Adaptive radiation of monograptids after the Late Wenlock crisis

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Succession of late Wenlock graptolites in the Kursala Formation, Tien Shan (Kirghizia), documents of the early recovery phase after the global *C. lundgreni* Event. *Pristiograptus dubius* was the only survivor among monograptids. After displaying a mass occurrence and an increased variation, the *P. dubius* stem lineage splits into two main trends: line A, represented by *Pristiograptus idoneus* and line B, represented by *Colonograptus*? *praedeubeli*. The former leads to *Lobograptus*? *sherrardae*, a generalized forerunner of such diverse trends as linograptids, cucullograptids and possibly also neocucullograptids (via *Bohemograptus*). The latter initiates the *Colonograptus-Saetograptus* line. The *P. idoneus* – *L.*? *sherrardae* lineage shows distinct gracilization, an apomorphic feature, while the other one preserves ancestral robustness, a plesiomorphic character. Hence, the bulk of the later monograptids of Gorstian and Ludfordian age may be derived from the *P. dubius* stem lineage. In respect of this conservative lineage a non-cladistic approach is prefered, because its morphological spectrum and evolutionary potential, and as we believe its specific identity, were preserved, in spite of numerous speciation events, until the early Pridoli.

Key words: global bioevents, *C. lundgreni* Event, graptolites, monograptids, adaptive radiation.

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Hermann Jaeger
in memoriam

Introduction

While considering etched and well-preserved graptoloids of early Gorstian age, Urbanek (1966, 1970) recognized a remarkable similarity between early representatives of such diverse groups as the Linograptinae, Cucullograptinae, and Neocucullograptinae. The resemblance manifests itself in the sicular and the proximal part of the rhabdosome of *Neodiversograptus nilssoni* (Barrande 1850), *Lobograptus progenitor* Urbanek 1966, and *Bohemograptus bohemicus* (Barrande 1850) (Fig. 6B–D) which indicates that the differences between those, after all quite divergent, lineages were at first insignificant, increasing progressively in the course of the evolution. This allowed Urbanek (1966: p. 384, Pl. 8; 1970: p. 204, Pl. 8) to posit that all the three subfamilies must have shared a common but still unknown ancestor.

This fairly bold conclusion has most recently been confirmed by Koren' and her colleagues (Koren' & Rinenberg 1988; Koren' 1991b, 1992) as a result of their studies on the unique sequences comprising late Wenlock pelagic deposits in South Tien Shan. Among the abundant graptolite fauna including also a number of new species which appeared after the *Cyrtograptus lundgreni* Event, Koren' (1992) has recognized *Lobograptus? sherrardae* (Sherwin 1974) as the best candidate for a common ancestor of the main Ludlow monograptid groups. Its stratigraphic occurrence in the *L.? sherrardae (C.? praedeubeli)* Zone of the late Wenlock and wide geographical distribution (Australia, Central Asia, Arctic Russia, and Arctic Canada) as well as the traits of its sicula, the proximal portion of the rhabdosome and the thecal morphology leave few doubts as to whether it could be considered the so far 'missing link' for the entire plexus of the Ludlow linograptids, cucullograptids, and perhaps also neocucullograptids as well as spinose monograptids (*Colonograptus, Saetograptus*).

More than that, studies by Koren' provide an insight into the patterns and mechanisms of the recovery of the monograptid fauna, which followed the great extinction caused by the *C. lundgreni* Event. There is convincing evidence that new lineages which appeared after the crisis may be immediately derived from the persistent stock represented by *Pristiograptus dubius* (Suess 1851). One of the survivors of the *C. lundgreni* Event, this species has become enormously fragment in fossil assemblages, which was associated with a high level of variation. Then it differentiated into a number of species, thus initiating a very early stage of the great Homerian radiation of monograptids (Fig. 1). The data presented by Koren' (1990, 1991b, 1992) together with a penetrating study conducted by Jaeger (1991), and a recent paper by Lenz (1993), based on isolated, three-dimensional specimens from Arctic Canada, throw a new light on the incipient stage of the diversification of the conservative pristiograptid stem into a number of progressive lines of evolution. Materials collected with 1 cm resolution in Europe and in Central Asia provide a reliable basis for the understanding of the evolutionary relationships of *P. dubius* and the descendant species. The data available outline as well the overall aspects of the late Homerian adaptive radiation which followed the *C. lundgreni* Event.

In the present paper we offer a review of current opinions on possible environmental causes of the *C. lundgreni* Event and we characterize its filtering effect due to selective extinction of different ecological and taxo-

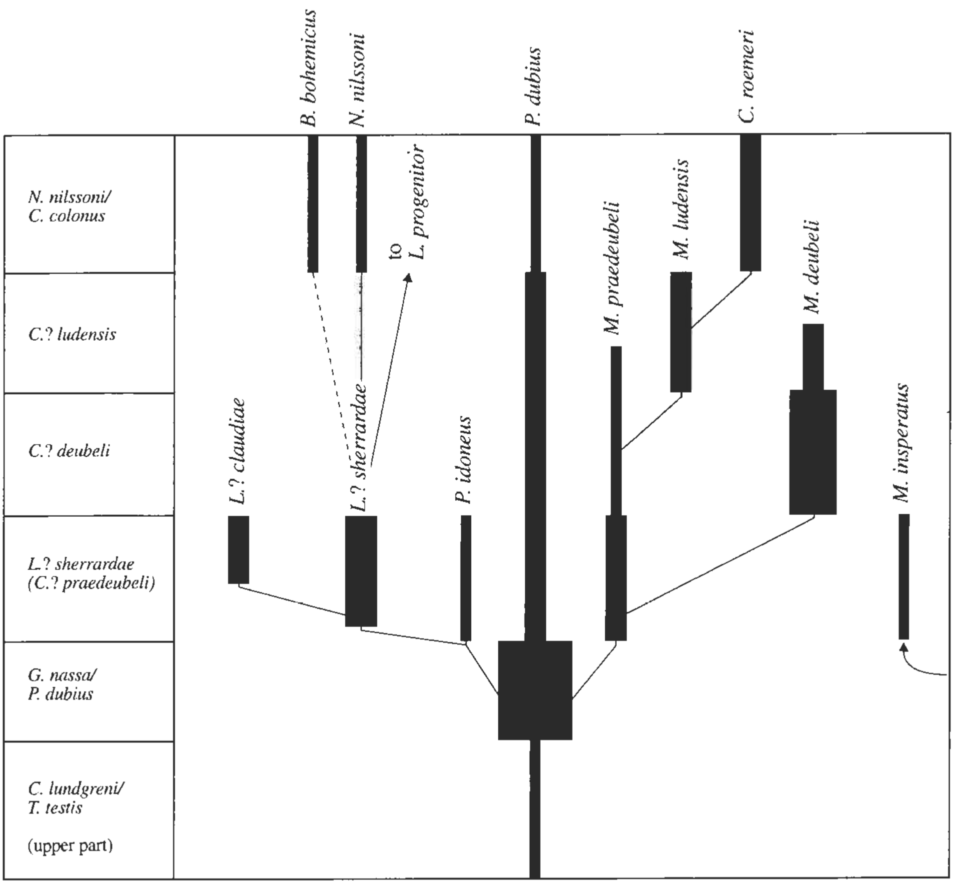


Fig. 1. Phylogenetic relationships, stratigraphic distribution and abundance of late Homerian monograptids as revealed in the Kursala Formation, northern slope of the Alai Range, South Tien Shan, Kirghizia (after Koren' 1992, modified). Bent arrow at the right indicates the possible appearance by immigration, while the thickness of black lines corresponds to the relative abundance in fossil assemblages.

nomic groups. However, the importance of a mass extinction should not be assesed by its destructive effect alone, but also by radiations of new groups that follow later. Therefore, the aim of the present paper is foremost to provide a description, an anatomy of this adaptive radiation, and also to suggest certain explanations of the phenomena observed.

The possible causes of the *C. lundgreni* Event

The environmental background of graptoloid mass extinction at the top of the *C. lundgreni/T. testis* Zone has been recently analyzed in a number of papers. As geochemical studies (Jaeger 1991) have revealed no traces of iridium enrichment below, within and above the extinction horizon in Thuringia, the extraterrestrial causes may be rather safely ruled out.

Eustatic explanations. — The possible terrestrial conditions which triggered the *C. lundgreni* Event should be of global nature, as mass extinction took place on vast areas, and was identified on all major palaeocontinents. One of the most common explanations, offered in literature dealing with mass extinction of marine faunas, are bathymetric changes. The Silurian has been recently reviewed and analyzed from this point of view by Johnson *et al.* (1991). Extinctions on a large scale are usually correlated with regressions, or at least shallowing events are considered a common denominator among the environmental changes resulting in mass extinction. Thus, Kaljo & Märss (1991: p. 147) in their study of the East Baltic data have arrived at a conclusion that in graptoloids 'diversity peaks and minima... coincide surprisingly well with phases of sea-level rise and lowering'.

This idea has been recently elaborated by Johnson and McKerrow (1991) in their study on the Silurian sea-level and faunal changes. Thus shallowing during the *C. lundgreni/T. testis–N. nilssoni/C. colonus* time (with its maximum in the *C.? ludensis* Zone) may be related to the great extinction of graptoloids at the top of the *C. lundgreni/T. testis* Zone. This glacio-eustatic mechanism provided, according to the above authors, the most probable cause of the sea level changes observed in the Silurian. Regression in the late Homerian is now generally accepted as a world-wide phenomenon (Kaljo *et al.*, in press). It would, hence, coincide climatically with cooling. This line of reasoning may be supported by observation (Paškevičius 1986) that in the South Baltic area sediments around the *C. lundgreni/T. testis* Zone became microlaminated. Paškevičius related this to seasonal changes of the climate. Therefore, regressions and climatic changes may operate synergetically.

There seems to be little doubt now about the crucial role of the glacio-eustatic factors in the dramatic terminal Ordovician mass extinction (Barnes 1986; Berry *et al.* 1990; Goodfellow *et al.* 1992; Koren' 1987, 1991a; Robertson *et al.* 1991). As compared with the *C. lundgreni* Event, the Ordovician one was a complex, step-wise process, composed at least of three phases. Each phase was probably related to a certain stage of the end Ordovician glaciation. The ecological disturbances lasted long enough for groups conditioned to disturbance to appear (the *Hirnantia* fauna), and for biotic changes become distributed into a number of separate events. Nothing like this could have been expected in the case of the *C. lundgreni* turnover, which clearly was a single act play. The common element, however, is the possible participation of glacio-eustatic mechanisms, as a dominant factor or a factor acting in combination with other agents. However, to what extent the case of the terminal Ordovician extinction could be extrapolated on later Silurian bioevents is an open question. Moreover, no reliable evidence of a late Wenlock glaciation has been recognized so far.

Hydrochemical explanations. — Quinby-Hunt & Berry (1991) suggested recently an entirely new approach to the causes of the late Wenlock global bioevent — namely a hydrochemical theory of extinction. Their starting premises are: high global average temperature during the Silurian and the lower oxygen atmospheric concentration. Both factors were responsible for an extensive oceanic anoxia. One can imagine the graptoloid habitat as the oxygenated surface layer plus some part of the hypoxic deeper stratum of the ocean. With expanding anoxia the depths of the graptoloid habitat would become shoaler and only those graptoloids which were surface dwellers would survive. Thus the *C. lundgreni* Event may be visualized as an expansion of anoxic waters into the graptoloid habitat, either caused by vertical advection, related to some tectonic changes as suggested by Wilde *et al.* (1990), or caused by a change of the oceanic redox conditions. The latter mechanism is considered recently as a more probable one.

The paper by Quinby-Hunt & Berry (1991) is an application of a general model of hydrochemical regime of the Lower Palaeozoic oceans (suggested earlier by Berry *et al.* 1987) to the late Wenlock changeover. Based on some recent analogues,this model assumes the presence of a suspended layer with anoxic waters, at rather low depths and far from the bottom. It leaves only a relatively thin layer of pelagic surface waters available for life. It is still an open question to what extent this model could be extrapolated on Palaeozoic seas and oceans.

There are, however, certain data which may provide some empirical evidence in favour of the model in question. Thus, the appearance of dolomite, interbedding graptolitic shales instead of limestone, in the latest Wenlock, may be considered an indication of the expansion of anoxia in the world's oceans. Deep-sea dolomitization occurs only under an increased reducing potential of sediments. Quinby-Hunt & Berry (1991) quote the Silurian section in Taimyr, described by Obut *et al.* (1965), as so far the only site displaying such a lithofacial change. However, Ulst (1974: p. 106) observed in the Silurian sections of Latvia a 1 m thick bed of laminated dolomite (Ancia member of the Riga Formation) immediately underlying the *P. parvus* Zone. She considers this bed a marking horizon, characteristic of abrupt facial changes around the late Wenlock changeover. It is usually interpreted as a reflection of a short-term sea-level lowering. This is little doubt that the East Baltic dolomite interbedding may also be interpreted along the lines suggested by Quinby-Hunt & Berry (1991). More findings of such dolomitic interbeddings at proper stratigraphic setting may strengthen the reliability of the hypothesis in question. A similar change of lithofacies (an increase in carbonate content), was recognized at the time of the *C. lundgreni* Event on the Polish Lowland (Tomczykowa 1988: p. 26). As the *G. nassa/P. dubius* Zone is already situated within the carbonate-rich bed (Henryk Tomczyk, personal communication), the Homerian extinction horizon may be traced by geophysical sounding over the distance of hundreds of km.

While earlier opinions frequently emphasized the principal role of tectonism among the causes of faunal crises and extinctions of graptoloids, recent opinions ascribe them a rather modest significance. The continental plate movements and their collisions (orogenic events) or swellings of mid-ocean ridges are now generally considered either as merely regional in their effects or too slow to explain fairly rapid Silurian sea-level changes (Johnson & McKerrow 1991). The much debated closure of intercratonal basins creates a similar situation, as the pelagic realm of adjacent seas offered alternative habitat for plankters. One could conclude that tectonism *per se* is insufficient to explain the entirety of the phenomena.

Summing up, one should agree with the cautious opinion of Jaeger (1991) that the causes of his 'big crisis' are still subject to speculation. A number of facts provide evidence for changes in the lithofacies around the extinction horizon in different regions of the world. Some of them were mentioned above. They correspond to some, not yet identified, global oceanographic disturbance, which severely affected the graptoloid assemblages. Such profound oceanographic changes are probably best reflected in carbon isotope (^{13}C) curves, with a depletion noted in some sections at about the *G. nassa/P. dubius* Zone. This is considered a cumulative effect of different factors, all contributing to reduced bioproductivity (Corfield *et al.* 1992; Corfield & Siveter 1992). Earlier, Jaeger (1959) defined the factors responsible for the 'big crisis' as anorganic (abiotic) in nature (e.g. temperature, oxygen concentration, current systems, etc.). The 'boundary coal seam' (a 10 cm thick alum slate with a very high content of coaly matter), observed by him in Thuringia, has been ascribed directly to the catastrophic mass mortality of plankton caused by such abiotic factors and leading to accumulation of organic remains (Jaeger 1959). He has compared the graptoloid crisis at the end of the *C.lundgreni/T. testis* time — both in its extension and in probable causation — to the mass extinction of planktonic foraminiferans in the Late Cretaceous.

Hence, the most recent discussions focus on two alternative explanations: the glacio-eustatic and the hydrochemical one. However, the problem is still unresolved, and in the future some new viewpoints could emerge as to the nature of the agents involved in this event.

The filtering effects of the *C. lundgreni* faunal turnover

We know, nevertheless, that this disturbance had a lethal effect on the macrozooplankton (graptoloids) and was also injurious for conodonts. Benthic communities suffered much less or even survived across the extinction boundary displaying a more or less vigorous radiation. Thus the Wenlock coral fauna reached its maximum diversification being at the same time represented by cosmopolitan taxa. A high degree of endemism is usually related to the reduction of diversity. In the opinion of Kaljo &

Märss (1991), 'the late Wenlock regression seems not to affect seriously the corals'. Although they understood the *C. ludensis* Zone as 'late Wenlock' there is no evidence of any substantial changes at the top of the *C. lundgreni/T. testis* Zone either. Copper & Brunton (1991: p. 252) have found 'no evidence for any reef extinctions or turnover phases during the Silurian'. In their opinion, there is no clear correlation between sea-level changes proposed for the Silurian and the distribution and development of reefs on a global scale.

Coral and stromatoporoid bioherms are common throughout the Wenlock-Ludlow boundary, and except for some local situations, show no traces of crisis near the end of the Wenlock over wide areas of the world. Likewise most trilobite and ostracode species survive the critical horizon (Thomas *et al.* 1989; Siveter 1989), while brachiopod faunas reveal no substantial changes (Boucot 1990; Bassett 1989).

At the regional scale, the decline of graptoloid diversity may be accompanied by a co-eval radiation or expansion of some benthic taxa. In Barrandian (Kříž 1992), the *C. lundgreni* Event coincided with a distinct change of the benthic fauna. However, instead of displaying an impoverishment of the diversity, the change is marked by the abrupt appearance of a new and rather rich brachiopod and trilobite community. This new community has recently been found in a number of localities, always in the same stratigraphic position. Thus, the great *C. lundgreni* changeover, expressed by a numerical decline of the graptoloid taxa is generally associated with great spreading of the benthic fauna. Therefore, one could conclude that the *C. lundgreni* Event has a double meaning — for graptoloids it was an extinction event, while for most benthic groups it was merely a spreading event. At the same time these planktic groups demonstrate most clearly the rule that each mass extinction is followed, after some interval, by radiation.

This incongruity between the changes in the pelagic and benthic communities near the end of the Wenlock, undermines the current explanation that low sea-level stands affected organisms mainly through the reduction of habitable shelf area. If this had been true the benthic organisms would have been the most affected. Paradoxically enough, it was mostly planktic groups that suffered the most. This sequence of events seems to become a distinct pattern of faunal changes in non-benthic groups. The above-mentioned incongruity means that there is no direct causal relationship between regression and diversity drops in such groups as graptoloids or conodonts.

A hypothetical causal relation should be searched in climatic effects of sea-level changes (Jablonski 1986). According to Johnson & McKerrow (1991: p. 166), 'melting ice caps could govern both sea-level changes and the character of oceanic water masses controlling the evolution of planktic faunas'. Thus an intermediate causal factor might be temperature — a powerful agent controlling the distribution of recent planktic organisms. The cold water currents and sharp thermal gradients could be an effective agent of mass elimination of presumably stenothermal graptoloids. Most probably the deterioration of climate was accompanied by significant changes in biological productivity of the ocean as well as in its circulation and chemistry. Hence, the onset of regression and the rapid cooling of the climate, triggered most probably a series of changes (the domino effect!), which resulted in a substantial breakdown of the physical and biological structure of the ocean. However, geological evidence of such climatic change is still unsatisfactory.

But even if we accept this or a similar point of view, it still remains unclear whether it was glaciation or deglaciation that brought about the most adverse environmental conditions for the existing lineages of planktic groups. During the Late Ordovician bioevent the major extinction of graptoloids (the *pacificus* Event of Koren' 1991a), may probably be related to the onset of climatic cooling, to the beginning of the growth of the Gondwana ice caps and regression. Spreading of floating ice over vast oceanic areas made the surface layers particularly inimical for stenothermic planktic organisms. On the contrary, the renowned *Hirnantia* fauna disappeared with the rise of sea-level due to a great climate warming at the end of the Late Ordovician ice age! By analogy one can conclude that also in the remaining cases of mass extinction, involving the glacio-eustatic mechanisms, it was the onset of glaciation which probably had a most deleterious effect on the plankton. Moreover, it seems that monograptids as the dominant group of macrozooplankton, were especially vulnerable to the cooling of the climate, as the benthic groups, some with planktic larvae, were not particularly affected.

The filtering effect of the *C. lundgreni* Event was thus a twofold one: on the one hand it accounted for the differential survival of the benthic and planktic taxa with an extremely severe killing effect for the last ecological group, and on the other it was responsible for a marked difference in the rate of survival amongst the specialized and non-specialized taxa of the monograptids. The only survivor represents a non-specialized morphoecological type. However, the survival of a nonspecialists should not be considered a general rule, as the plectograptine retiolitids which crossed the extinction boundary represented an extreme case of specialization among all the Graptoloidea.

A double role of the conservative *Pristiograptus dubius* stem line

The recovery after the *C. lundgreni* Event was achieved mainly by means of local speciation from indigenous survivors. Speaking about 'local speciation', we are having in mind that certain transient stages of speciation may be traced in the fossil material collected in the depositional areas under study, while the category of 'indigenous survivors' includes those relic species which are known to have survived across the *C. lundgreni* extinction boundary in place and continued to exist for some time. The environmental disturbance during the *C. lundgreni* Event was so radical that among monograptids only a single species — *Pristiograptus dubius* is known to have survived in Europe and Asia. It was associated with *Gothograptus nassa* (Holm 1890) — a new species which appeared after the event and immediately reached its acme, as well as *Pseudoplectograptus praemacilentus* (Bouček & Münch 1952) and *Pseudoplectograptus* sp., the rare relics from the *C. lundgreni/T. testis* Zone. Immediately above, they form the *G. nassa/P. dubius* Zone (or the former Interregnum of Jaeger 1959), their association deserving the name of a relic (Urbanek 1970, 1993).

As a rule, both species display a mass occurrence, probably a taphonomic equivalent to a population burst during their life time (Fig. 2). This phenomenon appeared to have occurred globally (Europe, Central Asia, Africa, Arctic, and Northeast Russia among the others). There is little doubt that the mass occurence observed in the sequences formed in different facial environments corresponds to the population burst of *P. dubius* during the life time of numerous generations. In the monofacial condensed strata (Thuringia, Tien Shan) deposited almost certainly at a steady rate and studied with a high resolution sampling, such a burst has been recognized solely within a short episode in the *G. nassa/P. dubius* Zone.

This is certainly true in respect of the *P. dubius* stem line, representing a persistent and, at the same time, conservative lineage. It is clear that this persistent lineage played a significant, albeit somewhat underestimated, role in the evolution of the Silurian monograptids. This role was a twofold one. The lack of specialization and the presumed eurybiotic nature of its adaptations (1) enabled it to survive through many biotic crises, which plagued the history of the late Silurian graptoloids. As a result, the *P. dubius* stem line continued through time as a conservative group, showing an exceptional permanence of stasis. In fact, the record available suggests some limited microevolutionary oscillations, or even a zig-zag evolution within the lineage, which, however, again and again was able to return to what may be called the standard morphotype (Urbanek, in press). The other (2) also frequently undervalued role for this persistent group, was to be the source of new progressive lineages which split from the stem group in post-crisis situations. The most recent data support earlier assumptions concerning the highly important role of the genus *Pristiograptus* in the evolution of Late Silurian graptoloids (Rickards *et al.* 1977: p. 62) and indicate for a particular significance of *P. dubius* stock.

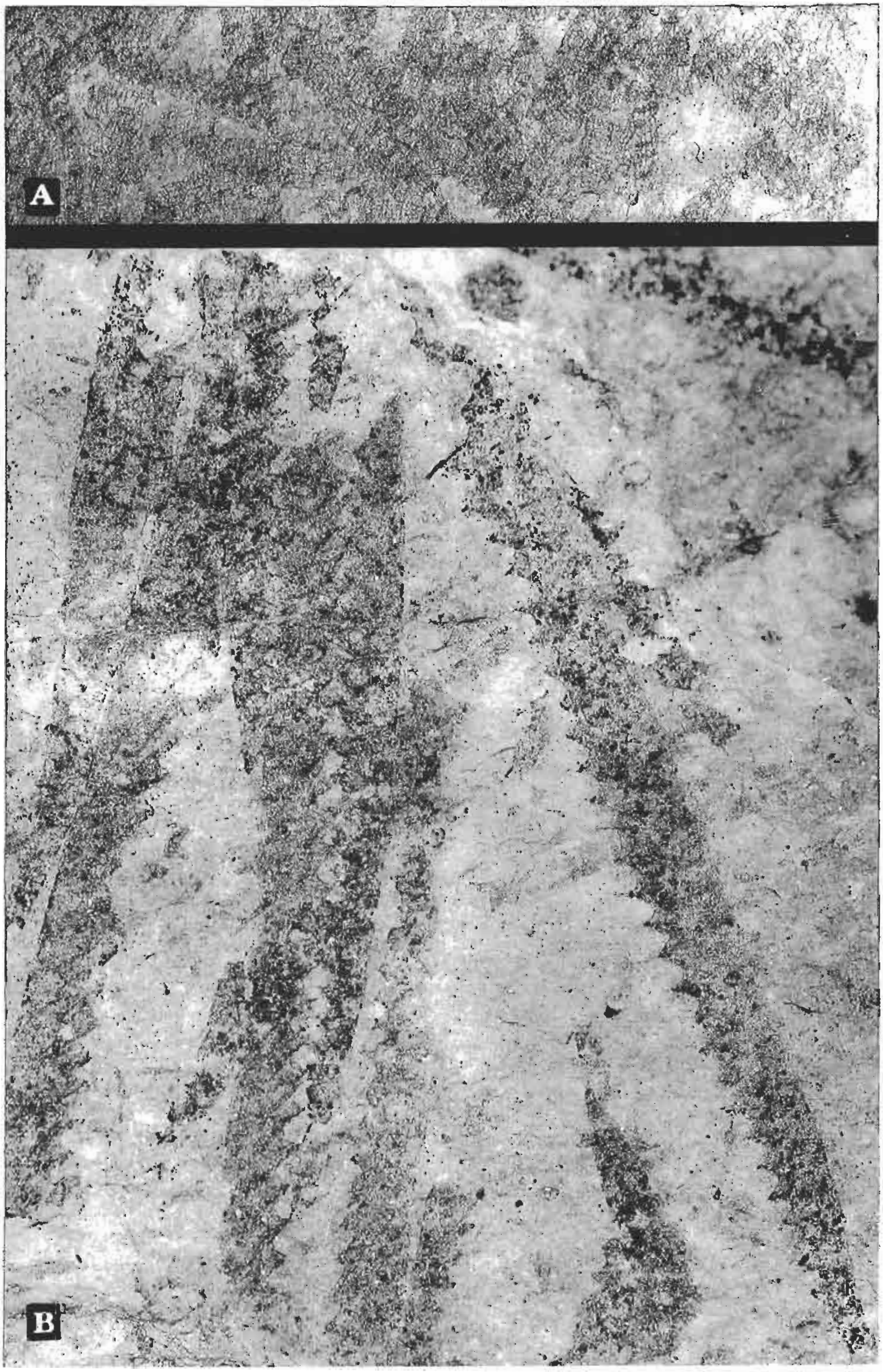
During the recovery which followed the *C. lundgreni* Event, the *P. dubius* stem line was immediately subjected to a population explosion. This mass increase may be interpreted as an immediate effect of an ecological release which followed the radical extermination of the intragroup competitors as well as a probable decimation of the predators. Urbanek (1970, 1993) proposed an explanation of the related phenomena assuming a certain general conceptual framework. Increase in abundance is, according to him, an element of the so-called post-event syndrome. Other elements are the low diversity of the relic assemblages and, in some cases, also the reduction of size of the surviving species (a diminutive phenotype), caused directly by the severity of the environmental conditions. The decrease in diversity of the late Homerian relic assemblages may be easily ascribed to the mass extinction which followed the *C. lundgreni* Event. It wiped out the diversified fauna of early Homerian age, comprising taxons and morphoecological types characteristic of the Llandovery and of the most of the Wenlock Series. The great proliferation of the surviving species is therefore related to the extinction event and to the ecological situation created by it, such as ecological release and the presence of vacant habitats.

In the case of the *Pristiograptus dubius* stock, its period of proliferation started immediately after the *C. lundgreni* Event and lasted at least through the *G. nassa/P. dubius* Zone. Mass occurrence of *P. dubius* associated with *G. nassa* or represented monospecifically is a remarkable feature of the graptolite-bearing sediments of this age on vast areas (Fig. 2). Remarkable abundance of *P. dubius* may be directly observed on bedding planes within the above mentioned Zone. In Tien Shan sections as many as 20 rhabdosome fragments may be seen on a surface of 10 cm^2, although large slabs were not available. The *G. nassa* and *P. dubius* usually occur monospecifically in alternating layers, although mixed assemblages, usually with predomination of one species, are also observed. The former species occurs in virtually countless accumulations, dozens of times more frequent than any of the plectograptines in the overlying horizons. Proliferation of *P. dubius* and its dwarfed variety may be observed on large areas and is interpreted as an unique event in the history of the species, directly related to the 'big crisis' (see Jaeger 1991: p. 309, Fig. 1). Other acme horizons observed in *P. dubius* vertical distribution were on local or regional scale, while the *G. nassa/P. dubius* burst reveal probably a global extent.

Population burst and generation of variation

One of the most important consequences of the numerical increase and high abundance is generation of great genetic variation. This classical thesis of population (or ecological) genetics was advanced decades ago by Ford (1931), to be later elaborated into a common wisdom of evolutionary biology. The recognition, besides the standard morphotype of *Pristiograptus dubius frequens* Jaekel 1889 of a number of transients and deviants in populations (chronodemes) from the *G. nassa/P. dubius* and *L.? sher-*

Fig. 2. Typical monospecific assemblages from *G. nassa/P. dubius* Zone. Kursala Formation, section 10, Tul' village, Alai Range, South Tien Shan, Kirghizia; × 5. ☐A. *Gothograptus nassa* (Holm 1890). ☐B. *Pristiograptus dubius* (Suess 1851).


A
B

rardae (*C.? praedeubeli*) zones may convincingly be ascribed to the side effects of the population burst that lasted over the time span of many generations.

Some fraction of variation observed during the periods of proliferation, in both extant and fossil populations, has obviously an aberrant or teratological character. Much of the variation, however, represents more successful attempts and is eventually used in speciation. Such are numerous transients recognized by Koren' (1992) between *P. dubius* and *Pristiograptus idoneus* Koren' 1992 as well as between *P. dubius* and *Colonograptus? praedeubeli* (Jaeger 1990). A possible relaxation of selection pressure might have enabled rapid speciation of even more extreme deviants, e.g. those responsible for the isolation of the proximal thecae in *Lobograptus? claudiae* Koren' 1992 or the ones accounting for an unusual, trumpet-like shape of the sicula in *Colonograptus? deubeli* (Jaeger 1959) (Figs 8C, 9C–D). One should agree with Mayr (1963: p. 619) that 'aberrant types produced during such periods disappear as rapidly as they appear', and only few achieve lasting success.

Ample variation imposes an uneasy task on a taxonomist, especially so in graptolite research, for the morphological concept of the species, which prevails there, involves some arbitrary judgments. Thus, no wonder that Jaeger (1991: p. 326) has found it difficult to decide whether the single rhabdosome with some degree of isolation in the first theca, as observed by him, represents merely an aberration of the *C.? praedeubeli* rhabdosome, or one should assign it to a new species.

A somewhat different instance of variation related to the period of proliferation is represented by diminutive *Pristiograptus dubius parvus* Ulst 1974. This widely distributed morphotype (Jaeger 1991) was formally ranked as a subspecies or a species. In fact, it well may be an ecophenetic variant, caused by severe environmental factors hindering the development of both the colony and the zooids (Urbanek 1993). The other possible explanation is fixation of a mutation which produced a dwarfed phenotype featuring better adaptation to adverse conditions than the standard type did (Jaeger 1991). This stunted or dwarfed form displayed a mass occurrence in some areas immediately after the *C. lundgreni* Event, but was later replaced by a normal and much larger *Pristiograptus dubius frequens* Jaekel 1889, which turned it into an episode without lasting phylogenetic consequences. Small size and high abundance, as well as lack of morphological specializations characterize *P. dubius parvus* as a probable r-strategist in the sense defined by McArthur & Wilson (1967: p. 149), and ever since frequently used in literature. It seems safe to suppose that its colonies reproduced early, after attaining certain minimum size. Also the generation turnover was probably accelerated as compared with standard morphotypes. The remaining late Homerian monograptids were probably also r-strategists, although less extreme than *P. dubius parvus.* They contrast with taxa produced in result of Gorstian adaptive radiation, represented by clear-cut specialized adaptive types (Urbanek 1966), making an impression of distinctive K-strategists.

Ecological consequences of an increased abundance and variation

An increase in the range of variation has also some immediate ecological implications. Combined with an ecological release, ample variation should result in broadening the occupied ecological niche. It is fairly certain that within the *G. nassa/P. dubius* and *C.? praedeubeli* Zone huge and variable populations (patches) of *Pristiograptus dubius* increased their ecological amplitude, using a wider spectrum of food resources and penetrating some new microhabitats. Such common effects of ecological release opened for them new evolutionary opportunities, e.g. ecological access to a number of niches appearing free due to the mass extinction of potential competitors. A certain degree of competition may, however, be expected from co-eval plectograptine retiolitids. This group survived the *C. lundgreni* Event and rapidly diversified into a number of taxa showing a high evolutionary turnover.

Nevertheless retiolitids displayed a distinct and quite different adaptive type, using most probably food resources somewhat different from those of regular graptolites. Thus, a certain partitioning of the graptoloid niche into a retiolitid and a monograptid subniches was the most probable outcome of their competition (Urbanek 1993: p. 41).

The broadening of the primary pristiograptid niche owing to mass abundance and an increase in variation afforded new opportunities for initial diversification, e.g. in the utilization of resources, later favoured by selection. This resulted in an incipient cladogenesis manifesting itself in two main divergent trends, towards *P. idoneus* and *C.? praedeubeli*, respectively, with simultaneous preservation of the stem group (Fig. 3). One can say that at this early phase of adaptive radiation the *P. dubius* populations literally made their way to those new niches which were potentially available. A centrifugal mode of selection was operative at this stage. After new descendant lineages appeared and most of the niches were filled, competition from newly formed species limited the stem lineage's further prospects for diversification. The resulting stabilizing selection caused a reduction of variation and slimming of the niche occupied by the conservative *P. dubius* stem lineage. Thus its variation and potential to diversify was to some extent controlled by a sort of a feedback mechanism. Mass extinction could always trigger new possibilities of diversity reduction, while rediversification involved reduced variation within the stem lineage due to the competition from the daughter species. In this way the *P. dubius* stock was able to preserve a lot of simple plesiomorphic features.

The phylogenetic pattern of early diversification

A detailed study on the morphology and stratigraphic distribution of the new monograptid taxa recognized in the late Homerian provides a rather safe foundation for phylogenetic inferences (Jaeger 1991; Koren' 1992; Koren' & Suyarkova 1994; Lenz 1993). The overall pattern of adaptive radiation is defined by a single event — an early schism into the main phylogenetic branches, which occurred in the early *L.? sherrardae* Zone (Fig. 3). Both diverged, as far as the stratigraphic resolution permits to establish, simultaneously from the conservative *Pristiograptus dubius* stem line, giving rise to the *Pristiograptus idoneus* and the *Colonograptus? praedeubeli* lineage, respectively. The prospective importance of this speciation event, however, was by far greater than that of all later changes, as this schism (using O.M.B. Bulman's wording) determined the major trends in the future monograptid evolution.

The bulk of later monograptid species either evolved (1) from line A or B as shown in the diagram (Fig. 3) or may be derived directly (2) from the persistent *P. dubius* lineage owing to later iterative speciations. Only a certain fraction of post-Homerian monograptids appeared as a result of (3) a multiple invasion of immigrants (cf. Urbanek 1993).

Moreover, this early schism also defined the two prevailing morphoecological types of later monograptids: the descendants of line A are slim and gracile with a small sicula and tubular thecae, while the derivatives of line B have not only preserved the robust pristiograptid foundations of the rhabdosome but even tend to increase the robustness of this element. Thus in respect of the overall rhabdosome shape, line A displays the predominance of synapomorphies, while line B is essentially symplesiomorphic. Therefore, the early schism may be considered one of the most dramatic events in the history of the late Silurian monograptids. Gracilization and robustness may define very approximately the early divergence of the niches and the trophic demands of the evolving lineages. There is evidence that during the Llandovery adaptive radiation, splitting into slender and robust types also played an important role. In the early Ludfordian, *Bohemograptus* split into the gracile line and the robust line. This tendency amongsts monograptid groups, to produce either very slender or very robust rhabdosomes was observed also by Rickards *et al.* (1977: pp. 92–93).

Pristiograptus dubius s. l. survived the speciation event, called herein 'the early schism', without noticeable changes in the morphological type. We accept the *P. dubius* lineage as a single stem species, which should not be subdivided into a number of sequential taxa. This contradicts, of course, the cladistic practice of setting the species boundaries at the speciation events. In our opinion, however, such an approach better accomodates the empirical data which suggest the survival of the ancestral species after the appearance of the daughter species — *P. idoneus* and *C.?*

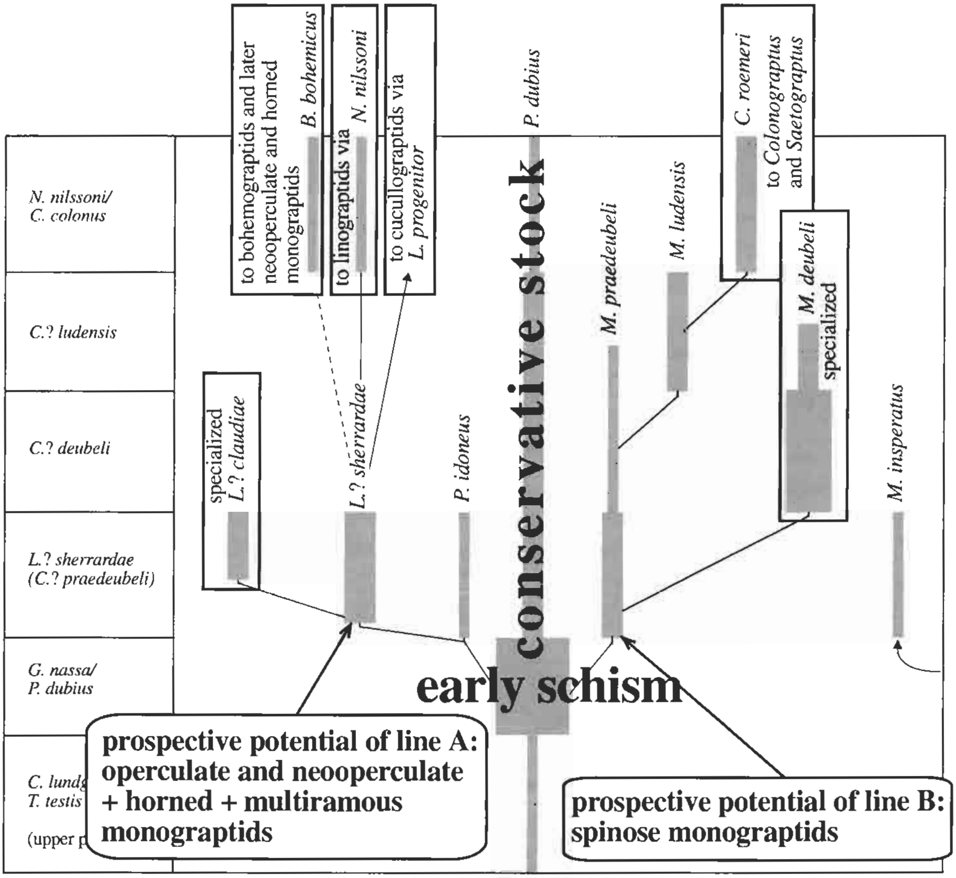


Fig. 3. Diagram showing the main trends of morphological changes during the late Homerian adaptive radiation of monograptids. What is meant by horned monograptids is the *Bohemograptus cornutus* group (further explanations in the text).

praedeubeli. The evolutionary potential of the stem species also remains essentially unchanged.

Meaning of the early schism. — The early schism, the separation from the *Pristiograptus dubius* stock of the two divergent lines of evolution, each representing quite a different trend of future changes, has been manifested by only minor modifications of the ancestral morphotype. The first representatives of the new lineages (*P. idoneus* and *C.? praedeubeli*, respectively), display only insignificant changes of the *P. dubius* 'Grundplan'. They are expressed in the proximal end development (the attenuation of the proximal end, its gentle dorsal curvature or a ventral bend), combined with some changes in the shape of the sicula (the ventral curvature or a flaring aperture), as well as in the appearance of gentle lateral elevations on the thecal apertures.

The adaptive significance of these minor traits is not obvious although probable. The curvature of the proximal end may be, in the light of the recent studies by Rigby (1990), adaptively significant, thanks to causing the rotation of the rhabdosome, and ensuring a higher feeding efficiency as compared with rectilinear ancestral types. The initial dorsal curvature, characteristic of the *P. idoneus–C.? sherrardae* line, was, however, later lost in the evolution of descendant species (in advanced cucullograptids and linograptids and still earlier in bohemograptids), or replaced by a ventral curvature.

The appearance of such features may be explained as a means of producing a certain degree of difference rather than in terms of a specific function resulting in the adaptive superiority over the ancestral type. Such character difference was an asset in avoiding severe intragroup competition in huge and crowded *P. dubius* patches during the time of proliferation. At the same time they outline the directions of future ecological expansion. Some other minor traits develop into persistent and crucial adaptations of certain groups, as for instance the apertural elevations in cucullograptids (Urbanek 1966). Some others are truly enigmatic, e.g. the trumpet-like sicula in *C.? deubeli* or the attenuation of the proximal end in *P. idoneus* etc. We are ignorant whether such characters, individually or in compound, played the role of key-adaptations, distinguishing divergent trends of further specialization. More probably, they were merely an outward expressions (correlates) of certain intrinsic characters which had been decisive for the evolutionary potential of each lineage at the early stage of divergence. Nevertheless these minor and newly introduced traits 'stamped' the earliest representatives of the divergent directions of further specialization. It is tempting to use after Simpson (1949, 1953) the term 'token' to denominate such minor but stable morphological characters, having no evident functional significance, but providing a characteristic marker (or emblem) distinguishing a given lineage or group.

Branch of gracile forms. — The A line, represented by *P. idoneus* and *C.? sherrardae* as its successive links, displays a distinct trend toward the size reduction of the sicula, the gracilization of the thecae and the gradual development of a dorsal curvature in the proximal part of the rhabdosome (Figs 4–5). The more advanced *L.? sherrardae* Sherwin 1974 exhibits a pronounced dorsal curvature in the proximal part of the rhabdosome and slight elaborations of the apertural border, developed as gentle elevations (Fig. 6). That is why Koren' (1992) suggested that it should be tentatively assigned to the genus *Lobograptus*, while a less advanced *P. idoneus*, with straight thecal apertures and a lesser dorsal curvature, was treated as a representative of *Pristiograptus*. In fact, both morphospecies present a difficult task for a taxonomist, which may be solved only by some arbitrary judgement. Far more important, however, is the fact that *Lobograptus? sherrardae* is truly intermediate in its characteristics, resembling strongly the earliest representative of cucullograptids, *Lobograptus progenitor*, on the one hand, and the earliest linograptid, *Neodiversograptus nilssoni*, on the other (Fig. 6A–C). It also exhibits, via *P. idoneus*, close relations with regular pristiograptids from the *P. dubius* group. Moreover, *L.? sherrardae*

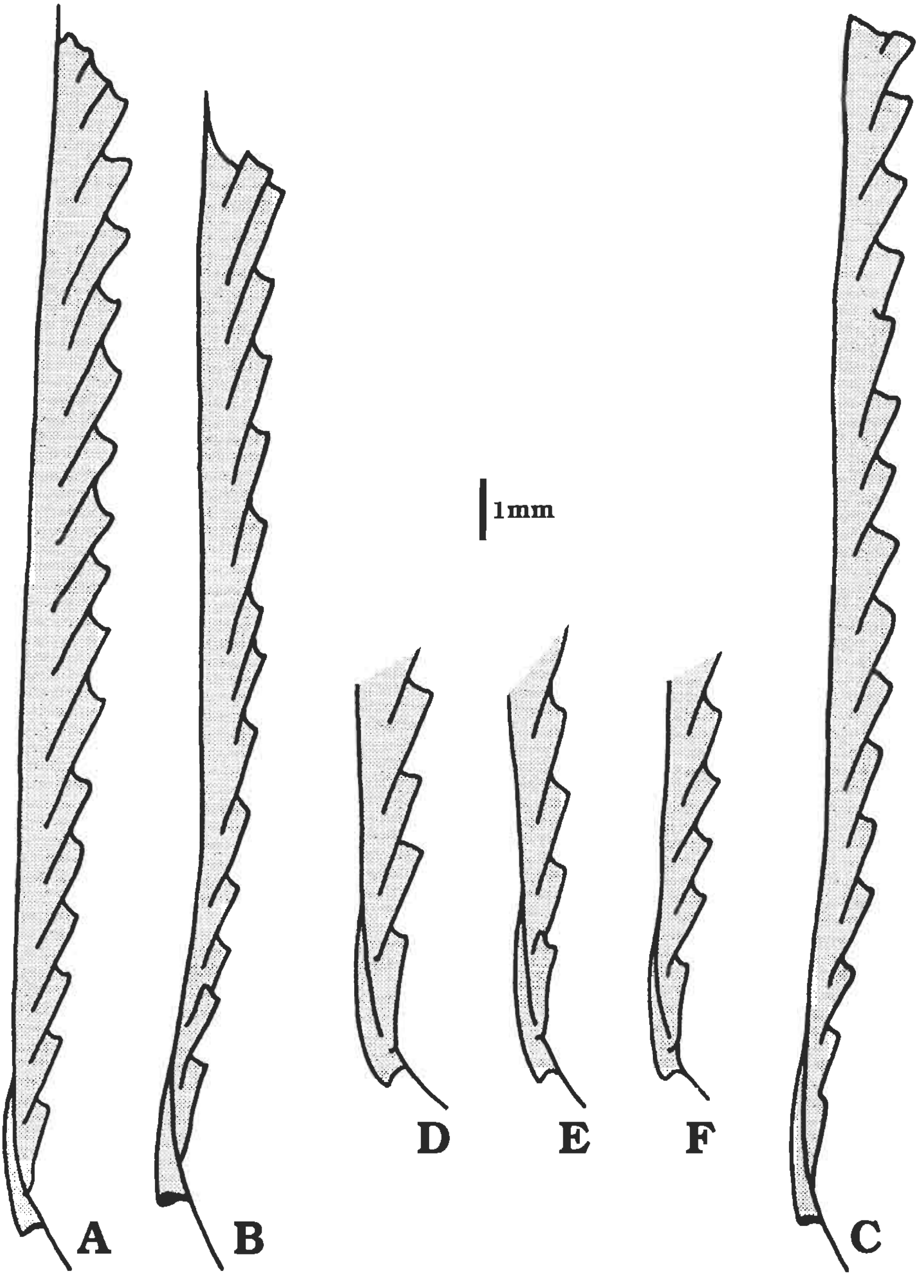


Fig. 4. Outline drawings of monograptids illustrating the *P. dubius–P. idoneus* transition. *L.? sherrardae (C.? praedeubeli)* Zone, Kursala Formation, Alai Range, South Tien Shan. ❑A. *Pristiograptus dubius* (Suess 1851), proximal part of the rhabdosome with curved sicula morphologically transient to *P. idoneus* Koren' 1992. ❑B–F. *Pristiograptus idoneus* Koren' 1992 proximal parts of rhabdosome with different degree of dorso-ventral curvature (B–C) and sicular portions of the rhabdosome showing a morphological spectrum in the degree of curvature (D–F).

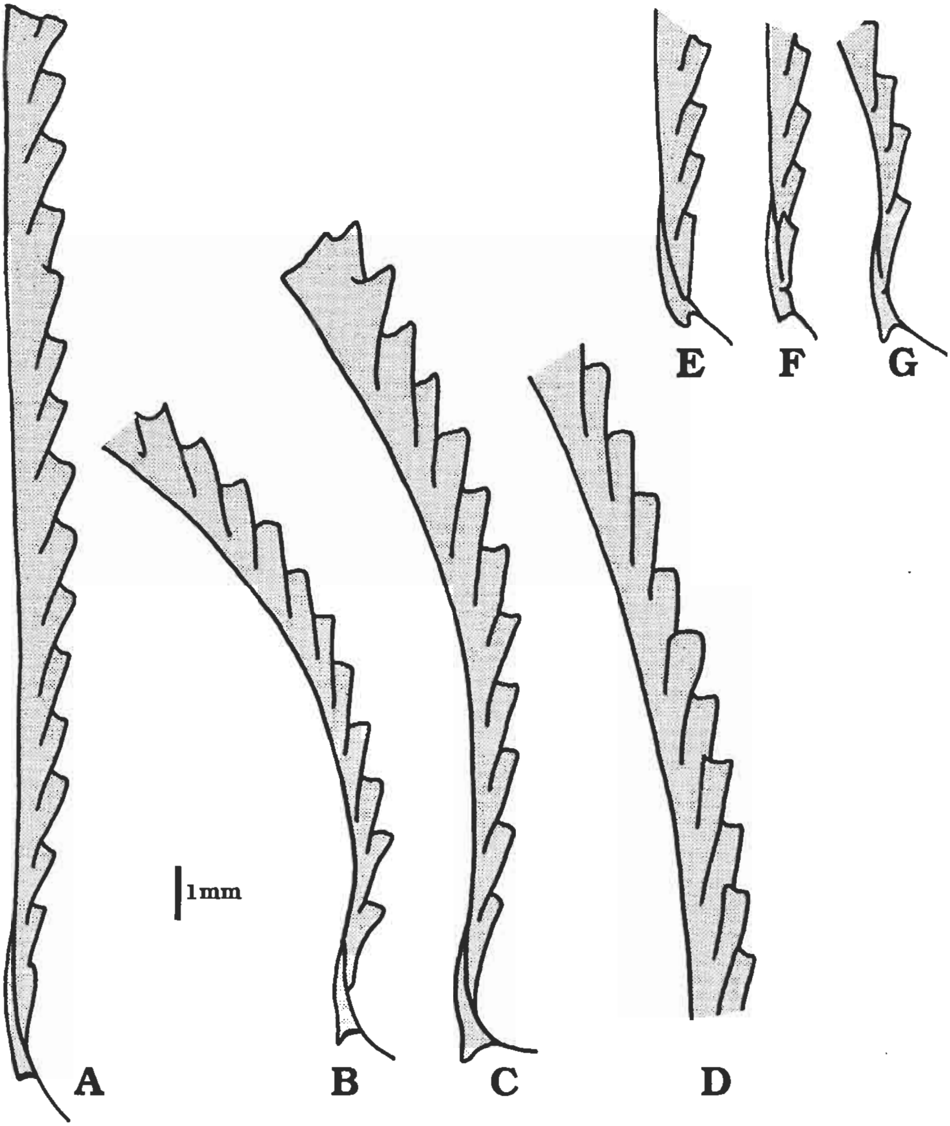


Fig. 5. Outline drawings of monograptids illustrating the *P. idoneus–L.? sherrardae* transition. *L.? sherrardae* Zone, Kursala Formation, Alai Range, South Tien Shan (after Koren' 1992, simplified). ❑A. *Pristiograptus idoneus* Koren' 1992, the presumable ancestor of *L.? sherrardae*, proximal part of the rhabdosome with a slight dorso-ventral curvature. ❑B–D. *Lobograptus? sherrardae* (Sherwin 1974) with strong dorsal curvature of the rhabdosome (B–C) and distal part of the rhabdosome (D). ❑E–G. Gradual transition between *P. dubius* (E), *P. idoneus* (F) and *L.? sherrardae* (G) traced at sicular portion of the rhabdosome.

is separated only by a small morphological discontinuity from *Bohemograptus bohemicus* which may also be derived from it, assuming few morphological changes (Fig. 6D). *Lobograptus cornuatus* described by Lenz (1993) from the *C.? praedeubeli* level of Arctic Canada is in our opinion

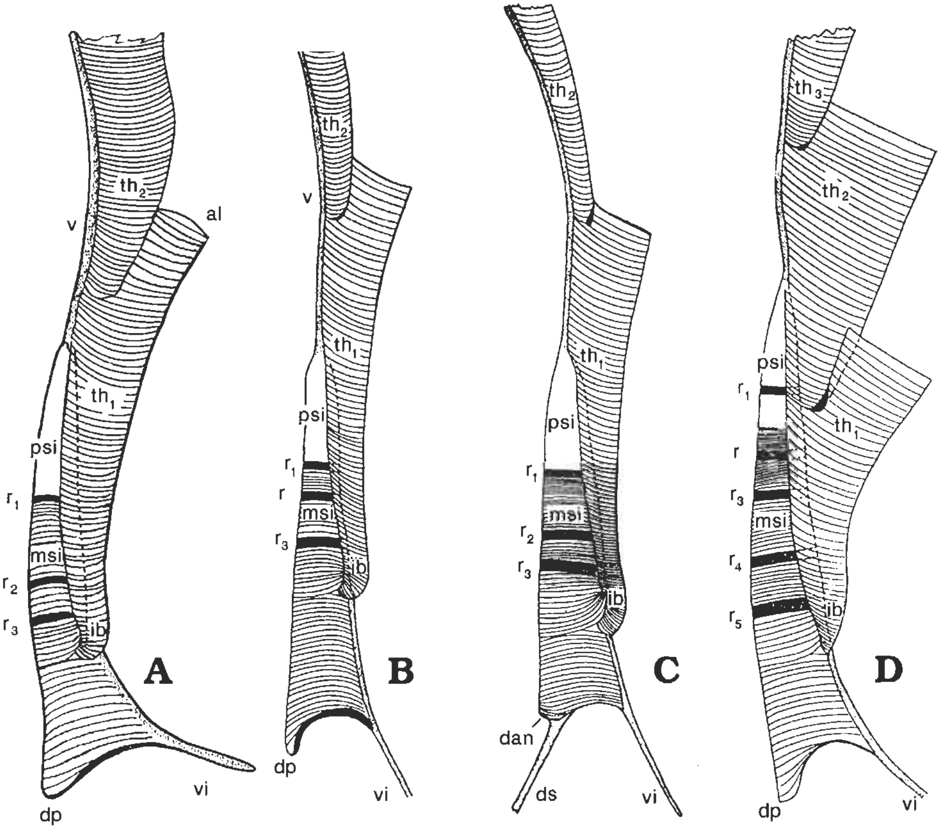


Fig. 6. Proximal parts of rhabdosome as seen on isolated bleached specimens (after Urbanek 1970 and Koren' 1992, modified). In A fusellar lines are conjectural, in B–D simplified. ❑A. *L.? sherrardae* (Sherwin 1974). ❑B. *Lobograptus progenitor* Urbanek 1970. ❑C. *Neodiversograptus nilssoni* (Barrande 1850), a monograptid morph. ❑D. *Bohemograptus bohemicus* (Barrande 1850).

conspecific with *L.? sherrardae.* It is only because his material consists of short fragments, that Lenz (1993: p. 496) has arrived to the conclusion that 'the rhabdosome is apparently straight throughout', differing in this way from *L.? sherrardae* and *L. progenitor.* Otherwise his paper has provided most valuable data on the sicular and thecal morphology of this earliest forerunner of the lobograptid trend.

Thus in its own Zone, *L.? sherrardae* attained only a small degree of divergence from its pristiograptid ancestors, while its lobograptid specialization (gentle elevations of the apertural border) or linograptid features (increase in the width of the sicular aperture combined with a slight dorsal curvature in the proximal part of the rhabdosome) were insignificant. Nevertheless, its morphology is unique among the collateral contemporaries, making *L.? sherrardae* an almost perfect candidate for a common ancestor for both linograptids and cucullograptids (see Figs 3–6). It represents one of those forms, which were christened 'synthetic', 'prophetic' or 'mixed' types in classical pre-Darwinian and early post-Darwinian palaeontological literature (Darwin 1962). They combine features characteristic of a few independent trends of future evolution. It is appropriate to mention here, however, that the future scope of morphological and ecological changes (e.g. the ability to form sicular cladia or produce complex apertural apparatus) was totally unpredictable at the *L.? sherrardae* level of evolution! Yet the prospective evolutionary potential of its descendants was exceptional and included i.a. such novelties as the multiramous rhabdosome and a new skeletal tissue, the last one being an invention of the advanced bohemograptids (microfusellar tissue, Urbanek 1970).

Branch of robust forms. — The course of events within line B may be traced in the first place due to the studies of Jaeger (1959, 1991). His *C.? praedeubeli* marks the first step towards more advanced or more specialized derivatives of this line (Fig. 7B). It preserves largely the *P. dubius* habitus except for the slight ventral curvature of the proximal end or the presence of incipient symmetric lappets (elevations) on the aperture of th$_1$.

It is difficult to understand why Jaeger (1991: p. 326) insists that the derivation of *C.? praedeubeli* from its most likely ancestor (*P. dubius*), 'would need quite a number of qualitative transformations'. It is clear that these differences are small and mostly quantitative in nature.They could have been bridged as a result of a single speciation. Moreover, Jaeger has not found transients between *P. dubius* and *C.? praedeubeli*. Instead he mentions (Jaeger 1991: p. 319) a fairly mosaic variation within populations of *C.? praedeubeli*, with variants representing different degrees of expression of disparate *C.? praedeubeli* characters, combined with those of *P. dubius*. This variation might be also interpreted as a lateral transition towards *C.? praedeubeli*, without producing, however, a long series of sequential populations. Therefore, it is no wonder that Koren' (1990, 1992) does not share this somewhat agnostic stance of Jaeger's, deriving *C.? praedeubeli* immediately from the conservative *P. dubius* stem line and assuming later bifurcation of its lineage into the *C.? deubeli* and the *C.? ludensis* (Murchison 1854) *(=Monograptus vulgaris* Wood 1900*)* lines (for the nomenclatorical problem involved here see Jaeger 1991: p. 334).

The phylogenetic role of *C.? praedeubeli* within line B is comparable to that of *L.? sherrardae* in line A. On one hand, it has been shown to produce a rather specialized sideline represented by *C.? deubeli* (see below), on the other hand, it was a starting point for progressive lines leading eventually to *Colonograptus* and *Saetograptus* (see Figs 1, 3).

The successive links of the above evolutionary line may be seen in *C.? ludensis*, then *C.? gerhardi* (Kuehne 1955) followed by typical representatives of *Colonograptus*, *C. roemeri* (Barrande 1850), and *C. colonus* (Barrande 1850), in the overlying *N. nilssoni/C. colonus* Zone. The evolution of the *C.? praedeubeli–C.? ludensis–C.? gerhardi* lineage was very gradual ('gleitende Evolution' of the German authors), showing an overlap of the variation range between the ancestral and the daughter species and involving mostly quantitative and statistical changes.

At present it is difficult to say whether *C.? ludensis* or *C.? gerhardi* were the forerunners of the earliest *Colonograptus* species. The latter has more elaborated lateral elevations but also a somewhat specialized thecal morphology, while *C.? ludensis* is relatively delayed in the expression of the first character. There is, however, little doubt that true colonograptids of

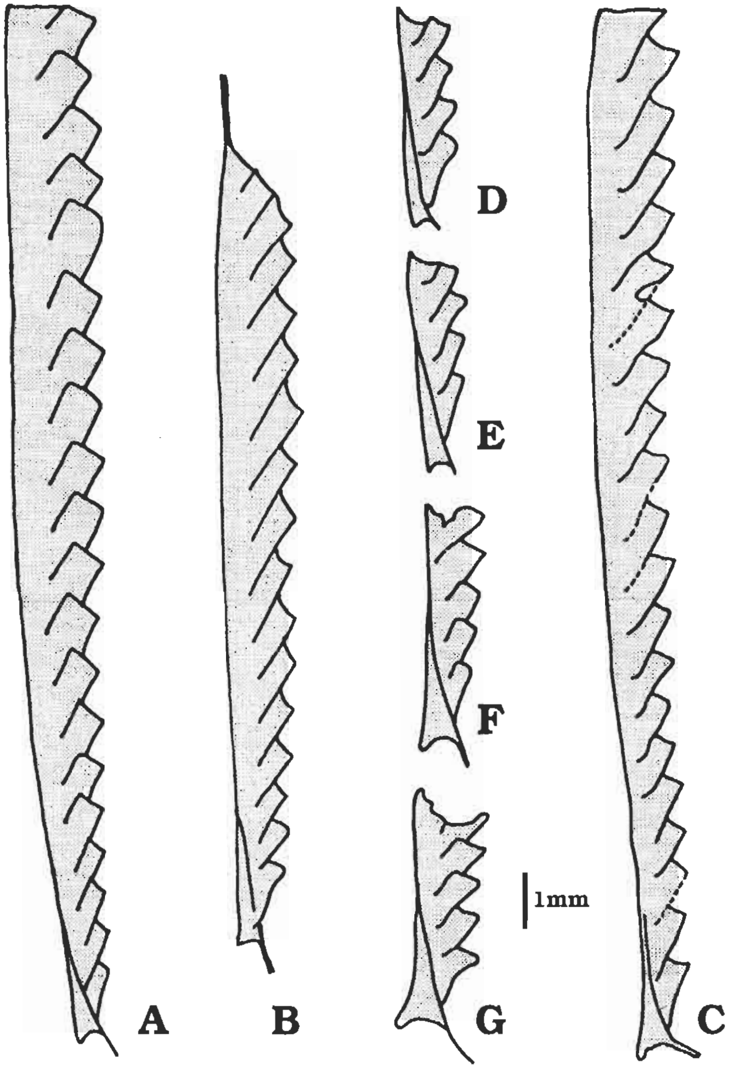


Fig. 7. Outline drawings illustrating the *P. dubius–C.? deubeli* transition. *C.? praedeubeli–C.? deubeli* Zone, Kursala Formation, Alai Range, South Tien Shan, Kirghizia. ❑A. *Pristiograptus dubius* (Suess 1851). ❑B. *Colonograptus? praedeubeli* (Jaeger 1990). ❑C. *Colonograptus? deubeli* (Jaeger 1959). ❑D–G. Variants displaying morphological transition from *C.? praedeubeli* to *C.? deubeli*.

the *N. nilssoni/C. colonus* Zone emerged from the populations of the *C.? ludensis–C.? gerhardi* plexus. The novelty first acquired at the *C.? praedeubeli* stage of phylogeny, namely the gentle lateral elevations of the apertural border in th_1, became strongly elaborated. They attained quite a different character due to a perceptibly increased expressivity (enlargement) and penetrance (spreading onto a number of proximal thecae). This adaptive type proved later to be very persistent and characteristic of the entire Gorstian. It did not disappear until the *S. leintwardinensis* Zone.

It is difficult to judge whether the gentle elevations of the apertural border, a novelty (apomorphy) distinguishing *L.? sherrardae* and *C.? praedeubeli* from their *P. dubius* ancestors, represent homological or merely homoplastic structures. The morphogenetic effects, although different in degree (expressivity), are approximately similar. In the light of Koren's (1992) observations on *L.? sherrardae*, these elevations are slightly better expressed in the proximal part of the rhabdosome. As a result of the polar organization of graptolite colonies (Urbanek 1961, 1972), phylogenetically novel characters can be introduced into the rhabdosome either proximally or distally and thus are to be more pronounced towards one of the ends. In the case in question, the new character must have been introduced from the proximal end. This is in contrast with the prevailing distal introduction of phylogenetic novelties in most of the later cucullograptids. Line B also displays an orthodox proximal introduction of the novel trait. In spite of this, we are rather inclined to accept an independent origin and possibly a different genetic basis for the paired apertural elevations formed in lines A and B, respectively.

The use of generic names established for the well-defined Gorstian species groups, presents great difficulties when applied to the late Homerian taxa. The low degree of expression of diagnostic features (apertural lobes and elevations) make them hardly discernible while their phylogenitic significance, as markers of particular terends is doubtless. Nevertheless, an introduction of new generic names to lump those early representatives of the Ludlow genera like *Ludensograptus* Tsegelnjuk 1976 seems inappropriate. We have suggested for the time being a tentative classification used in the text of the present paper.

The present study closes a long debate on the role of *P. dubius* in the phylogeny of late Silurian monograptids. Some preliminary ideas that colonograptids may be derived from the *P. dubius* stock were expressed even earlier (Urbanek 1963: p. 196, footnote; Hutt *et al.* 1972; Rickards *et al.* 1977). These views were rather skeptically evaluated by Jaeger (1978: pp. 39–43), who regarded them as speculative. But he himself fall victim of his own discoveries, which in time provided substantiation for the above view! The assumption that *Lobograptus*, *Neodiversograptus* and *Bohemograptus* evolved by gracilization of a member of the pristiograptid stock in the 'low Ludlow', were expressed by Rickards *et al.* (1977: p. 82). Sherwin (1974: p. 234) noticed a great similarity between *L.? sherrardae*, *L. progenitor* and *N. nilssoni*. However, Koren' was the first to provide a factual substantiation to the view that the above mentioned trends are of *P. dubius* ancestry, and evolved directly from *L.? sherrardae*. She has supported at the same time the earlier tentative suggestion of Urbanek (1966, 1970) that those divergent lines had a common ancestor.

Specialized sidelines

Each of the two main trends of the evolution, which had appeared due to the early schism, produced sidelines represented by extremely specialized adaptive types (Fig. 3). This introduces an element of a certain symmetry

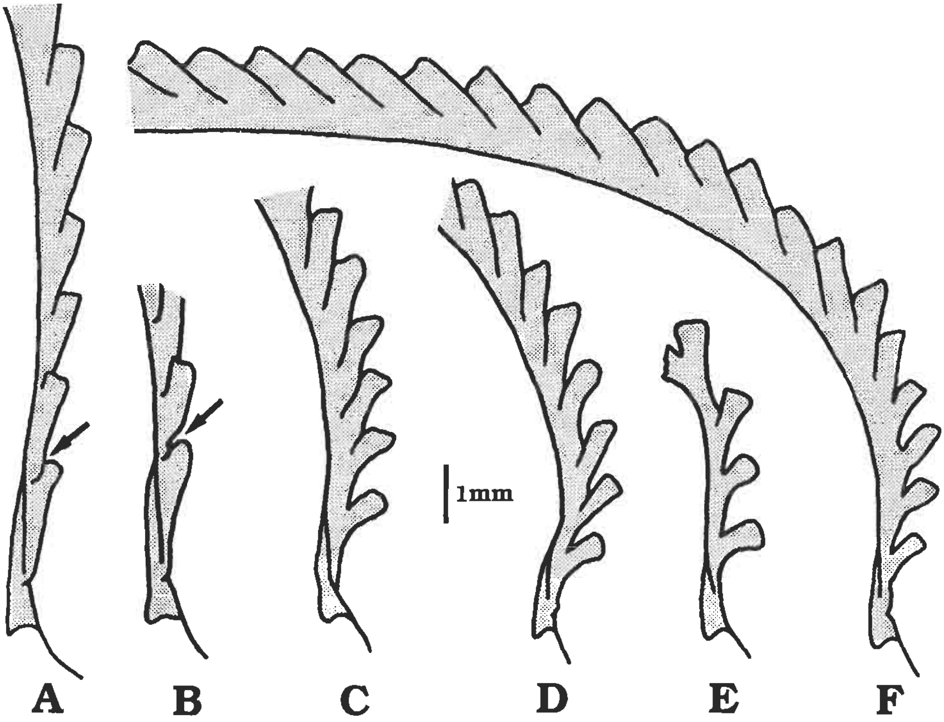


Fig. 8. Outline drawings illustrating the *L.? sherrardae–L.? claudiae* transition. Upper part of the *L.? sherrardae (C.? praedeubeli)* Zone, Kursala Formation, Alai Range, South Tien Shan (after Koren' 1992, simplified). ❑A–B. Proximal portions of rhabdosomes in *L.? sherrardae* (Sherwin 1974) displaying transient characters to *L.? claudiae* Koren' due to incipient degree of isolation of th_1 as indicated by an arrow. ❑C–F. Expressivity variants in *Lobograptus? claudiae* Koren' 1992 from less (C) to more advanced (D–E) types, and a specimen with a typically biform rhabdosome (F).

to the pattern of the adaptive radiation exhibited by late Homerian monograptids. Thus line A ends laterally with *L.? claudiae*, remarkable by its tendency towards isolation of the most proximal thecae (Fig. 8), a doubtlessly autapomorphic feature. The degree of isolation (its expressivity) and the number of thecae (3–6) affected by it (its penetrance) varies within the population (Fig. 8C–E). One can also trace the appearance and introduction of this novel character, first manifested by an insignificant notch separating the uppermost metathecal portion of th_1 from the adjacent th_2 (Fig. 8A–B). These observations by Koren' (1992) are not only evidence of a gradual course of speciation *L.? sherrardae–L.? claudiae*, but also a corroboration of the earlier ideas on the proximal introduction of some new characters in the evolution of many graptoloids and their further spreading due to increased expressivity and penetrance. At the same time, the morphology of the distal thecae leaves no doubt as to their *L.? sherrardae* ancestry. Representing a unique trend of a rather short duration, *L.? claudiae* has been recognized, besides Tien Shan, also in Novaya Zemlya

(Arctic Russia, Koren' 1992) and in Arctic Canada (A.C. Lenz, personal communication). Hence, the last mentioned taxon is a species established on a wide area, not an aberrant local variety.

The species in question was a short-lived one, being confined to the upper part of the *L.? sherrardae* Zone. Koren' (1992) has seen in it the terminal link, closely related to *L.? sherrardae* but marked by a high degree of specialization. Against the background of coeval and later monograptids, the morphological trend represented by *L.? claudiae* is unique. However, similar patterns are seen in the Early Silurian, with a number of very successful lineages exploring the tendency. They include both the moderate ('triangulate monograptids', *Demirastrites*) and extreme expressions (*Rastrites*), of thecal isolation. The causes for the evolutionary failure in the case of *L.? claudiae* are difficult to define. Was it an improper ('inadaptive') combination of isolation with the rest of the organizational features of the colony, or was it rather a different environmental context? For the time being these questions must be left unanswered.

Line B produced *C.? deubeli* as an early product of specialization. This is most clearly expressed in the unusual shape of its sicula, doubtless an autapomorphic feature (Figs 7C, 9C–D). At the same time evolution from *C.? praedeubeli* to *C.? deubeli* displays all possible transients from standard to modified, rightly called the *M. hercynicus*-type of the sicula (Jaeger 1959). Therefore, the limit between these two species could be set only arbitrarily, although the initial and the terminal form differ sharply (Jaeger 1991: p. 328). On the other hand, the Tien Shan material reveals a smooth transition from *C.? praedeubeli* to *C.? ludensis* with a considerable overlap in the variation range of both species (Koren' & Suyarkova 1993). Recent opinion expressed by Lenz (1993: p. 495) that *C.? praedeubeli* is a more likely ancestor to *C.? ludensis* than to more specialized *C.? deubeli* pays no attention to the numerous transitions in both directions.

The flaring aperture of the metasicula and the trumpet-like shape of the entire sicula are among the diagnostic features of *C.? deubeli.* They are not, however, unique. First of all, siculae of a similar shape occur sporadically as deviants within the populations of different stratigraphic horizons as, for example in *Bohemograptus* (Urbanek 1970) and *'Monograptus' ultimus* (Jaeger in Kříž *et al.* 1986). Such deviants were not included in the norm of the corresponding species, with a few exceptions, however. It was only later, that the Early Devonian (Lochkovian and Pragian) monograptids started to display the trumpet-like siculae (Jaeger 1978). This is, indeed, a graphic example of a 'Zeitsignatur' in the phylogeny of graptoloids.

The reason why the *M. hercynicus*-type siculae offered no or only limited success in Silurian times but opened rather wide opportunities in the Lower Devonian are obscure. The most probable explanation which may be suggested is that only in Devonian monograptids the trumpet-like siculae were constituents of a balanced adaptive syndrome. Although *C.?*

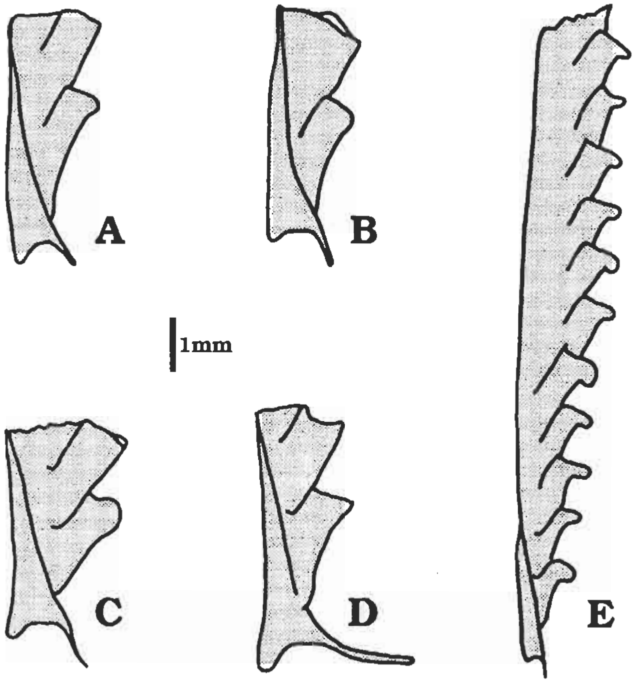


Fig. 9. ❑A–D. Morphological series illustrating sicular parts of rhabdosome from *C.? praedeubeli* (A) to *C.? deubeli* (B–D). ❑E. *'M.' insperatus* Koren' 1992, an aberrant species from the *C.? deubeli* Zone, Kursala Formation, Alai Range, South Tien Shan (after Koren' & Suyarkova 1994, simplified).

deubeli represented a fairly widespread species and existed through the *C.? deubeli* and *C. ludensis* zones, it left no descendants. This could probably be ascribed to its high degree of specialization, which first ensured its temporary biological success but soon eliminated it from the evolutionary scene.

Both sidelines represented by extremely specialized types, may be considered evolutionary experiments. Their appearance had been possible only because of the relaxation of selection, as well as of the genetic and epigenetic homeostasis during the early stage of adaptive radiation. This aspect of the late Homerian radiation of monograptids provides a good illustration of Mayr's (1963: p. 619) conclusion that during periods of proliferation 'even rather improbable genotypes may have a chance to survive for a while. Inevitably they give way, however, to more successful types in related branches'.

An instance of migration

Koren' (1991) has described from the *L.? sherrardae (C.? praedeubeli)* Zone of the Kursala Formation another unusual monograptids — *'M.' insperatus*

(Fig. 9E). It is characterized by the presence of distinct and rather uniformly developed paired apertural lobes on all thecae of the rhabdosome. While the apertural lobes resemble in shape those in *Colonograptus*, their penetrance surpasses what can be seen in any Ludlow colonograptid. Koren' has found *'M.' insperatus* as nearly isomorphic to *'M.' branikensis* Jaeger 1986 from the early Pridoli, although certainly the two species are not related phylogenetically. The position of *'M.' insperatus* is so isolated among the coeval monograptids, that Koren' (1992) suggested a cryptogenetic origin for this species. In this way, it would be the only case of the immigration of an alien element during the early phase of the adaptive radiation of monograptids after the *C. lundgreni* Event. This may be either evidence that the vacant habitats were almost completely sealed by 'inflated' *P. dubius* populations, preventing any invasion, as suggested recently by Urbanek (1993), or that the mid-ocean reservoir of graptoloid fauna was also affected by the environmental changes caused by the *C. lundgreni* disturbance, which resulted in a decreased migration pressure from the ocean into the marginal seas.

A striking resemblance of *'M.' insperatus* to much later Pridoli types, makes it a graphic example of a 'precocious form', to use Bulman's (1944–1947) terminology. Such an erratic appearance of morphologies which are ahead of time (or at least of the prevailing fashion of the time) is a well-established feature of the phylogeny in different groups. A number of terms were suggested to designate such early appearances, from 'Vorformen' or 'Vorpostenform' suggested by German palaeontologists (e.g. Schindewolf 1952) to 'heraldic evolution' as proclaimed quite recently by Rickards (1988). Some term is needed, although by using it we are not explaining the nature of the phenomenon. One could hypothesize that the 'insperatus' morphology is an effect of fixation of a mutation with a high expressivity and penetrance, producing a distinct, although rather little specific phenotypic effect (paired apertural lobes). The relative severity of the effect, as compared with standard colonograptids, may be explained by the tolerance of the environment during the time of an ecological release. However, judging from its fate *'M.' insperatus* proved to be adaptively inferior as compared with endemic pristiograptids. The problem of the precocious forms may be explained assuming that a number of nonhomological mutations may produce similar effects, such as apertural lobes. Nevertheless, some traits which remain unrecorded in the fossil state (behavioural, physiological etc.) may be crucial for the survival or extinction of the species with otherwise similar morphology.

Conclusions

The present paper may be summarized in the following four conclusions:

(1) *Pristiograptus dubius* is the only monograptid which survived the *C. lundgreni* Event in place, without retreating to a refugium. It is known to

have flourished on vast areas in the marginal seas and basins, immediately after the crisis (that is in the *G. nassa/P. dubius* Zone). The mass occurrence of *Pristiograptus dubius*, which may be explained in terms of an ecological release, was accompanied by an increase of variation followed by a period of rapid diversification into a number of new species (adaptive radiation). Hence, the case in question, provides good evidence for the conclusion that adaptive radiation is usually preceded by 'an evident and sometimes dramatic release of variability' (Simpson 1953: p. 228). Moreover, the release is immediately related (probably by a population — genetic mechanism) to the period of proliferation displayed by the ancestral species.

(2) The early phase of the adaptive radiation studied herein is characterized by a paucity of the lineages which evolved from the *P. dubius* conservative stock. Only two lineages were involved in the 'early schism', which defined the opposite trends of further diversification into slender (branch A) and robust (branche B) descendants of *P. dubius*. Contrary to many Early Silurian lineages, which were initially rather slender, Late Silurian monograptids starting from moderately robust forms, developed divergent trends, on one hand towards more robust types, on the other hand towards extremely slender stocks. Both lines mentioned above produced some generalized and some specialized types. An instance of the generalized type within line A is *L.? sherrardae*, a presumed common ancestor of linograptids, cucullograptids, and probably also neocucullograptids (via *Bohemograptus*). A similar role was played by *C.? praedeubeli* within line B. The generalized types display the prevalence of ancestral features (symplesiomorphies) with only a few traces of specialization (future synapomorphies). The presence of generalized types may be considered a remarkable feature of adaptive radiation. Moreover, such species as *L.? sherrardae* resemble the synthetic types which emerge during adaptive radiation and possess characters proper to the later divergent evolutionary trends.

While the generalized types produced descendant taxa, each representing a distinct adaptive type, the specialized taxa both on lines A and B, left no descendants and became extinct after a shorter (line A) or somewhat longer (line B) time. The generalized types of the late Homerian adaptive radiation have an exceptionally great evolutionary potential, being responsible for the bulk of post-Homerian monograptids. This highly diversified faunal assemblage originated, with only a few exceptions, monophyletically from a single ancestor, namely from *P. dubius*.

(3) Some of the descendant lineages, the cucullograptids and neocucullograptids in particular, were subjected to secondary radiations. Thus, the Gorstian cucullograptid adaptive radiation produced more evolutionary lineages than the late Homerian radiation from the *P. dubius* stock did. At the same time, cucullograptid species are morphologically clear-cut, while the earliest products of the late Homerian diversification are less clearly defined because of the scarcity of characters available. Therefore the

assignment of the earliest species to the genera, erected on the well-defined Gorstian fauna poses a difficult task and is largely arbitrary. The fact remains that this early divergence defined the trends of future evolution for most of the late Silurian monograptids. However, these trends are morphologically only slightly outlined as most of the key-features were to appear only later. Branching off is therefore not synonymous in this review with the sudden appearance of the entire adaptive syndrome. On the contrary, later adaptive radiations were only variations of a certain adaptive type. Hence, ample splitting cannot *per se* be a measure of the significance of the given adaptive radiation.

(4) The history of the late Silurian monograptids provides conclusive evidence of a pivotal role played by the conservative *P. dubius* stem line in the graptoloid evolution. Like some others persistent lineages, the *P. dubius* stock was characterized by presumably highly eurybiotic adaptations, permitting this species' survival through at least three biotic crises. On the other hand, the lack of morphological specialization opened possibilities to introduce new changes and modifications. Thus the *P. dubius* stock was at the same time a persistent lineage with the permanence of a near-stasis, as well as, periodically, a source of new progressive lineages. As a result of adaptive radiation in late Homerian-early Gorstian time, linograptids (*Neodiversograptus)*, cucullograptids (*Lobograptus)* and neocucullograptids *(Bohemograptus)*, as well as spinose monograptids *(Colonograptus)* were produced. In the early Pridoli, 'neocolonograptids' (the *ultimus-lochkovensis* group) branched off the stem line (Urbanek, in press) This exceptional double role of the *P. dubius* stock is a remarkable feature of the late history of Graptoloidea.

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Streszczenie

Współczesne badania nad kryzysem biotycznym jaki dotknął monograptidy w późnym wenloku (tzw. zdarzenie *C. lundgreni*), pozwalają ocenić zarówno skalę masowego wymierania (przeżywa tylko jeden gatunek, *Pristiograptus dubius*), jak i przebieg procesów składających się na wczesny etap odradzania fauny graptoloidowej. Duże znaczenie dla poznania tych ostatnich miało zbadanie obfitej fauny z formacji Kursala, w górach Tien Szań (Kyrgystan). Różnicowanie się szczepu *Pristiograptus dubius* było poprzedzone jego masowym występowaniem i zwiększoną zmiennością. Następnie doszło do oddzielenia się dwu głównych linii ewolucyjnych: linii A, reprezentowanej przez *P. idoneus* oraz linii B, którą wyznacza pojawienie się *Colonograptus*? *praedeubeli*. Pierwszy gatunek dał początek *Lobograptus*? *sherrardae*, stanowiącemu wspólnego przodka tak rozbieżnych trendów ewolucyjnych jak linograptidy (*Neodiversograptus nilssoni*), kukullograptidy (*Lobograptus progenitor*), a prawdopodobnie także neokukullograptidy (za pośrednictwem *Bohemograptus*). Natomiast *C.*? *praedeubeli*, przedstawiciel lini B, zapoczątkowuje rozwój charakterystycznych dla wczesnego ludlowu monograptidów „kolczastych" (*Colonograptus*, *Saetograptus*).

Rozejście się wspomnianych linii ewolucyjnych określone jak „wczesna schizma", wyznacza zarazem główne kierunki ewolucji monograptidów ludlowu.