Phyletic evolution of the latest Ludlow spinose monograptids

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The spinose latest Ludlow (Ludfordian) graptolite *Monograptus (Uncinatograptus) spineus* is not related to the lobate-spinose monograptids of the late Wenlock. It developed independently as a result of phyletic evolution from hooded *M. (U.) acer*, *M. (U.) protospineus* sp. n. being a transient link. Cumulative effects of gradual and directional changes within this lineage resulted probably in feeding specializations that enabled separation of niches. Previously described *M. (U.) acer* and *M. (U.) aculeatus* are defined as chronosubspecies, the latter representing a more advanced stage of evolution. A biostratigraphic subdivision of late Ludfordian in graptolite facies is suggested.

Key words: graptolites, monograptids, phyletic evolution, hypermorphosis, Ludlow, Late Silurian.

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Introduction

Monograptus (Uncinatograptus) spineus (Tsegelnjuk 1976) is undoubtedly the most remarkable species recognized in the latest Ludlow (Ludfordian) graptoloid faunas of the East European Platform (Tsegelnjuk 1976). It is the only monograptid with a lobate-spinose apertural apparatus, this being composed of an apertural lobe with long paired spinose outgrowths placed in the antero-lateral corners of the lobe itself (Figs 1D, 7C–E: s). Such morphology is reminiscent of Late Wenlock monograptids of the *M. priodon* – *M. flemingi* group, but against the background of the co-eval fauna *M. (U.) spineus* is unique in Late Ludlow. However, recent studies on the latest Ludlow (late Ludfordian) graptoloid fauna isolated chemically from the well-known Mielnik-1 borehole (the Polish part of the East European Platform; cf. Urbanek 1966, 1970) provide evidence concerning its affinities. This taxon is the terminal link in a lineage comprising four sequential taxa: *Monograptus (Uncinatograptus) acer acer* (Tsegelnjuk 1976) → *M. (U.) acer aculeatus* (Tsegelnjuk 1976) → *M. (U.) protospineus* sp. n. → *Monograptus (U.) spineus* (Tsegelnjuk 1976). This lineage reveals a distinct morphological and temporal sequence in the changes affecting a number of characters. The key changes are associated either with the gradual development of the dorsal curvature of the rhabdosome or (and chiefly so) with the apertural apparatus, resulting in the elaboration of an apertural lobe with spines, a unique combination for Ludfordian monograptids (Fig. 1A–D).

Consequently, *M. (U.) spineus* cannot be regarded as a cryptogenic element in the late Ludfordian fauna. On the contrary, it is a product of evolutionary changes which are traceable *in situ*, within the fossil record available in the Mielnik boring.

The material illustrated in the present paper is housed at the Institute of Palaeobiology of the Polish Academy of Sciences (abbreviated as ZPAL) in Warsaw, Poland.

Crucial evolutionary changes

Morphological changes were primarily expressed in the structure of the apertural apparatus, whilst the overall shape of the rhabdosome was subject to only slight modifications. The ancestral type of the apertural apparatus may be seen in such species as *Monograptus (Uncinatograptus) uncinatus* Tullberg 1883 and is represented in *M. (U.) acer acer* (Fig. 1A) by a single apertural lobe, a derivative of the dorsal wall of the metatheca. The lobe is made up of a double series of fuselli with a zig-zag suture in the middle. Such lobes, devoid of any outgrowths or spines, were formally assigned to the 'uncinatus' type of apertural accessories, as defined by Jaeger (1978). The apertural lobe in *M. (U.) acer aculeatus* represents the same structural type.

The next stage in the morphological evolution of the apertural apparatus within the lineage is represented by a transient sequential species, described herein as *Monograptus (Uncinatograptus) protospineus* sp. n. This form, in addition to the lobe proper, possesses a pair of well-defined but short and blunt antero-lateral processes (Figs 1B, 6A–F: alp). Examination of isolated and bleached specimens has revealed their microstructure (Fig. 1C: alp). They are composed of three to four of bent fuselli superimposed over the antero-lateral corners of the lobe proper.

A still more advanced stage of evolutionary change can be observed in *Monograptus (Uncinatograptus) spineus* which, in addition to possesing an apertural lobe proper and a pair of antero-lateral processes, also displays true apertural spines (Figs 1D, 2A–B, 7C–E: s). Situated on the antero-lateral processes doubtlessly inherited from the 'protospineus' stage of the morphological evolution, these spines represent a new acquisition attained

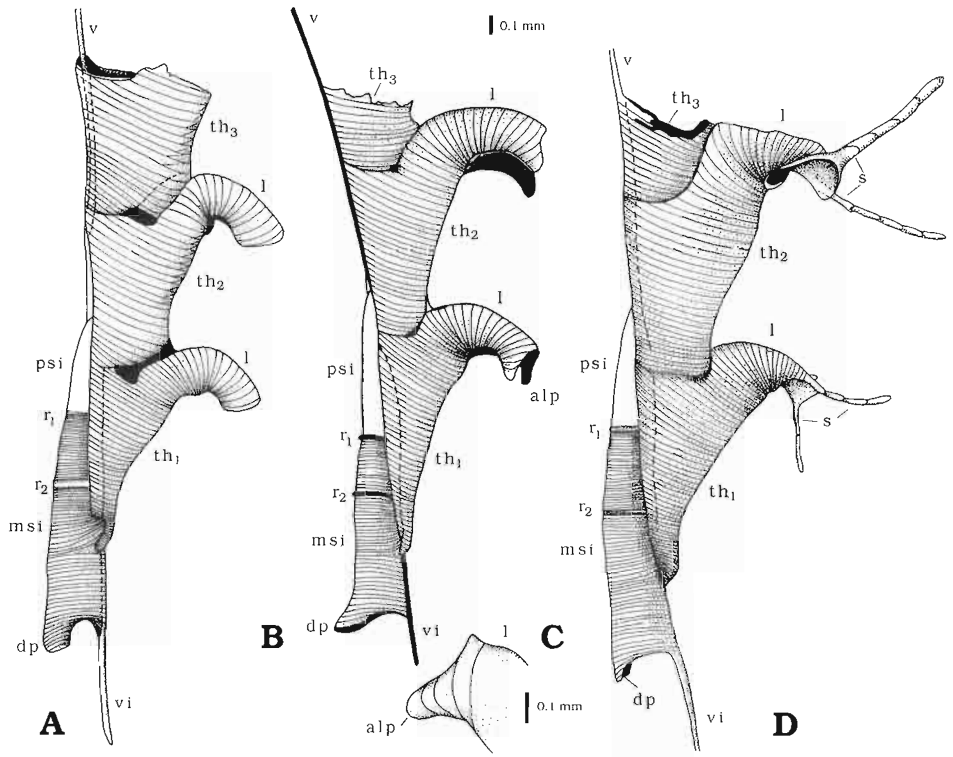

Fig. 1. Morphological changes within the *Monograptus (Uncinatograptus) acer* → *M. (U.) spineus* lineage as seen in proximal parts of the rhabdosome. Diagrammatical camera lucida drawings based on bleached specimens isolated from Mielnik-1 borecore. ❑A. *M. (U.) acer acer* (Tsegelnjuk 1976), *M. acer* Zone. ❑B–C. *M. (U.) protospineus* sp. n., lateral view of rhabdosome (B) and fusellar structure of antero-lateral process (C), *M. protospineus* Zone. ❑D. *Monograptus (U.) spineus* (Tsegelnjuk 1976), *M. spineus* Zone. Abbreviations: alp — antero-lateral processes, dp — dorsal process of metasicula, l — apertural lobe proper, msi — metasicula, psi — prosicula, r$_1$–r$_2$ — successive sicular rings (annuli), s — apertural spines, th$_1$–th$_3$ — successive thecae, v — virgula, vi — virgella.

during the *M. (U.) protospineus* → *M. (U.) spineus* phyletic transition. They are made of superimposed fusellar bands, with fuselli heads (f$_1$–f$_5$) projecting somewhat outwards and accounting for the 'telescopic' appearance of the entire structure. The spines are fairly long (0.28–0.35 mm in th$_1$ and some 0.50–0.60 mm in medial and distal thecae), being usually preservationally deformed in different ways. In life, however, they probably projected laterally from the antero-lateral corners of the lobe proper (Fig. 2).

Monograptus (U.) spineus is the terminal, and clearly highly specialized species of the lineage. It disappears from the Mielnik borehole sequence, when the fauna is replaced by a low-diversity assemblage including *Pristiograptus dubius* s. l. and *Linograptus posthumus* and occupying beds of considerable thickness before monograptids of Přidoli age make their first appearance. This situation may be seen as a substantiation of the

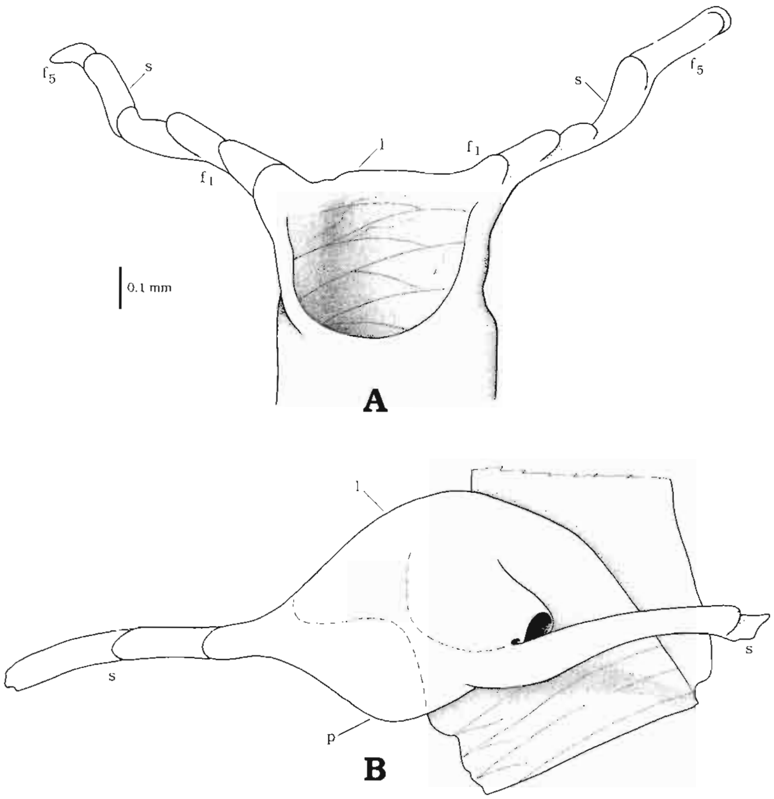

Fig. 2. Apertural apparatus in *Monograptus (Uncinatograptus) spineus* (Tsegelnjuk 1976) seen in two contrasting states of preservation. Camera lucida drawings of bleached specimens from Mielnik-1 boring, depth 760,15 m, *M. spineus* Zone. A. Proximal theca with the apertural lobe flattened and aperture exposed. B. Distal theca with the apertural lobe compressed over the aperture. Note the presence in addition to the lobe proper (l) of paired apertural spines (s) made of a number of fuselli (f_1–f_5) and a promontorium (p).

concept of the *M. spineus* Event advanced by Koren' (1993). She is convinced that the assemblage of the *M. spineus* Zone was wiped out by a biotic crisis, leaving only a few non-specialized hold-overs. The bulk of the early Přidoli fauna is therefore composed of newcomers (immigrants), which initiated their own lineages, starting from relatively non-specialized morphological types closely related to the conservative *P. dubius* stem species (Urbanek in press).

The course of the morphological change described above fully agrees with the stratigraphic sequence of the species involved (Fig. 3). There is no doubt that the *M. (U.) acer* → *M. (U.) spineus* sequence represents a true evolutionary lineage based on direct ancestral-descendant relations. Directional changes within a single lineage without any branching or splitting of the line of descent together with a gradual and cumulative pattern of change qualify this mode of evolution as phyletic (according to the definition made by Simpson 1944 and frequently used ever since). The

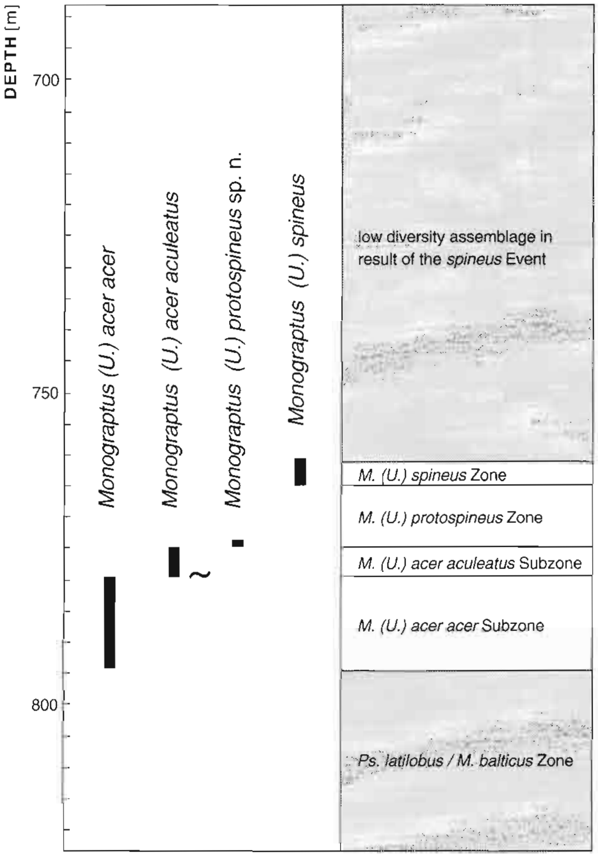

Fig. 3. Stratigraphic sequence of the taxa from the *Monograptus (Uncinatograptus) acer* → *M. (U.) spineus* lineage as encountered in the Mielnik-1 borehole section. Note the replacement of the successive taxa in time and the resulting zonal subdivision. The *M. acer acer* and *M. acer aculeatus* Subzones combine into *M. acer* Zone.

lineage in question is thus an instance of phyletic evolution in the Ludfordian monograptid fauna. Its successive links represent sequential species (chronospecies) which appeared as a result of transformation as opposed to true speciation (multiplication of species).

Associated morphological changes in the lineage

Not unlike most monograptid phyletic lines studied so far, morphological changes within the *M. (U.) acer* → *M. (U.) spineus* lineage were focused on the apertural apparatus. Other thecal characters were only moderately affected by change, although the rhabdosome developed increasing dorsal curvature. This may conveniently, although only approximately, be estimated by the angle of divergence D, contained between the dorsal line of rhabdosome and a straight line crossing the middle of the metasicular aperture and the apex of prosicula (Fig. 4: asterisks) and measured beyond the latter point.

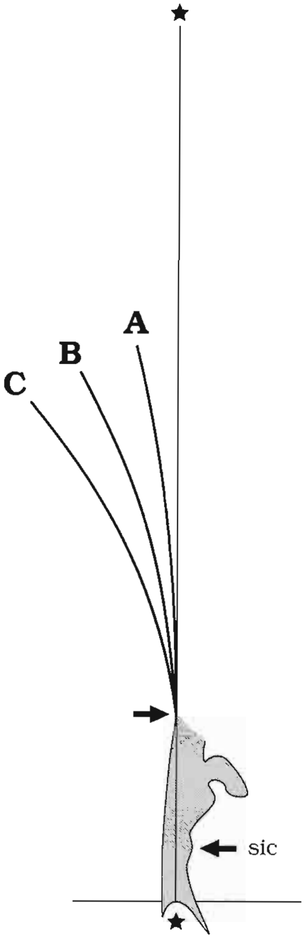

Fig. 4. Dorsal curvature of the rhabdosome within the members of the *acer-spineus* lineage, measured by D, the angle of deviation of the dorsal line of the rhabdosome from the straight line (denoted by asteriscs), and defined by the apex and center of the sicular aperture. A. Maximum dorsal curvature observed in the lower zonal populations of *Monograptus (Uncinatograptus) acer acer*. B. Maximum dorsal curvature observed in higher zonal populations of *M. (U.) acer aculeatus*. C. Dorsal curvature measured in *M. (U.) protospineus* sp. n. and in *M. (U.) spineus*. Note a progressive increase in the degree of the dorsal curvature as shown by A–C.

In the early populations (depth 792.70 m) of the lineage, represented by *Monograptus (U.) acer acer*, the rhabdosome is straight (D=0) or the dorsal curvature is insignificant (Fig. 4A). Somewhat higher (depth 791.90 m and 790.55 m), the observed D varies from 0° to 6°, involving no more than a few most proximal thecae. In geologically youngest populations (depth 774.50 m), assigned herein to *M. (U.) acer aculeatus*, a phylogenetically more advanced member of the lineage, the dorsal curvature is expressed more distinctly, with D attaining some 17° and involving a greater proportion of the rhabdosome (Fig. 4B). Although the material available is too scanty to be analyzed statistically [the total number of proximal fragments of rhabdosome was 30 and 5 for *M. (U.) acer acer* and *M. (U.) acer aculeatus* respectively, usually 1–4 in one sample] there is no doubt that the increase of dorsal curvature within *M. (U.) acer* s. l. was gradual and progressive. Nevertheless, an arbitrary limit between the two subspecies in question may be set in the Mielnik-1 boring at the depth 780.00 m (Fig. 3, denoted by ~).

A still higher degree of curvature (D ~ 25°) is a feature characteristic of the two later members: *M. (U.) protospineus* sp. n. (only 2 proximal fragments available) and *M. (U.) spineus* (Fig. 4C). The latter species is represented by 12 proximal fragments. It seems that a further increase in the dorsal curvature was insignificant and its degree became essentially stabilized at the 'protospineus' level. Any further change of the rhabdosome curvature was then replaced by progressive modifications of the apertural apparatus, which also began at the 'protospineus' stage of evolution.

Other minor changes of a purely quantitative nature may be seen in the shape of the ventral wall of the proximal thecae. In the early populations, assigned herein to the *M. (U.) acer acer*, ventral walls are straight and thecae strictly tubular. The later populations, referred to *M. (U.) acer aculeatus*, display a gentle sigmoidal curvature of the wall, which produces a somewhat narrower 'neck' beneath the genicular bend. This thecal character is even more strongly pronounced in *M. (U.) protospineus* sp. n. (Fig. 6A: arrow) and in *M. (U.) spineus*.

There is little doubt that both the dorsal curvature and the gentle sigmoidal thecal shape developed gradually within the lineage. In a single chronodeme (single rock sample), one could observe rhabdosomes varying from straight to slightly bent (Mielnik, interval 792.70–790.55 m) as well as proximal thecae with either straight or ventrally incised walls (Mielnik, depth 790.55 m).

A certain reduction in the rhabdosome length has also been recorded. Whilst *M. (U.) acer acer* features fairly large rhabdosomes, the terminal link, *M. (U.) spineus* has shorter rhabdosomes. The transient link *M. (U.) protospineus* sp. n. is represented by specimens too fragmentary to infer the size of the rhabdosome. This conclusion has, however, only a tentative meaning as they depend heavily upon the preservation state and the conditions of chemical treatment of preserved remains.

Summing up one can conclude that the sequence of evolving populations, regarded here as *M. (U.) acer* → *M. (U.) acer aculeatus*, displays a truly gradualistic pattern of change (shift of the mean in one or two traits). In contrast to this *M. (U.) protospineus* sp. n. and *M. (U.) spineus* are morphologically distinct and although immediately related are separated by a small discontinuity from respective ancestral species. It seems that they appeared by fixation of a single mutation (or a few mutations), responsible in each case for minor but distinct morphological effects.

The evolutionary meaning of spinosity in monograptids

A distinctly directional effect observed within this lineage led to the emergence of highly specialized spinose forms. Spinosity is also a feature common to the terminal species in many Late Silurian monograptid lineages, e.g. *Lobograptus cirrifer* Urbanek 1966, *Cucullograptus aversus* *rostratus* Urbanek 1966, *Neocucullograptus kozlowskii* Urbanek 1970, and *Monograptus* (*Testograptus*) *testis* (Barrande 1850) (see Urbanek 1966, 1970; Urbanek & Teller 1974). All this brings about the problem of the significance of spines. In the past, this problem was frequently seen in an almost metaphysical perspective, spines and spinosity being considered an immanent property of the advanced (senile, gerontic) phases of the phylogeny. The best illustration of such an approach was Beecher's (1898) classical study on spinose brachiopods and trilobites. Today such explanations can hardly be convincing, although there is no denying that spinose monograptids as a rule represent the terminal species of graptoloid lineages. This implies their rather specialized nature as a product of long-lasting directional evolution and therefore makes them easy victims of extinction during drastic environmental disturbances. There is little doubt, however, that spinosity *per se* is not directly related to the forthcoming extinction of the lineage.

I would suggest that the development of apertural spines in monograptids as the result of feeding specialization among related species, leading to the division of the niche between the spinose and non-spinose species. Although the specific functions of the apertural spines are obscure and may be multiple (trophic, protective, supporting, or sinking preventing), I would suggest that they provided foremost an easy way to produce a large character difference in the trophic apparatus, so important for the co-existence of related species within a single niche and leading to a decrease of within group competition.

Comparative morphology of apertural lobes and spines

The highly elaborated apertural apparatus of *Monograptus (U.) spineus* may anatomically be resolved into several components acquired at different stages of phylogeny (Fig. 5). The foundation of the entire structure is provided by the lobe proper, inherited from common *M. (U.) uncinatus*-like ancestors. This basic structure was preserved without any significant changes in late Ludfordian monograptids, which are directly related to the *M. (U.) acer – M. (U.) spineus* lineage, as defined above. Therefore I suggest to name this structural element the 'acer' acqusition.

Antero-lateral processes constituting the next component (Fig. 5) were acquired at the 'protospineus' stage of phylogeny and the last element, the spines proper, did not appear until the *M. (U.) spineus* stage. Thus, the results of the phylogenetic changes were cumulative, new characters being added to the existing structural elements rather than replacing them (Fig. 5). Hence, the base of the spine in *M. (U.) spineus* is a homologue of the antero-lateral process in *M. (U.) protospineus* sp. n. However, the structure in question was transformed from a tape-like into a rode-like one. Another addition which appeared at the 'spineus' stage of evolution was the promontorium, a protruding anterior edge of the lobe proper. Its

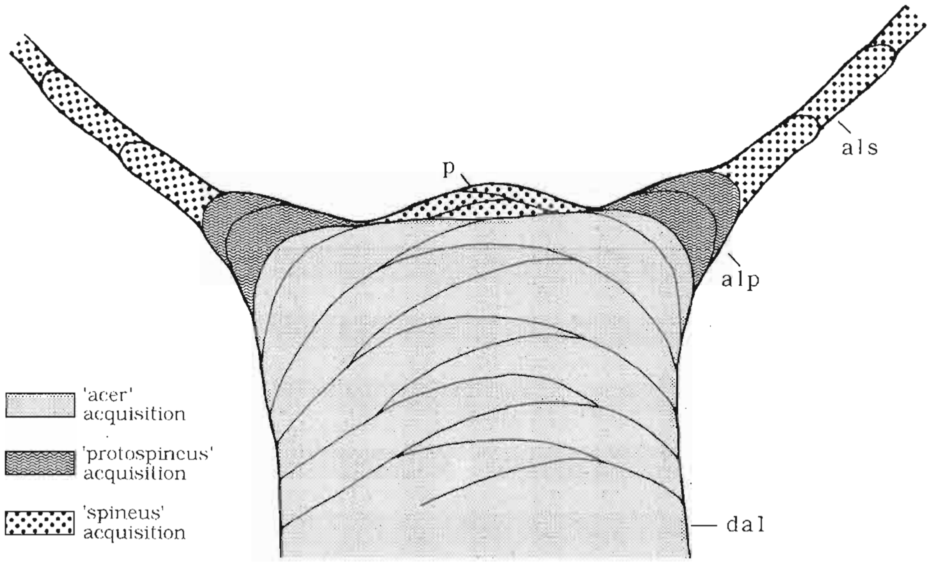

Fig. 5. Morphogenetic components of the apertural lobe in *Monograptus (Uncinatograptus) spineus* revealing the cumulative effect of terminal additions (differently shaded) to the ancestral structures (hypermorphosis). Note the presence of protruding anterior edge of the lobe called the 'promontorium' (p). Abbreviations: alp — antero-lateral processes, als — antero-lateral spines, dal — dorsal apertural lobe, p — promontorium.

angular shape may have foreshadowed the never-realized appearance of the third spine.

Such a mode of morphological evolution strongly resembles other instances of phyletic evolution recognized among monograptids, e.g. the *Cucullogratus hemiaversus* → *C. aversus* → *C. aversus rostratus* lineage (Urbanek 1966) or the *Neocucullograptus inexspectatus* → *N. kozlowskii* lineage (Urbanek 1970).

The phenomenon of addition of new characters to the terminal growth stages of the ancestral structure is well known and has been described by numerous authors in almost every group of animals. A surprisingly large number of terms has also been proposed to denote this mode of morphological evolution in somewhat different contexts. For some students, the essential point was that the addition of a new structural element to the already existing ones meant a certain prolongation of growth or morphogeny, or a terminal addition of a new growth stage. It is worth mentioning in this respect the concept of hypermorphosis of de Beer (1940: pp. 31, 77), applied to the graptoloid thecal characters by Westoll (1950), and criticized and modified in certain respects by Bulman (1951) and Urbanek (1960, 1973). Some other notions may also be applied with a greater or lesser accuracy to the problem in question (see de Beer 1940: p. 77). There is a danger, however, that this terminological redundance may obscure the nature of the processes involved which in our case boil down to a gradual and additive mode of evolutionary change.

Stratigraphical setting of the lineage

The late Ludfordian fauna appears in the East European Platform after the *N. kozlowskii* Event (Urbanek 1993). The event resulted in the extinction of specialized early Ludfordian representatives of *Neocucullograptus* and *Polonograptus*, as well as of the last *Bohemograptus*. However, the appearance of the new fauna was preceded by a low diversity assemblage composed of relatively common *Linograptus posthumus* and *Pristiograptus dubius* s.l. In turn they gave way to true late Ludfordian fauna represented by *Pseudomonoclimacis latilobus* (Tsegelnjuk 1976), *Pristiograptus dubius fragmentalis* (Bouček 1936), *Monograptus balticus* Teller 1966, *Monograptus hamulosus* Tsegelnjuk 1976, and *Monograptus (Formosograptus) formosus* Bouček 1931. They appeared in a rapid succession (in fact almost simultaneously), marking a single graptolite assemblage zone, namely the *P. latilobus/M. balticus* Zone.

The first representative of the *M. (U.) acer* → *M. (U.) spineus* lineage, *Monograptus (U.) acer* appears above the last named zone, defining in this way the lower boundary of the eponymous zone. This zone is subdivided into lower and upper subzone, by the presence of the corresponding index subspecies: *M. (U.) acer acer* and *M. (U.) acer aculeatus*. The next horizon is marked by the occurrence of *M. (U.) protospineus* sp. n., which in the Mielnik borehole is represented by a thin bed (some 40 cm thick). The material from the Gushcha 4015 borehole of Volhynia examined by the author in 1983 with a kind permission of Dr. P. Tsegelnjuk, reveals that a form conspecific with our *M. (U.) protospineus* sp. n. is also present there. That is why *M. (U.) protospineus* Zone is tentatively recognized in the present paper as a separate unit. It is followed by the *M. (U.) spineus* Zone, defined by the occurrence of the eponymous species and recognized as a biostratigraphic unit by Koren' (1992) in Tien Shan sections (Kyrgystan). *M. (U.) spineus*, described from Volhynia is also present in E Poland and in Central Asia. I agree with Koren' that the species in question is a good candidate for a standard index fossil of the late Ludfordian. Its extinction is related to the next faunal turnover, mentioned above (p. 3) and preceding the appearance of an abundant early Přidoli assemblage. Therefore, the sequence encountered in the Mielnik borehole reveals a clear temporal replacement in the vertical distribution of the members of the *acer-spineus* lineage (see Fig. 3, for vertical range and stratigraphic subdivision). Consequently they are interpreted as chronospecies (or subspecies) within a single line of descent.

In other areas, the sequence within this lineage is less clear. According to Tsegelnjuk, all species of the *acer–spineus* lineage co-occur within a single assemblage and are associated with *Pseudomonoclimacis latilobus* and *M. balticus*. This conclusion may probably be explained by the low resolution, used in the study of vertical distribution of his borecore material, rather than by real differences in distribution. However, Koren' (personal communication) also mentions the co-occurence of *M. (U.) acu-*

leatus and *M. (U.) spineus* in the sections from the Kursala Formation of Tien Shan (Kyrgystan). Moreover, all these species are reffered by her to a broadly understood *M. (F.) formosus/M. (U.) spineus* Zone of the late Ludfordian.

Taxonomy and nomenclature of lobate-spinose Ludfordian monograptids

In spite of the short history of investigation, the taxonomy and nomenclature of Ludfordian lobate-spinose monograptids is not free from complexity. Initially Tsegelnjuk (1976) described two species of hooded and spinose (lobate-spinose in the terminology applied in the present paper) monograptids from the borehole material of Volhynia, to which he has given the name of *Acanthograptus spineus* and *A. aculeatus*. As the generic name *Acanthograptus* is preoccupied by *Acanthograptus* Spencer 1878 (see Přibyl 1983), used to designate a common dendroid genus, Tsegelnjuk's generic name is invalid. Moreover, quite recently Tsegelnjuk (personal communication) has established that the holotype of *'A.' aculeatus* is in fact devoid of spines. It is a normally hooded monograptid, closely related to *'A.' spineus*, but what was previously observed as spine-like or claw-like outgrowths represent merely intersections of the apertural lobe with the bedding plane. Nevertheless, following Koren' (in press), I recognize the validity of Tsegelnjuk's specific name and the taxon designated by it. However, I consider this taxon to be a subspecies, characterized by a simple apertural lobe but a distinct dorsal curvature. It is one of the members of the *M. (U.) acer* → *M. (U.) spineus* lineage, namely *Monograptus (Uncinatograptus) acer aculeatus* (Tsegelnjuk 1976).

The subspecific rank for this taxon is accounted for by its minor morphological difference from a form identified by Tsegelnjuk (1976) as *Heisograptus acer*. Except for the degree of the dorsal curvature, which is hardly discernible in *M. (U.) acer* and quite distinct in *M. (U.) aculeatus*, the forms are practically identical. Such minor morphological differences may even be evaluated as intraspecific variation. However, taking into account the progressive nature of the change in the character in question and its potential stratigraphical significance, we propose to distinguish two sequential subspecies — a lower zonal *M. (U.) acer acer* and a higher zonal *M. (U.) acer aculeatus*. The range of their zonal variation fits within a single chronospecies and a given sample may be difficult to assign to one of the subspecies, in view of the gradual nature of changes (pp. 6–7). By delegating *M. (U.) acer* to his genus *Heisograptus* Tsegelnjuk (1976: p. 103), made a rather unfortunate decision. The type species of the genus: *M. micropoma* (Jaekel 1889) has apertural lobes composed of microfusellar tissue as shown by Urbanek (1958), and consequently there is little sense to make this generic name comprise numerous hooded monograptids with a normal fusellar structure of the lobes. In this way the single *M. (U.) acer* – *M.*

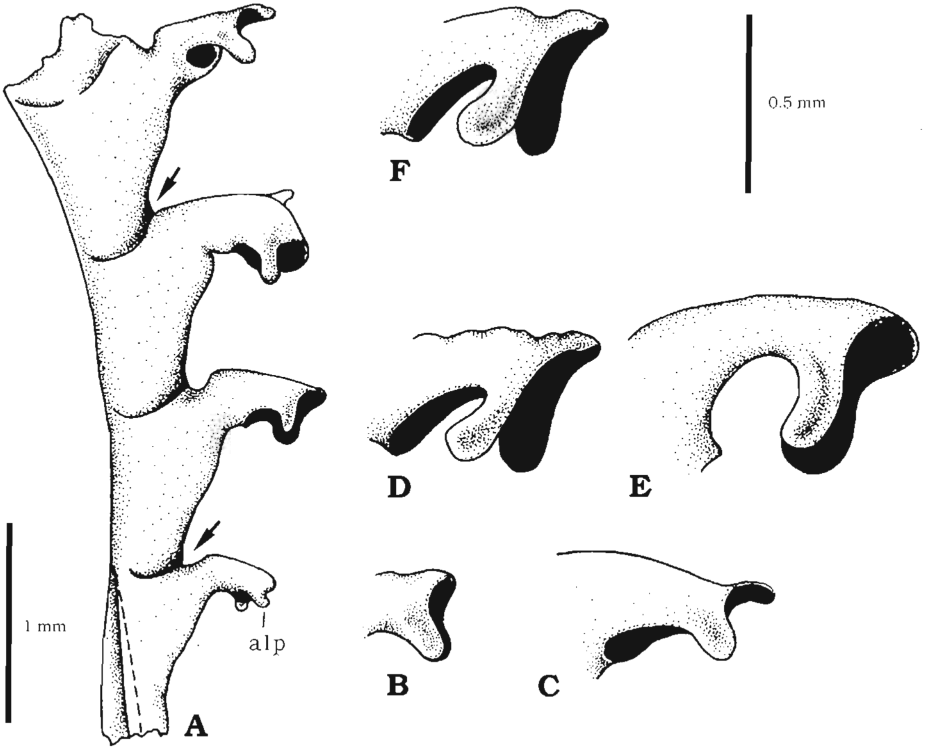

Fig. 6. *Monograptus (Uncinatograptus) protospineus* sp. n. Rhabdosome fragments isolated from Mielnik-1 borehole, depth 773.50 m, *M. protospineus* Zone. A. Proximal fragment with apex of prosicula preserved (ZPAL G. XVII/2). B–F. Different size and shape of antero-lateral processes on apertural lobes of the thecae. Arrows indicate slight incisions at the base of thecae. Abbreviation: alp — antero-lateral processes.

(U.) spineus lineage has been artificially partitioned into two genera, which are either technically invalid or irrelevant.

M. (U.) protospineus sp. n. is ranked as a distinct chronospecies for several reasons: (1) it is separated from its forerunner by a small morphological discontinuity (p. 7), (2) it started a new trend in the evolution towards spinosity, and (3) its thecal characters are readily discernible when flattened. The same holds true for *M. (U.) spineus*, which differs distinctly from its ancestor in having long apertural spines, and belongs to one of the most characteristic species among Late Silurian monograptids. It represents a structure which has not been previously observed in any Ludfordian graptoloid species. Otherwise it retained a number of features shared with its non-spinose forerunners and this is one of the reasons why I assign it to *Monograptus (Uncinatograptus)*. The other reason is that *M. (U.) spineus* did not speciate and consequently did not produce any derived species (a species group). Hence, the erection of a new genus or subgenus is unjustified, in spite of its morphological distinctness.

Description of a new species

Family Monograptidae Lapworth 1873
Genus *Monograptus* Geinitz 1852
Subgenus *Uncinatograptus* Tsegelnjuk 1976
Type species: *Monograptus uncinatus* Tullberg 1883

Monograptus (Uncinatograptus) protospineus sp. n.

Figs 1B–C, 6A–F, 7A–B.

Monograptus cf. *formosus* Bouček; Teller 1966: p. 554, Fig. 12.

Holotype: Fig. 7A, ZPAL G. XVII/1.

Type locality: Mielnik IG 1 deep boring, East European Platform, E Poland.

Type horizon: late Ludfordian, *M. protospineus* Zone, Mielnik-1 bore core, depth 773.15 m.

Derivation of name: From Greek *proto* — beginning, giving rise to, and Latin *spineus* — spiny, thorny.

Diagnosis. — Hooded monograptid with finger-like antero-lateral processes on thecal apertural lobes. Dorsal curvature in the proximal part of the rhabdosome.

Material. — Six semi-flattened rhabdosome fragments, including sicula, medial and distal parts, all etched from matrix.

Description. — Sicula (Fig. 1B) straight, approximately 1.5 mm long, with the prosicular apex situated immediately above the apertural lobe of th_1. Prosicula (psi) 0.53 mm long, provided with a distinct apertural ring (r_1). Metasicula (msi), 0.95–1.00 mm long, with a single ring (r_2), situated approximately one-third of the distance from the prosicula to the metasicular aperture. Metasicular aperture somewhat expanded (width 0.40 mm), in result of the presence of a strong, tongue-like dorsal process (dp), some 0.12 mm long. Initial bud situated 0.30 mm from the margin of the metasicular aperture. Virgella robust, 0.80 mm long.

Thecae are uniform throughout the rhabdosome, narrower at the base (0.30 mm at th_1, and 0.45 mm at th_3 up to 0.80 mm in distal thecae), widening towards the aperture, with ventral wall either gently sigmoidal or almost straight. Overlap in proximal thecae very small, increasing in distal ones to 1/3. Apertures are provided with strongly developed, subhorizontally oriented, apertural lobes, resembling in their overall shape the apertural lobes observed in *M. (U.) acer* (Tsegelnjuk 1976). They are fairly long (measuring transversely), 0.50 mm in th_1, 0.60 mm in th_3, and 0.80 mm long in distal portion of the rhabdosome (Figs 6A, 7A).

The species-specific feature of the lobes, observed in all thecae of the rhabdosome are paired antero-lateral processes (Figs 1C, 6B–F: alp). They have a finger- or tongue-like shape and are directed downwards (proximally), being 0.15 mm long in proximal thecae and 0.30–0.40 mm long in the distal ones. Due to their position and length, antero-lateral processes are readily discernible on specimens seen on the bedding planes.They provide an easy identification of the species in question (Figs 6B–F, 7B), which otherwise is very similar to *M. (U.) acer aculeatus* (Tsegelnjuk 1976).

The rhabdosome is distinctly dorsally curved (dorsally concave), with the curvature starting at the prosicular apex. The angle of deviation (D) measured between the long axis of the sicula and the course of virgula along th_1–th_4 is approximately 25°–26°. The degree of the dorsal curvature is similar to that in *M. (U.) spineus* and distinctly stronger than that in *M. (U.) acer aculeatus* (Fig. 4). The N, number of thecae in 10 mm, cannot be directly measured because of the lack of longer fragments but may be estimated as being about 12 in distal part of rhabdosome.

Comparison. — Bleached specimens reveal that the microstructure of the apertural lobes proper do not differ from that in other representatives of the *M. uncinatus* group of monograptids. The apertural lobe is made thus of a double series of fuselli, producing a broad zig-zag suture (Fig. 1B–C, l). The only addition to this basic structure are antero-lateral processes discussed above (p. 2), representing a novelty initiating a trend towards spinosity (Figs 1B–C, 6: alp).

Phylogeny. — The position of *M. (U.) protospineus* sp. n. within the *M. (U.) acer–spineus* lineage is clearly defined by its morphology and stratigraphical occurrence. Morphologically, it foreshadows the truly spinose *M. (U.) spineus*, and stratigraphically, it occupies the short interval between last appearence of *M. (U.) acer aculeatus* and first appearanceof *M. (U.) spineus*. In contrast to the abundant populations of the ancestral and descendant species, *M. (U.) protospineus* sp. n. is represented by few specimens and was very short ranging. All this indicates that it was a truly transient link, subject to a rather rapid transformation into a more advanced morphological type, represented by *M. (U.) spineus*. However, in spite of this it was rather widely distributed (East European Platform, Central Asia, see below). Hence, a certain bottlenecking of the lineage, at the 'protospineus' stage of evolution, was probably expressed merely by a numerical decrease but not by the reduction of the area of distribution.

Occurrence. — *M. (U.) protospineus* sp. n. has been found in the Mielnik-1 borehole in the interval between 773.50 m and 773.15 m. Hence, the thickness of the type stratum is approximately 0.4 m. However, the examination of the Gushcha-4015 borehole material (made kindly available to the present author by Dr. P. Tsegelnjuk in 1983), revealed the presence at the depth of 758.50–763.00 m of a conspecific form in a stratigraphic position fully analogous to that in Mielnik. Moreover, the form described by Teller (1966) from the Łeba-3 borehole (W Pomerania,

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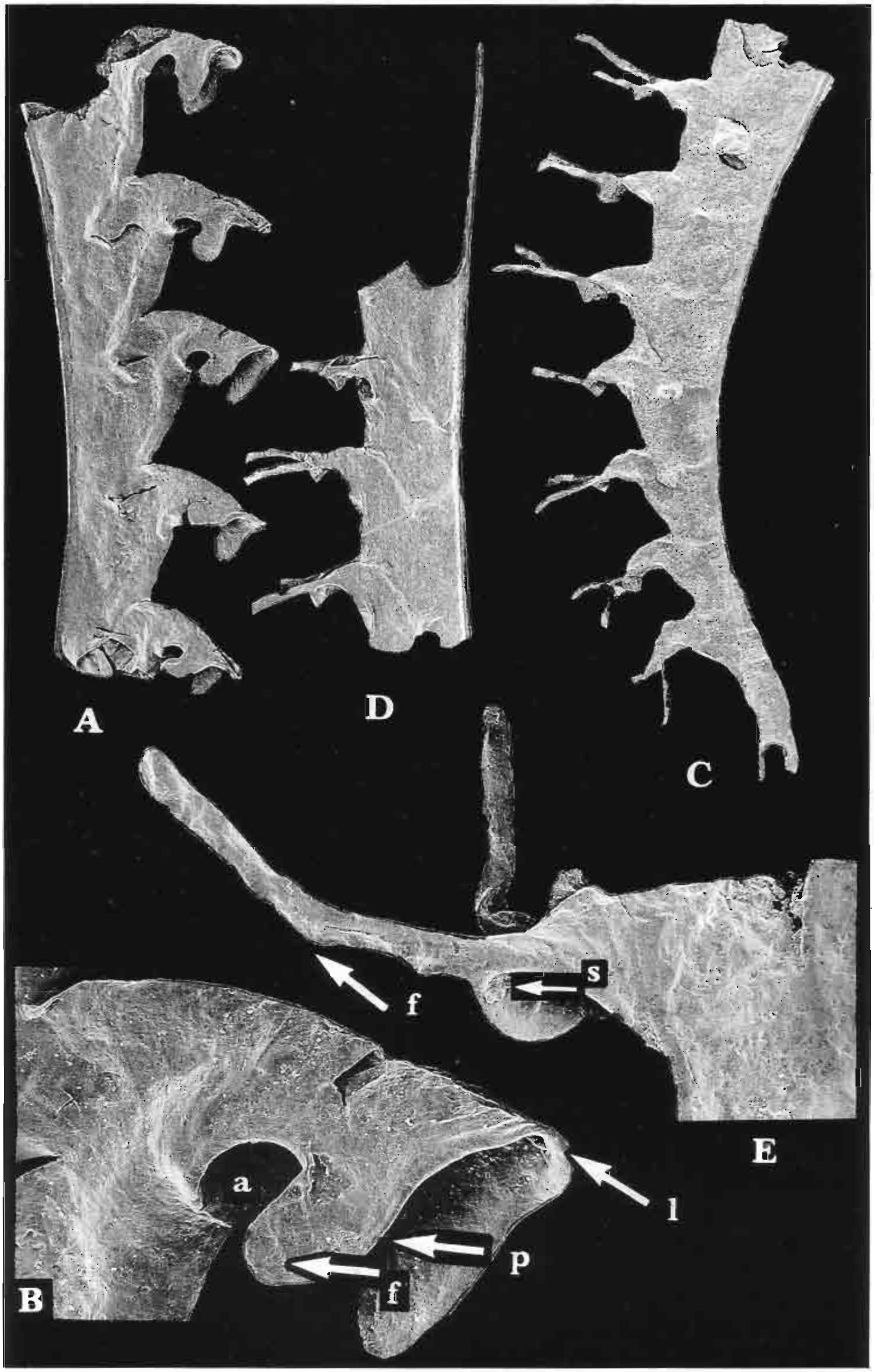
Fig. 7. Late Ludfordian spinose monograptids isolated from Mielnik-1 borecore. ❑A–B. *Monograptus (Uncinatograptus) protospineus* sp. n.: distal fragment of rhabdosome (A, holotype ZPAL G. XVII/1) and details of apertural apparatus (B), both in lateral view, depth 773.50 m, *M. protospineus* Zone. ❑C–E. *Monograptus (Uncinatograptus) spineus* (Tsegelnjuk 1976): proximal (C) and distal (D) part of rhabdosome and details of apertural apparatus (E), all seen laterally (ZPAL G. XVII/3–5), depth 760.15 m, *M. (U.) spineus* Zone. A × 25, B, E × 100, C–D × 20. Abbreviations: a — aperture, f — traces of growth lines (fuselli), l — apertural lobe proper, p — antero-lateral process, s — base of spine.


A
D
C
f
s
E
a
l
p
f
B

Poland) and identified by him as *M.* cf. *formosus,* with its first appearance situated about 50 m above the last appearance of *M. balticus*, is doubtlesly identical with *M. (U.) protospineus* sp. n. and confirms its wide occurrence at a consistent stratigraphical horizon.

Koren' & Sujarkova (in press) have found a probably conspecific form in their sections in the Alai Range (South Tien Shan, Kyrgystan). Its stratigraphical position is, however, less clearly defined.

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Streszczenie

Rozpoznana na podstawie głębokiego wiercenia Mielnik IG-1 (E Polska) sekwencja fauny graptolitowej, wskazuje na wyraźną dwudzielność najwyższego ludlowu (piętro ludford). Dominujące we wczesnym ludfordzie monograptidy z podrodziny Neocucullograptinae wymierają pod koniec poziomu N. *kozlowskii*, w wyniku jednoimiennego zdarzenia (kryzysu biotycznego). Miejsce zubożałego zespolu reliktowego zajmuje następnie zróżnicowana fauna, wsrod ktorej szczegolne znaczenie przypada przedstawicielom *Monograptus* opatrzonych tekami typu „uncinatus”. Pojawiają się one po dłuższej przerwie w zapisie paleontologicznym (tzw. „Lazarus effect"). Powyżej tego poziomu rozwija się linia filogenetyczna, złożona z następstwa: *M. (Uncinatograptus) acer acer* – *M. (U.) acer aculeatus* – *M. (U.) protospineus* sp. n. – *M. (U.) spineus*. Ten ostatni posiada obok płatów aperturalnych także dlugie kolce i jest charakterystycznym gatunkiem przewodnim poinego ludfordu. Stopniowa i kierunkowa ewolucja w obrębie tej pojedynczej linii stanowi przykład tzw. „ewolucji filetycznej". Zmiany ewolucyjne miały charakter kumulatywny i nowe elementy strukturalne byly dodawane do już istniejących (hypermorfoza) *M. (U.) protospineus* sp.n. reprezentuje ogniwo posrednie i ma platy aperturalne opatrzone zaczątkowymi wyrostkami, na których w dalszym przebiegu filogenezy powstaly prawdziwe kolce aperturalne. Niezwykłe podobienstwo *M. (U.) spineus* do „kolczastych" monograptidow poinego wenloku jest więc wyrazem homeomorfii.