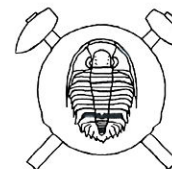


Joint occurrences of body- and trace-fossil communities (Ordovician, Barrandian area, Czech Republic)



Společné výskyty asociací body-fosilií a ichnofosilií v ordovických sedimentech Barrandienu (Czech summary)

(5 text-figs.)

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Rich associations of benthic fauna accompanied by diversified assemblages of ichnofossils have been found in the Ordovician of the Barrandian area, namely in the Klabava Formation ("Euloma Shales"), in the Šárka Formation (facies of black shales with concretions), in the Letná Formation (layers with the *Drabovia redux* Community), in the Zahořany Formation and in the *Polyteichus* Facies of the Bohdalec Formation. The associations of body- and trace fossils in the Letná, Zahořany and Bohdalec Formations are comparable to the *Dalmanella* Community of the Caradocian of North Wales; the remaining mentioned associations have no described analogies. As the number of analysed associations is limited, their comparison shows rather individual differences than recurring features. However, data compiled by Pickerill and Brenchley (1991) on palaeoenvironmental indicators of marine siliciclastic facies (which comprises also body-fossils and trace fossils) are of the use in the analysis of joint occurrences of body-fossil and trace fossil assemblages.

Key words: Ordovician, Czech Republic, Barrandian area, benthic assemblages, trace fossils.

Introduction

Relatively little attention has been paid to a regularity of joint occurrences of specific body- and trace-fossil assemblages, regardless both the groups separately served for erecting of general facies models [Boucot (1975): benthic assemblages; Seilacher (1967), Frey et al. (1990), Bromley and Asgaard (1991): ichnofacies]. Solving environmental problems of particular sedimentary units, many authors prefer either body- or trace fossils. Furthermore, pictorial reconstructions of ancient fauna and flora usually omit in-faunal elements [and generally most of soft-bodied animals; e.g., Augusta – Burian *in* Dvořák – Růžička (1972)].

Ordovician sediments of the Barrandian area (central and western Bohemia) involve several formations and facies rich both in body fossils and in ichnofossils. The published attempt to synthesise the data (Mikuláš 1998) was focused mostly to the regional palaeogeography and basin development. Aims of the present contribution are the following: 1. To compare the joint occurrences of rich body- and trace fossil assemblages from the Barrandian area to those described from abroad; 2. To look in these joint occurrences from the point of view of function of the overall benthic assemblages; 3. To present pictorial reconstructions of selected benthic assemblages from the Bohemian Ordovician; 4. To discuss a temporal and spatial structure of the benthic assemblages and ichnoassemblages in the Barrandian Ordovician.

Previous work

The statement given in the introduction that the topic of comparison of ichnoassemblages and benthic communities is seldom studied does not mean that there are no

published data on the joint occurrences of body and trace fossils. However, the purpose of these references varies substantially. The joint finds of traces showing their tracemakers *in situ* are important for obvious reasons and therefore they have been described in detail (e.g., Osgood 1970, Mikuláš 1990, Over 1988, Pickerill – Forbes 1978, West – Ward 1990). Papers dealing with the Precambrian–Cambrian boundary (e.g., Landing et al. 1988) also consider the body- and trace fossils altogether, because of the stratigraphical and evolutionary significance of both the groups. Descriptive papers providing a palaeontological information mainly for a local public (e.g., Gibson – Gastaldo 1989, Gutschick – Sandberg 1978) may also reflect joint occurrence of the body and trace fossils. Obviously, there is a lot of sedimentary units which have provided both the body and the trace fossils but each group has been elaborated separately by different authors with a little attempt to synthesise the data.

For the purpose of the present contribution, the papers using the body and trace fossils altogether to understand various aspects of sedimentary environments are the most relevant. The paper by Savrda – Bottjer (1989) on the Jurassic Possidonia Shales (Germany) is an example from the post-Palaeozoic. Papers of Pickerill – Brenchley (1979), Brenchley – Pickerill (1980), Hurst – Pickerill (1986), and Pickerill – Hurst (1983) described and interpreted body and trace fossil assemblages from Ordovician and Silurian siliciclastic sequences showing dominance of brachiopods in the benthic fauna from Wales and from Nova Scotia, Canada. Finally, a synthesis of sedimentological and palaeontological criteria for recognition of sedimentary environments in marine siliciclastic facies was published by Pickerill – Brenchley (1991). These authors suggested typical body- and trace fossil assemblages for various sedimentary environments, con-

sidering obviously both the knowledge of the joint occurrences of both the groups, and the data published separately for each of the groups.

The most detailed study of this kind is that of Pickerill – Brenchley (1979) from the Caradocian of the north Wales. In the clastic shallow marine sediments, ichnofossils show generally similar range of taxa as in the Barrandian, being represented by variable suite of ichnogenera including *Cruziana*, *Rusophycus*, *Trichophycus*, *Skolithos*, *Planolites*, *Gyrochorte*, *Diplocraterion*, *Arenicolites*, and *Teichichnus*. In terms of “classical” ichnofacies, this assemblage is referred as a coexistence of the *Skolithos* and *Cruziana* Ichnofacies in a shallow subtidal inner infralittoral shelf environment, and it is accompanied by several “shallow water” marine benthic assemblages. The *Howellites* Community, found in muddy siltstones, is composed of ecologically tolerant forms and is expected to live in depths less than 25 m. It is accompanied by trace fossils *Skolithos*, *Planolites*, and *Teichichnus*. The *Dinorthis* Community had occupied shifting coarse-grain substrates under high physical energy, in depths ca. 10 m, and less-energetic settings of finer sands in depth ca. 25 m. *Planolites* and *Chondrites* are the only joint traces. The *Dalmanella* Community had lived on a fine sand bottom with reduced sedimentation rate, in a depth ca. 25 m. It is accompanied by rich trace fossil assemblage including *Cruziana*, *Rusophycus*, *Trichophycus*, *Lockeia*, *Arenicolites*, *Skolithos*, and *Planolites*. The *Nicolella* Community had occupied calcareous silt and fine sand bottom in low energy settings, in depths of ca. 30 m. Discernible trace fossils are rare (*Skolithos*, *Planolites*) but the substrate is completely bioturbated which had substantially reduced the visible trace fossil diversity.

Hurst – Pickerill (1986) described a rather simple ichnoassemblage (*Chondrites*, *Palaeophycus*, *Planolites*, *Helminthopsis*) passing through several shallow-water (estimated depth 30–60 m) associations of benthic shelly fauna from the Llandoveryan of Nova Scotia (Canada). The associations had been controlled mostly by the substrate and by rates of the sedimentation. From the same area, the Llandoveryan sediments provided more diversified ichnofauna referred by Pickerill – Hurst (1983). Red shale facies deposited in shoreface environments have no body fossils but various traces belonging to *Chondrites*, *Gordia*, *Helminthopsis*, *Palaeophycus*, *Planolites*, and *Scalarituba*. Mottled mudstone facies are interpreted as shallow subtidal, with low sedimentation rates. They are extensively bioturbated, most bioturbation being represented by *Chondrites*; other trace fossil belong to *Planolites*, *Lingulichnus*, *Palaeophycus*, *Helminthopsis*, *Gordia*, *Teichichnus*, and *Skolithos*. Among the body fossils, *Lingula* in vertical life position has been found. Storm generated, shallow subtidal “lenticular facies” have in places extremely strong bioturbation and articulated shells of *Dalmanella primitiva*. Facies of laminated black shales have no fossils and ichnofossils as a result of low oxygen joint with low energy settings.

As mentioned above, Pickerill – Brenchley (1991) proposed a synthesis of the characteristic features of marine siliciclastic facies, using both benthic shelly fauna and ichnofossils as the indicators. For brackish lagoonal environments, body fossils are usually restricted, low diversified; sometimes the shell beds are present. Trace fossils of those environments are imperfectly known but generally low diversified, having ichnotaxa of “classical” *Ptilonichnus*, *Glossifungites*, *Cruziana*, and *Zoophycos* ichnofacies. Shoreface environments: Body fossils: The Palaeozoic assemblages characterised by brachiopods, bivalves and gastropods. Diversity generally low but may be increased by introduction of allochthonous faunas by storm, tidal and wave activity. Trace fossils: Typically “classical” *Skolithos*, more rarely *Ptilonichnus* and *Cruziana* ichnofacies, depending, among others, on substrate mobility. Diversity low. For inner (shallow) shelf environments, the Palaeozoic body fossils assemblages showing moderate abundance, predominated by brachiopods, are suggested to be characteristic; in inner fronts of deltas, faunas can be sparse due to the low salinity. Trace fossils are normally represented by moderate- to high-diversity *Cruziana* and/or *Skolithos* Ichnofacies. Middle shelf: Body fossils should form high-diversity assemblages, in the Palaeozoic dominated by brachiopods, trilobites, and echinoderms. Trace fossils are highly diversified as well, represented by repeating *Cruziana* and *Arenicolites* assemblages. Outer shelf: In the Palaeozoic, the body fossils are rare, represented by brachiopods and trilobites. Bioturbation is generally intense but low to moderately diversified. Slope and basinal environments have, in addition to pelagic fossils, benthic trilobites and hyolithids; trace fossil content varies depending on energy. *Skolithos*, *Arenicolites*, and *Glossifungites* “classical” ichnofacies are common in submarine canyons and fans, the *Zoophycos* Ichnofacies may characterise the low-oxygen slopes, and the *Nereites* Ichnofacies is typical in quiet but oxygenated parts of the deep basins.

Joint occurrences of body and trace fossils in the Barrandian area

Comparison of the data published by the above-mentioned authors to the situation in the Barrandian show numerous analogies. On the other hand, some assemblages, their combinations and their appurtenance to lithological and presumed environmental context remain specific for the Barrandian. One of the differences between the Barrandian and the scheme published by Pickerill – Brenchley (1991) consists in the fact that the term “shelf” is difficult to apply in the Barrandian Ordovician. During most of the Ordovician, only limited area of the “shelf” (occupying probably depths of several tens of metres only and a lateral extent of few kilometres at the maximum) had taken place in the Prague Basin (cp. Mikuláš 1998). The remaining part of the basin had been compo-

sed of the slopes and the floor of the trench, which is estimated to be several hundred meters deep. However, most of the settings presumed in the Barrandian Ordovician may be described in common terms of marine sedimentary environments.

Trace fossil communities in the Barrandian area were described in several minor papers (Mikuláš 1988–1997) which were summarised by Mikuláš (1998). Benthic assemblages of the Barrandian area are described from most part in terms of brachiopod communities erected by Havlíček (1982), who also suggested their relations to Boucot's (1975) classification of benthic assemblages.

Lower Tremadocian (Třenice Formation)

Coarse-grained greywackes and polymictic fine-grained conglomerates attributable to a surface of alluvial fans yielded the *Hyperobolus feistmanteli* Community which

may be correlated with Benthic Assemblage 1 of Boucot's (1975) classification. One locality only provided a trace fossil assemblage, consisting of unusually thick-lined *Bergaueria* and rare *Skolithos* (Mikuláš 1998).

No previous authors have given another example of the *Bergaueria*-dominated ichnoassemblage accompanied by presumably shallow-water inarticulate brachiopod benthic community. Generally, the characteristics of the shoreface environment published by Pickerill – Brenchley (1991), i.e. low-diversity brachiopod assemblage and the *Skolithos* "classical" ichnofacies applies.

Arenigian (Klabava Formation)

Central depression of the basin had mostly clay substrates locally with increased share of coarser-grained terrigenous detritus. The benthic assemblage consists of trilobites and small obolids (the *Rafanoglossa* Community

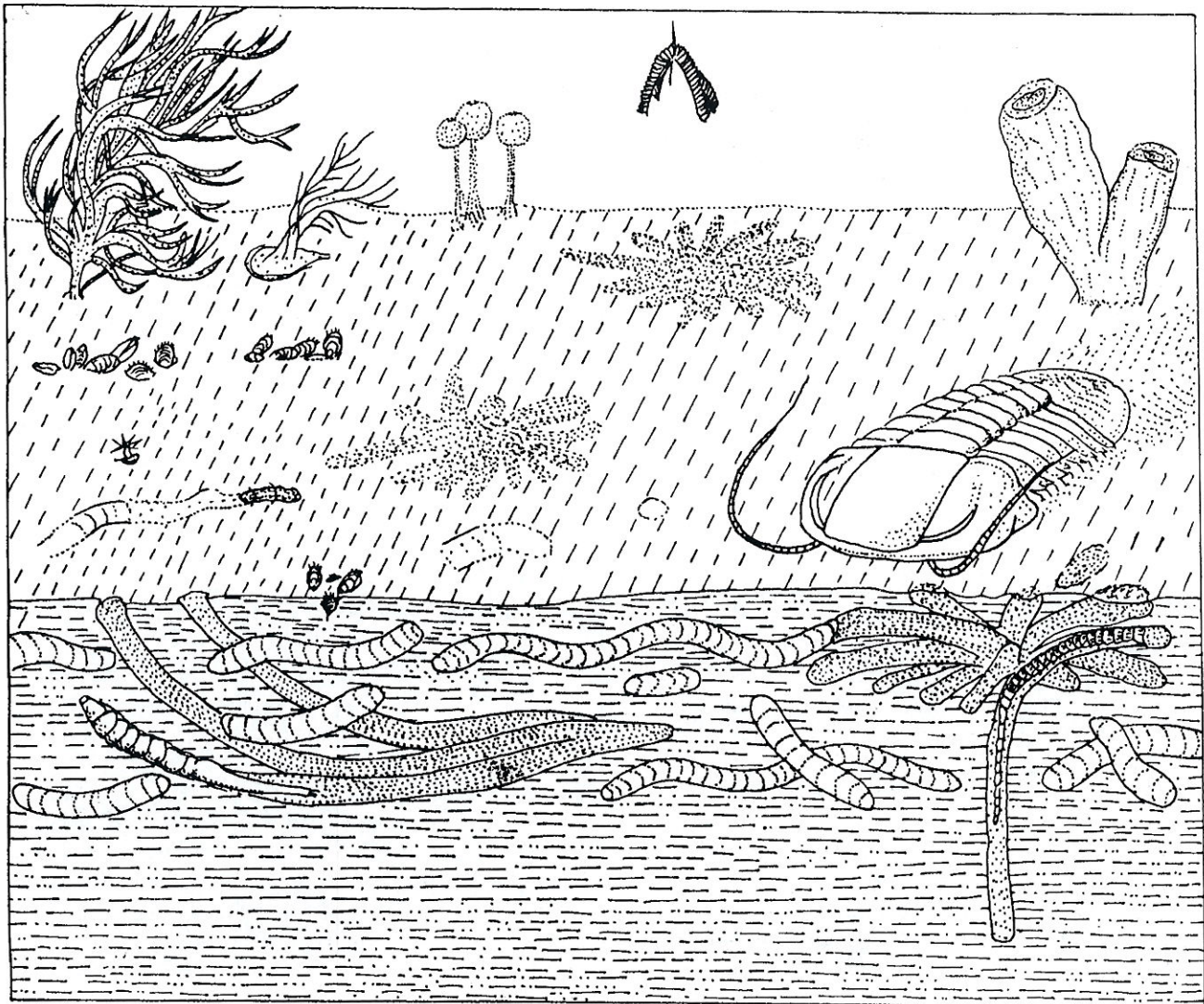


Fig. 1. Reconstruction of flora and fauna of the Klabava Formation (facies of "Euloma Shales"), Arenigian of the Barrandian area. Plakton is represented by *Tetraraptus*; benthic forms on the sea floor involve algae, sponges, small obolid brachiopods, and the trilobite *Euloma*; in-faunal elements are speculative tracemakers of star-like traces *Glockerichnus*, meniscate *Ancorichnus* and branching *Phycodes* (possibly polychaete "worms").

representing probably the Benthic Assemblage 3). This assemblage is accompanied by variable subsurface feeding traces (*Ancorichnus*, *Phycodes*, *Glockerichnus*); cp. Fig. 1. Shallow-water tuff substrates hosted a monospecific *Nocturnellia nocturna* Community (B.A. 2) which is in places joint with dense assemblages of the trace *Bergaueria*. Rather shallow-water red greywackes and shales having a *Leptembolon insons* Community (B.A. 1–2) yielded poorly diversified *Zoophycos*–*Planolites* ichnoassemblage (Mikuláš 1998).

Also the Arenigian benthic communities and their combinations are not directly comparable to any of the particular assemblages described by Pickerill – Brenchley (1979), Hurst – Pickerill (1986) or Pickerill – Hurst (1983). The shallow-water occurrence of *Zoophycos* coupled with low-diversity inarticulate brachiopod com-

munity would point to the “brackish lagoonal environments” following the scheme by Pickerill – Brenchley (1991); in the Barrandian Ordovician, it is placed to the position of the “inner shelf”, showing, however, rather low energy of waving and currents and therefore partially isolated from the open sea; therefore there is a slight controversy only. The assemblage with the bergauerians and *Nocturnellia* shows a similar status as the combination of the assemblages in the Tremadocian. It falls to the characteristics of the shoreface environment given by Pickerill – Brenchley (1991), which is in a good agreement with the presumed situation in the Barrandian. The *Rafanoglossa* Community accompanied with abundant and diverse subsurface fodinichnia (occupying the middle of the trench) cannot be directly compared with any combination suggested by Pickerill – Brenchley (1990).

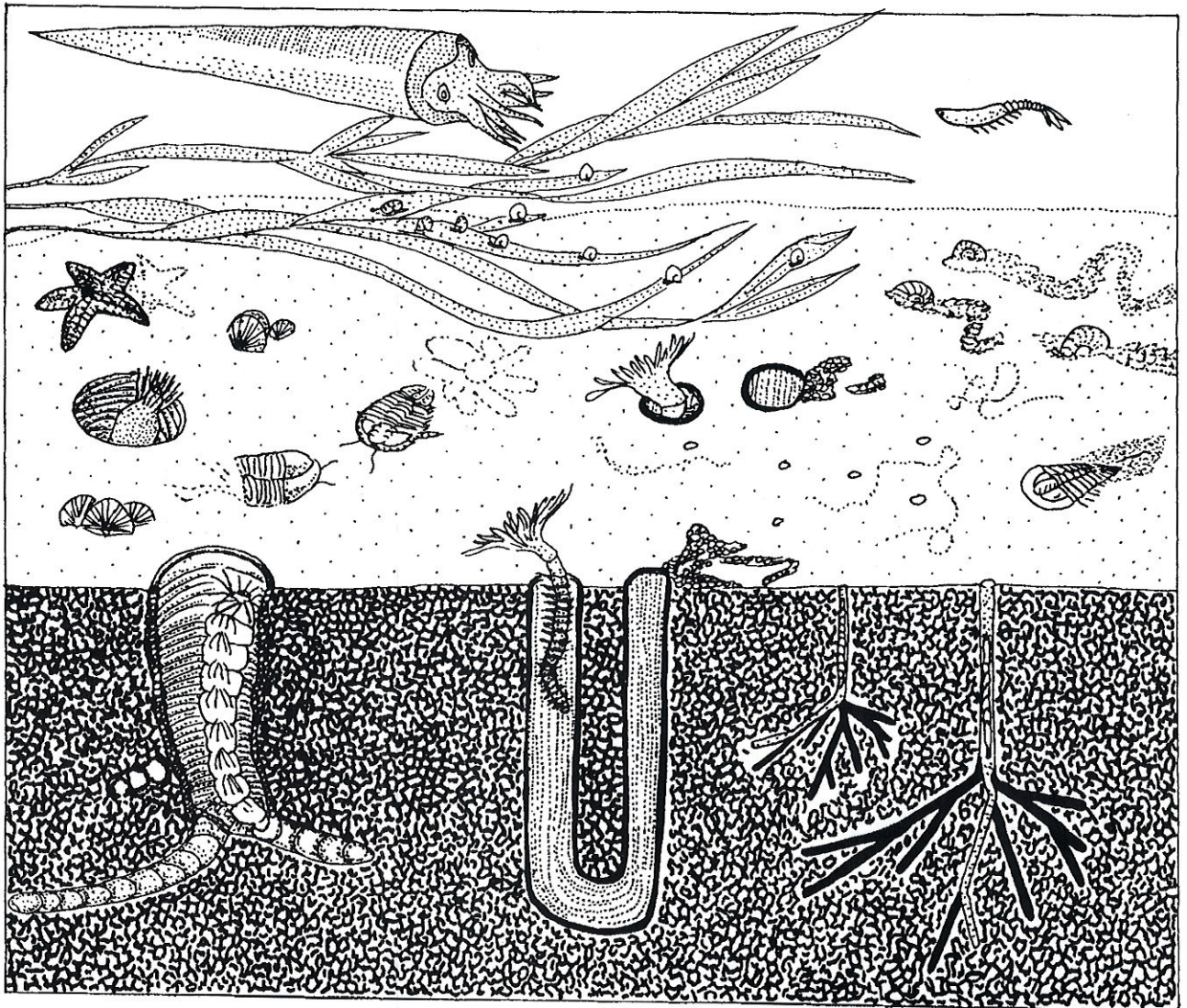


Fig. 2. Reconstruction of flora and fauna of the Šárka Formation (facies of black shales). Llanvirnian of the Barrandian area. Plakton is represented by an orthocone nautiloid, phyllocarid and algae with epiplanktonic gastropods; benthic forms on the sea floor involve orthid brachiopods, trilobites *Placoparia* and *Ectillaenus*, an asteroid and gastropods making *Nereites*-like traces; in-faunal elements are speculative (e.g., polychaete) tracemakers of traces *Brdichnus* (left), lined *Arenicolites* (in the centre) and *Chondrites* (right). Surface traces were not preserved for taphonomic reasons, parts of traces from deeper tiers were well-preserved in siliceous concretions.

Llanvirnian (Šárka Formation)

Black shale lithofacies of the Llanvirnian Šárka Formation is characterised by the *Euorthisina* Community (B.A. 3 to 4) having diversified trilobites, ostracods, bivalves, less diversified brachiopods, a.o. In the western (probably shallower) part of the basin, this fauna is accompanied by trace fossils *Chondrites*, *Arenicolites*, and *Zoophycos*-like trace *Brdichnus* (Fig. 2). Facies of oolitic iron ores is poor both in fossils and ichnofossils (fragments of inarticulate brachiopods, *Planolites* and *Bergaueria*; Mikuláš 1998).

The sedimentary environment of the oolitic iron ores and the joint body and trace fossils had been probably very specific. It falls outside the Pickerill – Brenchley's scheme, having, however, some common features mainly with the shoreface environments. The central part of the Prague basin occupied by the *Euorthisina* Community applies clearly to the "slope and basinal environments", having both pelagic and benthic fauna and trace fossils attributable to the *Zoophycos* and *Nereites* "classical" ichnofacies.

Dobrotivian (Llandeilian; Dobrotivá Formation)

Facies of quartzites (i.e. the Skalka Quartzite) have a poor fauna (fragmentary orthid brachiopods; approx. B.A. 2) and a monotonous *Skolithos* ichnoassemblage. Among the facies lying closely to the presumed axis of the basin, rhythmically alternating layers of sandstones and shales yielded locally trace fossils *Phycodes*, *Diplocraterion*, *Cruziana* and *Rusophycus* or a monotonous dense assemblage of *Dictyodora*. Mixed sediments of clays and sands have common *Zoophycos*. These facies are very poor in shelly fauna. In the black shales, occupying most of the presumed basin trench, the diversified trilobites, gastropods, molluscs, echinoderms and several common species of brachiopods (i.e. the *Paterula circina* Community covering B.A. 3 to 6) are accompanied in places by the traces *Chondrites*, *Arenicolites*, and *Palaeophycus* (Mikuláš 1998).

The facies of the quartzose sandstones having *Skolithos* and the poor brachiopod fauna shows a good agreement with the criteria given by Pickerill – Brenchley (1991) for shoreface environments. The presumed central part of the basin shows nice examples of various "slope and basinal environments", having poor benthic and pelagic faunas and low-diversity ichnoassemblages attributable with reservations to "classical" *Arenicolites* and *Zoophycos* Ichnofacies; however, as in many other cases, these ichnoassemblages may be better understood without their forced identification with any of the "classical" ichnofacies.

Lowermost Berounian (Lowermost Caradocian; Libeň Formation)

Sandy substrates (i.e. the Řevnice Quartzite) usually have common *Skolithos* or (when alternating with black

clay sediments) *Pragichnus* and no shelly fauna. Presumably deeper parts of the sandy substrates yielded in places the *Drabovia dux* Community with abundant articulate brachiopods and trilobites (presumably B.A. 3), which is in one locality joined with trace fossil assemblage (*Asteriacites*, *Diplocraterion*, *Planolites*).

The shoreface and basinal environments had changed a little from the Dobrotivian. Newly, the *Drabovia dux* Community, accompanied by rather low-diversity (but poorly known) assemblage of "classical" *Cruziana* Ichnofacies, falls to the Pickerill – Brenchley's (1991) criteria for inner (shallow) shelf environments. Particularly the *Dalmanella* Community of the North Wales Caradocian (Pickerill – Brenchley 1979) joint with occurrences of *Cruziana*, *Trichophycus*, *Lockeia*, *Arenicolites* and *Planolites* is comparable.

Lower to Middle Berounian (Letná Formation)

Areas with prevailing sandstones and subgreywackes yielded in places the *Drabovia redux* Community (referred to Benthic Assemblage 3), rich in orthid brachiopods and diversified dalmanitid, trinucleid, asaphid and calymenid trilobites. This community is accompanied by a moderately diversified ichnoassemblage (e.g., *Phycodes*, *Arenicolites*, *Rosselia*; Fig. 3). The main lithofacies, i.e. sandstones and subgreywackes intercalated with greywackes, siltstones and clay shales, contains in many places rich ichnoassemblages (e.g. *Cruziana*, *Rusophycus*, *Didymaulichnus*, *Fustiglyphus*, *Gyrochorte*, *Phycodes*, *Chondrites*, *Teichichnus*, *Squamodictyon*) but the shelly fauna is poor (rare *Dalmanitina socialis*; cp. Mikuláš 1998).

The *Drabovia redux* Community, joint with rich ichnoassemblage clearly attributable to the "classical" *Cruziana* Ichnofacies in rhythmical greywacke-shale layers, is comparable with the Pickerill – Brenchley's (1991) criteria for inner shelf, and it might be compared (as well as most of the occurrences of the *Drabovia*, *Drabovia-Aegiromena* or *Hirnantia* Communities in the Barrandian) with the *Dalmanella* Community of the North Wales. Also the notice of the authors that the faunas can be sparse in inner fronts of deltas applies well for the Barrandian. The status of the *Drabovia redux* Community joint with *Phycodes*, *Arenicolites* and *Rosselia* seems to be more complicated. It suits well to the Pickerill – Brenchley's (1991) criteria for the middle shelf (diverse brachiopod, trilobite, and echinoderm assemblages; diversified trace fossils represented by repeating *Cruziana* and *Arenicolites* associations), but in the present model of the Barrandian area I prefer the position of this community rather in the "protected" shallow shelf, because it falls better to the logic of the spatial and temporal development of the basin (cp. Mikuláš 1998).

Middle to Upper Berounian (Zahořany Formation)

The *Drabovia-Aegiromena* fauna (rich orthid and strophomenid brachiopods, trilobites, cystoids, bryozoans,

Barrandian area” by J. Sovák, created in 1996–1997 under the leadership of Dr. V. Turek and Dr. R. Prokop (National Museum, Prague) and exhibited in the National Museum in 1998–1999. Supplemented are trace fossils and in-faunal elements. The hypothetical soft-bodied animals have been reconstructed according to a presumed ethological function of joint trace fossils, and after recent analogies, published, e.g., by Bromley (1996).

Although no direct evidence of hunting the in-faunal elements by other members of the assemblages [as described by Bergström (1967)] is known from the Barrandian Ordovician, we may presume numerous predator-prey relationships among vagrant benthos and in-fauna. Most of sediment-feeders or chemosymbionts used organic mass from microplankton. They might represent a usual prey of larger vagrant benthic forms as trilobites (suggested on Fig. 3).

In any case, we need the ichnological record if we attempt to reconstruct both composition and function of ancient benthic assemblages.

Temporal and spatial structure of the benthic assemblages and ichnoassemblages in the Barrandian Ordovician

As shown above, it should be concluded that both the benthic communities and the ichnoassemblages of the Bohemian Ordovician occur mostly in presumed positions in the basin, and their joint occurrences are seldom in controversy with the summary of main features of marine siliciclastic facies published by Pickerill – Brenchley (1991). However, the above-shown comparison is based on very generalised terms, as the “classical” ichnofacies, or, e.g., “high-diversity assemblages dominated

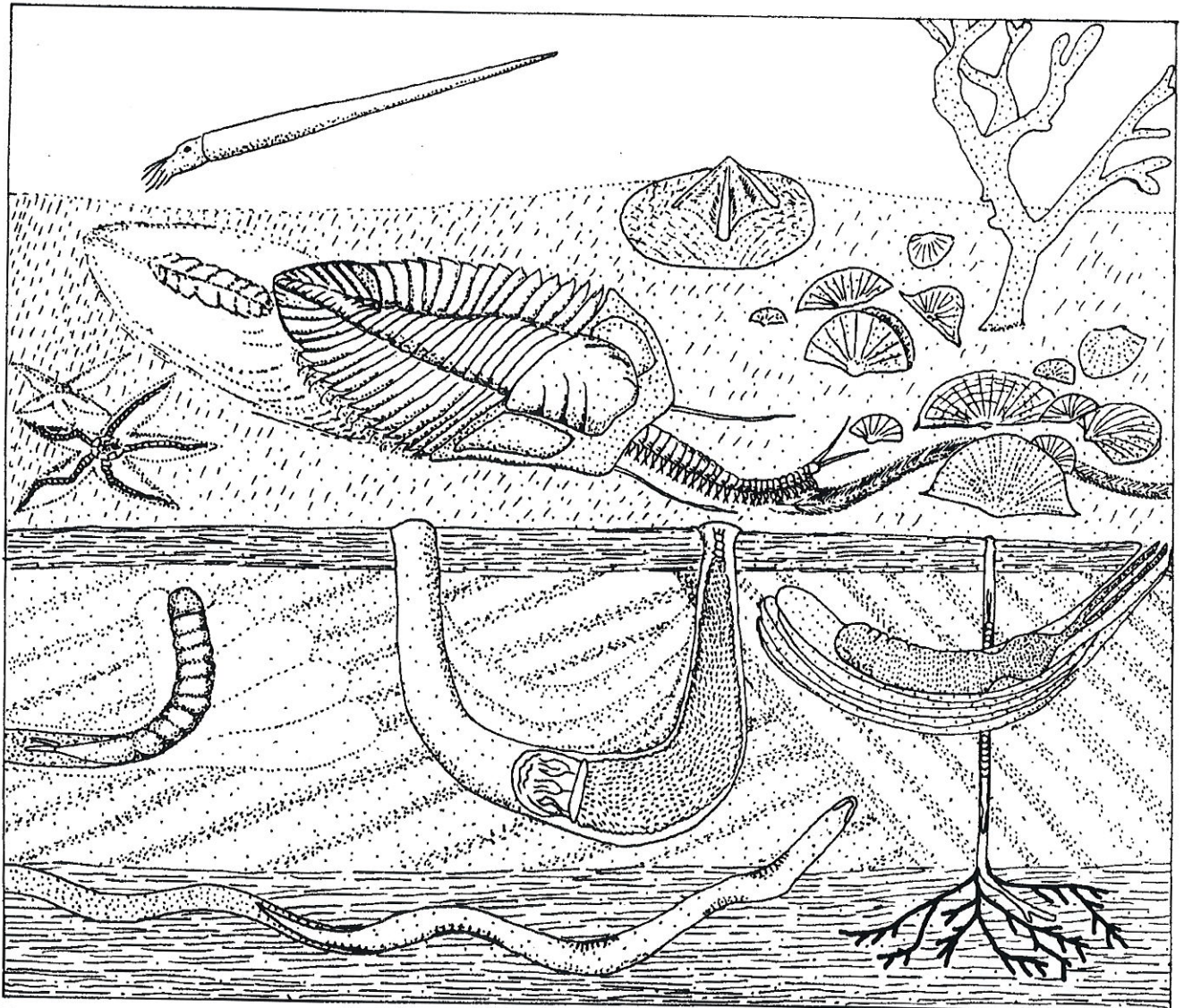


Fig. 5. Reconstruction of flora and fauna of the Bohdalec Formation (the *Polyteichus* Facies). Uppermost Berounian of the Barrandian area. Plakton is represented by an orthocone nautiloid; benthic forms on the sea floor involve bryozoans *Polyteichus* and *Batostoma*, orthid and strophomenid brachiopods (e.g., *Svobodaina*, *Aegiromena*, *Rafinesquina*), calymenid trilobite leaving the resting trace *Rusophycus* to prey on an annelid “worm”, and the ophiuroid *Taeniaster* in its resting burrow, *Asteriacites lumbricalis*; in-faunal elements are tracemakers of *Phycodes*, *Rhizocorallium* and *Teichichnus* (upper tier), *Planolites* and *Chondrites* (deep tier).

by brachiopods". If we study the benthic communities and the ichnoassemblages in greater details, there are obvious differences of temporal and spatial distribution between single ichnoassemblages and benthic communities associated with them. For example, the *Drabovia–Aegiromena* Communities, placed by Havlíček (1982) to a relatively narrow range of Benthic Assemblages 3–4, passed slightly changed through numerous different ichnoassemblages (Mikuláš 1998, Figs. 8–11).

Havlíček (e.g., 1982), studying the brachiopod communities, interpreted most of the lithological and faunistic changes in the Barrandian Ordovician as a result of local tectonics in the basin, and a little importance is given by him to global eustatic events. On the other hand, Chlupáč – Kukul (1988), studying mostly lithology and sedimentology (roughly also the trace fossils, as observed during the field work, were included), found the eustatic events the most important and the local tectonics was given by them only a secondary influence.

The Barrandian Ordovician shows a relatively long time interval of continuous siliciclastic sedimentation where the body- and trace fossil assemblages may be observed. Therefore the obtained data suggest to formulate some more general conclusions on the temporal and spatial structure of the benthic assemblages and ichnoassemblages, and consequently on various aspects of differences and similarities of both the forms of the fossil record. However, there are numerous complications in interpreting the data. For comparison of different benthic assemblages, a cluster statistical analysis offers to be used, regardless the complication following an uneven value or subjectivity of some taxa. It would be probably even more difficult to find reasonable criteria for a statistical comparison of similarity/difference of ichnoassemblages from various localities; for example, presence/absence of elite trace fossils as *Zoophycos* or *Thalassinoides* is much more important than the presence/absence of *Planolites* or numerous other facies-crossing forms. In this state of the study, I have desisted from the use of the cluster analysis, letting the presented conclusions supported only by the description of the assemblages on a non-quantitative level.

There is an obvious reason for the differences in lateral changes and temporal stability of the two groups: the ichnofossils do not preserve the fossil organisms but the fossil behaviour (e.g., Crimes – Droser 1992, Bromley 1996). Three other factors are expected to influence the distributional patterns:

1. Taphonomic reasons. The *Drabovia–Aegiromena* brachiopod benthic assemblages had passed almost untouched through a storm wave base, but the ichnoassemblages had changed substantially in the same situations (Mikuláš 1998, Figs. 8–11). The reason might be that the occasional storm sedimentation had influenced much more a preservation potential of the trace fossils than that of the body fossils.

2. Different effects of local and global changes. Appearance of the dark clay sedimentation after transgres-

sive events had always been joined with the appearance of simple ichnoassemblages dominated by *Chondrites* and *Planolites* though it cannot be concluded that only these traces had a high preservational potential; brachiopod benthic assemblages had been also reduced in diversity and density in these situations, but not so strongly (cp. Mikuláš 1998, Figs. 10–11). The global eustatic events might influence much more an oxygenation of the upper part of the substrate than the local (e.g., tectonic) changes. Therefore, the trace fossils, formed mostly by in-faunal elements, reflected them very sensitively. On the other hand, frequent local fluctuations of physical energy and rate of sedimentation might have stronger effects on benthic shelly fauna than on the ichnofauna.

3. Differences of extinction and recovery patterns between in-fauna and sessile or vagile shelly fauna. The "Plus ca change" theory concluded that frequent changes of the environment might retard evolution, because the changes lead to a selection of opportunistic organisms (Sheldon 1996). As suggested preliminarily by Mikuláš (1997), following this hypothesis, it is likely that the persistence and temporal changes of in-faunal communities (i.e. the tracemakers of many ichnofossils) should be different than the persistence of the shelly fauna (consisting mostly of the forms living on the bottom), because the environmental fluctuations in the sediment show different dynamism (they are usually much less frequent, but as shown above, they may be more prominent in some situations) compared to the niches of the sea floor. This theory may be applied, with some reservation, to the interval of the Berounian (Caradocian) Stage (Mikuláš 1998, Figs. 8–11), showing the persistence of the *Aegiromena–Drabovia* faunas, but the considerable variety of the ichnoassemblages even in presumably similar to identical sedimentary environments in different times. As an example, siltstones of the Zahořany Formation are in most localities highly bioturbated by the *Zoophycos* tracemaker, but no *Zoophycos* has so far been found in the siltstone facies of the overlying Bohdalec Formation (cp. Figs. 4 and 5).

I believe that the trace fossils could give much more evidence for the patterns of extinctions and recovery than generally presumed. The ichnofossils are usually regarded as a facies-related record of the fossil behaviour, which is essentially correct; they, however, still remain traces of particular organisms, in most cases of the non-shelly fauna. In the cases as the Ordovician of the Barrandian area, the comparison of the body- and trace fossils, after a careful recognition and elimination of other influences, should be used to test the "Plus ca change" theory, or to formulate new hypotheses on the extinction and recovery patterns.

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Společné výskyty bohatých asociací body-fosilií a ichnofosilií v ordovických sedimentech Barrandienu

Bohaté benthické fauny doprovázené rovněž bohatými ichnospolečenstvy byly v ordoviku Barrandienu zjištěny zejména v klabavském souvrství (eulomové břidlice), v šareckém s. (facie černých břidlic s konkrecemi), v letenském s. (polohy se společenstvem *Drabovia redux*), v zahofanském s. (řada lokalit) a v polyteichové facii bohdaleckého souvrství. Společenstva body-fosilií a ichnofosilií v letenském, zahofanském a bohdaleckém souvrství jsou srovnatelná s *Dalmanella* Community v caradoku severního Walesu (Pickerill – Brenchley 1979), zbyvajících zmíněné asociace nemají popsané zahraniční obdoby.

Při nevelkém množství analyzovaných společenstev (jak v Barrandienu, tak v zahraničním paleozoiku) ukazuje jejich srovnávání spíše individuální rozdíly mezi jednotlivými společnými výskyty než opakující se rysy těchto situací. Na většinu společných výskytů body-fosilií a ichnofosilií v ordoviku Barrandienu lze však s různou mírou přesvědčivosti aplikovat údaje Pickerilla – Brenchleyho (1991). Tito autoři publikovali tabulku paleoenvironmentálních indikátorů mořských siliciklastických facií zahrnující body-fosilie i ichnofosilie, která je podle mého názoru použitelná jako základní schéma klasifikace společných výskytů body-fosilií a ichnofosilií.