

GEOLOGICAL NOTES

Chitinozoan Contribution to the Ordovician and Lower Silurian Paleobiogeography¹

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ABSTRACT

Relationships between various Lower Silurian chitinozoan assemblages are established using statistical methods such as calculation of the number of species in common and similarity coefficient. Conclusions clearly indicate that Eastern Canadian chitinozoan fauna are distinct from those of the north Gondwana margin. The proposed relationships are refined by the use of more rigorous analytical techniques such as correspondence analysis and cluster analysis. The results are compared to the paleogeographic reconstructions available for the Ordovician and the Lower Silurian. They show that chitinozoans are useful not only for stratigraphic correlations, but also, as their paleogeographic distribution seems to be linked to paleolatitudes, they can be used to document plate tectonic dynamics.

Introduction

Palynologists are well aware of the fact that some widely separated contemporaneous chitinozoan assemblages are very similar while other assemblages that are proximal geographically to each other are very different. The existence of some widespread species in all chitinozoan assemblages allows long distance correlation and supports the idea that chitinozoans are valuable stratigraphic fossils and not subject to provincialism. On the other hand, some detailed studies have documented a facies control on isochronous chitinozoan assemblages which suggests that the facies are responsible when dissemblance occurs in assemblages of the same age (Laufeld 1974; Mannill 1972). This problem was encountered during a study of Ordovician chitinozoans from eastern Canada where, despite the existence of some species known elsewhere, the distinctiveness of the eastern Canada assemblages made close comparisons with other assemblages difficult. This led Achab (1988), from an empirical and also intuitive approach, to recognize that the geographic distribution of Ordovician chitinozoans was linked to paleolatitudes. A subsequent, more quantitative approach, using simple statistical techniques, such as the calculation of the number of common spe-

cies and the calculation of a similarity coefficient (Achab 1991), confirmed the distinction between the high latitude Ordovician microfaunas from the north Gondwana margin and the low latitude Laurentian and Australian microfaunas.

Paleobiogeographical studies of chitinozoa distribution are very few. Achab (1991) gives an overview of the literature on Ordovician paleobiogeography. For the Silurian, very few authors have elaborated on the chitinozoa provincialism. Laufeld (1979) concludes that the provincialism, on the generic level, is less pronounced in Silurian times than in the Ordovician. By comparing a Llandovery-Wenlock fauna from southern Ohio and northern Kentucky on the specific level with Baltoscandia, the Brabant Massif, Anticosti Island and Great Britain, Grahn (1985) concludes that provincial affinities exist between those faunas, while faunas from Spain (Cramer 1964) and North Africa (Taugourdeau and de Jekhowsky 1960) are dissimilar to those from southern Ohio and northern Kentucky.

The aim of this study is to perform a simple statistical comparison on Lower Silurian (Llandovery) chitinozoan microfaunas. The suggested links between the various regions during the Ordovician and the Lower Silurian are then tested and refined by using correspondence and cluster analyses.

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Data Selection

For a biogeographical study, the database should reflect the real time range of a species for a certain region, thus eliminating as much as possible the paleoecological control on presence or absence. Fortunately this paleoecological control on the distribution of chitinozoan is not very strong. Apart from their clear absence in certain conditions, like reefs (Laufeld 1974), chitinozoan fauna are present in a wide variety of sedimentary rock types. In open marine environments their abundance and diversity is more strongly controlled by the hydrodynamics than by the environmental factors. This led Paris (1981) to the conclusion that chitinozoan have a pelagic or epipelagic mode of distribution.

This led us to postulate that the total vertical distribution in a certain region, as compiled from all the studied sections and representing different environments, reflects to a great extent the true stratigraphical range of a species in that region.

Choosing relatively large time intervals eliminates the problems that arise with the detailed correlation of sections within a region and between different regions, and increases the number of species per region and per time interval, making the statistical treatment more reliable.

The three time intervals chosen for the Ordovician correspond to the North American Ordovician Series: Canadian, Champlainian, and Cincinnati, dividing the Ordovician in intervals representing more or less equivalent periods. The use of the sub-periods (Canadian, Dyfed and Bala) as proposed by Harland et al. (1989), would divide the Ordovician into very unequal intervals. The Lower Silurian in this study is equivalent to the Llandovery. This epoch is considerably shorter than Ordovician time intervals, but not enough data from Wenlockian strata are available for the moment to include them in this study.

The species were included in the database after a critical assessment of the taxonomy by the authors so that the species name may differ from the original assignments. The list of references used for each of the intervals is given in Appendix A, which is available from *The Journal of Geology's* Data Depository, free of charge upon request.

Comparison Techniques for the Lower Silurian

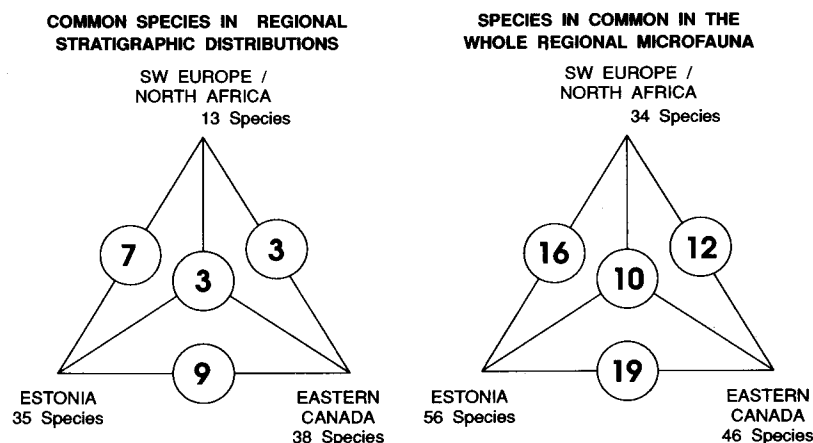
The previous comparison of Ordovician microfau- nas (Achab 1991) involved three increasingly precise calculations: (i) the calculation of the number of common index-species used in various regional zonations; (ii) the number of common species oc-

curing in the synthetic stratigraphic range charts of selected chitinozoan species, as established for different regions, and (iii) the number of common species counted when comparing the whole known regional microfauna. For this last comparison, all the regional information, even punctual, on chitinozoan microfaunas was taken into account.

The same three-step approach was applied to Lower Silurian chitinozoans. However, the first approximation based on index-species is only possible for Estonia and southwest China (Yangzi Region). The detailed regional zonation, proposed by Nestor (1990) for Estonia, has, for the Llandovery, only two species (*Angochitina longicollis* and *Conochitina emmastensis*) in common with the Yangzi Region regional zonation, proposed by Geng and Cai (1988). The calculation of common species occurring in synthetic range charts was performed on range charts available for southwest Europe and North Africa (Paris 1988), as well as for Estonia (Nestor 1990). A range chart for eastern Canada was compiled based on data available from Anticosti (Achab 1981), the Chaleurs Bay region in Gaspé (Asselin and Achab 1989), and more recent unpublished studies.

The calculation of the number of common species from the synthetic range charts and the whole regional chitinozoan microfaunas (figure 1) shows similar results. These results also corroborate those obtained for the Ordovician: The lowest number of common species are observed between assemblages of the north Gondwana margin (North Africa and southwest Europe) and those from Laurentia (eastern Canada). The Estonian microfauna, like that of Baltoscandia during the Ordovician (Achab 1991), has approximately the same number of common species with eastern Canada (Laurentia) and the southwest Europe and North Africa (north Gondwana margin).

This first attempt was complemented by a more precise and comprehensive comparison involving the calculation of the number of common species and the similarity coefficient between pairs of regions. An existing Ordovician Dbase-III database, supplemented with the information on Lower Silurian species, was used. The records include the name of the species, its stratigraphic distribution, the locality, the author name and the year of publication. The following available data were integrated: for eastern Canada, data from Anticosti (Achab 1981) and Chaleurs Bay (Asselin and Achab 1989); the Brabant Massif, Martin (1973), Verniers (1982) and Van Grootel (1990); for Podolia, Laufeld (1971); for Baltoscandia, Laufeld (1974), Nestor (1976, 1980a, 1980b, 1984, and 1990) and Grahn



LOWER SILURIAN

(1978); for North Africa and southwest Europe, Paris (1981 and 1988), Hill and Paris (1985), and Schweineberg (1987) and for the United States, Grahn and Bergström (1984, 1985) and Grahn (1985).

The calculation of the number of Lower Silurian common species and the Dice similarity coefficient was performed on this database. The results of the Lower Silurian are presented in table 1. The number of common species is indicated in the upper right half of the table, and the similarity coefficients are reported in the lower left half. In this matrix table, the higher numbers of common species, relative to total numbers of reported species for the respective regions, and the higher values of the similarity coefficient, suggest a close relationship between the two geographic regions considered.

From both the coefficient similarity matrix and the number of common species matrix, a potential relationship is inferred between Baltoscandia, eastern Canada, the United States, the Brabant Massif, and Podolia. In contrast, North Africa shows the lowest similarity with all these regions.

This approach by simple comparison, applied to Lower Silurian chitinozoans, confirms the results obtained for the Ordovician. The eastern Canada microfauna is distinct from that of the north Gondwana margin. It also indicates a potential link between the Brabant Massif, Baltoscandia, and Podolia.

Correspondence and Cluster Analysis

In order to quantify the postulated Ordovician and Lower Silurian links and to gain more precise information on the nature of the relationship obtained from the simple comparison techniques

Figure 1. The number of common species between SW Europe-North Africa, Estonia, and eastern Canada (sides of the triangles) and between the three regions (center) found in the regional stratigraphic distributions charts (left triangle) and the whole regional microfaunas (right triangle) for the Llandovery.

used above, correspondence analysis and cluster analysis were applied to our database. The correspondence analysis was performed directly on a raw data table, since this matrix is actually a contingency table where each value represents the presence (1) or absence (0) of a corresponding species in a corresponding region. The cluster analysis is done with the factor scores of the regions resulting from the correspondence analysis. This procedure ensures a better evaluation of distances between groups, a direct linkage between the distance representations of correspondence and cluster analysis, elimination of useless noise in the data and consequently, better segregation and clustering of the groups.

Correspondence Analysis. Correspondence analysis is a type of factorial analysis similar to principal component analysis. In addition to reducing the number of space dimensions of the data set, the correspondence analysis preserves the euclidian distances between both samples (species) and variables (regions) in the same space of reduced dimensions (Legendre and Legendre 1979). The dimension of this space is smaller than the mini-

LOWER SILURIAN	NORTH AFRICA	BALTO-SCANIA	EASTERN CANADA	BRABANT MASSIF	PODOLIA	UNITED STATES	COMMON SPECIES
NORTH-AFRICA	13	3	3	3	2	2	
BALTOSCANIA	0.170	23	8	7	4	6	
EASTERN CANADA	0.150	0.310	28	11	2	6	
BRABANT MASSIF	0.170	0.310	0.440	22	3	4	
PODOLIA	0.220	0.290	0.120	0.220	5	3	
UNITED STATES	0.190	0.390	0.330	0.270	0.460	8	
	DICE COEFFICIENT						

Table 1. Matrix combining the number of common species (upper right half) and the Dice similarity coefficient (lower left half) for the considered regions during the Llandovery.

mum size of the data set. Moreover, the location of each species in the multivariable space is at the barycenter of the regions; the reverse is true for a region being at the barycenter of the species. The barycenters are linearly related to the center of gravity of variables. This property is due to the fact that the data table analyzed is a contingency table. Regions that plot close together on the graph have higher assemblages affinities and vice versa. Also, species that plot close to a region can be considered as characteristic or endemic to that region, while species that plot in a position intermediate between two or more regions are common to these regions. The relative distances between the points representing species and those representing regions are proportional to the affinities between species which occur and characterize the areas. A great advantage of this procedure is that it eliminates the useless noise in the data without losing the essential information.

Cluster Analysis. Cluster analysis is a technique of automatic classification that separates heterogeneous data into consistent groups of more homogeneous characters and illustrates the affinities between these groups by means of a dendrogram. Similarity between groups is shown on the graph by smaller values at the knot value on the graduate scale.

The algorithm used for the aggregation of data is based on variance with inertia criteria. This approach is particularly suitable when the initial data were previously transformed in factorial coordinates by correspondence analysis (Lebard et al. 1979). Instead of looking for the nearest point in the reduced factorial space of the factorial analysis, the program aggregates pairs of data points in order to minimize the loss of inertia of the entire data set. Using correspondence coordinates, cluster analysis can also give the position of the dendrogram knots for plotting on the factorial plane, which makes the interpretation easier. The cluster analysis was performed on the first four factorial axes of the correspondence analysis.

The factorial and cluster analyses were performed on four intervals: Lower Ordovician, Middle Ordovician, Upper Ordovician, and Lower Silurian.

Lower Ordovician

Figure 2a shows the first factorial plane corresponding to 53% of variation of the correspondence analysis for the Lower Ordovician and illustrates the relationship between regions and species distribution. Regions and microfaunas can be lumped in

three groups. Group (1) includes the United States, Spitsbergen, Australia, and eastern Canada; group (2) is composed of Bohemia, North Africa, and southwest Europe; and group (3) contains only Baltoscandia.

Southwest Europe, North Africa, and Bohemia form a group with a large number of regional species represented by the three circles in close proximity on the factorial scattergram (figure 2a). Eastern Canada, Australia, the United States and Spitsbergen form another clear group, also characterized by a large number of regional species. Baltoscandia differs from the two groups because of its numerous endemic species. The distinctiveness of the three groups is emphasized by the low number of common species.

Cluster analysis (figure 3a), based on 78% of variation, also reveals three distinctive groups during the Lower Ordovician. The first one contains Bohemia, North Africa, and SW Europe, the second eastern Canada, the United States, Australia, and Spitsbergen. Although linked to the second group, Spitsbergen is less closely related in the dendrogram than in the factorial scattergram. This is because the factorial scattergram shows the variation of only two of the axes, instead of the four used in the cluster analysis.

Baltoscandia forms a third group; however, the distance between Baltoscandia and the two other groups is not much greater than the distance between those two groups.

Middle Ordovician

Figure 2b illustrates the relationship between the regions and the species distribution for the Middle Ordovician microfaunas. For this interval, the pattern is approximately the same as for the Lower Ordovician. Eastern Canada, the United States, and Australia still form a group with clear affinities separated from a second group composed of southwest Europe, North Africa, and Great Britain. The Baltoscandian assemblage is still isolated from both other regional groups, but there are now, compared to the Lower Ordovician, a higher number of species with an intermediate position between Baltoscandia and the two other groups.

Integrating a greater amount of variation than the principal plane of the correspondence analysis (47% of variation), the dendrogram, with 78% of variation, also suggests (figure 3b) that the groups are becoming closer on the diagram, or that the overall variation between the regions is decreasing. However, the three groups identified during the Lower Ordovician are still present, with a clear

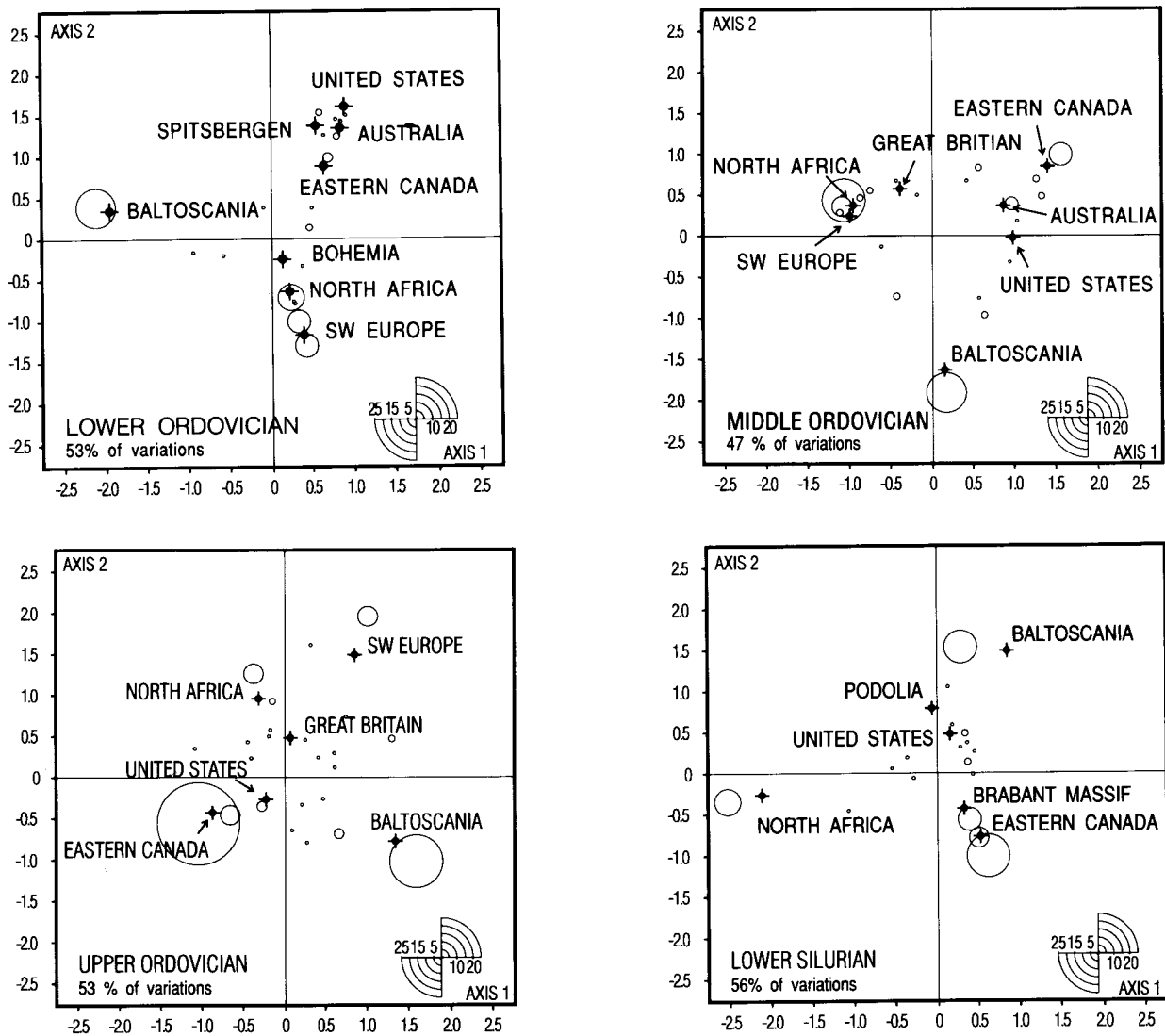


Figure 2. Distribution of the species (circles, proportional to the number of species) and the regions (crossed dots) of the principal plane, formed by the two first axes of the correspondence analysis for the Lower Ordovician (*a*), Middle Ordovician (*b*), Upper Ordovician (*c*) and the Lower Silurian (*d*).

link between eastern Canada, the United States, and Australia and between North Africa, southwest Europe, and Great Britain. The Baltoscandia assemblage now shows intermediate affinities between both groups, instead of its very isolated position in the Lower Ordovician.

Upper Ordovician

The Upper Ordovician scattergram also shows an increase of the number of common species in the various regions. It seems that now, the variation within the groups is as great as the variation between the groups. Nevertheless, elements of the

previous grouping persist (figure 2*c*), with a first group consisting of eastern Canada and the United States, a second including southwest Europe, North Africa, and Great Britain, and a third one corresponding to Baltoscandia, still in an isolated position.

The cluster analysis emphasizes the attenuation of the segregation between regions suggested by the correspondence analysis. The dendrogram (figure 3*c*) suggests that, except for the clear link between Great Britain and North Africa and that of eastern Canada and the United States, the clustering for the Upper Ordovician is more heterogeneous compared to that of the previous Ordovician intervals.

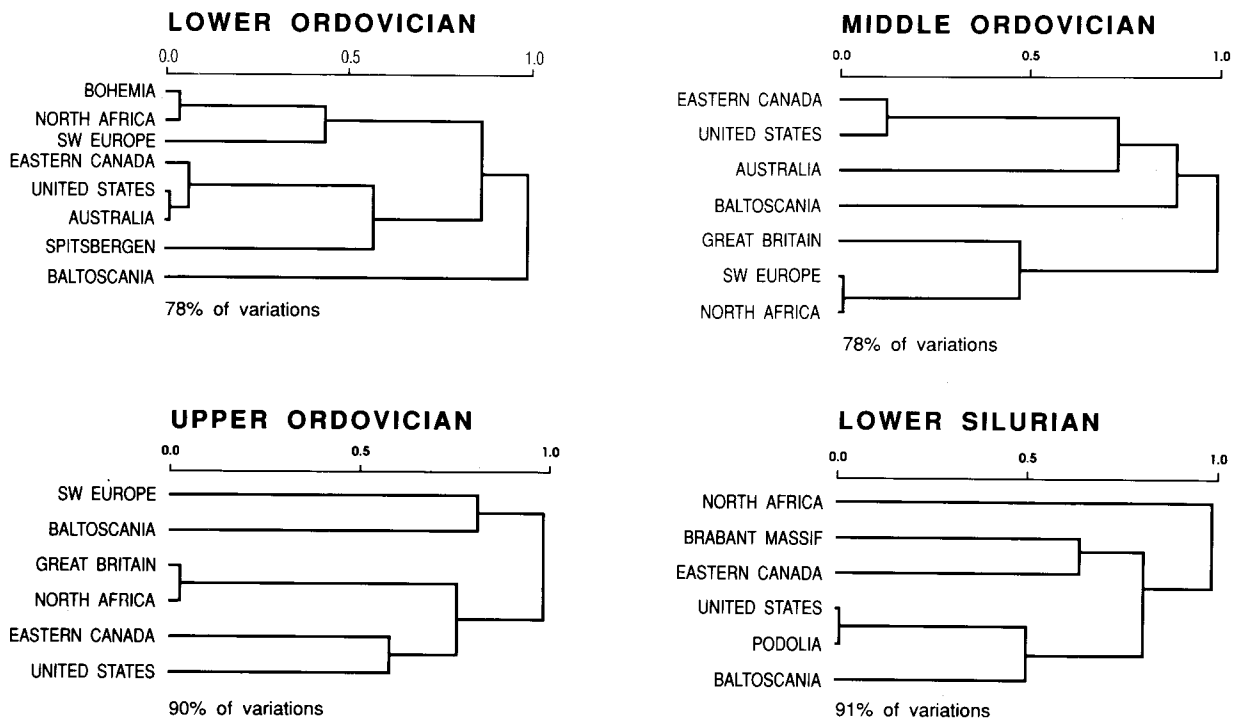


Figure 3. Dendrograms classifying the regions by their relative distances in the volume formed by the first four factorial axes for the Lower Ordovician (a), Middle Ordovician (b), Upper Ordovician (c) and the Lower Silurian (d).

Lower Silurian

In the Lower Silurian, the position of the regions on the factorial scattergram (figure 2d) differs noticeably from that observed during the Ordovician. Again, we can lump the microfaunas into distinct groups. A first one, clearly differentiated, corresponds to North Africa and occupies an isolated position. The second group, consisting of the Brabant Massif and eastern Canada, is not so clearly individualized from the third group, which includes the United States, Podolia, and Baltoscania. The last two groups share a large number of species, while only a limited number of common species are observed between these groups and North Africa. In other words, the variation within the regions of the two last groups is as important as that between them.

The cluster diagram (figure 3d) emphasizes the strong bipolar character of the factorial scattergram. North Africa is clearly separated from the cluster regrouping the Brabant Massif, eastern Canada, the United States, Podolia, and Baltoscania. In this latter group, Baltoscania, Podolia, and the United States are linked together, as are eastern Canada and the Brabant Massif.

Paleobiogeographic Significance

Correspondence and cluster analyses results obtained for the various intervals considered in this study show a clear segregation of Gondwana microfaunas from Lower Ordovician to Lower Silurian. Consequently, the results also support the northward shifting of Baltica from Lower Ordovician time, where it is very isolated on the scattergram (figure 3a), to the Upper Ordovician (figure 3c) and Lower Silurian (figure 3d), where the relation between Baltoscania and low latitude regions such as eastern Canada and the United States becomes closer. The upward displacement of Avalonia starting in the Early Ordovician and its subsequent collision with Laurentia (in the Early Devonian?) (McKerrow 1988) also seem to be documented here (figure 3b,c) by the gradual detachment of Great Britain in the Middle to Upper Ordovician from the North Africa-southwest Europe group, and by the integration of the Brabant Massif into the equatorial cluster during the Llandovery (Lower Silurian). Our study is not conclusive on the debate as to whether Avalonia and Baltica are two different plates, separated by the Thornquist sea (sensu McKerrow and Cocks 1986) or that Ava-

lonia is the southern extension of the Baltic plate (Paris and Robardet 1989; Robardet et al. 1990). However, the isolated position of Baltoscandia on the Ordovician scattergrams (figure 2a to c) and the closer relationship between Avalonia (Great Britain) and Gondwana (North Africa and SW Europe) during the Middle Ordovician does favor a separation between the Baltic and Avalon plates.

The similarity and links proposed for different regions and the clustering obtained are in fact mathematical manipulations of data. From a paleontological point of view, these results should have a paleoecological significance and so express the biogeographic distribution of the microfaunas and their respective regional specificity. Our results are compatible with the known geographic distribution of some chitinozoan assemblages. For example, for the Lower Ordovician, *Velatachitina* and *Eremochitina* faunas have only been reported from southwest Europe and North Africa, regions lying on the north Gondwana margin and occupying a high-latitude position (figure 4). During the same period, the *Fustichitina* genus was restricted to low latitudes. Thus, the statistical affinities between eastern Canada, the United States, Spitsbergen, and Australia on the one side and North Africa, southwest Europe, and Bohemia on the other, reflect their paleolatitudinal position.

The paleolatitudinal influence is also expressed during the Middle Ordovician. *Sophonochitina* is a characteristic north Gondwana genus while *Conochitina subcylindrica* and *Conochitina pirum* are species restricted to low latitudes and are reported from Laurentia and Australia (Achab 1988: figure 2).

The same is true during the Upper Ordovician, where *Armoricochitina nigerica* and *Calpichitina lenticularis* assemblages are well known from the north Gondwana margin, while *Hercochitina* species are abundant in Laurentian faunas (Achab 1988: figure 3). In the Lower Silurian, the strong dichotomy between two main groups of clusters is also expressed by *Pterochitina deichaii* assemblages, apparently restricted to high latitudes, and *Spinachitina maennili*, occurring in intertropical regions (figure 5).

Conclusions

Correspondence and cluster analyses performed on chitinozoan assemblages seem to be an interesting tool for the identification of regional chitinozoan microfaunas and the understanding of their paleogeographic significance. Chitinozoans appear to be useful not only for stratigraphic correlation, but also as a tool for documenting plate tectonic dynamics. The northward shifting of Baltica and the detachment of Avalon from Gondwana are demonstrated by their positions relative to the other regions on the scattergrams and clusters. By refining the chitinozoa stratigraphy and clearing the taxonomic problems that still exist, their paleotectonic usefulness can be significantly improved.

In this study, the choice of the species used to name the typical regional assemblages (e.g. *Velatachitina*, *Spinachitina maennili*) was subjective, based on our own experience. On the scattergram of the correspondence analysis, the chosen species fell within their clustered regions. However, it

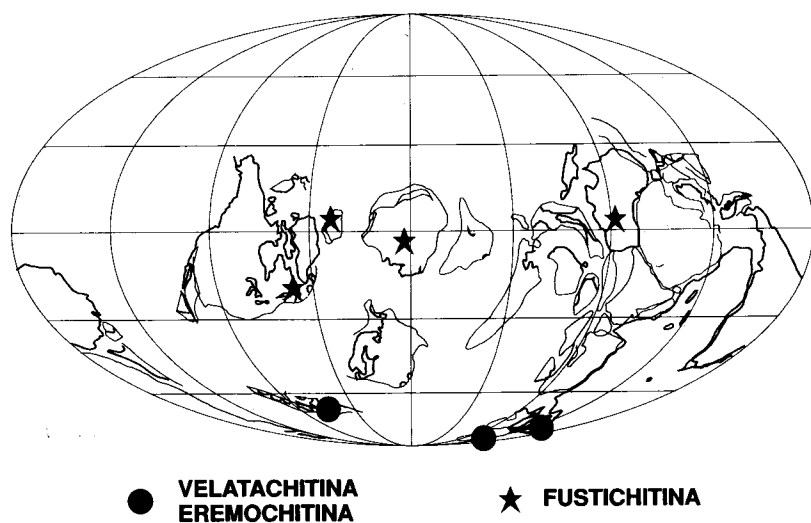
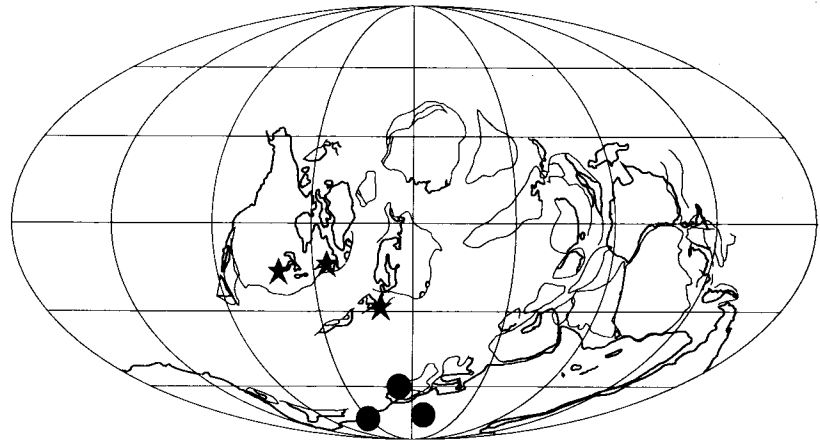


Figure 4. Distribution of Lower Ordovician chitinozoan assemblages characterized by *Fustichitina* and *Velatachitina-Eremochitina* (map after Scotese and McKerrow 1990).

Figure 5. Distribution of Lower Silurian chitinozoa assemblages characterized by *Pterochitina deichaii* and *Spinachitina maennili*. Map after Scotese and McKerrow (1990).



★ SPINACHITINA MAENNILI ● PTEROCHITINA DEICHAII

would be more objective to select the characteristic species by a statistical method. The plot of the different species on the scattergram of the correspondence analysis, as obtained for this study, can be a tool for this selection; however, the number of common species is too high and the choice will remain subjective. To reduce the number of potential characteristic species, facilitate the choice, and obtain the most representative and characteristic species, the statistical method to be used must take into account the relative abundance of the various species in an assemblage and their stratigraphic range. These two parameters can be incorporated in the database and weighted to better characterize chitinozoan assemblages and thus get

a better segregation of microfaunas and their characteristic components.

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