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ON THE BATHYMETRIC DISTRIBUTION OF GRAPTOLITES

The mode of life of graptolites, with their differentiation according to the depth of habitat in particular, has been the constant focus of researchers. For the first time the bathymetric control of graptolite distribution was discussed by Berry (1962), Skevington (1969), Berry and Boucot (1972) and, in a more advanced form, by Erdtmann (1976 a, b). It should be noted that Bulman (1964) also assumed that graptolites may have lived at various depths in the sea. Obut (1964), Kozłowski (1971), Kirk (1978) link the life of graptolites with the euphotic zone of the sea, while the last author believes that the morphology of graptolite rhabdosomes is suggestive of their bathymetric differentiation within the above zone.

A viewpoint similar to the ideas expressed by Erdtmann (1976 a, b) and based on the study of graptolites and facies of the East Baltic Silurian (partly also Ordovician) will be presented below. In our discussion we proceed from the fact recognized by a number of authors (Paškevičius 1968; Gailite, Rybnikova and Ulst 1967; Kaljo and Jürgenson, 1977 etc.), namely, that a rich and diversified assemblage of graptolites was distributed in the central part of the sea occupied by the basin facies. Towards the coast the role of graptolites decreases quickly — the transitional facies still yield numerous graptolites associated with trilobites, ostracodes and brachiopods from the *Clorinda* community (in the Llandovery) as well as from the *Dicoelosia* — *Skenidiodes* (in the Wenlock and more rarely from the *Dayia* (in the Ludlow) communities; but in carbonate deposits of open-shelf and shally facies there occur only few graptolite remains. This is clearly shown in fig. 1, which also explains the terminology used in our paper. In Britain the same (in broad terms) facies pattern of distribution was suggested by Elles (1939).

The transitional facies belt may be wider or narrower due to tectonic reasons, but usually, comparatively many graptolite specimens occur only in the outer half of the belt. In its inner half graptolites are insignificant.

According to Kaljo and Jürgenson (1977), the width of the transitional facies belt averages 100 km with a minimum width of 20 and a maximum

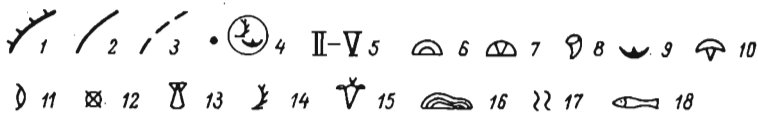
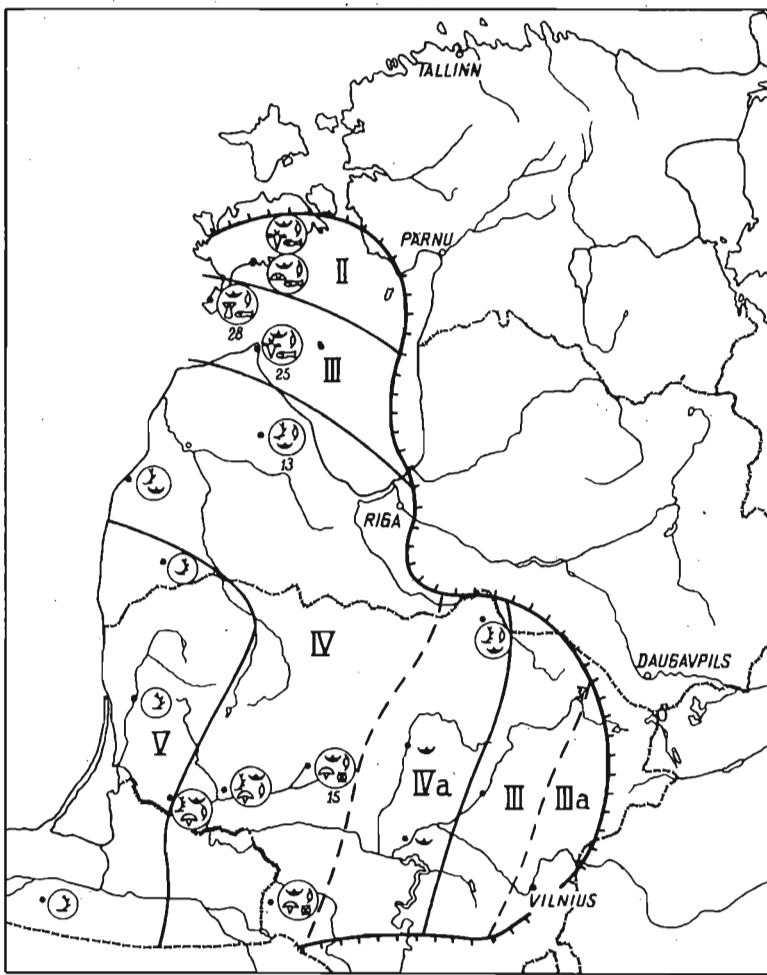


Fig. 1. Facies zonation of East Ludlow (simplified from Kaljo and Jürgenson 1977). 1 boundary of the present distribution of Ludlow deposits; 2 boundary of facies belt; 3 boundary of lithological difference; 4 borings, circles denote the predominating groups of organisms the figure shows the content of detritus; 5 facies belts (facies):

II shally facies composed of various grainy limestones (bio- and lithoclastic), at places with developed bioherms; more characteristic are brachiopods, ostracods, corals and Agnatha; there occur interbeds of lagoonal rocks with eurypterids; III open-shelf facies consisting of detritic and muddy-detritic clayey limestones which are in part nodular and with marly interbeds, communities are dominated by brachiopods, ostracods and Agnatha, sometimes molluscs. In more eastern parts of the facies belt (III a) interbedding of grainy and clayey limestones and dolomites can be observed (at places with gypsum); IV transitional facies composed of marls and clay with limestone lenses and interbeds. In the eastern part of the belt, within the limits of Lithuania, prevail marls (IV a). More common are brachiopods, ostracods, trilobites and in some sections graptolites, at places there are abundant crinoids; V basin facies composed mainly of graptolite-bearing clays;

6 stromatoporoids; 7 tabulate corals; 8 rugose corals; 9 brachiopods; 10 trilobites; 11 ostracods; 12 echinoderms; 13 pelecypods; 14 graptolites; 15 eurypterids; 16 calcareous alge; 17 worm tracks; 18 fishes.

of 160 km. This means that within 50 km (but sometimes within only 20 km) rocks with abundant graptolites were replaced by those where graptolites were almost entirely absent.

Assuming the planktonic and euphotic mode of life of graptolites one might expect fairly numerous graptolite fossils also in shallow-water shelf deposits. But there are very few of them.

Various reasons have been proposed to account for this, such as 1) destructive effect of high energy environment in the shallow sea; 2) biological barrier, and 3) differences of neritic and pelagic graptolite assemblages.

The destructive effect of the environment is by all means an important factor in the formation of graptolite taphocoenoses (Erdtmann 1976 a). But, in our opinion, the major influence is the quantitative regulation of the taphocoenosis composition and, to a smaller extent, the selective destruction of less stable rhabdosomes (the physical and chemical durability of rhabdosomes or their parts seems to show little variation in a number of graptolite genera).

In order to understand the situation as it is, we shall turn to some materials concerning the East Baltic Ordovician and Silurian.

According to Pölma (1973; 700 thin sections studied) in the Ordovician graptolite detritus can be observed in clayey limestones and marls of the Latvian structural facies zone. There, the total share of detritus amounts to 13 per cent, of which the graptolite-containing "varia" group accounts for as much as 7 per cent. The pure and clayey limestones of the Estonian-Lithuanian structural-facies zone, with the average detritus content equal to 25 per cent, contain almost no graptolite detritus. Pölma believes that the rocks he studied are deposits of moderate (Estonian — Lithuanian zone) and medium (Latvian zone) depths below the wave base (especially so in the Latvian zone). The facies model of the Baltic Silurian (Kaljo *ed.* 1970 suggests that the marls of the Latvian zone are related to the transitional facies belt.

Detritus of Silurian rocks has been studied by Aaloe (1977) on the strength of the data from 300 thin sections. He stated, strongly in line with the above, that the role of graptolites in the composition of organogenous detritus is limited to the transitional and deeper facies.

Etching graptolites from carbonate rocks helps to better understand their distribution in shelf areas. Thus Männil (1976) having etched organic fossils from about 2,000 samples weighing up to 0,5 kg, arrived at the following conclusions which he had presented at the Graptolite Symposium at Tallinn:

a) shelf facies of some stratigraphic intervals in particular, yield much more abundant graptolites than is customarily believed (see also Elles 1939);

b) carbonate facies mostly contain certain specific graptolite species;

c) the majority of species occurring in limestones display a discontinuous distribution; some of them are distributed within a narrow interval (zone) over a wide territory (for instance, *Gymnograptus linnarssoni*, which has been recorded from Oslo to Moscow);

d) in relatively near-shore facies, a very limited number of graptolite species can be observed often no more than a single species, as is the case with *Amplexograptus cf. fallax* in Northern Estonia. Towards the open sea the number of species gradually increases.

Considering the data offered by Nölvak (1972 and personal communication), we may add that in limestones (especially at some levels) graptolite siculae are much more common than fragments of rhabdosomes.

In his work Männil (1976) makes wide use of the terms "shelf" and "carbonate" facies. These are difficult to translate into the exact language of facies analyses. But in spite of this limitation, his data and the results of his study of detritus allow us to make two conclusions as far as the neritic graptolites are concerned:

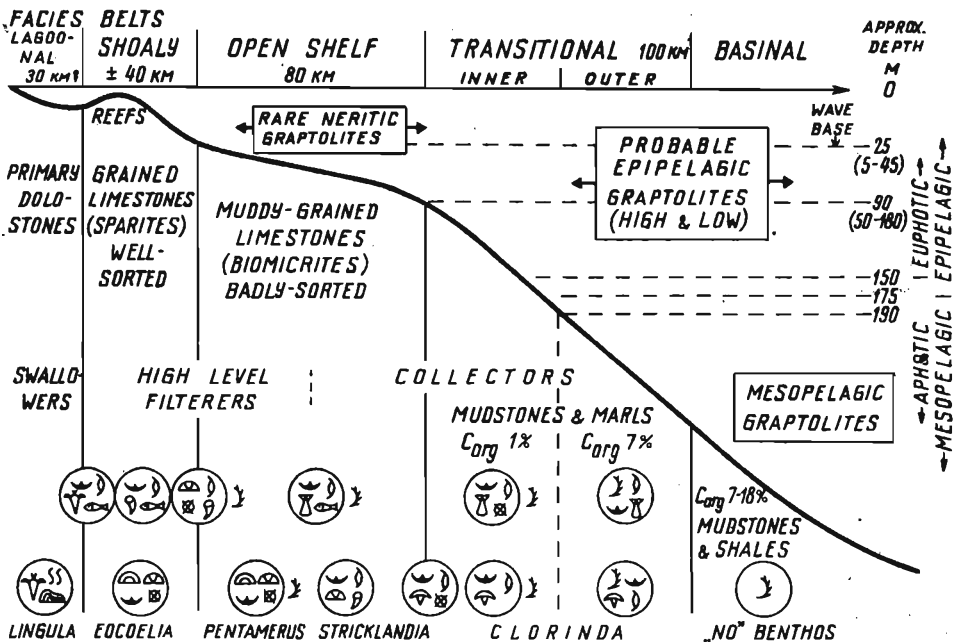


Fig. 2. Bathymetric distribution of main graptolite assemblages. The figure is based on the data on the East Baltic Silurian. The bathymetric curve is plotted with regard to the average width of facies belts, to the depth of the wave base and to the average inclination of the shelf surface and the continental slope (see the text). Boundaries between the photic and pelagic zones have been drawn according to Hedgpeth (1966). Distribution of dominating trophic groups, brachiopod-dominating communities and predominating organisms groups over the facies belts is shown on the basis of our data (predominant groups are marked with symbols in the circle; graptolite being the only secondary group to be denoted with a symbol next to the circle). The content of organic carbon is listed according to Jürgenson (see Kaljo and Jürgenson 1977).

For explanation of symbols see fig. 1.

1) A rather small amount of graptolite fragments (detritus) in the carbonate rocks of the shelf can be interpreted as evidence of the scarcity of graptolites inhabiting the neritic sea, for it is quite unlikely that numerous graptolites could have suffered complete (traceless) destruction, at least, in the open-shelf facies belt (see fig. 2), within whose bounds the sea-bottom is below the level of the constant wave action. In the transitional facies belt, where the number of graptolite macroremains increases, the role of their detritus also becomes greater.

2) The neritic part of the sea was inhabited by a specific and not numerous graptolite assemblage whose diversity increased in the direction of the open sea. An impoverished though regular composition of the assemblages, as observed over quite extensive areas, indicates that its qualitative structure could hardly be affected by destructive processes. Otherwise, one would have to assume a very fine mechanism of selective destruction operating over wide territories. But this does not seem to be the case.

Zima (1976) analyzed the significance of biological barrier for graptolite distribution. He correctly noted the great importance of feeding conditions as a factor of animal distribution. Taking into account analogous relations of phyto and zooplankton in modern seas and what is known as the boundary effect, he postulates that graptolites displayed a zonal pattern of distribution around the land masses. The zones of phyto- and zooplankton overlapped only in part with phytoplankton being confined to an area closer to the coast-line.

But a more detailed treatment of spatial relations between the phyto- and zooplankton in present-day seas (Beklemishev 1957; Bogorov 1959 etc), however, convinces us that the boundary effect, so characteristic of plankton seasonal assemblages, cannot be of decisive significance for the distribution of cumulative taphocoenosis of graptolites which is the object of palaeontological studies. On the contrary, the biological data show that a positive correlation between the phyto- and zooplankton as well as between the plankton and the benthos is by far the more common pattern of distribution. Bogorov (1959) even stressed that life in the euphotic layer influences the development and distribution of biota all along the sea-water column.

Some authors (see above) suggested a bathymetric differentiation of graptolite assemblages. We also think this probable but not to the degree illustrated by Berry and Boucot (1972) in their model.

Depending on conditions, phytoplankton can live in the euphotic zone roughly up to a depth of 100—150 m. Small numbers of graptolite remains in shallow-water deposits suggest that the neritic and epipelagic environment is not suitable for graptolites in spite of the abundance of food (see also Erdtmann 1976 b).

The wave base depth varies from sea to sea: Anderson (1971) gives

a value of 5—15 m, while on the eastern shelf of the Caspian sea it reaches 25—45 m (see Nestor and Einasto 1977). This means that more than half of the euphotic zone is hydrodynamically comparatively quiet. Nevertheless graptolite remains in muddy-detritic deposits of open-shelf facies are rare.

The Silurian Paleobaltic Basin was a pericontinental sea on the margin of a very low, almost flat Fennosarmatian continent (see the facies analysis in Nestor and Einasto 1977; Kaljo and Jürgenson 1979). It is most probable that the sea floor was also gently sloping. According to Heckel (1974) the bottom dip in such basins ranges from 0.4 to 2 m. per 1 km. Taking into account the character of the continent we shall use for our calculations not the average but a little lower rate of inclination (0,8 m/km). The depth of the wave base will be taken as 25 m. According to our model this depth is the lowest limit of distribution of well-sorted grained limestones (sparities) of the shally facies (see figs 1, 2). Then, at the average width of the open-shelf facies belt (80 km according to Kaljo and Jürgenson 1977), the depth of the sea near the shelf margin would be estimated at 90 m (with a minimum inclination of 50 m and a maximum of 180 m — see Heckel 1974). This is somewhat below 133—140 m, the values presented on the average for the present day shelves (Fairbridge 1966, a.o.) but fully within the known variation range (20—600 m).

As stated above, fairly numerous graptolites remains begin to occur in the outer half of the transitional facies belt. Our facies model classifies that belt as a continental slope (Nestor and Einasto 1977), but we believe that this slope was not too steep either. It would suffice to have the seafloor dip twice as great as above (2 m/km) for the lower water layers in the middle of the transitional belt not to fit into the euphotic zone.

The increase of the number of graptolite remains on the rocks of the outer part of the transitional facies belt (see fig. 2) is accompanied by a considerable rise in the content of organic carbon which is as high as 7 and 18 per cent in the rocks of outer part and the basin facies respectively (Kaljo and Jürgenson 1977):

Pyrite is also common in these deposits. Similar data have fairly been published earlier (Bulman 1964; Erdtmann 1976 b, a.o.), we agree with the usual interpretation of these facts as an evidence of oxygen deficiency in the course of sedimentation in the near bottom layer. These is a further proof of this in that the role of benthic organisms decidedly decreases in the outer part of the transitional belt, while these organisms are almost entirely lacking in the basin facies.

There are no data at our disposal enabling us to determine the depth of the ocean within the basin facies belt; neither do we know the thickness of the near bottom layer of anaerobic water. However, the rapid increase in the abundance of graptolite remains in the facies belt, the depth of which reaches the aphotic zone, together with their scantiness in the

more shallow water deposits suggests that the bulk of graptolites dwelled in a comparatively deep-water environment of mesopelagic zone. The only exception were those specific forms which were able to live under the conditions of neritic shallow water or of epipelagic zone.

Such a conclusion accords well with the variation curve of a number of Ordovician and Silurian graptolite taxa presented by Rickards (1978). Certain minima of this curve (in particular at the Ordovician-Silurian boundary and at the level of the topmost Wenlock) coincide with periods of regression and with a considerable eustatic drop in sea level observed in many regions of the world.

The change in basin depth could not have influenced the living conditions of the animals inhabiting the surface water layer so greatly, neither could it have caused such a drastic decrease in their numbers as shown by Rickards. But for deep-sea (mesopelagic) animals to which we attribute graptolites the shallowing of sea was doubtless a fatal factor.

It should be remembered, as some authors think, that in the early Paleozoic the ocean was not as deep as it is now, and therefore even small changes were of great significance. Sheehan (1973) suggested, by analogy with the Pleistocene glaciation, that due to the late Ordovician glaciation the ocean level lowered by 100 m. Taking into account the comparative shallowness of the Early Paleozoic ocean, we must consider such a eustatic drop in the sea-level very great; this doubtless rather seriously affected the living conditions of mesopelagic graptolites.

I do not believe the shallowing of the seas to be the only factor which led to the extinction of graptoloids in the Devonian, but we should not neglect it either.

The above considerations and conclusions arise out of the study of the evidence as observed in the East Baltic areas. It is fully possible that other parts of the Early Paleozoic ocean and shelf could yield richer neritic graptolite assemblages. The East Baltic case however, cannot be explained logically enough unless we consider the majority of graptolites to be mesopelagic animals.

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