

Oligophyly and evolutionary parallelism: A case study of Silurian graptolites

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Oligophyly may be defined as a restrictive factor in evolution leading to minimization of the number of phyletic lines owing to an occasional reduction by means of mass extinction as well as to their recovery from scanty survivors. The monophyletic origin of the vast majority of taxa finds its explanation in this succession of events, namely in the diversity reduction (DR) – rediversification (RD) sequence. In turn, the recovery from a few or a single ancestral species (near-monophyly or monophyly) causes a number of consequences for the evolution of emerging new taxa. They produce a particular class of systematic groups called genealogical domains. Such groups display an exceptionally close affinity and a similar evolutionary potential exhibited i.e. an abundant parallelism. In other words, the paucity of ancestry (oligophyly) explains why both the monophyletic origin and evolutionary parallelism are such common features of the phylogeny in most fossil groups. Parallelism is caused by the similarity of apomorphic tendencies (known as ‘underlying synapomorphy’ in phylogenetic systematics), which are among the most characteristic features of evolution within a genealogical domain. It is now evidenced that the vast majority of Late Silurian monograptid faunas are descendants of only two species – survivors from the severe *lundgreni* Event. Numerous cases of heterochronic parallelism and evolutionary repetitions observed within the repertoire of the Late Silurian monograptid faunas may be explained as a far reaching effect of oligophyly. Each ancestral species established its own genealogical domain displaying certain apomorphic tendencies. The same is true for the monophyletic origin and early radiation of Llandovery monograptids. Whilst graptolites provide numerous graphic examples substantiating the oligophyly concept, it is clear that the phenomena discussed are of a much more general nature.

Key words: Monophyly, oligophyly, mass extinctions, adaptive radiations, recoveries, genealogical domains, evolutionary parallelism, graptolites, Silurian.

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'...Classification consists in grouping beings according to their actual relationship, i.e. their consanguinity, or descent from common stocks'.

(Charles Darwin in his letter of 26 July 1843 to George R. Waterhouse. In: F. Burkhardt (ed.), 1996 *Charles Darwin's Letters*).

Introduction

Ever since Darwin, a far-reaching goal of systematics has been to understand classification in terms of evolutionary history. In this sense, biological systematics may be considered a historical science (Ghiselin 1996). However, it is clear that classification can be neither explained by nor deduced from the general theories or rules of evolution. Classification may be derived from the knowledge of the course of evolution, understood as a narrative about the events which happened in the evolutionary history of a given group. Hence, in the light of the Darwinian tradition, the current task of systematics is to search for the main evolutionary events, or turning-points which shaped the major features of the evolution of a given group or taxon. In this way, one could also comprehend the essential patterns of classification within large systematic groups developing during long time intervals.

In the present paper I shall focus on biotic crises that led to mass extinctions, as factors shaping the important features of the future evolution in the group of survivors and therefore defining also the major features of their classification. Moreover, I will use the history of graptolites to support most of my considerations, although it is obvious that the phenomena discussed here are of a fairly general nature.

The concept of oligophyly and its implications for evolution and classification

One of the most obvious results of mass extinction is reduction of biological diversity, expressed both in the number of taxa and in the number of lineages which they represent. This effect has been well analyzed in numerous instances and the dynamics of such changes in diversity across the extinction horizons has been carefully recorded for a number of bioevents (Walliser 1996). Less understandable are further consequences of the reduction of diversity for the subsequent recovery, for the patterns of radiation, and for the essential features in the evolution of surviving lineages.

From the standpoint of phylogenetic systematics, the crucial factor of the post-event situation is the paucity of phylogenetic lines among the surviving groups of organisms. The results of mass extinctions may be compared to the bottleneck effect at the level of evolutionary lineages (Urbanek 1997). Therefore recovery starts from scanty ancestral taxa, frequently from a single species or only a few taxa, representing an even smaller number of lineages. I have termed (Urbanek 1997: p. 124) this common pattern of survival and recovery 'oligophyly' (from Greek *oligos* – few, scanty, and *phylon* – tribe, race), emphasizing in this way the initially strongly reduced number of surviving phyletic lines, later subject to recovery and re-radiation(s). Hence, such bottlenecking leads to an unusually low diversity among the survivors and, consequently, to a great phylogenetic uniformity of recovering assemblages. Urbanek (1997: p. 123) found

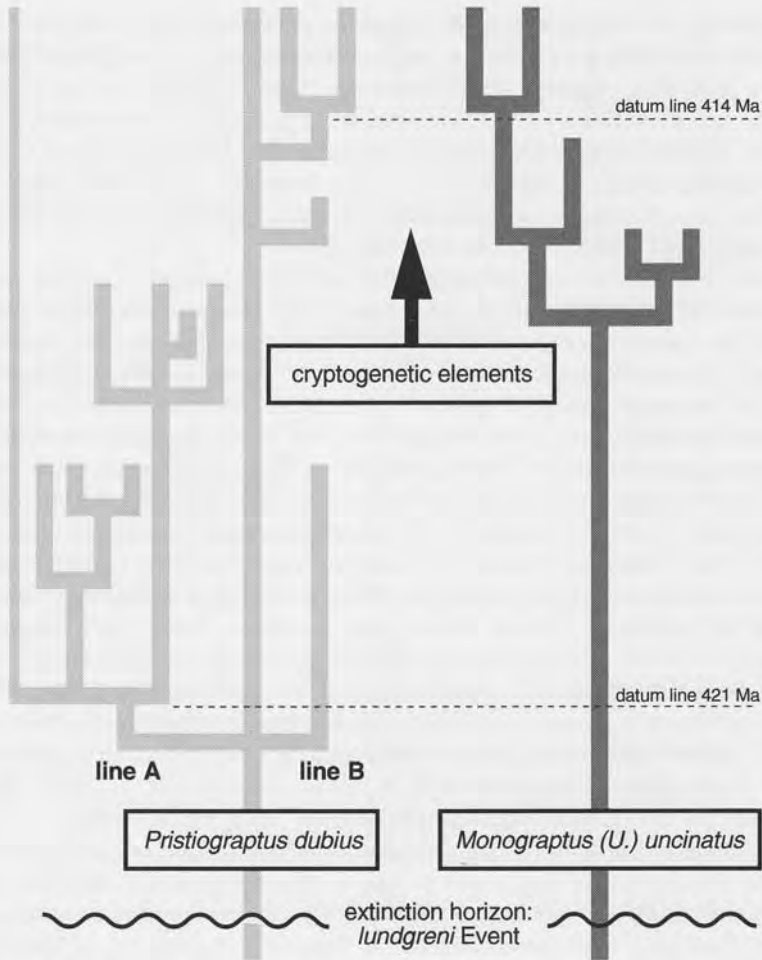


Fig. 1. Main phyletic elements within the Late Silurian monograptid faunas are represented by *Pristiograptus dubius*-related clades and by *Monograptus (Uncinatograptus) uncinatus*-related clades, both survivors of the *lundgreni* Event, as well as by the subsidiary cryptogenetic elements. Radiation pattern based on the data from Urbanek 1997, simplified; datum lines provide approximate numerical age (after Harland *et al.* 1982) for the lower boundary of Ludlow (base of the *nilssoni* Zone, 421 Ma) and for the lower boundary of Přidoli (base of *parultimus* Zone, 414 Ma) in order to define the time-scale for the processes discussed herein.

only three (and possibly even only two) phylogenetic elements in the entire Late Silurian monograptid fauna. I ascribed this paucity of phylogenetic elements to the severe effects of the *lundgreni* Event, survived only by representatives of two lineages: one represented by *Pristiograptus dubius* (Suess, 1851) and the other by *Monograptus uncinatus* Tullberg, 1883. It is now evidenced that the vast majority of later monograptid fauna are descendants of those two species (Fig. 1).

Oligophyly, which can be understood as scanty ancestry (monophyly, near monophyly or strongly restricted polyphyly), led consequently to an unusually close affinity among all derived taxa. They constitute what may be called a genealogical domain characterized by the proximity of common ancestry (Sluys 1989). Among the charac-

teristic features of evolution in such genealogical domains are widespread homeomorphy and especially parallelism as well as the occurrence of repeatedly evolving characters in several ingroup taxa. Numerous cases of heterochronic (diachronic) parallelism and evolutionary repetitions which are part of the evolutionary repertoire of the Late Silurian monograptid fauna (Urbanek 1996, 1997) may also be explained as a far-reaching effect of oligophyly. It is clear from the data that oligophyly should be included into evolutionary consequences of mass extinction (some of these consequences were already recognized by Jablonski 1986).

In more general terms, oligophyly may be defined as a restrictive factor leading to minimization of the number of phyletic lines in the course of evolution due to the occasional (or episodic, see Boucot 1994) bottlenecking of lineages by means of mass extinctions. Therefore 'minimization of polyphyly' is not merely a methodological principle of contemporary phylogenetic systematics, but an objective fact of nature documented for a large number of lineages. In other words: the evolutionary history of many groups passed through recurring periods of near-extinction and recovery from a few survivors, which represents an evolutionary strategy involving minimal polyphyly (= oligophyly or near-monophyly). In this respect, most taxa began under similar initial conditions, characterized usually by the scarcity of existing lineages and underwent a subsequent recovery from a strongly limited number of ancestors. Consequently they share an essentially similar evolutionary potential. In this way, similar initial conditions determine, to a large extent, the course of further evolutionary history for such groups, which above all is the function of the 'propinquity of descent' (using Darwin's 1859: p. 413 phrase). Moreover, it is clear that the principle of a monophyletic origin of 'natural' systematic groups would only be a mental scheme imposed upon nature by their students, were nature itself unable to create critical situations, when only a single, or very few, phyletic lines can go through 'the eye of a needle'.

I focus my attention herein on the processes occurring in time, but it is perfectly clear that similar processes may occur also in space and geographical distributions provide many instances of monophyly (Mayr 1969: p. 140). Dispersal across geographical (and ecological) barriers as a rule reveals a selective pattern. In the majority of cases only one species of a given group has the ability to transgress the barrier, to colonize the new environment and produce a new center of dispersal on the other side. Such events are fully compatible with the oligophyly paradigm, being just an alternative scenario. The only marked difference between the latter scenario and the previously suggested one is the replacement of mass extinction, by the ecological mechanism of barrier selectivity. In both cases, however, new groups originate and diversify from a limited ancestry, thus reinforcing the case for a monophyletic scenario. Moreover, it follows that the mass extinction is not a necessary prerequisite of oligophyly, although commonly it is.

The classical definition of monophyly as given by Haeckel (1868) was subject to different redefinitions, both less (Simpson 1961) and more (Henning 1982) restrictive. The monophyly criterion for the recognition of taxa at different levels has received much criticism (see Borkin 1983 for the review of earlier views and Baum 1992 for the recent standpoints). However, the criteria of monophyly and monophyletic origin are beyond the scope of the present paper. Suffice it to say that monophyly remains one of the paradigmatic concepts of systematics and a more or less strictly defined principle of monophyly or, in other words, the principle of exclusion of polyphyly is widely accepted both in routine systematics (Scotland 1992; Whiting & Kelly 1995) and in the

systematic concepts concerning the major organic phyla (Starobogatov 1994; Cavalier-Smith *et al.* 1996; Nielsen *et al.* 1996). Almost universal occurrence of monophyly (however, with notable exclusions due to hybridization and symbiogenesis) is usually explained by the essentially non-repetitive nature of events involved in the emergence of biological taxa, understood as unique complexes of traits and correspondingly unique sets of genetic information. Such unique combination of characters implies a unique ancestry. According to this view, a multiple origin of a natural taxon is a highly improbable or extremely rare event.

However, the phenomenon of parallel evolution, when taxa with strongly similar complexes of homological traits are produced independently, accounts for a situation when uniqueness of taxa is reduced and when a multiple (polyphyletic) origin of taxa can not be excluded *a priori*. One of examples are cynodonts, a group of mammal-like reptiles considered to be immediate ancestors of mammals. Numerous species of advanced cynodonts attained almost a mammalian grade of organization and may be considered potential ancestors of mammals. Hence, Tatarinov (1976: p. 207) is inclined to think that mammals originated from more than one cynodont ancestor. Yet in spite of this reasoning, Kielan-Jaworowska (1996: p. 620) has summarized most recent developments by stating that 'in the present state of knowledge, the monophyletic origin of mammals appears more probable and is supported by most palaeontologists'. There is, indeed, a remarkable asymmetry between the supply and demand in the phylogenetic machinery. From numerous potentially possible ancestors of a new group which appears due to parallel evolution, a very few or only a single one are usually realized. This contradiction is, in my opinion, resolved by the oligophyly concept, which assumes that monophyly is ensured not solely by the uniqueness of the biological systems involved but also by the periodic bottlenecking of the lineages due to mass extinction or dispersal selectivity. The oligophyly concept offers an historical explanation why the criteria of monophyletic origin could as a rule be met in classification. It also provides an answer why, in spite of the widely spread parallelism in the evolution of many groups, in most cases recognized taxa are not polyphyletic. This is so because their origin is usually preceded by a drastic reduction of diversity (and hence of the number of parallel lineages) to a very few or to a single evolutionary lineage, which then may experience recovery or transformation and subsequent re-radiation.

Restrictive function of mass extinction in graptolites

The starting condition for oligophyly is in most cases a drastic reduction of diversity, a function executed by mass extinctions. There is an ample literature dealing with the dynamics of extinction summarized quite recently by Benton (1995) and Sepkoski (1996), and a general model of recovery was offered by Courtillot & Gaudemer (1996). A general survey of the Ordovician and Silurian Bio-Events including i.a. data on graptolites is provided in Barnes *et al.* (1996) and Kaljo *et al.* (1996). The most common method of data analysis employed in such surveys is based on tracing how frequency distributions in the total number of taxa change across critical horizons in large systematic or ecological groups (diversity curves), a method inadequate for my reasoning. From the standpoint of the oligophyly concept, I am interested instead in the fate of particular taxa like genera or species, or even individual lineages and in the decrease of intragroup diversity at a low systematic level. This difference in approach

is best expressed in the understanding of the N_0 parameter, the initial number of taxa prior to recovery. This parameter serves in some mathematical models of recovery (Courtillot & Gaudemer 1996) to calculate the value of $N(t)$, the number of taxa that occur at time t . In most cases N_0 is simply the initial number of taxa in a given assemblage or a large systematic group, while for my purpose N_0 should be re-defined as the initial number of taxa in a given lineage at $t = 0$. Hence, in the case of the *lundgreni* Event, the pristiograptid lineage in the overlying *dubius-nassa* Zone ($t = 0$) has $N_0 = 1$, whereas for the *uncinatus* lineage $N_0 = (1)$, where brackets indicate the Lazarus effect involved in its survival (Urbanek 1993). Therefore for the entire monograptid stock $N_0 = 1 + (1)$ and for the graptoloids in general $N_0 \sim 4$. The redefined N_0 parameter clearly indicates that each *dubius* and *uncinatus* derived phyletic line originated from a single ancestor and consequently each produced a monophyletic group displaying propinquity of descent.

The analysis of the patterns of change of graptoloid taxa across the extinction horizons given by Štorch (1995) basically meets these requirements. A more recent study by Melchin *et al.* (in press) presents a high-resolution analysis of diversity data on a global scale for the entire Silurian but pays attention mostly to the numerical abundance of species with only a few remarks on extinction/survival of lineages or supraspecific taxa. However, some important data are summarized with regard to individual bio-events, which are important because of their exceptional magnitude and global significance, or due to an exceptionally good palaeontological record or both. Several are discussed in greater detail below.

The terminal Ordovician (late Ashgill) mass extinction belongs to one of the five greatest biotic events recognized within the Phanerozoic (Raup & Sepkoski 1982). Planktonic graptoloids were heavily affected as the vast majority of their species and approximately 11 Late Ordovician genera became extinct. Relic assemblages occurring within the *extraordinarius* Zone were extremely impoverished, composed of a few obviously non-specialized survivors the world over.

The effects of this major biotic crisis were best summarized by Barnes *et al.* (1996: p. 160) who wrote: 'at this time [late Ashgill, A.U.], all graptoloids became extinct with the exception of three or four diplograptid species currently assigned to *Normalograptus* and *Glyptograptus*. It was these few taxa which subsequently gave rise to a totally new, rapidly evolving fauna of the Silurian'. The first sentence of the quotation may be considered a superb summation – of the restrictive impact of mass extinction on diversity while the second sentence is a concise description of oligophyly, understood as recovery from a few survivors.

Re-diversification during the Early Silurian came from two independent stocks: newly emerging monograptids (in the *persculptus* Zone) and generalized diplograptid survivors such as *Normalograptus*. Uniserial scandent colonies of early monograptids represented an evolutionary novelty with a great prospective potential (a uniserial event according to Rickards 1988). However, in spite of the fact that the trend towards a uniserial arrangement of thecae (partial reduction of the second thecal series) was displayed in a number of Late Ordovician–Early Silurian diplograptids, there is strong morphological evidence that monograptids could be derived only from a particular diplograptid stock, displaying a certain type of early development. Thus, from the very beginning, the theca – th 1^1 grows upwards (an apomorphic feature) while otherwise, in the diplograptid type of development, th 1^1 initially exhibits a downward direction of growth. It is only in its distal

portion that th 1¹ starts to grow upwards, which results in a characteristic 'J'-like shape (a plesiomorphic trait). Diplograptids which display this type of development (e.g., *Glyptograptus*) should be excluded from the list of presumed monograptid ancestors; *Akidograptus* or *Parakidograptus*, for the same reason, is a far more probable candidate for this role (Li 1990; Koren & Bjerreskov 1997).

Although we still cannot finally resolve the problem of the origin of monograptids by presenting a morphocline, both the morphogenetic constraints and the course of events revealed by stratigraphy point to their emergence from a single species or from a group of very few closely related diplograptid species (mono- or pachyphyly). But even then their characteristic feature, namely the apertural budding of the first theca, developed gradually, and early monograptids from the *persculptus-vesiculosus* zones, like all diplograptids, still displayed subapertural budding due to the perforation or resorption of the sicular wall (Melchin 1994; Koren's personal information). Adaptive radiation started within the *vesiculosus* Zone at this early stage of the morphological evolution, whereas those monograptids that had already become uniserial represented still a transitional group of 'diplo-monograptids'. A true monograptid condition of the initial bud development, so characteristic of and persistent within the later Silurian uniserial graptoloids, represents most probably a parallel acquisition, attained independently in a number of lineages. This may be interpreted as evidence for their similar apomorphic tendencies (underlying synapomorphy) and, in the consequence, may also support the status of Monograptina as most probably a monophyletic group. This early diversification marked the beginning of an enormous Llandovery radiation of monograptids. It was accompanied by an almost simultaneous differentiation of the genus *Normalograptus* Legrand, 1987, a stem group for the Silurian diplograptids, making many attempts to modernize by a number of novelties its otherwise conservative biserial organization (Koren & Rickards 1996). Therefore, both the monoserial and the biserial stem group of Silurian graptoloids display an extreme decrease in diversity, only later subject to a rapid re-radiation.

Although less deleterious in its general effect, the *lundgreni* Event (late Wenlock, Homerian), was equally devastating with respect to monograptids. Among the diverse taxa which had comprised the pre-extinction assemblage, multiramous cyrtograptids were subject to final extinction, while single stiped monograptids and plectograptine retiolitids were severely affected by mass extinction. The only monograptid that survived the *lundgreni* Event *in situ* was *Pristiograptus dubius*, later the ancestor to the majority of Ludlow monograptids. Its phylogenetic role has been described above. The re-appearances of some taxa with distinct Wenlockian features [*Monoclimacis micropoma*, *Monograptus (Uncinograptus) uncinatus*] suggest a considerable significance of the Lazarus effect in the recovery of the Ludlow graptolite assemblage. However, the only factor of lasting effect for the further development of the Late Silurian graptoloid fauna was the re-appearance of *Monograptus (Uncinograptus) uncinatus*, which was to become the ancestor of Ludlow hooded monograptids. *Pristiograptus dubius* and *Monograptus (U.) uncinatus* represent extinction-resistant lineages, displaying a relatively generalized morphology as is the case with many surviving taxa (Kaiser & Boucot 1996). The entire Late Silurian monograptid fauna is composed of only these two phylogenetic elements plus some species of a cryptogenetic origin, such as *M. (Formosograptus) formosus* (Fig. 1). Some of these enigmatic forms may be eventually assigned to the *dubius* or the *uncinatus* stock, the ancestry of others staying open for long or maybe for ever. But the fact remains that the vast majority of the Ludlow monograptids may be safely derived

from only two ancestral species (Urbanek 1993, 1997). As shown by Jaeger (1959, 1991) and Koren' (1991, 1992), the rich Gorstian monograptid fauna was preceded world-wide by an extremely impoverished assemblage of the *dubius/nassa* Zone, directly overlying the *lundgreni* extinction. The few survivors of this interlude gave rise to the diversity of monograptids as well as of plectograptines (retiolitids). The evolutionary potential of these survivors of the *lundgreni* Event might be justly compared with that represented by the diplograptid generalists from the *extraordinarius* Zone that had survived the *pacificus* Event of the terminal Ordovician (Koren' & Bjerreskov 1997). A striking similarity in the course of events in both biotic crises provides foundations for the oligophyly concept. The crucial feature is the presence of diversity lows preceding the recoveries and re-radiations.

Summing up, it seems safe to conclude that major graptolite radiations are related to recoveries that followed drastic reductions of diversity. Such sequences of events have been observed in numerous cases prior to any theoretical evaluation and belongs to the canonical wisdom of classical palaeontology. Recently, this relation was called by Walliser (1996) the extinction-radiation (E-R) sequence. He stressed the significance of this somewhat paradoxical pattern when extinction events ultimately cause an increase in diversity. I would restate his reasoning by emphasizing rather the reduction of diversity as an immediate effect of extinction, preceding the ensuing radiation. A strong diversity reduction (DR) is a necessary prerequisite of major rediversification, RD (usually an adaptive radiation), producing in this way the following sequence: DR-RD (Fig. 2). The causal factor here is most probably relaxation of competition and vacancy of niches emptied by mass extinction (Urbanek 1993). Major radiations are frequently preceded by changes defining crucial adaptations of divergent evolutionary lines, like the invention of the nematophoric (planktonic) sicula during the dendroid/graptoloid transition or the appearance of a uniserial scandent rhabdosome prior to the radiation of monograptids. Structural foundations of a new adaptive types were sometimes formed during the early radiation phase, as the 'early schism' within the *dubius* stem lineage after the *lundgreni* Event (Koren' & Urbanek 1995). However, even in the former case some new and most crucial features of organization, such as the loss of bithecae in the anisograptid ancestors of graptoloids or the apertural budding of the first theca in early monograptids, were added to the primary foundations as evolutionary improvements, so the emergence of a new structural plan (Bauplan) was additive rather than saltatory.

Small-scale radiations follow a different pattern; they utilize the already existing adaptive innovations as was the case with cucullo- and neocucullograptids. These radiations are usually variations on a theme, as they represent modifications of a certain basic type (Urbanek 1996: p. 125). They are not preceded by a decrease of diversity; in fact they increase or maintain it. Moreover, such small adaptive radiations produce very closely related groups (which again may be considered genealogical domains). A good example is *Lobograptus*, where all species are descending from a common ancestor (*Lobograptus progenitor*), the terminal species being separated by only 2–3 speciation events from it (Urbanek 1966, 1995). A pattern of diversification essentially resembling that in *Lobograptus* is diagrammatically shown in Fig. 2 as subgroup B-H immediately related to its common ancestor B'.

According to the oligophyly concept, recovering lineages produced first a closely related group of taxa, termed a genealogical domain. But it is obvious in the examples that further divergence contributed to a rapid increase in within-group differences and

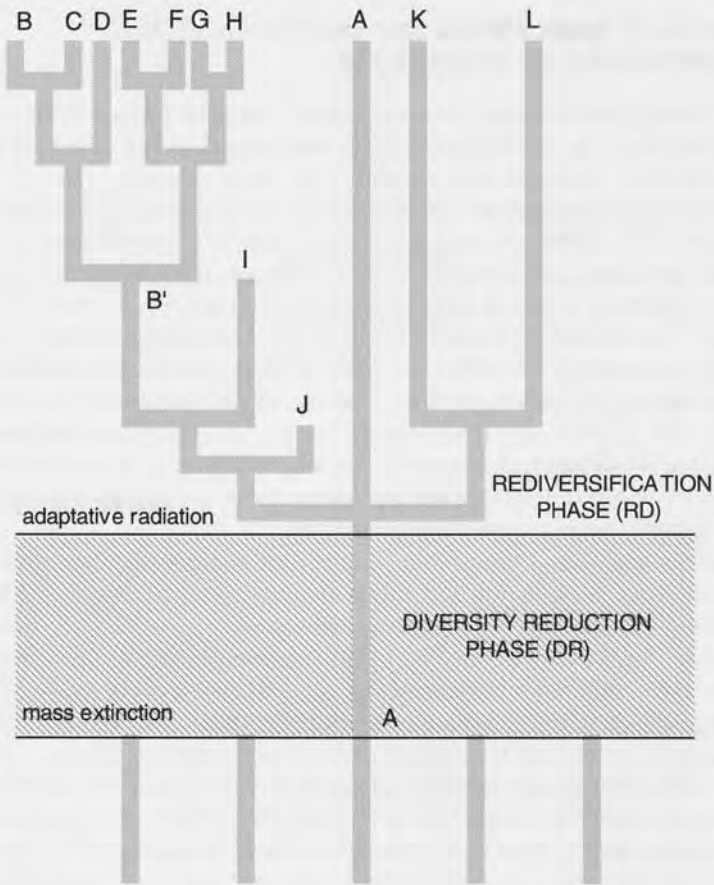


Fig. 2. An ideogram showing the diversity reduction (DR) – rediversification (RD) sequence during the recovery after mass extinction. Note that the only survivor (A) experience an adaptive radiation during the RD phase of the recovery. The end products of particular clades (B-L) produce a group of taxa displaying a proximity of common ancestry. This is particularly true of subgroup B-H immediately related to its common ancestor B' and displaying similar apomorphic tendencies, which in turn are distinctly different from those in K-L (an effect of the early divergence). Data from Koren' & Urbaneck 1995 and Urbaneck 1996, 1997, generalized.

eventually the most characteristic features of such domains, and the proximity of common ancestry faded away. Such was the course of events during the early Llandovery radiation, when monograptids, probably monophyletic in origin, soon lost the nature of a coherent genealogical group and split into a number of subgroups, each displaying their own apomorphic tendencies. The same is true for the late Homerian–early Gorstian radiation of monograptids, the survivors of the *lundgreni* Event. Their early divergence produced a number of evolutionary lines each displaying a different evolutionary potential, with a special position occupied by linograptids. From the very beginning they exhibited an ability to form compound colonies (an apomorphic feature) while retaining the plesiomorphic thecal characters. A vast majority of monograptids reveal a plesiomorphic overall colony shape while exhibiting various apomorphic tendencies in their thecal characters.

A theoretical framework for understanding the implications of oligophyly

A striking feature of evolution in genealogical domains (monophyletic groups of closely related taxa) is parallelism usually understood as an effect of repeatedly evolved characters, acquired independently by close relatives. One of the major debates in the recent phylogenetic analysis concerns the recognition criteria for parallelism (Webb 1994, 1996). An opinion prevails that true parallelisms are based on homologous structures, whilst convergences rely on the analogous ones. Hence, parallelism represents a special case of homology, which Plate (1922: p. 7) named 'homoiology'. As defined by Sluys (1989: p. 352), 'homoiologies are presumed to be independent evolutionary derivations, which develop from similar homologous precursors'. Abundant parallelism provides evidence of propinquity of descent (Gosliner & Ghiselin 1984: p. 260), and its presence is a common feature for numerous groups, both extant and fossil (such groups were listed by Gosliner & Ghiselin 1984: p. 264, and Sluys 1989: p. 351). Parallelisms are especially abundant in particular groups of organisms defined above as genealogical domains.

It seems obvious that a group recovering from a single survivor or from a few closely related ones eventually forms a genealogical domain (Urbanek 1997). A case study of parallel evolution in two genealogical domains of Late Silurian monograptids is given below. Such domains are first of all characterized by the proximity of their common ancestry and by similar apomorphic tendencies within all taxa or clades. This is best expressed in frequent instances of parallelism caused by both the common inherited genetic factors and the resemblance of the epigenetic system. The capacity repeatedly to develop synapomorphies (derived shared characters), called the underlying synapomorphy by Saether (1979, 1983) and Sluys (1989), may be considered one of the most characteristic features of evolution within a genealogical domain. Parallelism in them is frequently ubiquitous (rampant) and involves repeatedly evolving characters that are homologues. In turn, the presence of such parallelism is an indication of a common ancestry (monophyletic origin) as shown by Brundin (1976). It is especially true when parallelism is confined to a certain taxon (inside parallelism) and occurs in various subgroups of this taxon.

The concept of underlying synapomorphy implies a presumed common evolutionary potential in a given group based on persistent hereditary factors whose expression might be blocked and maintained in the genotype for millions of years (Sluys 1989; Urbanek 1996) or re-activated in the presence of some other genes and/or in a certain environmental situation defining the direction of selection. Therefore some authors appeal to the notion of canalized evolutionary potential (Sluys 1989), assuming that at the level of the epigenotype, potentially available genetic information is usually organized into a number of developmental channels owing to certain developmental constraints. The subsequent on- and off- switching of the genes (sometimes by a single mutation) may represent a repeated appearance of an apomorphic character in various clades. While I focus my attention on genotypic (mutational) and epigenetic constraints it is clear that selective factors are also necessary to produce such effects. A remarkable feature of underlying synapomorphy is mosaicism in the expression of certain characters. This situation, in my opinion fits in with the fossil record, where 'new features are often 'cut and pasted' on different groups at different times' (Shubin 1998). Such a pattern of parallel evolution

differs from classical orthogenetic schemes demanding a linear progression of key features within each lineage descending from a common ancestor. Moreover, when I refer to evolutionary potential, I usually have in mind close relatedness created secondarily due to oligophyly while orthogenetic concepts emphasized the significance of hereditary potential created during the earliest stages of the phylogeny of a given group.

The underlying synapomorphy concept has sometimes been criticized (Kitching 1996) for introducing the notion of a common ancestor with a presumed latent potential only later exhibited as apomorphic tendencies. According to the critics, such a reasoning has a relatively low explanatory potential and introduces a sort of undesirable predetermination to the understanding of evolutionary change (see also a similar criticism of latent potential concept in Tatarinov 1976: pp. 191–192). I believe that this controversy may be solved by interpreting the underlying synapomorphy as an unexpressed capacity of the entire genome or epigenotype to develop certain characters due to the appearance of even little specific mutations. It is of some interest that essentially the same explanation was suggested already by Darwin (1859: p. 161).

The recent studies on genealogical domains and evolutionary parallelism have developed rather independently from similar concepts of the past. But it is worth mentioning that 'the law of the homological series of variation' described by Vavilov as early as 1922 is, in a way, just another aspect of the same theme (see also Wake 1996). What Vavilov meant by this law were analogous spectra of the phenotypic and genotypic variation among related taxa, when strikingly similar traits occur with such a regularity that the presence of a character or a morph in a given taxon could be predicted on the basis of its presence in another taxa. The presumption of close relatedness provides an explanation for the homological series of variation. There are good reasons to believe that 'analogous variation' described by Darwin (1859: p. 159) in domesticated animals and cultured plants is essentially the same phenomenon as Vavilov's homological series of variation (Kozulina 1988; Ghiselin 1996).

Vavilov's ideas stimulated thinking of some palaeontologists to mention only Bulman (1933) and Rozanov (1974). Bulman described the repetition of similar themes (such as the number of the stipes and their direction of growth) in the evolution of different graptoloid lineages as 'programme evolution' and compared them with Vavilov's homological series of variation. Rozanov used a similar explanation for the appearance of strongly similar structures in the evolution of parallel lines of Cambrian archaeocyathids. He concluded that the structures in question may reasonably be considered homological. Moreover, the morphological traits in a homologous series may be arranged into a grid-like classification scheme, to some extent similar to the periodic system of elements. Empty cells permit prediction of the possibility of occurrence of some structural types, yet unknown but potentially likely to exist.

One may conclude that both concepts – that of the homological series of variation and that of the underlying synapomorphy – rely on the correspondence between the behaviour of genetic factors and the patterns of phylogeny. It seems also safe to generalize that palaeontological material abounds in instances of parallel evolution, Vavilov's 'law' being only a special case of this mode of evolution.

Recent phylogenetic studies emphasize the essential difference between parallelism and convergence. The latter concerns analogous similarity based on non-homologous structures (Sluys 1989). According to Gosliner & Ghiselin (1984: p. 258), 'convergence' means that the taxa began with different initial conditions and, by different pathways,

arrived at a similar condition'. The meaning of 'parallelism' emphasizes the significance of a common evolutionary potential, while 'convergence' puts emphasis on the role of selection. This corresponds to a primary and straightforward meaning of both terms in classical evolutionary theories but paradoxically makes them theory-laden. This fact explains why they were subject to such different approaches by different evolutionary theories: whilst neo-Darwinian theories, emphasizing the role of natural selection, usually underestimate the significance of evolutionary parallelism, the anti-Darwinian (auto-genetic) theories, stress especially the role of parallelism due to a common initial evolutionary potential as a factor determining the course of evolution (e.g., Schindewolf 1950 among palaeontologists and Lubischew 1982 among neontologists). The latter theories recognize parallelism at the expense of divergence and adaptive radiation, whilst to a selectionist evolutionary parallelism smells of intracausality (or autogenesis), that is evolution without selection, merely due to internal factors of organisms.

To make matters worse, many cladists have also been inclined to diminish the role of parallelisms because they obscure the significance of synapomorphies in establishing the phylogenetic affinities and undermine the universality of the principle of parsimony in the construction of phylogenetic trees. Some have denied the importance of parallel evolution as a phenomenon, some as a methodological problem or both (Hennig 1982; Eldredge & Cracraft 1980; Wiley 1981; Patterson 1982). Views have even been expressed that the concept of parallelism should be omitted from systematic studies (for an overview and critique of this radical approach see Gosliner & Ghiselin 1984: pp. 257–258). The reasonable solution is that the cladistic approach should be combined with the relaxation of the parsimony principle when we are dealing with rampant parallelism (Sluys 1989).

Nevertheless, the fact remains that parallelism, overestimated by some students and underestimated or even denied by some others, is not a peculiarity of evolution in a few groups, but a general rule. Exceptions are fairly few and in some groups (at the rank of order or suborder) parallel evolution often exceeds divergent evolution. In my opinion, this is largely due to the effect of the initial oligophyly (followed only by a modest divergence), upon the further evolution of many groups.

It is also clear that evolutionary parallelism is intrinsically related to monophyly. Parallelism in evolution of homological characters is an expression of close affinity between lineages which, in turn, in most cases may be ascribed to their monophyletic origin. This point has been raised many times (Schmalhausen 1947, 1969; Remane 1964; Mayr 1969; Ivanov 1988) but may be better explained only now in the light of the oligophyly concept. From the same principle it follows that although parallel evolution is a frequent mode of phyletic change, it is punctuated by mass extinctions that minimize the degree of polyphyly and in most cases ensure a monophyletic or near-monophyletic origin of the emerging new higher taxa. No wonder that Steinmann (1908) who visualized the entire history of the living world as events within innumerable parallel lines, attaining independently certain levels of organization, or 'phyletic stages' (such as fishes, amphibians, reptiles and birds or mammals) refuted the mere notion of extinction and accepted only pseudo-extinction due to phyletic transformation. I believe also that mass extinction is crucial for subsequent evolution of recovering groups because it creates proximity of common ancestry.

While classical palaeontology puts a strong emphasis on evolutionary parallelism, the pendulum has recently swung towards the undervaluing rather than overvaluing of

the significance of parallel evolution. Among the minority of students considering evolutionary parallelism equally important to divergence I would mention Tatarinov (1976) with his penetrating analysis of this evolutionary pattern in therapsids.

Parallelisms and evolutionary repetitions among Late Silurian monograptids

The Late Silurian monograptid fauna is composed essentially of only two phylogenetic elements, each descending directly from a single survivor of the *lundgreni* Event as mentioned above: either from *Pristiograptus dubius* or from *Monograptus (Uncinograptus) uncinatus*. Each survivor eventually produced a monophyletic genealogical domain displaying numerous cases of heterochronic (diachronic) parallelism based on independently acquired homological traits. The *dubius*-related genealogical domain was composed of a conservative stem lineage, represented by the persistent *P. dubius* itself, as well as of two progressive lines (named 'A' and 'B' line respectively in Koren' & Urbanek 1995 and Fig. 1 herein). The primary divergence between lines A and B (the 'early schism') involved only incipient slenderness (line A) or robustness (line B), but later each stock revealed a fairly different evolutionary potential. Representatives of line B combined their ancestral robustness with the development of paired lateral (bilateral) ear-like lobes or elevations (e), which were called 'blinders' (Fig. 3). The primary character state is expressed as triangular lobes (*Colonograptus* Přibyl, 1942), whereas the advanced one displays a pair of lateral spines, frequently shifted from the lateral to the postero-lateral position (*Saetograptus* Přibyl, 1942). Both astogenetic and morphological transients occur between these two character states, providing, in conjunction with their stratigraphic occurrence, a justification for the origin of all spinose monograptids (saetograptids) from a single ancestor, namely *Pristiograptus praedeubeli* (Jaeger, 1990), which, in turn, is an immediate descendant of *Pristiograptus dubius* (Suess, 1851). All saetograptids become extinct as a result of the *leitwardinensis* Event (Urbanek 1970), while most of the A-line derived taxa disappeared at the *kozłowskii* Event. This released the *dubius* stem lineage from competition, which resulted in the late Ludfordian and early Přidoli in a new diversification of the conservative pristiograptids, which were strongly reminiscent of the morphologies known from the Gorstian. As suggested by Urbanek (1993: p. 39) the extinction of the majority of intragroup competitors exploiting largely the same resources produces an effect of escape from competition and results in an ecological release. Certain aspects of this issue were discussed again by Koren' & Urbanek (1996: p. 146).

Thus both the late Ludfordian *Pseudomonoclimacis latilobus* (Tsegel'nyuk, 1976) and some early Přidoli monograptids, *Istrograptus*, *Neocolonograptus*, reveal lateral apertural lobes mimicking those of the B-line of the early Ludlow. In general, apertural elevations (e) were generated at least three times: in the Gorstian (eG), in the late Ludfordian (eL), and in the early Přidoli (eP), in the latter case – at least in two parallel lineages (Figs 3, 4). This was interpreted by Urbanek (1996, 1997) as an example of iterative evolution from the conservative *dubius* stem species, or, in other words, as a case of a heterochronic parallelism. The similarity is based on the homology of the structures involved, namely, the apertural lobes are made of the same specific skeletal tissue (fusellar tissue), displaying an identical arrangement of growth bands and showing the same relation to the thecal walls and the aperture (Urbanek 1996). This homological resemblance of morpho-

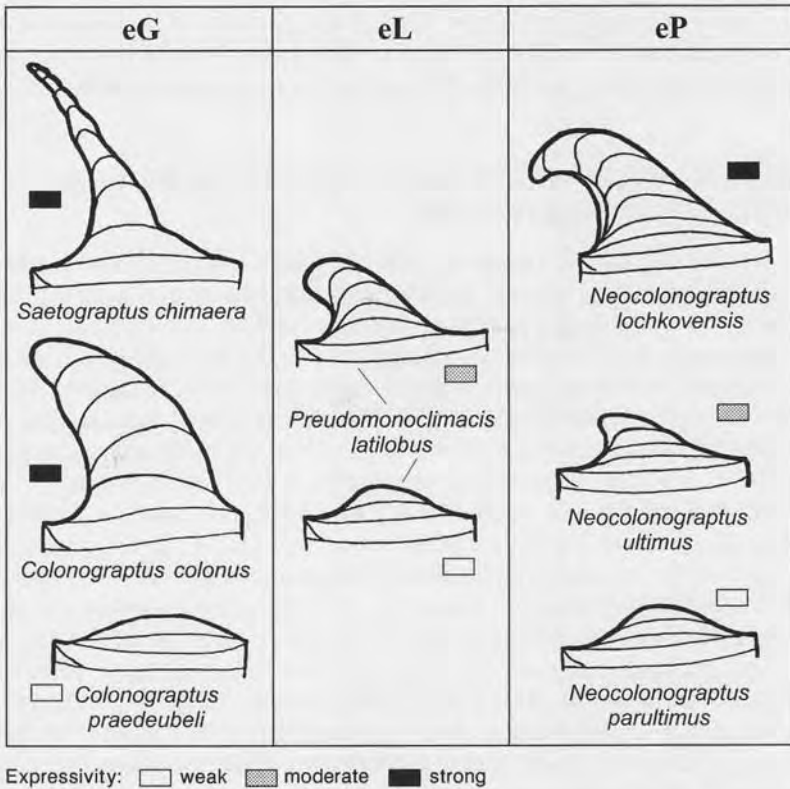


Fig. 3. The morphology and degrees of expressivity of the paired lateral elevations on the thecal aperture (e) which evolved within the Homerian–Gorstian (eG), Ludfordian (eL) and Přidoli (eP) iterative lineages deriving from the *Pristiograptus dubius* stem line: *Colonograptus praedeubeli*–*Colonograptus colonus*–*Saetograptus chimaera*; *Pseudomonoclimacis latilobus* displaying a low and a higher degree of expressivity; as well as *Neocolonograptus parultimus*–*Neocolonograptus ultimus*–*Neocolonograptus lochkovensis* lineage. Diagrammatically from camera lucida drawings; the same data were used to plot Fig. 4.

logical traits does not imply, however, a true synapomorphy because the characters in question were acquired independently, and at different times, every instance being connected with a distinct morphocline. Instead, it is a neat example of an underlying synapomorphy as defined above. *Neocolonograptids* of early Přidoli age are so remarkably similar to the earlier Ludlow colonograptids that they provide evidence that the *dubius* stem lineage featured essentially the same evolutionary potential during the Přidoli time as during the late Wenlock and Ludlow. This question was discussed in some detail in Urbanek (1996: pp. 120–123). He has also substantiated a non-cladistic understanding of the *Pristiograptus dubius* stem species (see also Koren' & Urbanek 1995), because this stem species survived a number of speciation events without a significant alteration of its evolutionary potential. Therefore an application of the 'nodal principle' demanding that after each speciation the ancestral species should be given different binominals seems unjustified. Although separated by at least 5 Ma, both *Colonograptus* and *Neocolonograptus* as well as *Istrograptus* (Fig. 4B, E, F) were derived from the same persistent species, namely *Pristiograptus dubius* (Fig. 4S–S'). Thus they represent a case of

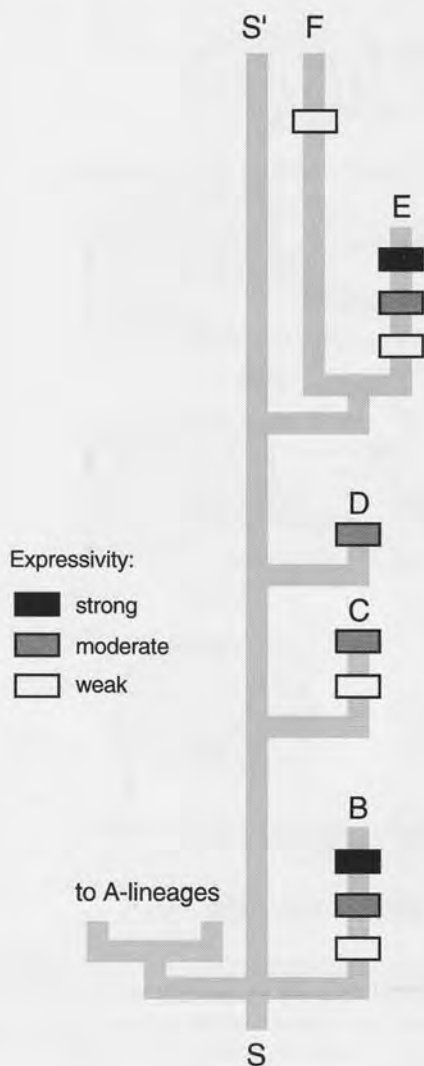


Fig. 4. The distribution and degree of expression (character state) of paired lateral apertural elevations (e) or lobes (such as shown in Fig. 3) within iterative clades (B-F) that branched off the *Pristiograptus dubius* stem lineage (S-S') and displayed apomorphic tendencies parallel to B line. Explanations: B – *Colono-graptus praedeubeli*–*Saetograptus chimaera* lineage, C – *Pseudomonoclimacis latilobus*, D – aberrant ?*petri*, E – *Neocolono-graptus parultimus*–*N. lochkovens* lineage, F – *Istrograptus trans-grediens* lineage displaying isochronous parallelism to E.

a heterochronic (diachronic) parallelism within a group of closely related taxa (a genealogical domain). In spite of a considerable time interval separating the origin of both the lineages, their ancestor was the same species, the long lasting *Pristiograptus dubius*, and they should be considered monophyletic by definition and by virtue of biological reasoning (Urbanek 1996, 1997).

Hence, the history of the *dubius*-related B group of Late Silurian monograptids (or genealogical domain B), may be restated in terms of the underlying synapomorphy (Fig. 4B–F). The recurrent generation of morphologically similar forms, based on homological structures displaying striking resemblance in minute details, may be considered as an expression of common apomorphic tendencies or as underlying synapomorphy.

The history of the *uncinatus*-related group may be visualized in the following way: the bulk of the late Wenlock hooked monograptids probably represented a monophyletic

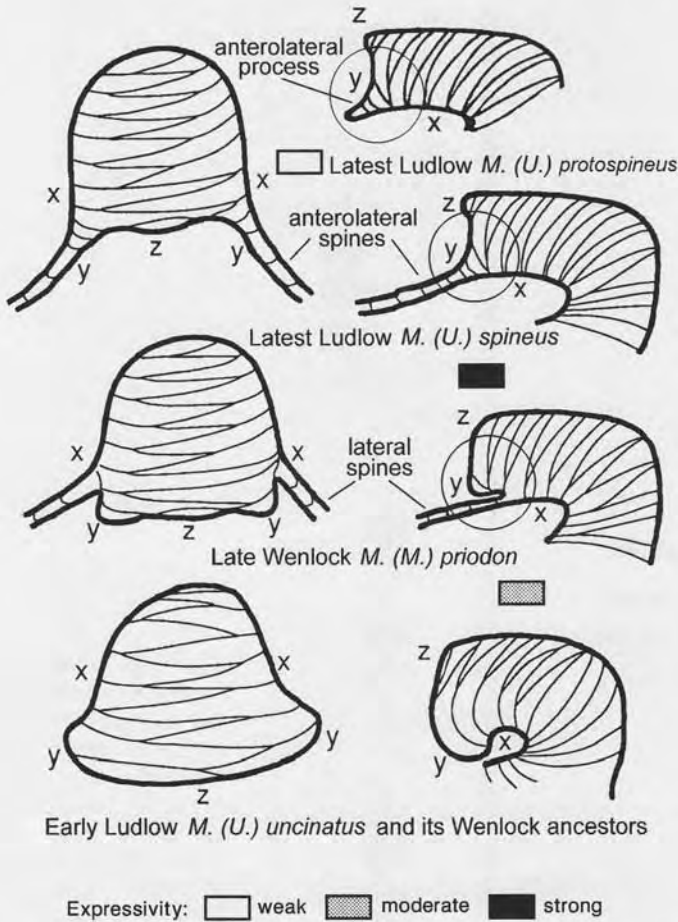


Fig. 5. The apertural apparatus in hooked monograptids of the late Wenlock, early Ludlow (Gorstian) and latest Ludlow (Ludfordian), seen ventrally and laterally. Note that the ancestral species is devoid of any additions to the single hooked apertural lobe while late Wenlock and late Ludlow ones are provided (encircled) either with lateral or anterolateral processes or spines displaying a different degree of expressivity; x, y, z are homologous points. After Urbanek 1996, modified.

group, and their common ancestor belonged to one of the few survivors from the severe *murchisoni* Event, which strongly bottlenecked monograptid lineages (see Štorch 1995). Some of the late Wenlock representatives, in addition to the unpaired apertural lobe, exhibited to a various degree paired apertural spines as is the case within the *priodon-flemingi* group (Fig. 5). The latest Wenlock spinose monograptids of the *testis* group assigned to *Monograptus (Terstograptus)* featured a specialized overall rhabdosome shape and extremely elongated spines. While all spinose monograptids became extinct following the *lundgreni* Event, the non-specialized hooked monograptids survived displaying only the Lazarus effect (Urbanek 1993). They were ancestors to *Monograptus (Uncinatograptus) uncinatus* recognized from the *nilssoni* Zone of the basal Ludlow and showing a single apertural lobe with no spines. This species was the ancestor to all the Ludlow hooded monograptids. They all lacked lateral spines with the exception of the

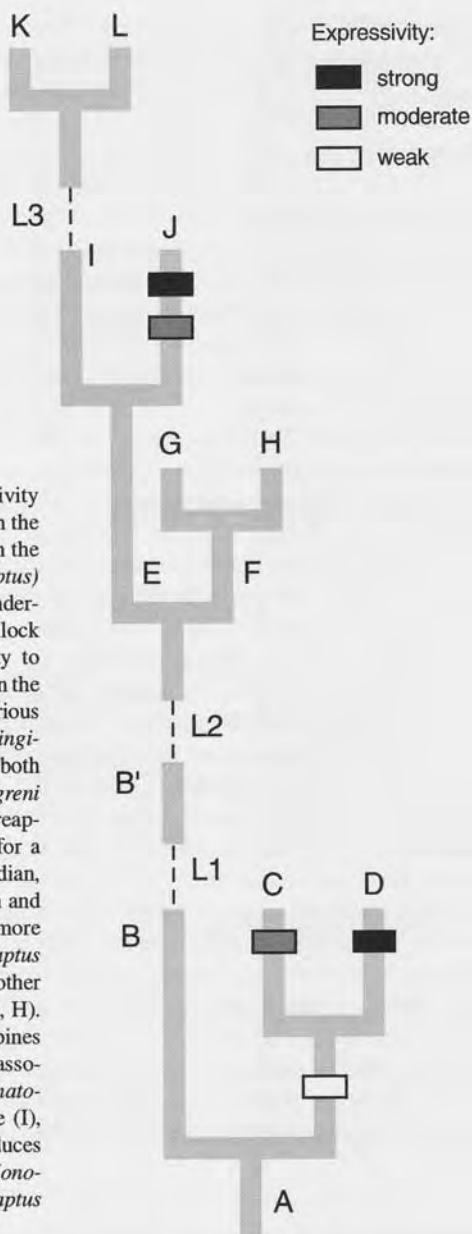


Fig. 6. The distribution and degree of expressivity of apertural processes or spines associated with the hooded apertural lobe (shown in Fig. 5) within the clades related to *Monograptus* (*Uncinatograptus*) *uncinatus* as interpreted in the light of the underlying synapomorphy concept. A common Wenlock ancestor of the stock (A) acquired an ability to develop lateral additions, which remain silent in the derived lineage B, but are expressed to a various degree in C [*Monograptus* (*Monograptus*) *flemingi-priodon*] and D [*Monograptus* (*Testograptus*)], both late Wenlock. Lineage B survives the *lundgreni* Event displaying a Lazarus effect (L1) and reappears in the early Ludlow (B') to disappear for a certain interval again (L2). Within the Ludfordian, the lineage is subject to certain diversification and splits into a somewhat more robust (E) and a more gracile (F) lineage, represented by *Monograptus* (*Slovinograptus*) – a possible forerunner of other Late Silurian gracile hooded monograptids (G, H). The reappearance of the lateral processes and spines remarkably similar to the late Wenlock ones is associated with lineage (J) [*Monograptus* (*Uncinatograptus*) *acer*-*M. (U.) spineus*], while lineage (I), after another Lazarus discontinuity (L3), produces hooded Přidoli monograptids (K, L) such as *Monograptus* (*Uncinatograptus*) *sp.* and *Monograptus* (*Dulebograptus*).

(*U.*) *protospineus* – *M. (U.) spineus* lineage (Figs 5, 6J). Sequential representatives of this lineage demonstrate a morphocline, showing a gradual development of antero-lateral spines (Urbanek 1996 and Fig. 5 herein). Thus the lobate-spinose morphotype reappeared in the latest Ludlow, as can be seen on the simplified cladogram, showing only some better known species (Fig. 6). The apertural spines in late Wenlock and late Ludlow monograptids are homologous as they are made of the same skeletal tissue, produced by the superposition of growth bands (fuselli) and occupy the same position in relation to the

main apertural lobe (Fig. 5, encircled). However, being acquired independently, they should be classed as homoiological as defined above and represent a doubtless case of homoplasy. A striking similarity in the overall shape does not exclude some highly characteristic differences in minute details (Fig. 5, encircled) – while in the Wenlock species spines are lateral, in the Ludlow ones they are situated antero-laterally (Urbanek 1996, 1997). A rather deterministic course of events in this case still leaves some room for contingency in the historical change. The significance of such subtle details for the recognition of homoplasy is particularly emphasized by Webb (1994, 1996).

It is also clear that classification in such groups as late Silurian monograptids cannot be based on morphology alone, because morphological similarity may be misleading. This explains also why genera play rather a subsidiary role in all considerations concerning Monograptina: the characters used for distinguishing the genera display too high a degree of evolutionary repetition. In all such cases the empirical knowledge of the course of events (the stratigraphic sequence) may help to establish the true nature of similarities used as a criterion for distinguishing taxonomic groups.

The history of the *uncinatus* genealogical domain may be described in terms of the underlying synapomorphy concept, and the recurrent derivation of the lateral spines in addition to the single apertural lobe was probably caused by certain apomorphic tendencies in the ancestral species. This underlying synapomorphy (in this case the capacity to develop lateral spines in addition to the regular hooked or hooded aperture) remain hidden (unexpressed) in most of the taxa within the *uncinatus* genealogical domain, being revealed only within certain subgroups (Fig. 6C, D, J) probably due to the subtle differences in the genetic background caused by selection. The hidden evolutionary potential implies the persistence of certain genetic and epigenetic factors through geologically long time intervals. As in the case of the *dubius*-related genealogical domain B, where the ability to form paired lateral apertural lobes ('blindlers') was maintained for approximately 5 Ma, the potential to form lateral spines on the unpaired lobe was preserved in the *uncinatus* stock for a similar time span (Urbanek 1996, 1997). The reasoning of a palaeontologist is essentially the same as that used recently by phylogenetic systematics (Saether 1983: p. 355; Sluys 1989: p. 358): the re-appearance of homologous traits results from re-expression of persistent hereditary factors or/and from re-activation of ancient developmental patterns. Both may be maintained in the genotype without being expressed for millions of years. Such a model of evolution suggested by these recent phylogenetic studies and implying a substantial retention of genes distinctly differs from the earlier schemes, based on classical population genetics, which assumed a steady replacement of genes in the course of evolution (allelic model of evolution).

Convergence amongst Late Silurian monograptids

Convergence is a result of selection acting on non-homologous structures but operating in a similar direction. The best example of convergence amongst Silurian graptoloids is that represented by the resemblance between the Cucullograptinae (a group essentially limited to the Gorstian) and the Neocucullograptinae (the early Ludfordian). Both groups evolved apertural apparatuses displaying a striking similarity, but based on a quite different skeletal fabrics (Fig. 7). While the Cucullograptinae used the regular fusellar tissue (Fig. 8C), the Neocucullograptinae newly invented and applied for the same

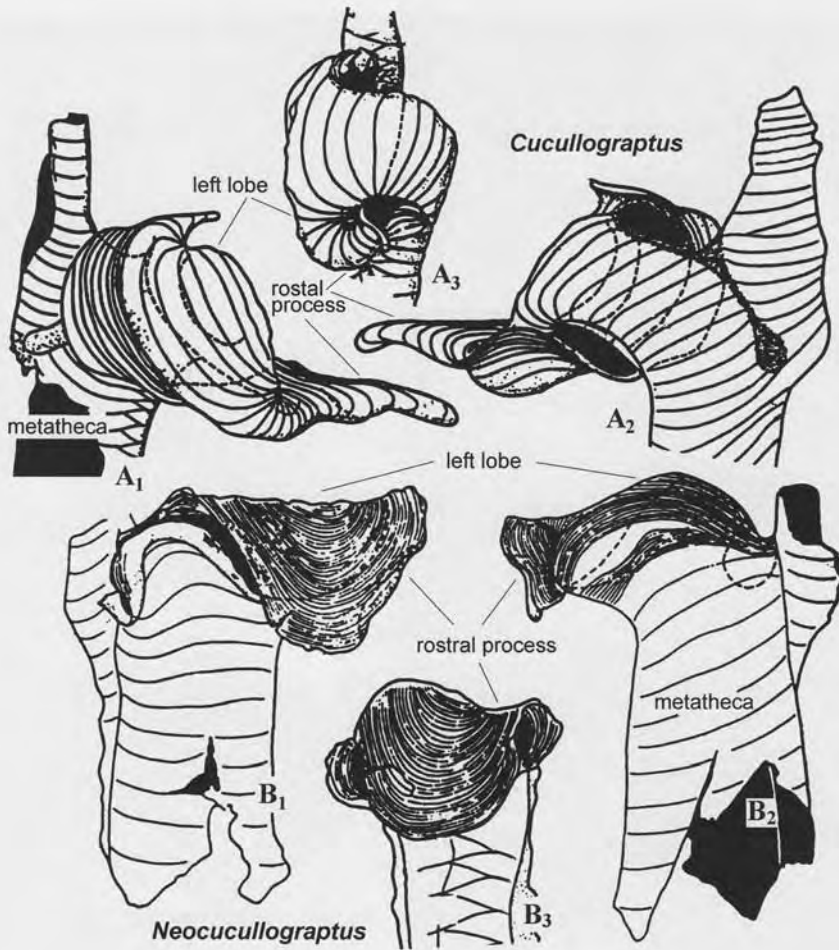


Fig. 7. Convergence as revealed by the morphological similarity in the structure of apertural apparatus of thecae in *Cucullograptus* and *Neocucullograptus* seen in reverse, obverse and in ventral view: A₁–A₃, apertural apparatus in *Cucullograptus aversus rostratus* Urbanek, 1960, early Ludlow, latest Gorstian; B₁–B₃, apertural apparatus in *Neocucullograptus inexpectatus* (Bouček, 1932), late Ludlow, Ludfordian. Note that in both cases the aperture is provided with a hypertrophied left apertural lobe forming a rostral process while displaying a quite different microstructure of skeletal tissue (after Urbanek 1966, 1970).

purpose a peculiar microfusellar tissue (Urbanek 1966, 1970 and Fig. 8A, B herein). In effect, the apertural apparatuses in both groups are fully comparable in essential topography as well as in some minor details, such as the presence of similar but not identical additional structures on the main lobe (tubular rostral process, different plates etc.).

In spite of this overall similarity, these apertural structures were produced at different times (neocucullograptids succeeding cucullograptids) and from a different ancestry. The common ancestor of all cucullograptids was *Lobograptus progenitor* Urbanek, 1966, which in turn, originated from ?*Lobograptus sherardae* (Sherwin, 1974), an immediate product of the early divergence from the *Pristiograptus dubius* stem species (the so-called 'early schism' of Koren' & Urbanek 1995). The common ancestor of all

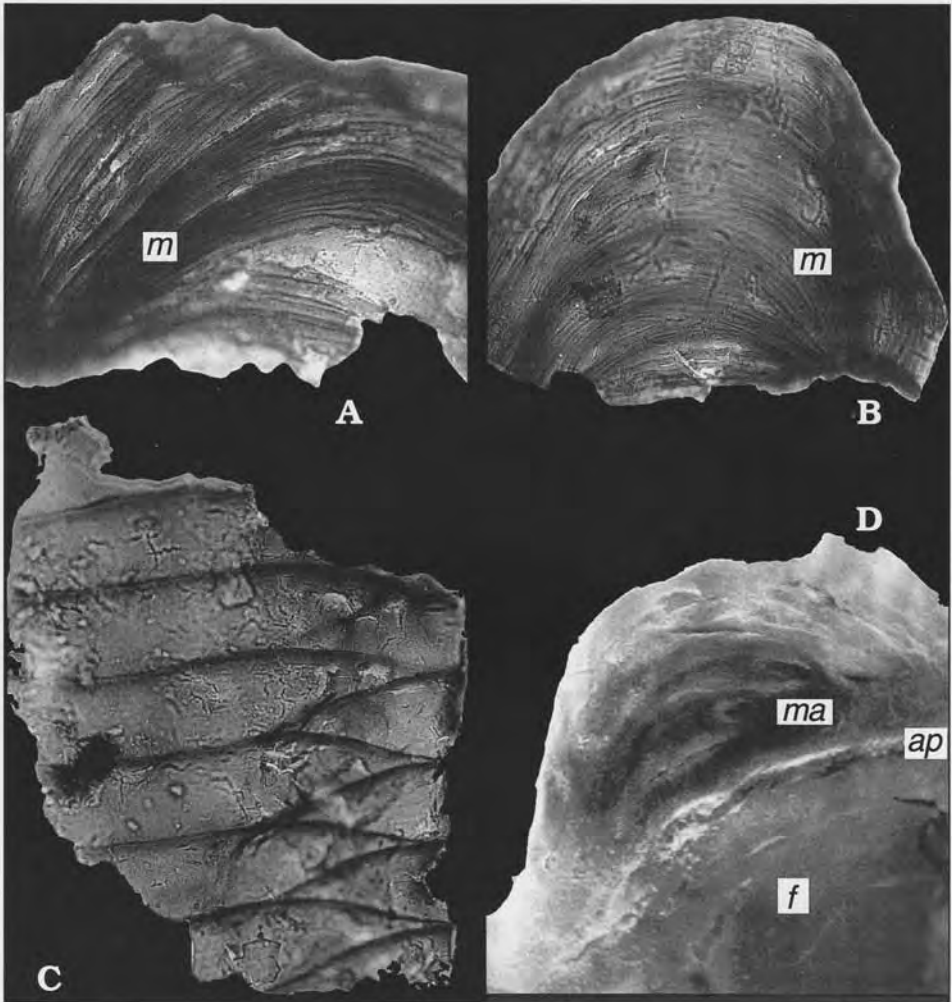


Fig. 8. Skeletal tissues of some neocucullograptids seen with an optical (A–C) and a scanning electron microscope (D). A, B. Bleached fragments of apertural lobe in *Neocucullograptus inexpectatus* revealing the structural pattern of microfusellar tissue (m). C. The standard fusellar tissue from a bleached fragment of a metatheca in the same species. D. An early phylogenetic form of a microfusellar addition (ma) to the aperture (ap) of a fusellar portion of the theca (f) in *Bohemograptus praecornutus* Urbanek, 1970 (early Ludfordian, Mielnik I.G. 1 bore core); A–C approximately $\times 120$, D approximately $\times 320$.

neocucullograptids is *Bohemograptus bohemicus* (Barrande, 1850), preceded by an earlier species, *Bohemograptus urbaneki*, displaying a close similarity to the earliest lobograptids as well as to early linograptids (Urbanek 1970; Rickards *et al.* 1995). Therefore neo- and true cucullograptids are rather closely related. Yet, in spite of this, they developed quite different, although analogous apertural structures. Moreover, they are so different morphologically not because they are so different genetically but due to the contingent nature of evolutionary change. The reason lies in the invention by the *Bohemograptus* lineage of a new peridermal tissue – the above-mentioned microfusellar

tissue – prior to its diversification and adaptive radiation. This new skeletal material appeared first as small and undifferentiated apertural additions (Fig. 8D), which only later were transformed into large and complex structures, the genuine apertural lobes (Figs 7, 8A–C). The novel material had been utilized in the morphogenesis of neocucullograptids by ‘evolutionary tinkering’ (or bricolage) as defined by Jacob (1983). Once invented and ‘close at hand’ (deposited around the aperture), it found an application in new structural designs. This is the only way how it could have happened to replace the regular fusellar material of which the thecae of most graptoloids were made.

The resemblance of the apertural structures in cucullo- and in neocucullograptids represents a border case of convergence and parallelism. The relationship of both lineages is close enough to expect that homeomorphy might have been caused by the evolutionary parallelism rather than by the convergence. However, fabrics are clearly non-homologous and in the case of neocucullograptids they are highly specific. On the other hand, however, the soft parts of the zooids (their cephalic disc and lophophore) exhibited a parallel evolution in both groups, expressed i.a. in the development of asymmetry and other common morphological traits. This may be expected because of the not too distant relationship between the ancestors of both lineages and the probable presence of a largely common genetic endowment. Both groups represent a very similar adaptive type, which Urbanek (1996, 1997) defined as ‘operculate’. They repeated essentially the same adaptive theme once in the Gorstian, and then in the early Ludfordian, although they used quite a different structural base each time. Such repetitions are a remarkable feature of the evolutionary history in the Late Silurian monograptids.

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Oligofilia i paralelizm ewolucyjny: przykład graptolitów sylurskich

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Streszczenie

Jednym ze skutków wymierania masowego było zmniejszanie się liczby przeżywających linii ewolucyjnych, z reguły reprezentowanych także przez nieliczne gatunki. Odradzanie się faun następowało więc od nielicznych przedstawicieli danej linii ewolucyjnej i w konsekwencji tworzące się nowe grupy taksonomiczne miały monofiletyczne lub prawie monofiletyczne pochodzenie. Ten czynnik systematycznie ograniczający ilość równoległe rozwijających się linii filogenetycznych otrzymał nazwę „oligofilii” (od gr. *oligos* – skąpy, nieliczny i *phylon* – ród, plemię, Urbanek 1997). W wyniku działania oligofilii odradzające się taksony stanowią szczególnie blisko spokrewnione grupy monofiletyczne, określane we współczesnej systematyce filogenetycznej jako domeny genealogiczne. Znamionym rysem ewolucji takich grup jest powszechny paralelizm ewolucyjny, świadczący o istnieniu określonych tendencji apomorficznych. Znajduje to wyraz w mozaikowym pojawianiu się danej cechy apomorficznej w różnych kładach należących do tej samej domeny genealogicznej (zjawisko „ukrytej synapomorfii”, ang. „underlying synapomorphy” Saether 1979, 1983). Historia odradzania się faun monograptidowych późnego syluru po zdarzeniu *lundgreni*, daje się dobrze zinterpretować w świetle koncepcji oligofilii i domen genealogicznych. Chociaż graptolity dostarczają szczególnie interesujących faktów na poparcie koncepcji oligofilii, nie ulega wątpliwości, że zasada ta ma ogólne znaczenie. Wskutek działania oligofilii odradzające się fauny złożone są z grup monofiletycznych, z których każda składa się z blisko spokrewnionych gatunków obdarzonych podobnym potencjałem ewolucyjnym. Warunkuje to częsty paralelizm ewolucyjny, stanowiący charakterystyczny rys zapisu paleontologicznego, odnoszącego się do historii różnych grup. Jednakże dalsze działanie oligofilii zapobiega polifiletycznemu powstawaniu potomnych taksonów, bowiem większość równoległych linii ulega eliminacji w wyniku wymierania masowego. Zasada oligofilii pozwala zrozumieć paradoksalny związek między monofiletycznym pochodzeniem większości taksonów szczebla ponadgatunkowego, ich w znacznym stopniu równoległą ewolucją oraz również monofiletycznym pochodzeniem powstających z nich grup potomnych.