

# Graptolite dynamics in Silurian and Devonian time

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On the basis of biostratigraphic data known at present some preliminary attempts are made to evaluate graptolite dynamics, that is changes in graptolite diversity in time and space within pelagic facies of Silurian and Early Devonian age. For the comparative studies of diversity fluctuations *versus* some major environmental changes a standard graptolite zonation is used. Several critical and more or less well studied stratigraphical intervals are chosen; among them the Ordovician/Silurian, Sheinwoodian/Gorstian and Gorstian/Ludfordian boundary beds. For each level the most complete reference sections are analyzed. Special attention is given to the graptolite extinction, specification and radiation events within these time intervals. They might have been partly connected with or influenced by the environmental factors as a result of eustatic sea-level and climate changes, alteration of anoxic conditions, migration of carbonate sedimentation in pelagic direction, and other globally detectable events. The graptolite evolution during the time of monograptid existence can be subdivided into three phases using the comparison of the amplitude of the extinction-origination events and repeatability of the synphasic cycles.

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## Introduction

Graptolite dynamics, that is, changes in species diversity with time and space, are shown to occur in pelagic facies of Silurian and Devonian age. Some preliminary attempts are made here to envisage fluctuations in diversity versus some major environmental changes, discernible on a world-wide scale. During this time interval the relative abundance of graptolite taxa can be exemplified by two zones. Species numbered 40 to 60 for the *triangulatus* to *turriculatus* zones (Llandovery), when they flourished. And it decreased to four to five species before their final extinction in the *yukonensis* Zone (the uppermost Pragian).

In general the Silurian and Devonian assemblages contain more than 400 species and subspecies. Most of them were of global distribution within the pelagic realm at equatorial and moderate palaeolatitudes. Synchronous zonal assemblages differ in diversity within the known regions, but a few taxa were found from one region only. The latter perhaps suggests some ecologically peculiar features within a certain basin. To a certain degree their limited distribution may, however, result from an inadequate sampling and incomplete studies.

A standard graptolite zonal succession for the Silurian and Lower Devonian (Koren 1984) is based on the graptolite occurrences from all the continents as well as a continuous biostratigraphical record and reliable regional zonations. At present there is no well-founded absolute time scale to measure duration of zones, though such attempts have been made on the basis of different approaches (Carter et al. 1980, Churkin et al. 1977, Harland et al. 1982). Graptolite zones are definitely of unequal duration, and, accordingly, one can not measure the speciation or extinction rate. All we can do is to analyse highs and lows in graptolite diversity per zone.

The above problem has previously been discussed in the literature for the entire time interval or for particular stratigraphic levels (Bulman 1964, 1971; Jaeger 1978; Rickards 1978; Koren 1979, 1982, 1983; Koren & Rickards 1979) both on regional and global scale. As a result a general picture of the Silurian and Early Devonian graptolite diversity has been obtained. The present paper is aimed at preliminary recognition of graptolite dynamics at a zonal level using a synthesis of the data available and some new results. However, the author met with some difficulties. For example, the picture of phyletic evolution with the rare exceptions is quite vague. In this re-

spect we refer to studies of triangulate monograptids by Sudbury (1958) and cucullo- and neocucullograptids by Urbanek (1966, 1970). Our knowledge of graptolite ecology, is the second weak point, though many interesting suggestions have been made in recent years (Berry 1973, 1979, 1984; Berry & Boucot, 1972; Berry & Wilde 1978, 1983; Erdtmann 1976; Kaljo 1978; Kirk 1969, 1972; Rickards 1975; Skevington 1974; Watkins & Berry 1977). These include graptolite depth stratification, automobility and other aspects. It was briefly summarised in a recent paper by Lenz & Chen (1985). One can not usually make a reconstruction of peculiar environmental features of the graptolite habitats on the basis of the sediment records which has successfully been shown for many benthic groups. Primarily we consider taphocoenoses not life communities. Besides the lithology of the typical graptolite-bearing rocks is fairly monotonous. Changes of environmental factors which have been critical for graptolite mass extinction and origination waves may not be reflected in lithoevents within pelagic sequences. They have to be searched for in the shelf direction.

We may conclude that graptolites inhabited the near surface pelagic environments, most probably they reached as far as mesopelagic water masses. It means that temperature gradient, nutrient supply (most probably phytoplankton) and biocoenotic relationships were the most important parameters responsible for graptolite ecological maxima and minima. The complex picture of abiotic changes which affected biotope facies is diagrammatically shown by Walliser (1984a, c). It is clear, that not a single causal mechanism triggered and stimulated the adaptive changes in graptolites. Evolutionary highs and lows via a long chain of actions and interactions have resulted from biotope transformations and deteriorations caused by plate tectonics, eustatical sea-level changes, as well as by climate fluctuations and oceanic current patterns. Physical-chemical parameters of water masses and land also contributed greatly to the development and productivity of oceanic plankton.

However, the absence of proper data and elaborate techniques prevent us from discussing those genetic relations between biotic and abiotic controls. Using available material we can only try to

evaluate the graptolite dynamics for several stratigraphic intervals.

A generalized graptolite zonation is taken as a basis for comparative studies of successive graptolite diversity changes within the Silurian and Lower Devonian (Fig. 1). We take three particular stratigraphic examples indicative of a diversity pattern during the most important environmental changes. They coincide with the *supernus* to *atavus*, *lundgreni* to *scanicus/chimaera* and *leintwardinensis* to *ultimus* s.l. zones. Each interval is of about the same duration, 4 or 6 million years or less. The stratigraphical levels chosen were studied thoroughly partly because they incorporate the system, series and stage boundaries, recently discussed and defined by subcommission on Silurian stratigraphy (Holland 1984, 1985; Bassett 1985).

## Approach

Three or four regions having the most complete and well known stratigraphic succession and faunal record were chosen to illustrate the graptolite dynamics. As a rule the mentioned sections are situated within facially different successions typical of slope zones of marginal cratonic seas and oceans. Frequency distribution curves are given for each region separately (Figs. 2–4). The column showing zonal assemblage structure summarizes biostratigraphic evidence for all the regional successions. It embraces species which appear within the unit, those surviving from the preceding one, and taxa which disappear between the two zonal boundaries. For each zone the total number of taxa is given.

Mass extinctions and appearances are considered as the most important bioevents. The first is used to explain an abrupt elimination of several lineages, generic and specific groups of cryptogenic origin. The term appearance in this case has a broad meaning and incorporates events of origination of new lineages and splitting of surviving ones as well as radiation events. Asterisks show the introduction of adaptive novelties; their relative size implies a different taxonomic significance. Both extinctions and appearances resulting in well pronounced culminations and lows mark widely detectable zonal boundaries which could be considered as event boundaries.

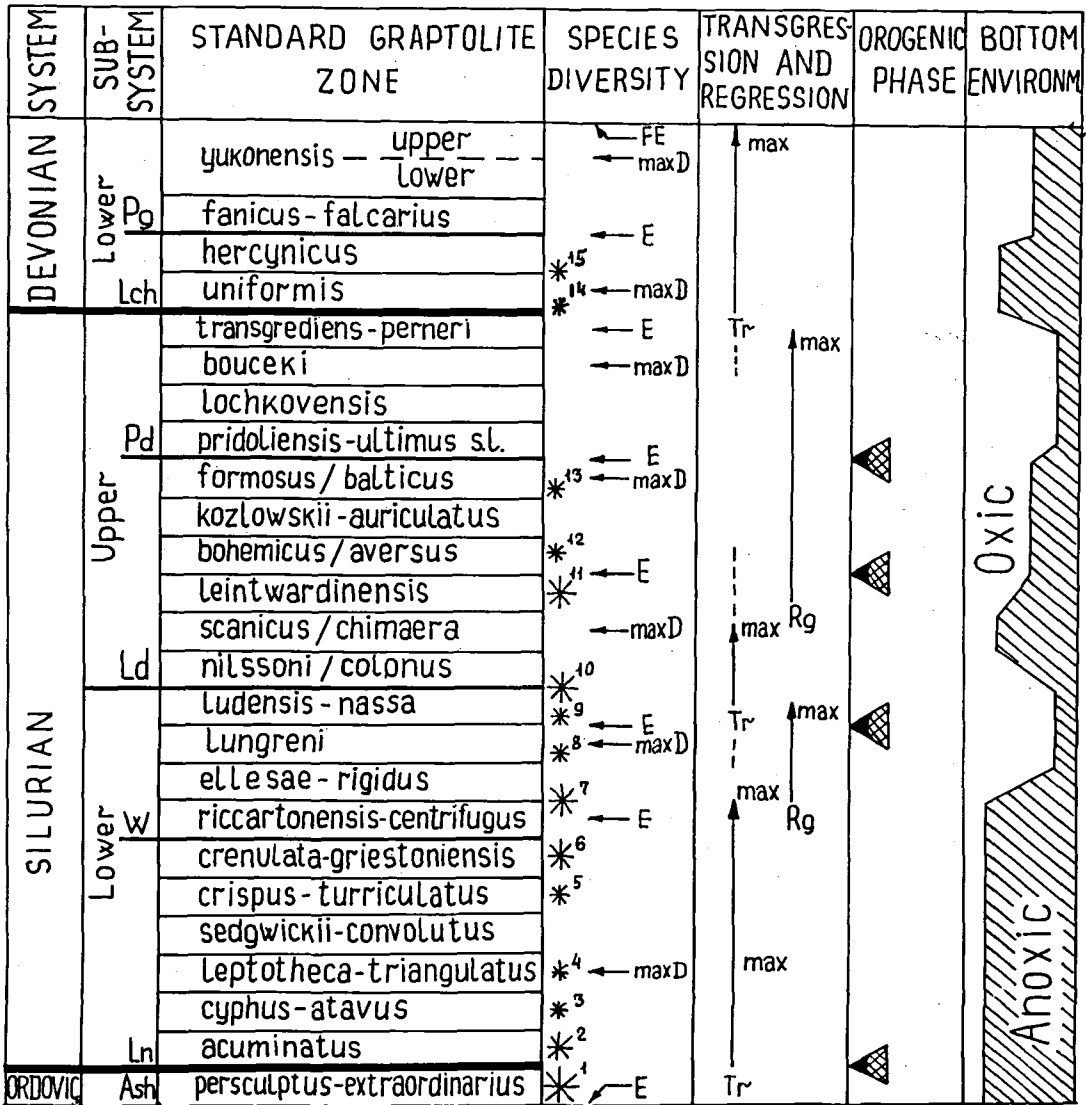


Fig. 1. Chart showing a generalised picture of graptolite dynamics against the major geological events in the Silurian-Early Devonian time. Abbreviations: E - extinction, D - diversity, Tr - transgression, Rg - regression. Asterisks and their size show the introduction of the new adaptive novelties of different taxonomic significans. They are as following: 1 - Suborder Monograptina (*Monograptus ceryx* Rickards et Hutt, 1970); 2 - Family Dimorphograptidae (*Akidograptus*, *Parakidograptus*); 3 - radiation in the "stem" atavograptids: *Přibylograptus*, *Lagarograptus*, *Coronograptus*; appearance of *Metaclimacograptus*, *Clinoclimacograptus*, *Rhaphidograptus*; 4 - radiation of the triangulate monograptids; appearance of *Rastrites*, *Diversograptus*, *Petalograptus* and other genera; 5 - *Monoclimacis*, *Sinodiversograptus*, the *Retiolites geminitzianus*, *Monograptus priodon*, *M. spiralis* and *Pristiograptus dubius* groups; 6 - Family Cyrtograptidae; 7 - new cyrtograptid lineages and the Plectograptinae Subfamily; 8 - cyrtograptid radiation; 9 - radiation within the Plectograptinae Subfamily and *P. dubius* group; an appearance of the common ancestor of the Linograptinae, Cucullograptinae and Neocucullograptinae Subfamilies; 10 - appearance of *Neodiversograptus*, *Bohemograptus*, *Saetograptus* and the *Monograptus uncinatus* group with subsequent radiation of newly formed stocks, including lobograptids in the *scanicus/chimaera* Zone; 11 - the Linograptinae Subfamily and new monograptids of the *M. uncinatus* group; 12 - *Neolobograptus* and *Neocucullograptus*; 13 - the *Monograptus formosus* group and several new monograptid lineages; 14 - the *Monograptus uniformis* and *M. aequabilis* groups; 15 - *Abiesgraptus*.

The diversity pattern shows the relative magnitude of extinctions, appearances and survivals plotted against some geological processes and events. Among them are eustatic sea-level and

climate changes, alternation of anoxic and oxic environments and to some degree the Caledonic orogenic phases.

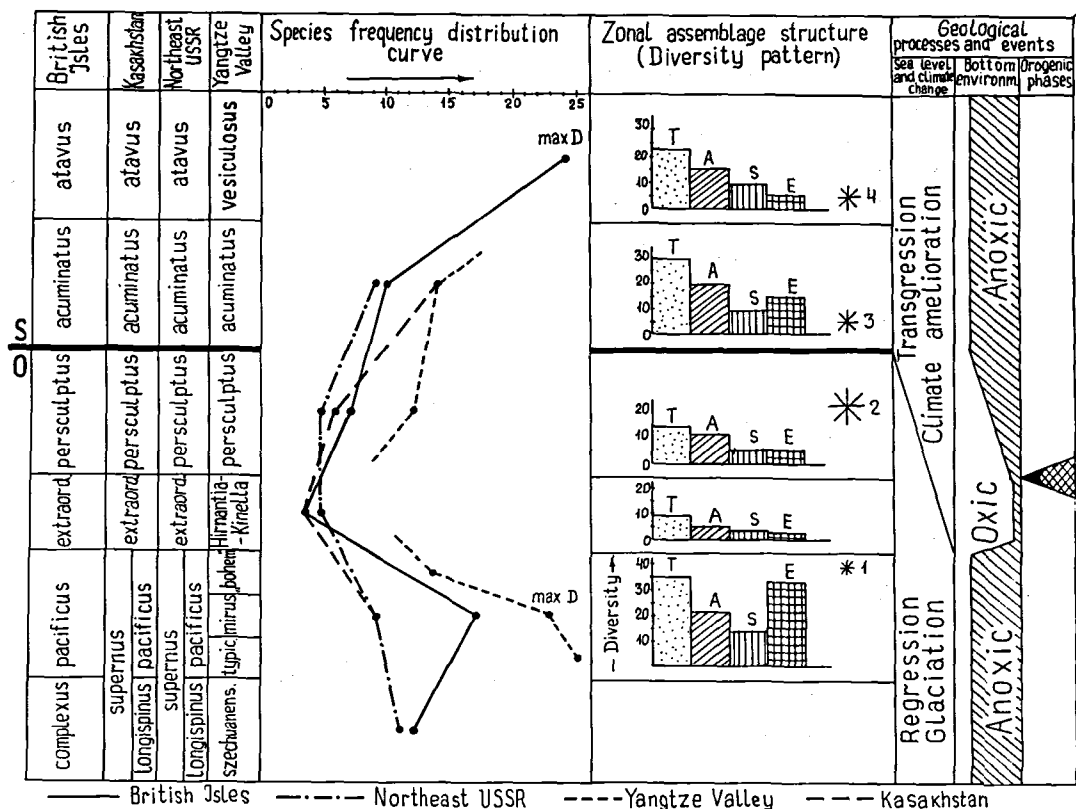


Fig. 2. Graptolite dynamics within the Ordovician-Silurian boundary interval (the *supernus* event). Abbreviations: D – diversity, A – appearance, S – survival, E – extinction, T – total number. Asterisks show the following bioevents: 1 – mass extinction of the Ordovician lineages formed by the Dicranograptidae, Nemagraptidae and Lasiograptidae Families, the Archiretiolitinae Subfamily and the *Climacograptus longispinus*, *C. latus*, *Paraorthograptus pacificus* and other diplograptid groups; 2, 3, 4 – see 1, 2, 3 on fig. 1. correspondingly.

### The *supernus* event

Major geological events take place at the Ordovician-Silurian boundary. The Ashgill glaciation and accompanying global climatic cooling and lowering of the sea-level are the most important (Brenchley 1984; Brenchley & Newall 1984). Orogenic movements of the Taconian phase which occurred approximately at the end of the glaciation have “resulted in structural remodeling of the Protoatlantic and Prototethys oceans” (Tomczykowa Tomczyk 1979). These events are reflected in contrasting changes in lithology and faunas (both faunal shift and immigration events), in replacement of anoxic environments by oxic ones (Barnes 1984). Many erosional effects took place in oceanic sediments, within cratonic sequences stratigraphic gaps are well documented. These events have drastically reduced

the extent of tropical and subtropical pelagic environments. The areal extent of the black shale sedimentation (anoxic environment) reached its maximum within the *supernus* Zone. It is almost absent in the *extraordinarius* Zone. A new expansion of anoxic water masses due to a global transgression starts in some regions in the *persculptus* Zone, becoming world-wide in the *acuminatus* Zone.

What are the graptolite dynamics at this time? It is shown at zonal and specific level for most representative sequences – British Isles, Kazakhstan, Northeast USSR and Yangtze Valley (Rickards 1976, Apollonov et al. ed. 1980; Wang et al. 1984; Koren et al. 1983; Stratigraphy 1984). The changes in diversity of synchronous graptolite assemblages are approximately the same for the three curves. Only a curve showing Yangtze Val-

ley graptolite changes is marked by unusually abundant graptolite associations. Two approximately equal diversity peaks at the *pacificus* and *atavus/vesiculosus* zones (25 to 35 taxa) is a common feature of all the sections discussed. The *extraordinarius-persculptus* diversity drop represents one of the most dramatic events in graptolite history.

Mass extinction of Ashgill taxa within the *pacificus* subzone can be illustrated by the zonal assemblage structure (Fig. 2). Only three diplograptid species survive at the *extraordinarius* boundary. Many important Ordovician lineages became extinct during this interval. Among them are: all the genera belonging to the Dicranograptidae, Nemagraptidae and Leptograptidae Families, as well as Archiretiolitinae Subfamily. Some Ordovician morphological relicts were recently

reported from the Llandovery of China (Stratigraphy...1984). Diplograptid faunas undergo a great crisis as exhibited by the extinction of the *Climacograptus* species groups, *Parorthograptus*, *Glyptograptus*, and other genera. The strongly impoverished the *extraordinarius* and *persculptus* zonal assemblages are represented by simple, non-specialised diplograptids all over the world (Koren 1983; Koren & Nikitin 1983). It was a time of pronounced deterioration of graptolite habitats. Nevertheless the most important evolutionary novelty – the origin of the uniserial monograptid colony – was introduced in *persculptus* time (Rickards & Hutt, 1970). The succeeding *acuminatus* Zone is characterized by the radiation in surviving diplograptid stocks. It is marked by the appearance and subsequent differentiation in new lineages represented by *Aki-*

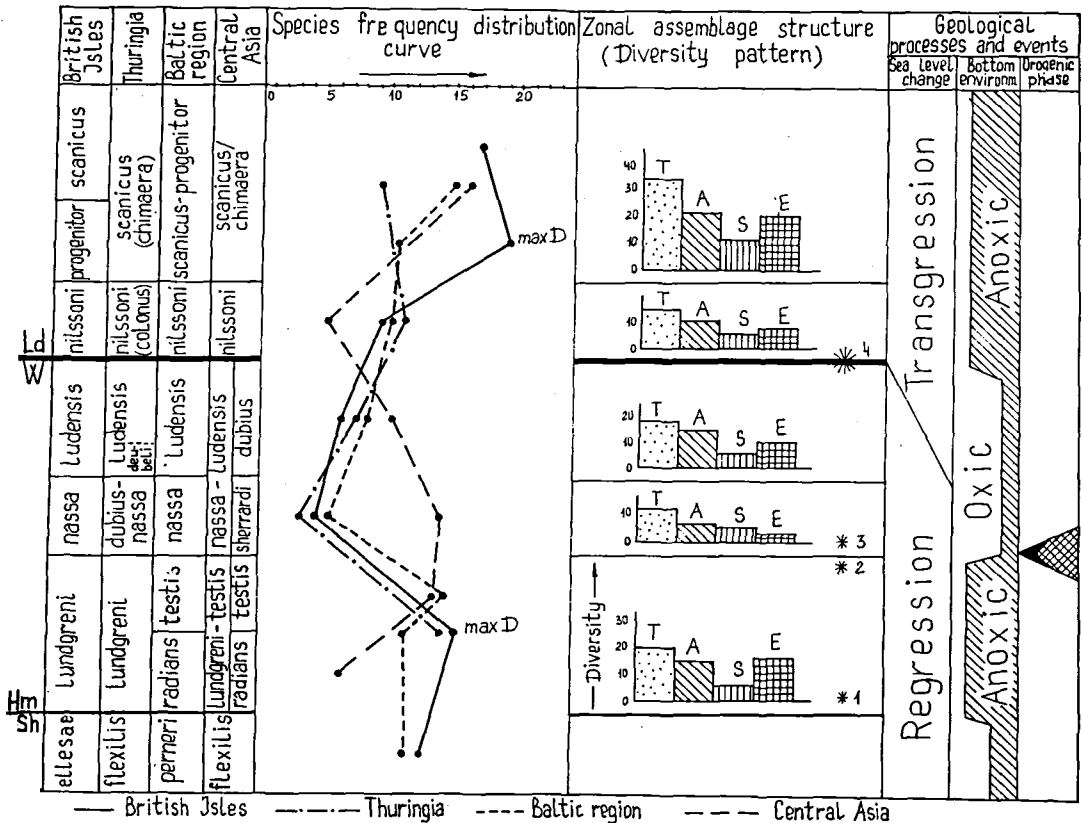


Fig. 3. Graptolite dynamics within the Wenlock-Ludlow boundary interval (the *lundgreni* event). Abbreviations are the same as in figs. 2 and 4. Asterisks shows the following bioevents: 1 - radiation within the Late Wenlock cyrtograptid stock; 2 - origin of a common pristiograptid ancestor of the Linograptinae, Cucullograptinae and Neocucullograptinae Subfamilies; 3 - radiation of pleclograptids and pristiograptids of the *Pristiograptus dubius* group; 4 - see 10 in fig. 1.

*dograptus*, *Parakidograptus*, *Cystograptus*, *Pseudoclimacograptus* and other genera (Rickards et al. 1977). The total number of species becomes twice as large, but most of new developing genera and species are short-lived and in general do not leave any descendents. Half of the zonal taxa become extinct by the *atavus* base.

The first radiation phase, predominantly within the newly formed monograptids of the *Atavograptus* stock, begins from the *atavus* or *vesiculosus* Zone and reaches its culmination during the *triangulatus* interval. Many origination events are known for synchronously developing diplograptid lineages (*Dimorphograptus*, *Raphidograptus* and others (Rickards et al. 1977).

The most dramatic evolutionary highs and lows can be interrelated through the long and complex chain of events with oceanographic and climatic changes well documented in sedimentary records on a global scale. Among them surface water cooling, changes in distribution of anoxic environments and level of carbonate compensation are of primary importance. The above events gave rise to profound biofacies changes and strong reduction of the amount of habitats.

### The *lundgreni* event

The Middle-Late Wenlock regression was gradual, but world-wide detectable. It had a least two maxima almost coinciding with the *flexilis* and *nassa* zones. The first level is characterized by the maximum of reef building, the second witnessed and extensive shallowing of cratonic seas and origination of widespread lagoonal facies. The geographical extent of anoxic environment strongly decreases as exhibited by black shale sedimentation except for the *lundgreni* Zone while extensive oxic environments were favourable for benthic fauna. The *nilssoni* shale transgression has brought about anoxic conditions with the last Silurian maximum within the *scanicus/chimaera* Zone.

The lithofacies changes at the Wenlock/Ludlow boundary in the caledonids (Prototethys; Tomčzykova Tomczyk 1979) and over the other territories (Central Asia, Canada) are partly attributed to the orogenic phase.

Regional biozonations for the British Isles, Thuringia, East Baltic and Central Asia were chosen (Rickards 1976; Jaeger 1959; Kaljo et al. 1984; Koren, Rinenberg, unpublished data). They represent the outer shelf (slope) and oceanic facies. All the sections are fairly complete and contain abundant graptolites. Three species frequency curves except for Central Asia (the Peshkaut section in South Fergana, unpublished data by Koren and Rinenberg) show a well pronounced evolutionary low at the *nassa-ludensis* and two diversity peaks for the *lundgreni* and *scanicus/chimaera* zones. A greater number of species in the *nassa-ludensis* Zone at the Peshkaut section in South Fergana reflect the radiation of the plectograptid lineages (*Gothograptus*, *Plectograptus*, *Holoretiolites*, *Spinograptus*). A drastic decrease of monograptid diversity (3 to 5 species) is similar in all the section discussed.

This time witnessed an abrupt termination of many Early Silurian lineages. The disappearance of the Cyrtograptinae subfamily marked by maximum diversity in the *lundgreni* Zone is the taxonomically most important. The *lundgreni* event of mass extinction strongly affected the composition of subsequent graptolite assemblages and the evolutionary trends of Ludlow monograptids as well. The disappearance of the *Monograptus priodon* and *Monoclimacis* stocks was also a very important phylogenetic event. Morphologically conservative and long-lived pristiograptid stock represented by *Pristiograptus dubius* (Suess) was subject to quite the opposite effect. There occur some speciation events resulting in appearance of *Pristiograptus deubeli* (Jaeger), *P. jaegeri* Holl. et al. and others. This was marked by the origination of some new apertural thecal structure – paired lateral lobes which progressively evolved and dominate among the other apertural structures of the Late Ludlow monograptids. The origination of a new important *Monograptus ludensis* lineage is most probably related to the *P. dubius* group. An even more phylogenetically important biological event is the appearance of the common predecessor for the Ludlow the Linograptinae, Cucullograptina and Neocucullograptinae Subfamilies which starts to develop at the *lundgreni/nassa* boundary. The cucullograptid radiation begins within “stem” lobograptids in the early *scanicus/chimaera* Zone and reaches a maximum at the end of it.

The total number of species after well pronounced drop in the *nassa* Zone slowly increase with the advance of the Early Ludlow transgression. Variable adaptive thecal apertures not long developed, reached a culmination in the *scanicus/chimaera* Zone. A relatively high proportion of taxa extinction characterizes each early Ludlow graptolite Zone.

The summary of the data shown leads to the following conclusion. The easily discernible large-scale abiotic and biotic environmental changes within the pelagic realm between the *lundgreni* and *scanicus* levels were of great ecological and phylogenetic significance for graptolite evolution. It is noteworthy that benthic groups were not greatly affected by the above changes. Late Silurian graptolites have never reached the earlier diversity in morphological structures. Since the beginning of the Ludlow

graptolites tried new adaptive paths some of which persisted till the end of Silurian, but most of them were successful only for a short while.

### The *leintwardinensis* event

There are only a few complete Upper Ludlow sections with continuous graptolite succession. In general, the Late Silurian is characterized by the regressive trend of sedimentation. Only the *scanicus/chimaera* and *formosus/spineus* zones suggest the distribution of transgressive anoxic water masses resulted in the black shale sedimentation reported from some regions. The environmental changes are well documented by the detectable lithoevents within graptolite sequences approximately beginning with the *leintwardinensis* Zone. These major events were mainly marked by an

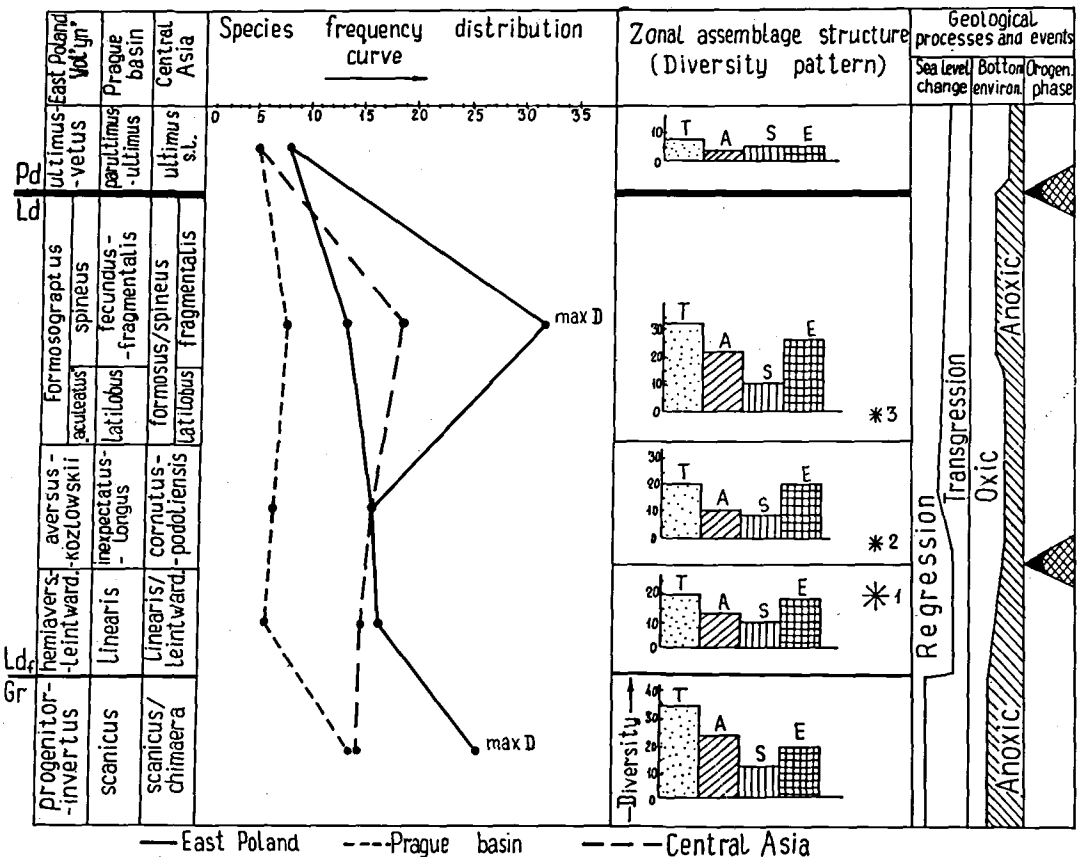


Fig. 4. Graptolite dynamics in Late Ludfordian - Early Pridoli time (the *leintwardinensis* event). Asterisks show the following bio-events: 1,2,3 - see 11,12,13 on fig. 1 correspondingly. Abbreviation for series and stages; Ash - Ashgill, Ln - Llandovery, W - Wellock, Ld - Ludlow, Pd - Pridoli, Lch - Lochkov, Pg - Pragian, Sh - Sheinwoodian, Hm - Homerian, Gr - Gorstian, Ldf - Ludfordian.

extensive carbonate sedimentation and rich benthic fauna. This implies the oxygenation of bottom waters and rapid biofacies shift. They may be connected with Late Caledonian orogenic movements within the Prototethys and the Protoatlantic. The cessation of graptolite shale sedimentation in Britain and Balto-Scandia in the *leintwardinensis* – *bohemicus* zones is probably one of the first consequences. Litho- and biofacies shift in slope environments is reflected in replacement of dark graptolite shales by cephalopode limestones (Barrandian, Morocco, Sardinia; Jaeger 1976). In the deeper basin and oceanic environments so called Ockerkalk or grey-greenish shale sedimentation have interrupted the graptolite-bearing sequences (Carnic Alps, Thuringia). The onset of deep-water carbonates falls at the *scanicus/leintwardinensis* boundary. They continue the section until the *transgrediens* Zone of the late Přidoli. Jaeger (1976, S. 278) considers this type of sediments as typical of the Prototethys and its margins. However, the author has recently found similar deep-water carbonates of the same age within the graptolite successions in the Polar Urals, Pai-Khoi and Central Asia. Their distribution in different palaeobasins suggests sedimentation in similar oceanic environments which are probably characterized by the low level of carbonate sedimentation and sea-floor scour. In the terminology introduced by Walliser (1984 a,b) they can be considered as the time-specific facies for the Late Silurian. As a result of facial reconstructions the habitats have strongly decreased judging from the limited number of graptolite occurrences. Within those biotopes which continued to exist some abiotic and biotic changes took place. A new phase of contractive morphological changes evidences new graptolite adaptive trends.

The sections chosen provide good examples of different pelagic facies – deep-shelf environments of marginal sea (East Polan, Volyn) and similar conditions within geosynclinal Prague Basin and the oceanic black shale sedimentation in South Fergana. The studies on graptolites and biozonations made by A. Urbanek, P. D. Tsegel'nyuk, A. Přibyl, R. E. Rinenberg and the author are still in progress. At present the data about graptolite dynamics within the *leintwardinensis* to *ultimus* s.l. zones are far from being complete. This is exemplified by species frequency curve (Fig. 4).

The left curve, plotted for the Prague Basin, seems to be quite smooth. That is possibly due to the poor or inadequate data about the Kopanina beds graptolites. There is a compound curve for East Poland and Volyn. The frequency of species for the *scanicus/chimaera* to *leintwardinensis* zones is based on the Urbarek's data (1966, 1970). For the *formosus/spineus* level two degrees of diversity are shown: one (13) shows the number of species in the Melnik borehole recognised by A. Urbanek (oral communication, 1985), the other (32) are from numerous boreholes of Volyn determined by Tsegel'nyuk (1981; The Silurian... 1983). The latter extremely high magnitude can at least partly be attributed to an artificial taxonomic splitting. The frequency curve for the Peshkaut section reflects evidence obtained from the continuous sequence of black shales and limestones similar to Ockerkalk with frequent graptolite events. The curve shows the number of taxa which can be recognized on the basis of flattened but well preserved material.

The general picture of the diversity pattern is as follows. The number of species per zone is approximately the same. However, the zonal assemblage structure allows us to conclude that graptolite dynamics were not even. The number of surviving taxa per zone is more or less constant. They consist of saetograptids (the *scanicus/chimaera* and *leintwardinensis* zones), pristio-graptids and bohemo-graptids (the *scanicus/chimaera* to *formosus/spineus* zones).

The diagrams show a distinct renovation in the composition of the Late Ludlow fauna within each zone. So, almost all lobograptids disappear in the lower zone. The earlier abundant cuculograptids, saetograptids and plectograptids disappear in the two subsequent units. The next wave of mass extinction is related to the end of the *formosus/spineus* Zone. In extent the event may be compared to that of the *supernus* Zone close to the Ordovician/Silurian boundary.

The major evolutionary events reflected in the appearance of adaptive morphological structures of high taxonomic rank can be assigned to the end of the *leintwardinensis* and beginning of the *cornutus* zones. The most important among them are: 1. an appearance of *Linograptus* able to produce numerous sicula cladia and 2. splitting of bohemo-graptid lineage and origination of specialized *Neolobograptus* – a possible neocucul-



lograptid ancestor whose phyletic evolution is typical of subsequent zonal phases (*cornutus* to *kozlowskii*; Urbanek, 1966, 1970). Another important phylogenetic event is that of the *formosus/spineus* Zone when the diversification of monograptids takes place and promotes several new lineages (Tsegel'nyuk, 1976, 1981). Several new specialized monograptids with apertural structures not seen since Llandovery, appear at the same time. For the last time the morphological and taxonomical diversity of Late Silurian graptolites reaches a maximum of a size which can be compared to that of the *scanicus/chimaera* zonal assemblage.

## Conclusions

To obtain a general idea about the dynamics of Silurian and Lower Devonian graptolites major extinction-origination events within the standard graptolite zonation have been outlined (Fig. 1).

The graptolite evolution during the time of monograptid existence is subdivided into three phases using a comparison of the amplitude of extinction and origination of taxa and the closeness of successive cycles.

The first phase is related to the Llandovery-Early Wenlock transgression marking the maximal spatial distribution of black-shale graptolite facies. Following the mass extinction event at the *supernus* Zone, the time of glaciation maximum, diplograptids and monograptids become first gradually and then abruptly very diverse. The most prominent Silurian peak is assigned to the *triangulatus* Zone when several synchronous and succeeding radiation events in already numerous lineages took place. The number of species totals 50 to 70. Graptolite dynamics in the Middle to Late Llandovery is more or less regular and persistent. The fauna is slowly losing its high diversity when in Early Wenlock time (the *riccartonensis* Zone) another mass extinction event took place.

The second Late Silurian phase (the *ellesae* to *transgrediens* zones) is a time of unstable abiotic environments. Eustatic transgressive and regressive sedimentation cycles, orogenic phases, alternation of anoxic and oxic environments, fluctuation in carbonate sedimentation depth, distribution of lime-rich water masses, and other

causes were responsible for frequent deteriorations and formations of new graptolite habitat or microhabitats. The areal extent of graptolite facies is markedly reduced. The complex genetic relations made the dynamics of Late Silurian graptolites extremely uneven and jerky. Frequent waves of extinction-origination events (Fig. 1) demonstrate that the ecological homeostasis of graptolites is disturbed. There are still several attempts to occupy new or existing ecological niches at introductions of new morphological structures, some of them prove to be successful for a while. The Early and Late Ludlow graptolites show two well pronounced diversity peaks. Another but smaller diversity maximum falls in the Middle Prídoli before the extinction of the most Silurian stocks.

During the third phase in graptolite evolution, that is during the Early Devonian, graptolites are characterised by an exclusively monotonous morphological thecal structure and very simple rhabdosomes. The last step in the adaptivity pattern is the appearance of a short-lived *Abiesgraptus*, which was able to produce both sicular and thecal cladia. However, the multistiped rhabdosomes became completely extinct by the end of the Lochkov. Since then evolution followed a phyletic speciation trend in some single lineages of uncinatid monograptids. The *uniformis* and *yukonensis* zones are marked by relative high diversity (8 to 9 taxa).

The final extinction of the remaining 4 to 5 species took place during a global Early Devonian transgression which brings about an extensive distribution of anoxic water masses as evidenced from sedimentary controls. Previously such effects supposedly were related to periods of graptolite diversification. So, we may suggest that the extinction of the group was strongly affected by peculiar biotic factors, primarily it may have been the break in trophic chains.

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## Dansk sammendrag

På grundlag af allerede eksisterende biostratigrafiske data foresøges det i afhandlingen at vurdere dynamikken i graptolit evolutionen som afspejlet i pelagiske aflejringer fra silur og tidlig devon. I de udvalgte tidsafsnit er uddøen og fremkomsten af

nye former af interesse. Disse ændringer er delvist forbundet med miljømæssige faktorer i forbindelse med eustatiske havniveau-ændringer og klimatiske skift, skift i anoxiske betingelser, forskydning af carbonat-sedimentationen i en mere pelagisk retning samt af andre globalt mærkbare ændringer.

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