

# Biotic crises and post-crisis recoveries recorded by Silurian planktonic graptolite faunas of the Barrandian area (Czech Republic).

Petr ŠTORCH

Geological Institute, Academy of Sciences of the Czech Republic, Rozvojová 135, 165 02 Praha 6 – Lysolaje, Czech Republic, e-mail: storch@gli.cas.cz

**ABSTRACT.** Evolution of the Silurian graptolite faunas of the Barrandian area was disturbed by eight biotic crises of a varying scale, most of which recognisable around the world. Adaptive radiation and immigration, or both combined, succeeded each crisis but resulted in a decreasing degree of recovery, leading to a progressive reduction in graptolite diversity. Such a picture of the decline of the graptoloidea in the Silurian suggests that, at that time, evolutionary response of the planktonic graptolites to large-scale environmental disturbances became less and less adequate. Major changes in graptolite diversity are comparable with sea-level fluctuations reflected by the sedimentary record and other Silurian biota. Adaptive radiations occurred among graptolites when sea-level rose along with rising temperature, and when the nutrient-rich, oxygen-depleted waters brought anoxic, graptolite-rich, black shale facies onto the wide shelves and epicontinental seas. Graptolite crises and mass extinctions are related to eustatic regressions with better water circulation and basinward retreat of the anoxic facies.

**KEYWORDS:** graptolites, Silurian, Barrandian area, bioevents, extinction, recovery, species-diversity curve

## Introduction

Eight large-scale biotic crises, characterised by sudden or stepwise reductions of species diversity, have been recognised in the history of the Silurian graptolites (figs. 1, 2). When stressful conditions improved, the graptolite fauna gradually recovered.

The magnitude and rate of the Silurian graptolite mass extinctions and recoveries recorded by Bohemian sections are shown by the species-diversity curves on figs. 1 and 2. The evolutionary impact of the biotic crises on graptolite faunas has developed. The Llandovery crises never brought the rich and diverse assemblages to near-extinction and always left some vigorous survivors. Reappearance of the temporarily missing taxa, as well as survivors immigrating from little affected refugia (Urbanek 1993), resulted in rapid recovery of the assemblages though on a little decreased degree of diversity. Even the late Ordovician extinction event, one of five major mass-extinctions in the Earth history, was followed by large and rapid recovery of the graptolite fauna. Adaptive radiation among normalograptid survivors began near the top of the Ordovician sequence along with a large post-glacial transgression.

In the lower and middle Llandovery (Rhuddanian and Aeronian stages) the first and largest of the Silurian adaptive radiations took place among planktonic graptolites. Stepwise diversification culminated during the early- to mid-Aeronian *triangulatus* – *convolutus* Biozones, when the zonal assemblages were comprised by more than 50 species. In the Barrandian area, the complex graptolite assemblage of the middle part of the *convolutus* Biozone (fig. 1) broke-down near the top of the Biozone (*convolutus* Event). The extinction was succeeded by the second radiation which culminated in the basal Telychian *linnaei* (*guericchi*) Biozone. The second extinction affected the graptolite faunas at the top of the Biozone (*utilis* Event). Graptolite diversity increased again up to the *spiralis* Biozone. In the uppermost Llandovery (the top of the *spiralis* Biozone), the graptolites suffered a third crisis (*spiralis* Event). The fourth adaptive radiation culminated in the lower Sheinwoodian *murchisoni* Biozone, when another extinction (*murchisoni* Event) quickly reduced the graptolite diversity to four species surviving in the *riccartonensis* and *dubius* biozones.

Following this event, graptolite assemblages never reached higher diversities. Assemblages after the *murchisoni* Event were composed of 10 – 15 species. The evolutionary response of local survivors to deteriorated environmental conditions became inadequate along with decreased immigration from little or non-affected refugia.

The next gradual rediversification gave rise to the moderately diverse lower Homerian faunas of the *lundgreni* Biozone. They were hit by another severe extinction at the top of the Biozone (*lundgreni* Event). The sixth crisis of the Silurian graptolite faunas has not been studied in the Barrandian area due deposition of the limestone sequence in which the graptolites are generally rare. This crisis was described by Urbanek (1993) above the lower Ludfordian *leintwardinensis* Biozone in the East-European Platform (*leintwardinensis* Event). The Ludfordian fauna rediversified again in the *inexpectatus* – *kozłowskii* biozones until it was reduced by a new extinction event at the top of the latter biozone (fig. 2, *kozłowskii* Event). The eighth extinction event affected the Pridoli graptolite fauna at the top of the *transgrediens* Biozone (Urbanek 1993), leaving few survivors among linograptids and monograptids (*transgrediens* Event).

This paper utilises rich and precise data on stratigraphical ranges of 268 graptolite species of the Lower Silurian of the Barrandian area (Štorch 1994a), completed by the data summarised by Bouček (1953), and by the new data on the upper Silurian graptolites, partly published by Přibyl (1983) and Štorch (1995).

In total, the stratigraphical ranges of 322 species have been incorporated in the present outline of the graptolite dynamics as recorded by the 30 Ma history of the Silurian System.

A maximum of 51 species in one graptolite zone has been recorded in the middle Llandovery *convolutus* Biozone. Some species, however, occur in the lower part of the biozone and some other appear in the upper part of the biozone. Other species may be restricted into a distinct part of the biozone. That is why so called immediate or **actual diversity** is preferred in generalised (figs. 1, 2) and detailed (fig. 3) diversity curves. The actual diversity is the joint occurrence of the species within one quarter of the graptolite zone.

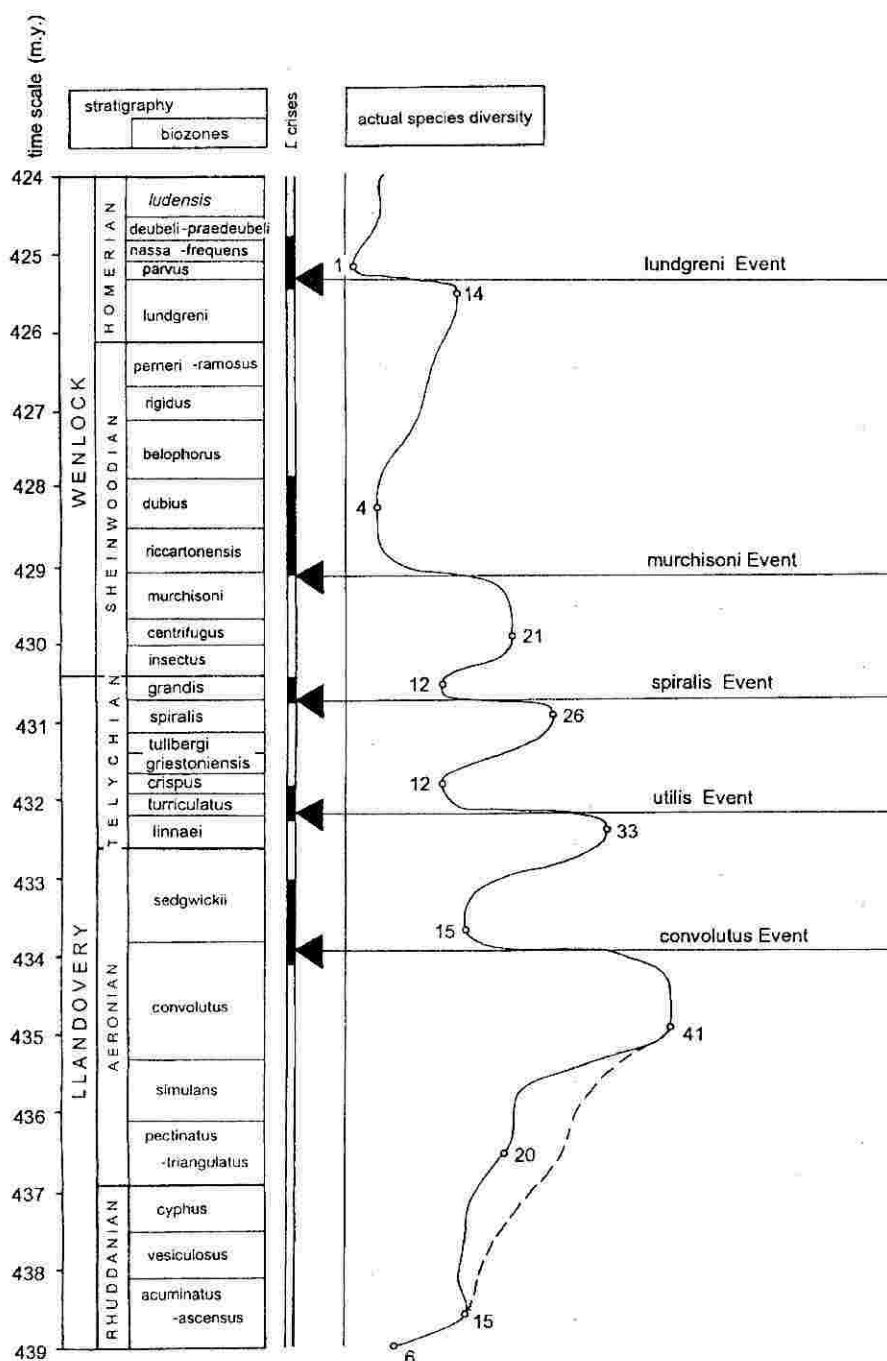


Figure 1. Lower Silurian crises and recoveries of the planktonic graptolite faunas: a generalized actual-diversity curve.

Explanations: Approximate duration of the graptolite biozones is related to the geological time scale after Harland et al. (1990). Actual, and/or immediate species diversity (open circles with numbers) include all the graptolite species within one quarter of the biozone. In the *vesiculosus* and *cyphus* biozones the diversity is lowered due to insufficient preservation of the graptolites which probably did not allow recognition of some closely similar and tiny species. Dashed line shows proposed growth of the diversity without this effect.

### Structure and behaviour of the graptolite assemblage during the extinction-survival-recovery cycle

Each of the eight crises was followed by a recovery of the graptolite assemblages leading to rediversification on a decreasing scale. Adaptive radiation and immigration, usually both combined, succeeded each crisis and resulted in decreasing degree of recovery. This, however, lead to a progressive reduction of diversity within the graptolite faunas. In general, the Silurian graptolites behaved

as a regressive group in the sense of Müller (1961). The following terminology (see also fig. 4) is based on that employed by Erwin and Kauffman (1993 MS) and Kauffman and Erwin (1995). It is simplified, however, and modified with respect to some specific features observed in the graptolite extinction, speciation, and radiation processes shown by Urbanek (1993) and the present study.

Sudden or rapid deterioration of the environment resulted in sudden or stepwise reduction of graptolite diversity. This interval is called the **mass extinction interval**. During the advanced stage of the mass extinction, less vigorous taxa disappear temporarily (lazarus taxa) or become extinct (victims of the mass extinction).

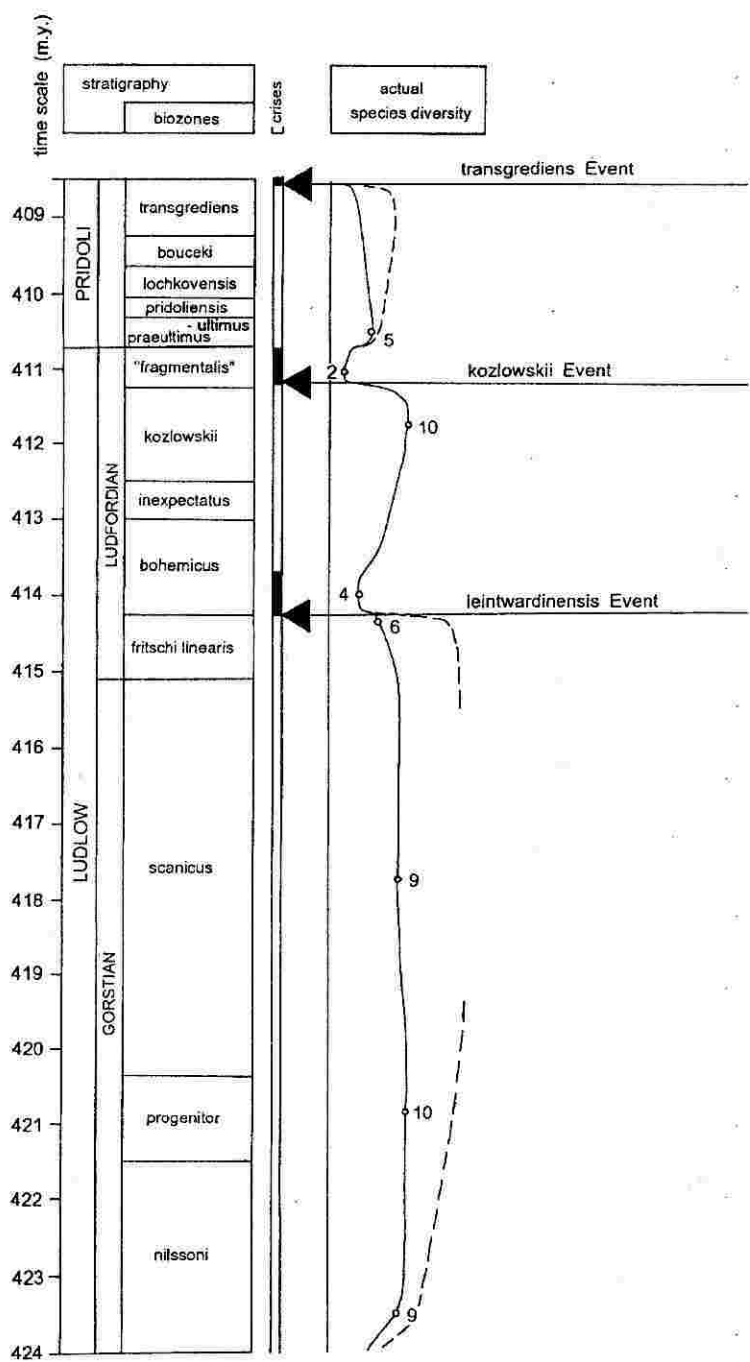


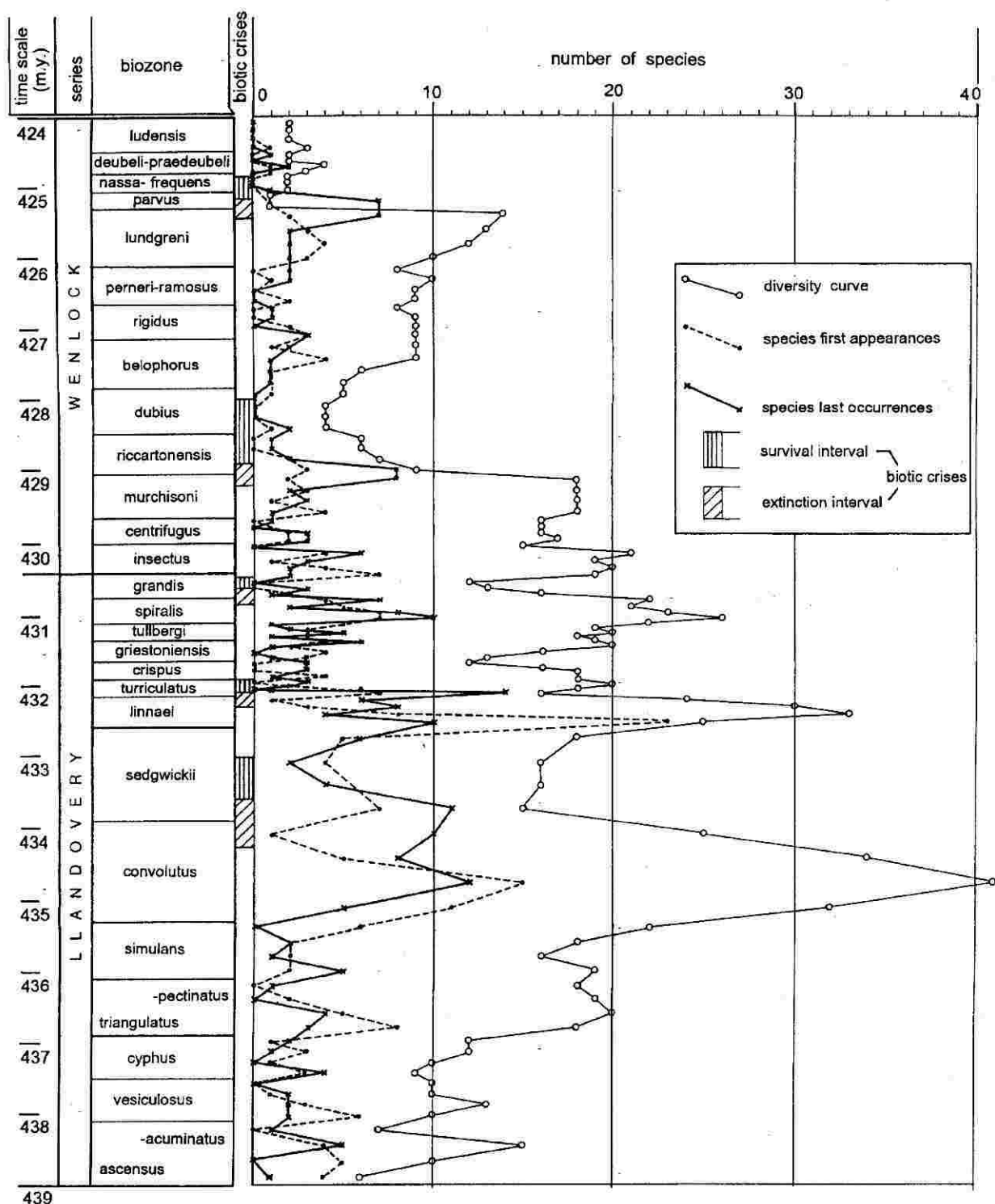
Figure 2. Upper Silurian crises and recoveries of the planktonic graptolite faunas: a generalized actual-diversity curve. For explanations see fig. 1. Largely biotrital limestone facies, unfavourable to graptolite preservation, may have reduced proposed graptolite diversity (dashed line) in some parts of the Upper Silurian sequence.

The **lazarus taxa** temporarily disappear from the fossil record, usually at or near the peak of mass extinction. They may survive elsewhere, in some refugia, and reappear during survival or recovery intervals as environmental conditions improve. The **victims**, however, are entirely eliminated from the fossil record.

The role of some taxa in graptolite assemblages may be diminished by severe conditions. When the conditions normalise these taxa may, or may not, reach their former share in the assemblage. These taxa are simply called **survivors**. Some of the survivors remain unchanged during the whole extinction-survival-recovery cycle. Neither their quantity or phenotype are markedly

affected. Such species are called **intact survivors**. They may be particularly tolerant of environmental changes or their habitat may be little, if at all, influenced by these disturbances.

Some species even evolve during the mass-extinction interval, adapt to severe conditions of the extinction event, and persist during the survival and recovery intervals. They are called **progenitor taxa**. Some progenitors are later eliminated by competition from immigrant or opportunistic taxa when severe conditions normalise (**failed progenitors**). Successful progenitors, however, give rise to new, common species and lineages during ensuing transgression.



**Figure 3.** Graptolite dynamics in the Lower Silurian of the Barrandian area. Actual species diversity is composed by the species passing through the reference interval (one quarter of the biozone), plus species which just evolved or immigrated and species which, in this interval, disappeared from the fossil record in the Barrandian area. Other two curves show the number of species last appearances (local or global extinctions) and the number of first appearances (indigenous speciation, immigration) respectively. Large radiations are marked by much increased speciation which was, however, accompanied by increased, though less so, extinction. During the crises, speciation and immigration almost ceased whereas the extinction frequency more or less increased.

The extinction interval is succeeded by the interval characterised by low diversity but high-density graptolite assemblage. The latter is called *survival interval* and immediately follows the major extinction. It is inhabited by surviving taxa composed by **local survivors**, progenitors, and, particularly, by so called **opportunistic**

**taxa**. In practice the survival interval spans between the end of mass-extinction with high extinction-frequency, and the new adaptive radiation and immigration.

A few of the surviving taxa become much more abundant when the most severe conditions disappear. They fill the free niches left by extinct taxa and dominate the low-



diversity but often high-density graptolite assemblages of the survival interval. The opportunists take the opportunity.

During the survival interval, the Lazarus taxa reappear in the fossil record together with the appearance of some **immigrant survivors of cryptic or semicryptic origin**. Unlike the Lazarus taxa, the immigrants lack any direct ancestors in the area and facies in question.

Some of the immigrants behaved as opportunistic taxa and became dominant components of the post-extinction graptolite fauna. They can be called **opportunistic immigrants**.

When severe environmental conditions improved, the graptolite fauna gradually recovered. The **recovery interval** is marked by evolution of new species from survived stems and, later on, by radiation of the new lineages. The dominance of the opportunistic taxa rapidly decreases.

## Brief characterisation of the individual crises

So called Late Ordovician and / or Ordovician-Silurian Boundary Event represents one of few major biotic crises in the Earth history. At that time the planktonic graptolites suffered the most severe decimation. Suddenly the highly diversified upper Ordovician graptolite faunas were extinct (ca 16 genera) leaving few survivors (Melchin and Mitchell 1991, Koren 1991a). Strongly impoverished relic assemblages of the topmost Ordovician *extraordinarius* and *persculptus* biozones are composed of several simple, non-specialised normalograptids all over the world.

In the *persculptus* Biozone, however, the new radiation started with great evolutionary novelty. The uniserial monograptid colony was introduced. Later on, it gave rise to rich Silurian monograptid faunas. The succeeding phase of the post-crisis recovery was marked by radiation within the survived normalograptid stock in the basal Silurian *acuminatus* Biozone. *Akidograptus*, *Parakidograptus*, *Cystograptus* and *Pseudoclimacograptus* (*Metaclimacograptus*) appeared. The total number of the species became twice as large, but most of the newly developed species and genera were short-lived and few left any descendants. The huge radiation developed in the *vesiculosus* and *cyphus* biozones and culminated during the course of the middle Llandovery *triangulatus* and *convolutus* biozones among the newly formed monograptids as well as within synchronously developing biserial taxa.

## Convolutus Event

The drastic reduction of faunal diversity at the top of the *convolutus* Biozone is well known from a number of places. However, it has not yet been studied in as much detail as the succeeding *sedgwickii* Biozone, with relic assemblage at the base, which is often developed in form of better oxygenated, graptolite free beds (in Spain, Poland, Scandinavia).

In Bohemia the maximum diversity of the Silurian graptolites (51 species) is reached in the *convolutus* Biozone. The actual diversity in the second and third fourths of the biozone reaches 41 species (figs. 1 and 3). The assemblage is characterised by large variety of highly specialised thecal and rhabdosomal morphologies (fig. 5).

Sudden break-down of the assemblage was observed near and at the top of the *convolutus* Biozone. Two-fifths of the former species (15 taxa) survived in the relic assemblage of the lower *sedgwickii* Biozone. Many

early and middle Llandovery lineages were terminated (namely biserial genera *Normalograptus*, *Pseudorthograptus*, *Neodiplograptus* and some monograptids – *Campograptus*, *Coronograptus*). *Petalograptus*, *Demirastrites* and *Rastrites* were severely reduced and temporarily disappeared. The survival and recovery intervals are marked by proliferation of some opportunistic species. (fig. 5). Later on, some opportunistic immigrants of cryptic origin appeared.

In the upper *sedgwickii* Biozone the diversity rapidly increased, due to both immigration and indigenous speciation among the surviving taxa. Some Lazarus taxa such as *Rastrites* and *Petalograptus* recorded a new and last evolutionary burst. The immediate diversity of 33 taxa has been attained in the *linnaei* Biozone.

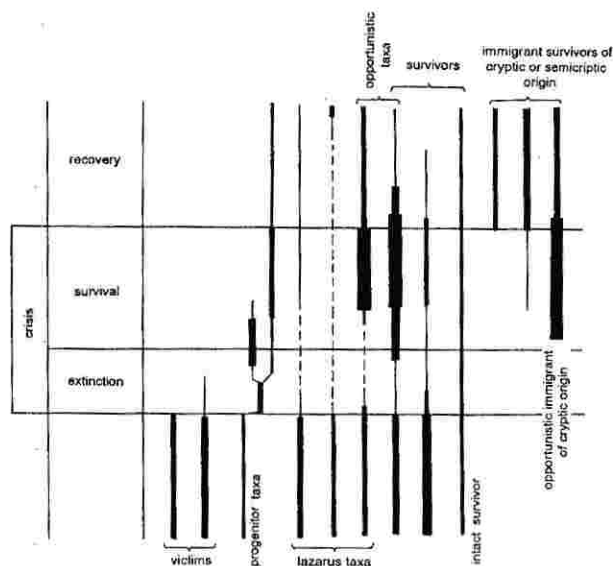


Figure 4. Graptolite extinction and recovery pattern: An ideogram based on Silurian graptolite faunas of the Barrandian area.

## Utilis Event

The new radiation was terminated by a second extinction event at the top of the *linnaei* Biozone. The *utilis* Event was described by Loydell (1994). It is particularly well recognisable in Spain and in Britain for instance.

In the Barrandian, the species diversity was reduced to about two-fifths of the former one (figs. 1 and 3). Extinction affected almost all graptolite stems but few were terminated (fig. 6). In the Barrandian area, *Metaclimacograptus*, *Glyptograptus* and *Stimulograptus* were entirely eliminated. The former two, however, survived high into the upper Llandovery elsewhere (Spain, Algeria). *Streptograptus* and *Rastrites* temporarily disappeared from Barrandian sections. They reappeared again in the later phase of the survival interval. The relic assemblage of the *turriculatus* Biozone was dominated by opportunistic survivors and, later on, by opportunistic immigrants (fig. 6). The brief appearance of some cryptic elements such as *Pristiograptus macrodon*, *Monograptus tureki* (? = *galaensis*) and *Petalograptus cf. schaueri* at the end of the survival interval is remarkable. They may be considered as unsuccessful immigrants.

In general, the *utilis* Event resulted in near-extinction of biserial graptolites with the exception of the family Retiolitidae and a few survivors among petalograptids and metaclimacograptids. The post-crisis recovery gave

rise to the late Llandovery (Telychian) fauna composed by *M. priodon* Stem and its relatives, and by pristiograptids of the *dubius* Stem which evolved from the *Prist. nudus* Group. Also *Torquigraptus*, *Streptograptus*, *Cochlograptus*, and *Pseudoplegmograptus* flourished and, later on, *Retiolites* and *Monoclimacis* appeared.

### Spiralis Event

Near the Llandovery-Wenlock boundary, at the top of the *spiralis* Biozone, the Telychian monograptid fauna was affected by another disturbance, so far recorded in Barrandian and at a slightly higher stratigraphical level by Melchin (1994) in Arctic Canada. Correlation of this extinction interval will need more attention in the future.

In the Barrandian, some species and genera became extinct at the end of the *spiralis* Biozone. Some others behaved as Lazarus taxa and returned when the environmental conditions normalised. There are however, some taxa, which have been little, if at all, affected (fig. 7). The relic assemblage is dominated by large, robust rhabdosomes. The population burst appeared in monoclimalacids (opportunistic species *Mcl. geinitzi*), large monograptids, and *Stomatograptus*. A peculiar immigrant of cryptic origin – *M. probosciformis* characterises the surviving assemblage, but it is ruled out in the course of the new recovery of the graptolite assemblage (fig. 7). Post-crisis recovery brought several prominent immigrants of cryptic or semicryptic origin to the Barrandian sections. These are *Mediograptus*, *M. cultellus*, *Cyrt. insectus* a.o.

### Murchisoni Event

The first of the biotic crises which nearly brought the Silurian graptolites to extinction affected the lower Wenlock assemblage of the *murchisoni* Biozone. It is prominent in many places throughout the world, but it has never been discussed except for a brief note by Koren (1987) and Štorch (1994b).

In the Barrandian, the species diversity dropped from 21 species to four survivors in the *dubius* Biozone (figs. 1 and 3). The environmental disturbance began in the *murchisoni* Biozone when some graptolite stems, such as *R. geinitzianus* Stem, disappeared whilst others gave rise to new, though short lived, species (*Mcl. adunca* – *M. radotinensis*). Major extinction affected the graptolites at the base of the *riccartonensis* Biozone when *Barrandeograptus*, *Mediograptus*, and *Cyrt. murchisoni* Group were terminated (fig. 8). Another taxa – *M. priodon* Stem, *Mcl. vomerina* Group and *Pseudoplectograptus* temporarily disappeared. Even non-specialised generalists, such as *Prist. dubius* Stem, were reduced. This was the time of origin and proliferation of *M. riccartonensis* (fig. 8). In this interval the bedding planes are crowded by isolated siculae which account for enormous juvenile mortality among the graptoloids. In the upper part of the *riccartonensis* Biozone the relic assemblage comprises common *M. riccartonensis* and *Prist. dubius* accompanied by extremely rare survived monograptids and, temporarily, by cryptic immigrants *Pseudoplegmograptus wenlockianus* and *M. solitarius*. The succeeding zone is marked by a great proliferation of *Prist. dubius* Stem, and by the appearance of the first immigrant survivor – *Str. antennularius*. The new recovery is demonstrated by the appearance of other immigrants (*M. belophorus*, *Plect. textor*) and the return of some Lazarus taxa (*Mcl. vomerina* Group, *M. priodon* Stem).

### Lundgreni Event

The new, middle Wenlock recovery of the graptolite fauna was gradual and never gave rise to the high-diversity assemblages which are known from Llandovery and Lower Wenlock strata (figs. 1, 2, 3). Moderate diversity was reached again in the *lundgreni* Biozone in which multiramose cyrtograptids proliferated, being accompanied by common rhabdosomes of several monograptid species, referred to *Testograptus*, *Streptograptus*, *Monoclimacis*, *Monograptus*, *Pristiograptus* and by plectograptid retiolitids. Another extinction event at the top of the *lundgreni* Biozone terminated all the graptolite stems with the exception of small non-specialised pristiograptids of the *Prist. dubius* Group and plectograptid retiolitids (figs. 9). The *lundgreni* Event is recognised world-wide. It is particularly well known owing to detailed analyses by Jaeger (1991), Koren (1987, 1991b), Lenz (1993), and Urbanek (1993).

The post-crisis relic assemblage is characterised by mass occurrence of *Prist. parvus* – a diminutive member of the *Prist. dubius* Stem. Soon the assemblage was enriched by another opportunist – *Gothograptus nassa*. The recovery interval brought about the appearance of *Plectograptus* and related plectograptids as well as the appearance and radiation of the *Prist. dubius* Group.

### Leintwardinensis Event

This event has been described by Urbanek (1993) from the East European Platform and by Koren (1993) from Tian-Shan. In Bohemia the interval in question is formed by bioclastic limestones in which the graptolite fossil record is inadequate for present study.

### Kozlowskii Event

The Silurian graptolite fauna suffered a 7th mass extinction at the top of the *kozlowskii* Biozone in the uppermost Ludlow. The *kozlowskii* Event is well recorded from the East European Platform (Urbanek 1993) as well as in the Barrandian (Štorch 1995). It corresponds with *podoliensis* Event described by Koren (1993) from Tian-Shan. A moderately diverse assemblage of the *kozlowskii* Biozone, composed of 10-12 species, disappears, and is replaced by a poor relic assemblage formed by two survivors. Specialised genera with ventrally curved rhabdosomes – *Neocucullograptus*, *Bohemograptus* and *Polonograptus* became extinct as well as small *Pseudomcl. dalejensis* (fig. 10). Multiramous *Linograptus* with simple pristiograptid thecae was not affected by the crisis but never proliferated. The second survivor – *Prist. fragmentalis* from the *Prist. dubius* Stem became more frequent in the survival interval and may be considered as an opportunistic taxon.

The recovery came as a result of immigration of alien faunal elements (Urbanek 1993). The most striking is an opportunistic immigrant of cryptic origin, the genus *Formosograptus* of torquigraptid appearance. Later on, pseudomonoclimalacids of the *Pseudomcl. ultimus* Group appeared.

### Transgrediens Event

A sudden decrease in graptolite diversity has been reported from many places, including the Barrandian, at the top of the Silurian sequence. It left few survivors and was soon followed by ingress of a new, Lochkovian assemblage. The emerging fauna comprises four to

five lineages of cryptic or semicryptic origin. In the Barrandian, the *transgrediens* Event has not been studied in detail.

## History and behaviour of the most successful Silurian graptolite stems

Some of the Silurian graptolite taxa and/or lineages successfully survived one or more mass extinctions (fig. 11). The most successful Llandovery graptolites are represented by both specialised and non-specialised forms. Non-specialised *normalograptids*, composed primarily of opportunistic and progenitor taxa, dominated relic assemblages after the late Ordovician mass extinction (after the *pacificus* Event). They also play a major role in the early phases of the post-crisis recovery (fig. 11). In highly-diverse, middle Llandovery assemblages, the generalised normalograptids were gradually replaced by more successful uniserial monograptids and by some newly originated biserial taxa (for instance *Petalograptus*), which were better adapted to their role within the highly diverse assemblage.

In some cases, mass extinctions interrupted evolutionary bursts of the specialised forms. Highly specialised taxa were particularly vulnerable to changes in temperature, nutrient supply and planktonic productivity. They were severely decimated but some of them survived the biotic crisis owing to great evolutionary potential and plasticity. This is why highly specialised *rastritids* and *petalograptids* survived the *convolutus* Event and *streptograptids* survived the *spiralis* and *murchisoni* events (fig. 11). Such taxa never proliferated in relic assemblages. They often briefly disappeared from the local fossil record but, later on, during the new radiation, they outstripped the opportunistic taxa.

Other taxa, namely *simple uniserial monograptids* such as *Prist. nudus* and *dubius* stems, *M. priodon* Stem, and, in part *Monoclimacis* and *Bohemograptus*, display a different strategy. They behaved as opportunistic taxa which filled free niches after the mass-extinction. They typically dominated the relic assemblages (fig. 11). Their share in the assemblage decreased when new indigenous speciation or immigration brought specialised taxa, better adapted to new environmental conditions.

A special case, which has not yet been explained, is represented by *Linograptus*. It survived three extinction events without any response in phenotype or population density. The only remarkable evolution was recorded after the last, *transgrediens* Event, when surviving *L. posthumus* gave origin to multiramous *Abiesgraptus*.

## What has been responsible for graptolite mass extinctions?

It was suggested by several authors (i.e. Koren 1987) that graptolite faunas developed depending on eustatic sea-level changes, climate fluctuations and oceanic current patterns. Primarily nutrient supply and organic productivity, temperature, and temperature gradient were responsible for the dynamics of epiplanktonic and mesoplanktonic graptolites.

Commonly the highly diverse assemblages proliferated in course of transgressive intervals, when high nutrient supply, perhaps, along with limited water circulation, allowed large extension of the oxygen-depleted nitrogen-compound rich waters onto the shelves and epicontinental

seas. According to Berry et al. (1987) and Berry and Wilde (1990) the oxygen-poor, nutrient rich waters offered the most hospitable habitats for graptolite faunas. Consequently, the anoxic black shales, which particularly extended along with rising sea level, contain the most rich and diverse graptolite assemblages.

As oppose to the transgressions, regressions brought better circulation and basin-ward retreat of the black-shale facies. They were accompanied by mass extinction among graptolites and other planktonic biota. Causal relations between the Ordovician sea-level changes and graptolite diversity were demonstrated by Fortey (1984).

The late Rawtheyan (middle Ashgill) *pacificus* Event occurred in the early phases of the Ordovician-Silurian boundary mass extinction. At that time both planktonic, nektonic, and benthic faunas were decimated (Brenchley 1984, a.o.). Extensive late Ordovician (Hirnantian) glaciation, centered in the southern hemisphere, was responsible for global cooling, glacio-eustatic regression and increased water circulation which disrupted the stable arrangement of the oceanic-water layering (Berry et al. 1987), and dramatically restricted potential graptolite habitats and food resources. Black-shale deposition almost ceased.

Large post-glacial eustatic transgression, which started in the *persculptus* Biozone at the top of the Ordovician sequence, was accompanied by progressive, accelerating rediversification of the relic graptolite fauna. Then, the lowermost Silurian strata show further eustatic transgression and rapid extension of graptolite rich anoxic sediments. Large lower and middle Llandovery radiation was interrupted by *convolutus* Event.

The *convolutus* Event correlates with the Sandvika Event – mass extinction among conodonts recorded by Aldridge et al. (1993). It was probably related to climatic change which changed oceanic circulation (Jeppson 1990) and decreased nutrient supply. It is accompanied by the basinward extension of the oxic facies.

The *utilis* Event was related to brief glacio-eustatic regression by Loydell (1994). The data on large extension of Gondwanan ice-cup was obtained from South America (Grahn and Caputo 1992).

The *spiralis* Event is coeval with the beginning of the conodont Ireviken Event described by Aldridge et al. (1993) and Jeppson (1993). Once again it is explained by climatic change which lead to reduction in organic matter productivity and basinward extension of the oxic sediments.

The *murchisoni* Event is related to mid-Wenlockian regression and another reduction of the anoxic facies.

The *lundgreni* Event was interpreted in the same way by Koren (1987). Indeed, the black-shale facies were strongly reduced at that time. The new transgression and extension of the black-shale facies culminated again in the *scanicus* Biozone.

The *leintwardinensis* Event accompanied a new large regression and the same interpretation is suggested for another upper Silurian mass-extinction events, which were always accompanied by sudden retreat of black-shale facies and the extension of carbonate deposition.

## Acknowledgements

The present study was carried out in frame of the Grant No 205/95/1516 (Grant Agency of the Czech Republic). English revision of the text was kindly provided by Prof. J. Ebert and Dr. D. Matteson.



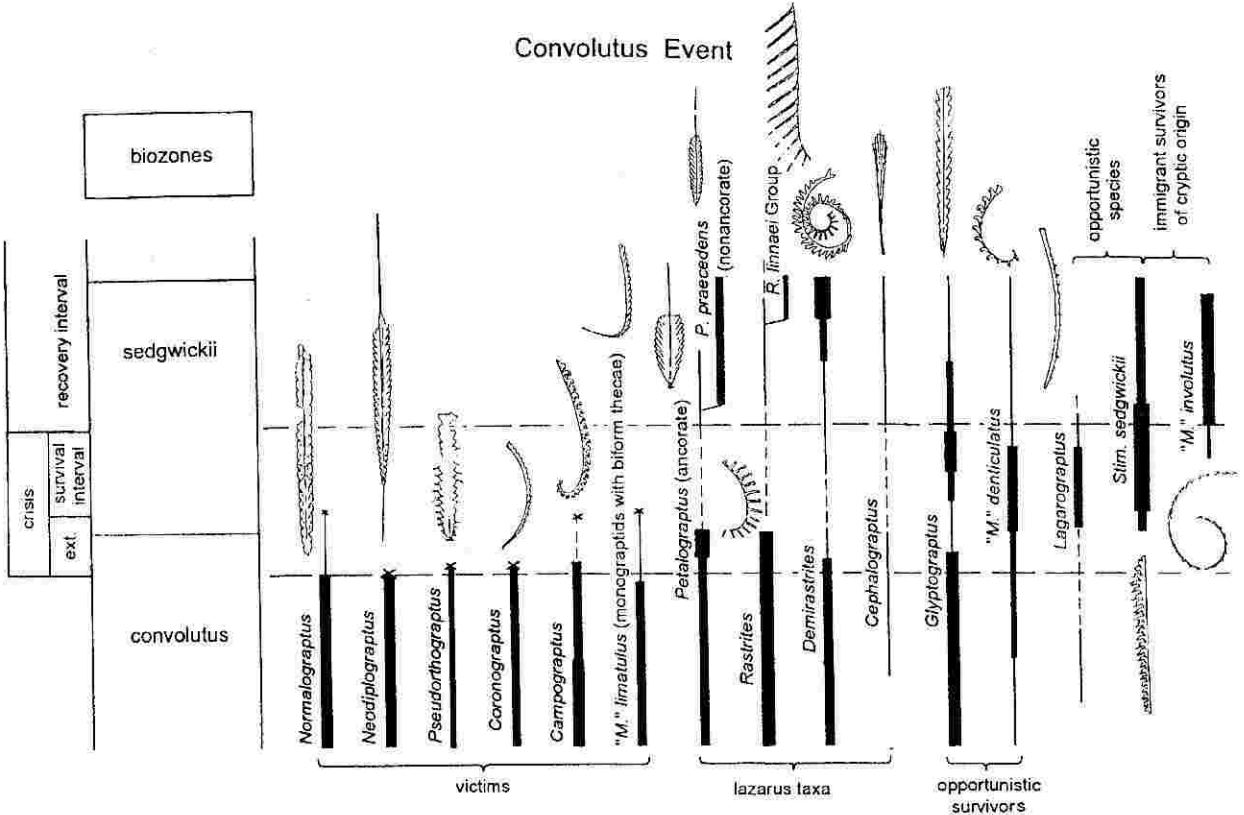


Figure 5. The convolutus Event: Extinction, survival and recovery among the most important graptolite species, species groups and genera in the course of the biotic crisis recorded in the latest convolutus and early sedgwickii biozones.

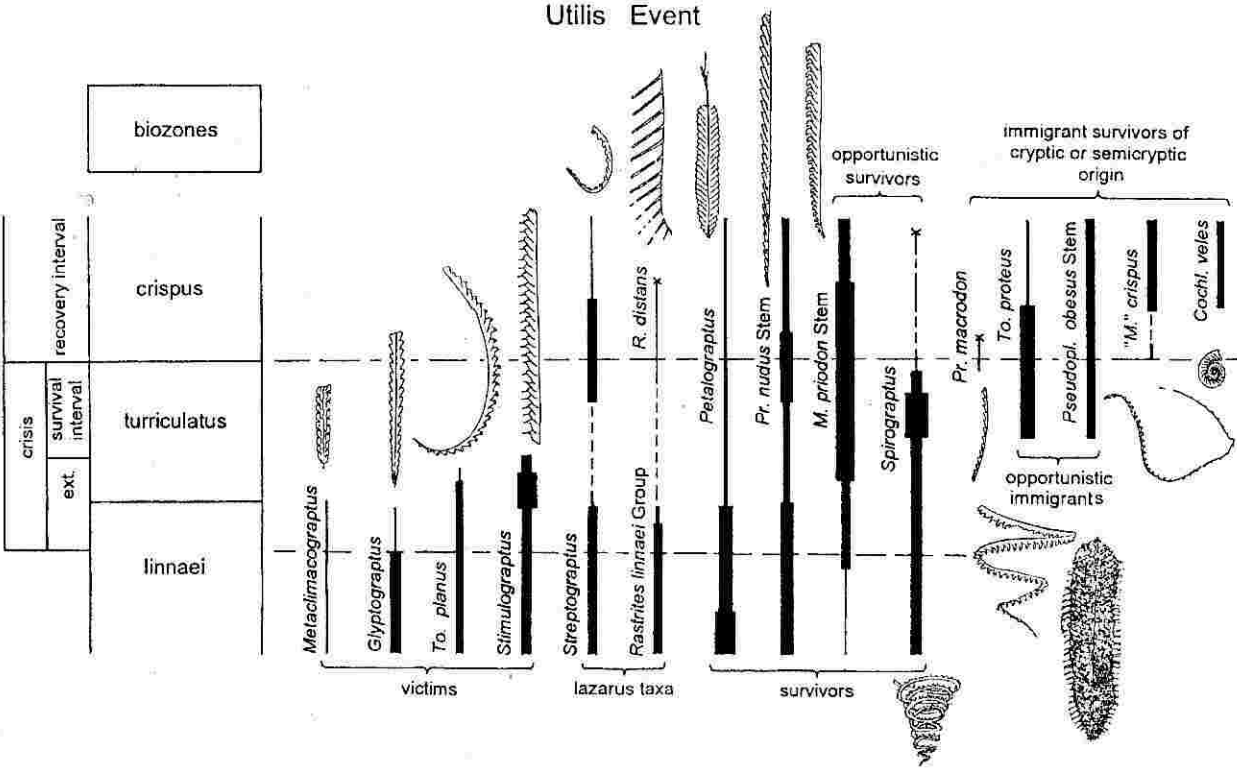


Figure 6. The utilis Event: Extinction, survival and recovery among the most important graptolite species, lineages (stems), species groups and genera in the course of the biotic crisis in the turriculatus and latest linnaei biozones.



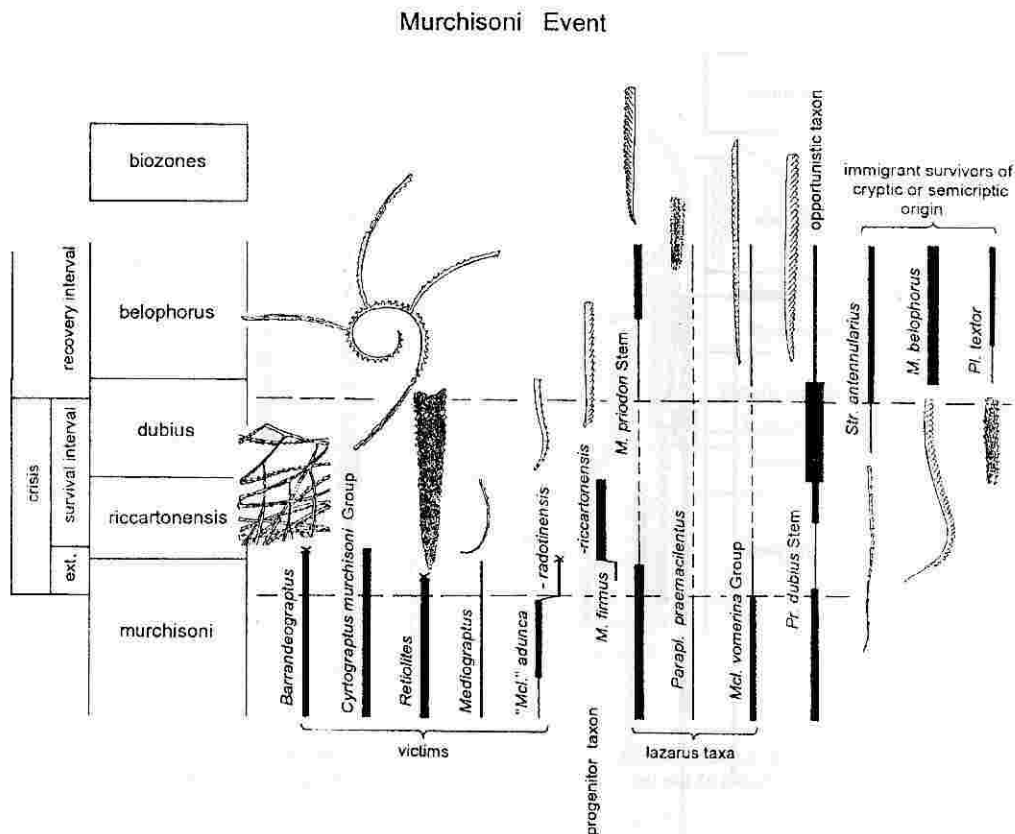


Figure 7. The *spiralis* Event: Extinction, survival and recovery among the most important graptolite species, lineages (stems) and genera in the course of the biotic crisis in the *grandis* and late *spiralis* biozones.

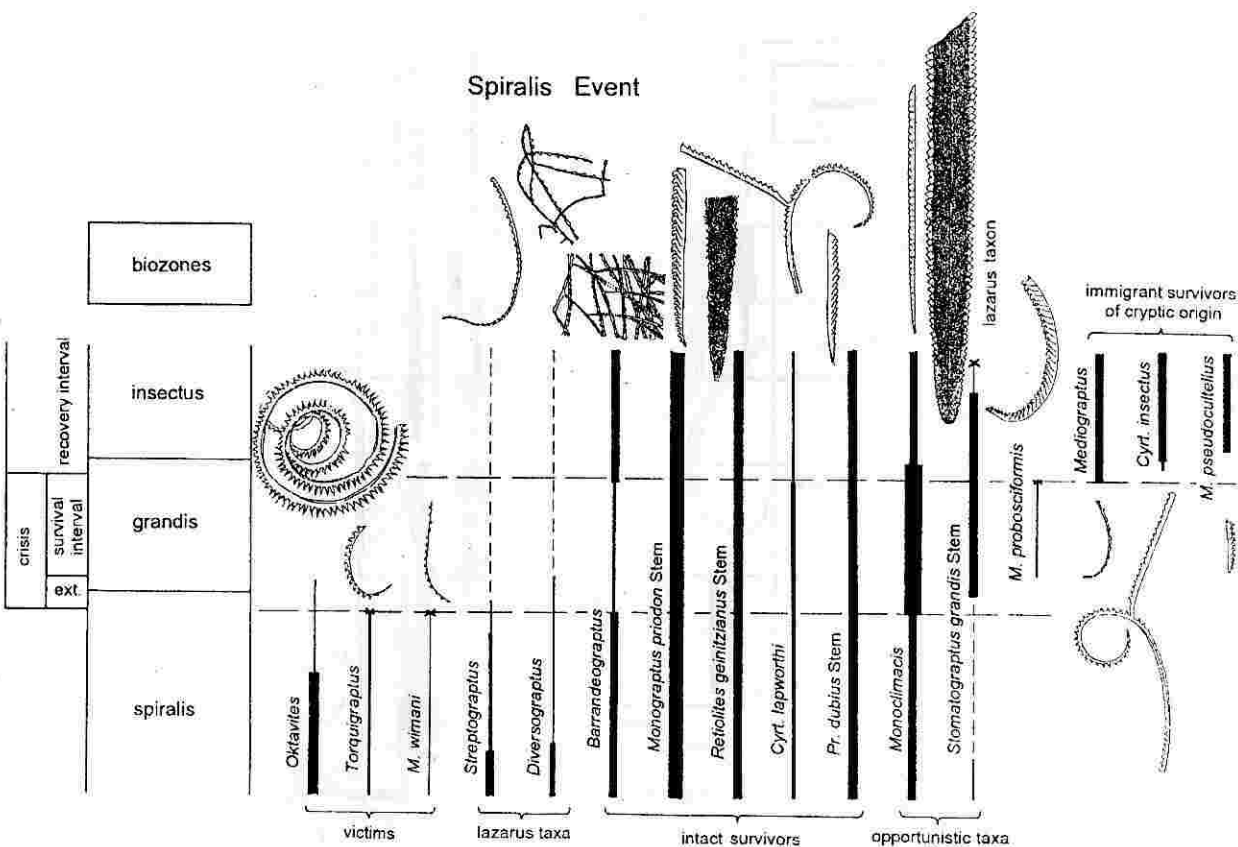


Figure 8. The *murchisoni* Event: Extinction, survival and recovery among the most important graptolite species, lineages (stems), species groups and genera in the course of the biotic crisis in the late *murchisoni*, *riccartonensis* and *dubius* biozones.

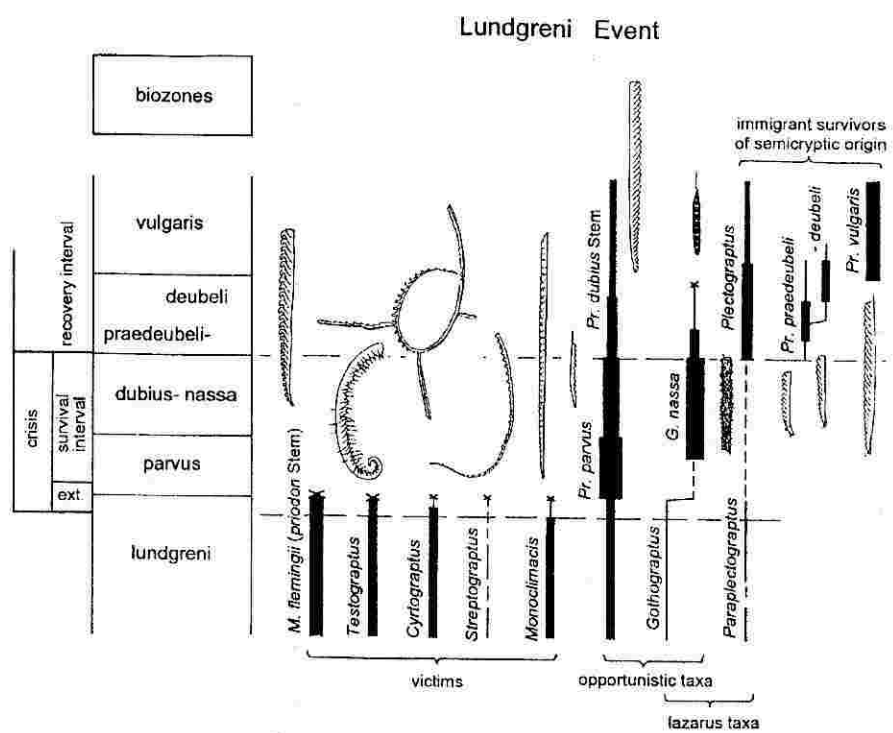


Figure 9. The *lundgreni* Event: Extinction, survival and recovery among the graptolite species, lineages (stems) and genera in course of the biotic crisis which affected the graptolite fauna at the top of the *lundgreni* Biozone and in the *parvus* and *dubius-nassa* biozones.

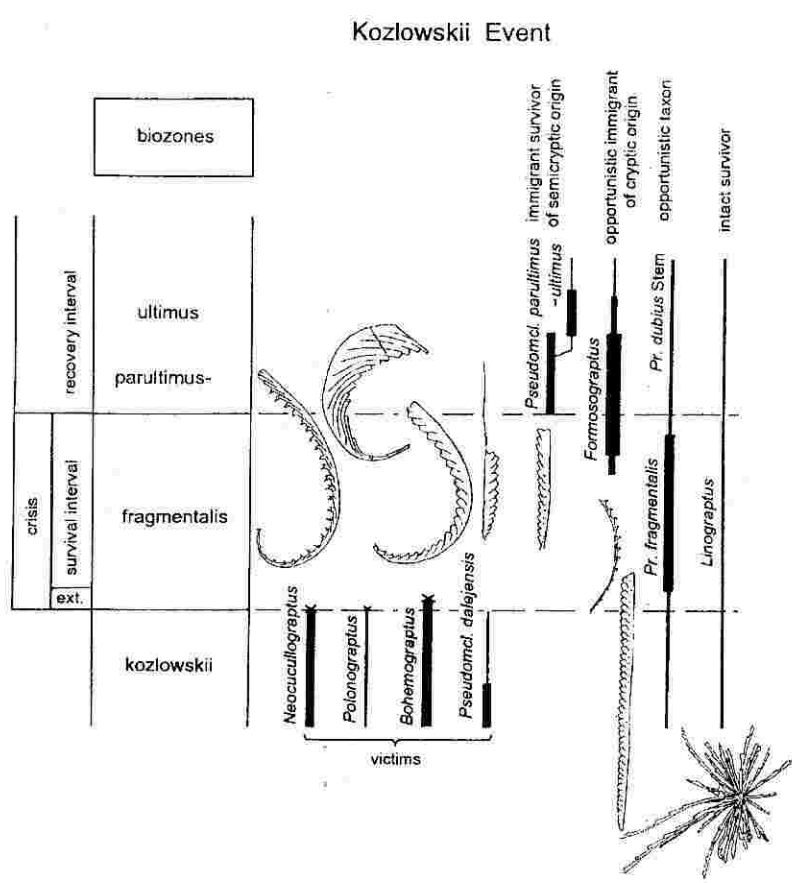


Figure 10. The *kozlowskii* Event: Extinction, survival and recovery among the graptolite species, lineages (stems) and genera in course of the biotic crisis in the *fragmentalis* Biozone.

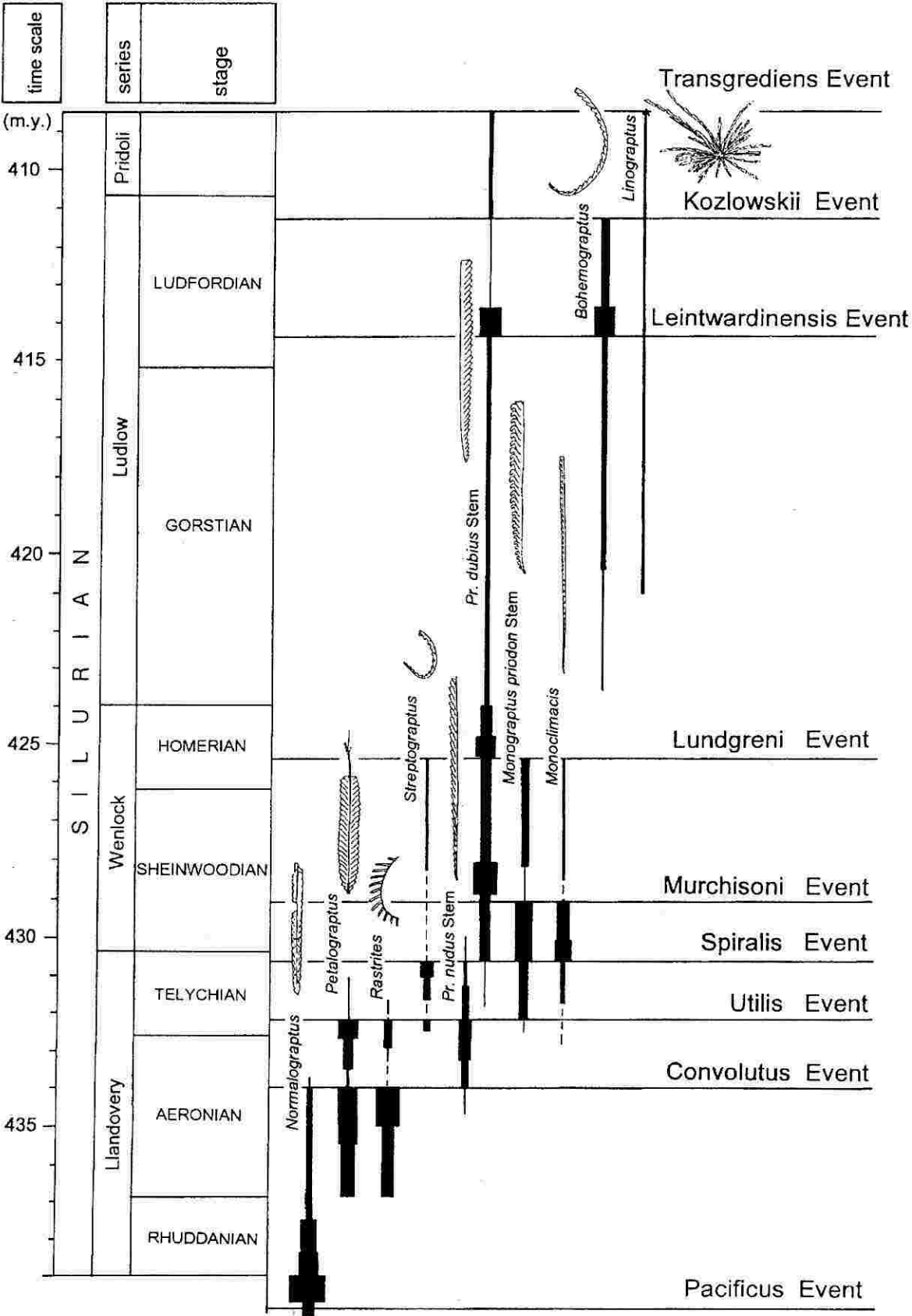


Figure 11. The most successful and long ranging Silurian graptolite stems and genera which survived at least one of the repeated crises.

## References

- ALDRIDGE R.J., JEPSON L. and DORNING K.J. 1993. Early Silurian oceanic episodes and events. *Journal of the Geological Society, London*, 150, 501–513.
- BERRY W.B.N., WILDE P. and QUINBY-HUNT M.S. 1987. The oceanic non-sulfidic oxygen minimum zone: a habitat for graptolites? *Bulletin of the Geological Society of Denmark*, 35, 103–114.
- BERRY W.B.N. and WILDE P. 1990. Graptolite biogeography: implications for palaeogeography and palaeoceanography. In McKerrow W.S. and Scotese C.R. (eds): *Palaeozoic Palaeogeography and Biogeography. Geological Society Memoir*, 12, 129–137.
- BOUČEK B. 1953. Biostratigraphy, development and correlation of the Želkovice and Motol Beds of the Silurian of Bohemia. *Sborník ústředního ústavu geologického, Oddíl paleontologický*, 20, 421–484.
- BRECHLEY P.J. 1984. Late Ordovician Extinctions and their Relationship to the Gondwana Glaciation. In Brechley P.J. (ed.): *Fossils and Climate*. 291–315. John Wiley and Sons.
- ERWIN D.H. and KAUFFMAN E.G. 1993 MS. Biotic recoveries from mass extinctions. *IGCP Project 335, First circular – April 1993*. Unpublished circular.
- FORTEY R.A. 1984. Global earlier Ordovician transgressions and regressions and their biological implications. In Bruton D.L. (ed.): *Aspects of the Ordovician System. Palaeontological Contributions, University of Oslo*, 295, 37–50.
- GRAHN Y. and CAPUTO M.V. 1992. Early Silurian glaciations in Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 99, 9–15.
- HARLAND W.B., ARMSTRONG R.L., COX A.V., CRAIG L.E., SMITH A.G. and SMITH D.G. 1990. *A geologic time scale 1989*. Cambridge University Press, 263pp. Cambridge, New York, Port Chester, Melbourne, Sydney.
- JAEGER H. 1991. Neue Standard-Graptolithenfolge nach der "Grossen Krise" an der Wenlock / Ludlow Grenze (Silur). *Neues Jahrbuch für Geologie und Paläontologie*, 182, 303–354.
- JEPSON L. 1990. An oceanic model for lithological and faunal changes tested on the Silurian record. *Journal of the Geological Society, London*, 147, 663–674.
- JEPSON L. 1993. Silurian Events: the Theory and the Conodonts. *Proceedings of the Estonian Academy of Sciences*, 42, 23–27.
- KAUFFMAN E.G. and ERWIN D.H. 1995. Surviving mass extinctions. *Geotimes*, 40 (3), 14–17.
- KOREN T.N. 1987. Graptolite dynamics in Silurian and Devonian time. *Bulletin of the Geological Society of Denmark*, 35, 149–159.
- KOREN T.N. 1991a. Evolutionary crisis of the Ashgill graptolites. In Barnes C.R. and Williams S.H. (eds): *Advances in Ordovician Geology, Geological Survey of Canada, Paper 90–9*, 143–156.
- KOREN T.N. 1991b. The *Lundgreni* extinction Event in Central Asia and its bearing on graptolite biochronology within the Homerian. *Proceedings of the Estonian Academy of Sciences*, 40, 74–78.
- KOREN T.N. 1993. Osnovnye rubezhi v evolutsii ludlovskikh graptolitov. *Stratigrafia, Geologicheskaya korelyatsia*, 1, 44–52.
- LENZ A.C. 1993. Late Wenlock – Ludlow (Silurian) graptolite extinction, evolution and biostratigraphy: perspectives from Arctic Canada. *Canadian Journal of Earth Sciences*, 30, 491–498.
- LOYDELL D.K. 1994. Early Telychian changes in graptoloid diversity and sea level. *Geological Journal*, 29, 355–368.
- MELCHIN M.J. 1994. Graptolite extinction at the Llandovery-Wenlock boundary. *Lethaia*, 27, 285–290.
- MELCHIN M.J. and MITCHELL C.E. 1991. Late Ordovician extinction in the Graptoloidea. In Barnes C.R. and Williams S.H. (eds): *Advances in Ordovician Geology, Geological Survey of Canada, Paper 90–9*, 143–156.
- MÜLLER A.H. 1961. *Grossabläufe der Stammesgeschichte*. G. Fischer. Jena.
- PŘIBYL A. 1983. Graptolite biozones of the Kopanina and Přídolí Formations in the Upper Silurian of central Bohemia. *Časopis pro mineralogii a geologii*, 28, 149–167.
- ŠTORCH P. 1994a. Graptolite biostratigraphy of the Lower Silurian (Llandovery and Wenlock) of Bohemia. *Geological Journal*, 29, 137–165.
- ŠTORCH P. 1994b. Llandovery-Wenlock boundary beds in the graptolite-rich sequence of the Barrandian area (Bohemia). *Journal of the Czech Geological Society*, 39, 163–182.
- ŠTORCH P. 1995. Upper Silurian (upper Ludlow) graptolites of the *N. inexpectatus* and *N. kozlowskii* biozones from Kosov Quarry near Beroun (Barrandian area, Bohemia). *Bulletin of the Czech Geological Survey*, 70, 65–83.
- URBANEK A. 1993. Biotic crises in the history of Upper Silurian graptoloids: a palaeobiological model. *Historical Biology*, 7, 29–50.