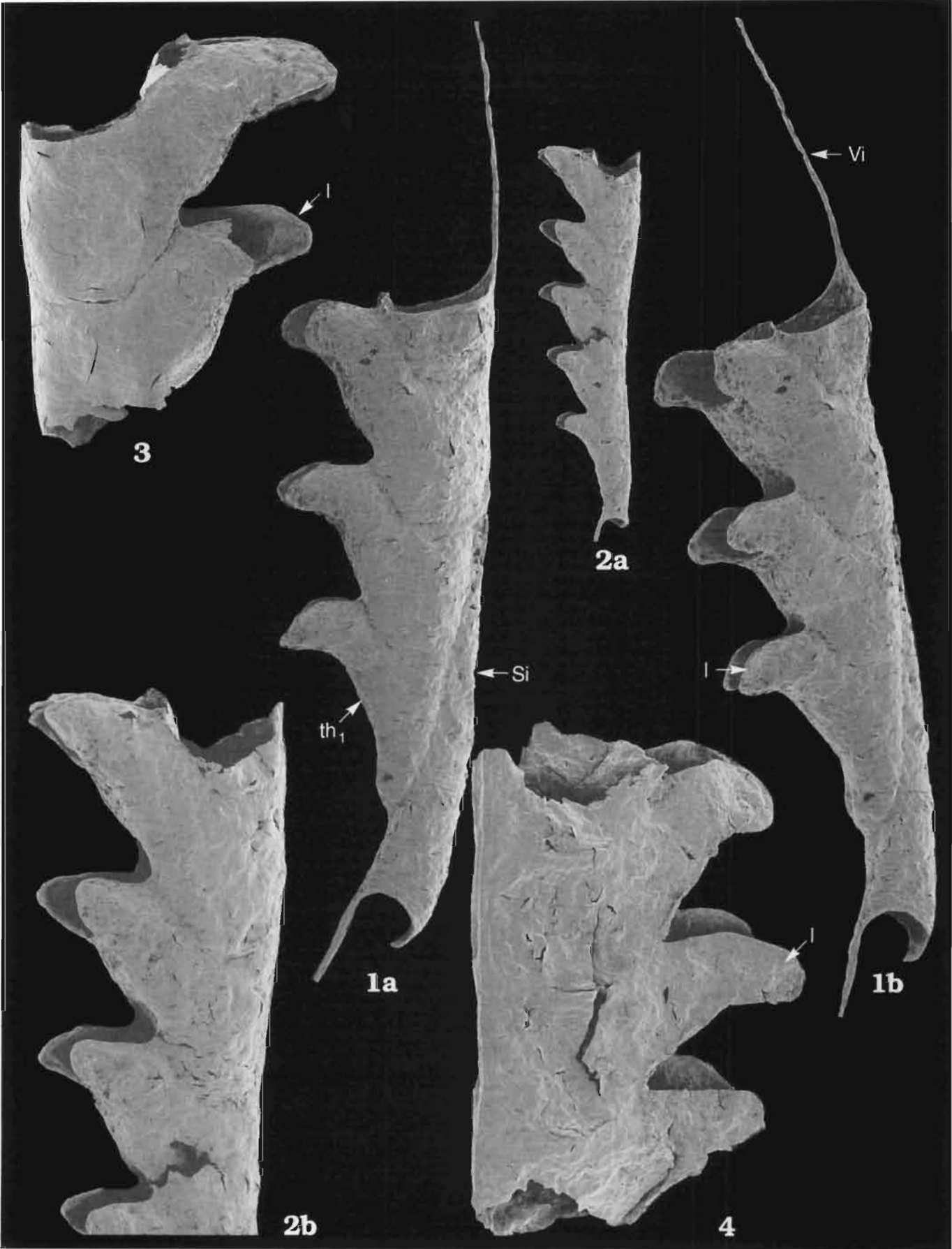


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 23

Neocolonograptus lochkovenski 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, *lochkovenski* Zone, *branikensis* Subzone; 1, 2b, 3, 4 × 50; 2a × 20.

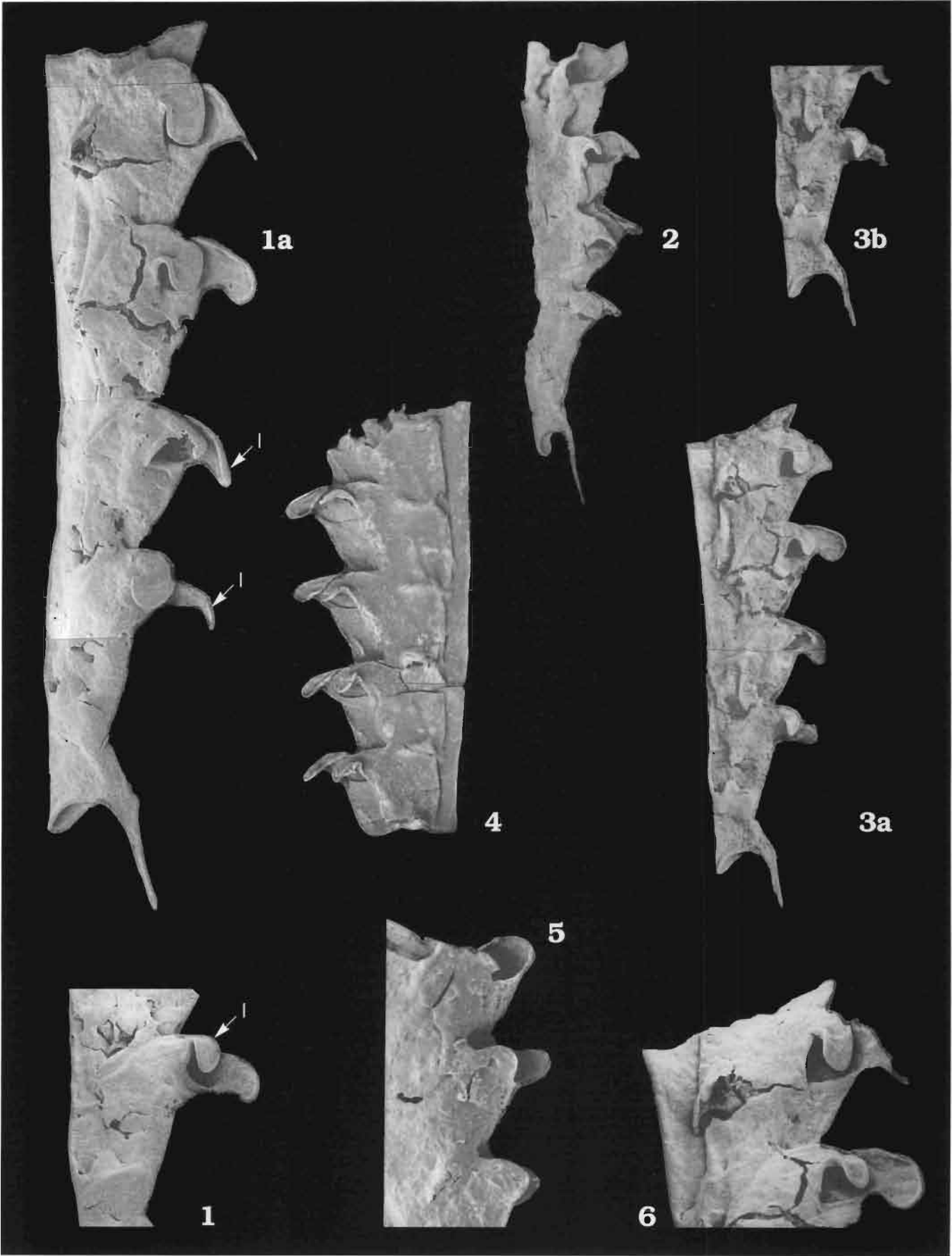


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 24

Neocolonograptus lochkovens *lochkovens* (PŘIBYL) 169

- 1–6. Proximal part of the rhabdosome (1–3) and the morphology of the proximal thecae (2–6). Note a strong development of the paired apertural lobes (l) in proximal thecae and their decrease in distal ones (5). Mielnik, depth 661.30 m, *lochkovens* Zone; 1 \times 25; 2 \times 12; 3 \times 17; 4, 5 \times 20; 6 \times 25.

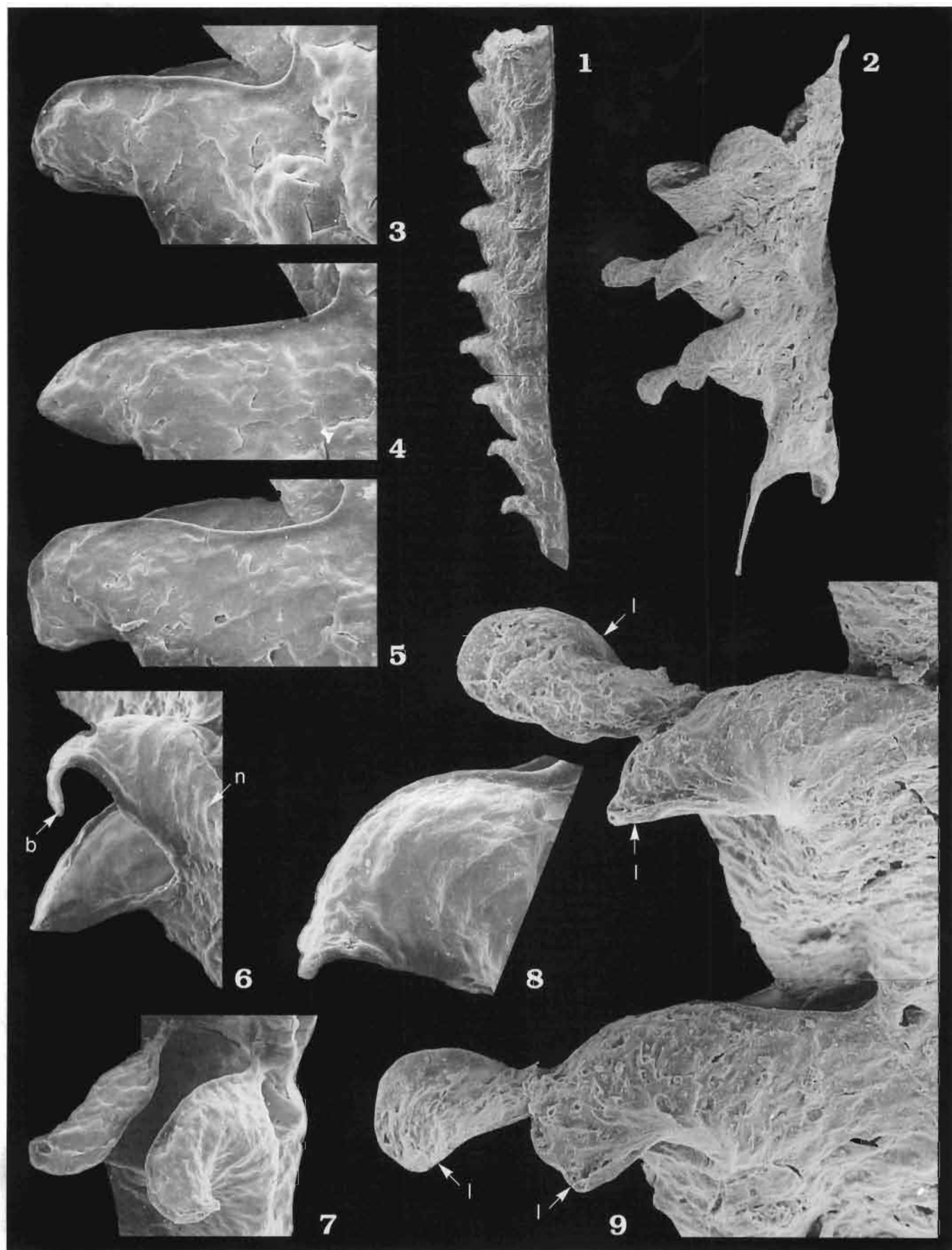


LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 25

Neocolonograptus lochkovens *lochkovens* (PŘIBYL) 169

- 1–9. Proximal parts of the rhabdosome with sacula 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 (l) 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; *lochkovens* Zone, *lochkovens lochkovens* Subzone; 1 × 12; 2 × 31; 3–5, 7 × 130; 6 × 140; 8 × 200; 9 × 94.



LATE LUDFORDIAN AND EARLY PŘIDOLI MONOGRAPTIDS FROM THE POLISH LOWLAND

PLATE 26

Neocolonograptus lochkovens *lochkovens* (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, *lochkovens* Zone, *lochkovens lochkovens* Subzone; 1a × 12; 1b, 2, 3a, 4a, b × 25; 3b × 45; 5 × 50.

