

LATE DEVONIAN TO DINANTIAN OSTRACODES (COMMENTS ON TAXONOMY, STRATIGRAPHY AND PALEOECOLOGY)

by

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(3 figures)

ABSTRACT. - Three groups of marine ostracodes are distinguished which characterize different sedimentary environments in the late Devonian and early Carboniferous. Despite their undisputed stratigraphical significance Entomozoaceans have been described as yet mainly from isolated localities or from incomplete sequences. The distribution of *Thuringian*-type ostracodes seems strongly controlled by the paleoenvironment. The same appears to be true for the benthic ostracode assemblages in shelf deposits. Preliminary attempts suggest that it may be possible to distinguish a number of late Devonian and Dinantian ostracode provinces. However, the boundaries between the same may be rather flexible in time and space.

RESUME. - Trois groupes d'ostracodes marins peuvent être distingués, chacun caractérisant un environnement sédimentaire différent au Dévonien tardif et au début du Carbonifère. En dépit de leur signification stratigraphique indiscutable, les Entomozoacées ont été décrites jusqu'ici surtout dans des localités isolées ou des séquences incomplètes. La distribution des ostracodes de type-Thuringien semble fortement contrôlée par le paléoenvironnement. Il en est de même des assemblages d'ostracodes benthiques dans les dépôts de plateforme. Des tentatives préliminaires suggèrent qu'il est possible de reconnaître plusieurs provinces d'ostracodes tardi-dévoniennes et dinantiennes. Cependant, les frontières qui les séparent sont peu précises dans le temps et dans l'espace.

INTRODUCTION

A review of our actual knowledge on late Devonian to early Dinantian ostracodes may produce quite contradictory feelings. On the one hand, there is the still increasing flood of papers on the subject, notably during the past two decades, as was already observed by Malz (1975). This may induce a false euphoria that the available data allow worldwide interpretations and applications. On the other hand, there is the repeatedly published opinion (cf. Sohn & Jones, 1984) that we have still a long way to go before final conclusions might be made. A broad-brush survey based on some recent review papers shows three main fields of interest amongst ostracodologists: taxonomy, stratigraphy and paleoecology/paleobiogeography. The present report is not meant as an exhaustive analysis of the actual state of affairs within each of these fields, but rather as a subjective anthology of some trends in the study on late Devonian and early Dinantian ostracodes.

TAXONOMY

The principal guides for a more or less uniform classification of ostracodes are the USSR Treatise on Ostracoda (Orlov, ed. 1960) and the (American) Treatise on Invertebrate Paleontology, Part Q, Ostracodes (Moore, ed. 1961). The classifications adopted in these publications show many differences, as partly explained by Moore (1961: Q422-Q429). Since then, important additional work has been realized. At present, two working groups intend to prepare completely revised volumes on ostracode classification, one on Paleozoic

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ostracodes and one on Post-Paleozoic ostracodes. However, several more years of painstaking studies will be needed before these revisions are published. Amongst the many new entities of ostracodes discovered and described since 1961 in the Devonian and Carboniferous are the usually silicified, "Thuringian-type" ostracodes. These are characterized by many genera and families with a strongly spinous carapace, which have been investigated by a.o. Gründel (1961, 1962) and Blütenstengel (1965) in the Upper Devonian and early Dinantian of Thuringia (German Democratic Republic). Also of some importance for ostracodologists is the repeatedly raised question, whether the genus *Cryptophyllus* (included in the palaeocopid family Leperditellidae in Moore, 1961) is really a true ostracode or not.

The application of new techniques such as the electron scanning microscope has enabled the detection of more details and a more refined definition of species and genera. However, Neale's (1978) statement concerning Cretaceous ostracodes that the generic criteria have become tenuous and that the generic assignment of species seems to change almost daily may be true to some extent also for Paleozoic ostracodes. Moreover, two groups of ostracodologists may be distinguished with quite opposite feelings about the possibility to identify unambiguously many smooth-shelled ostracodes such as Bairdiaceans. One group (including many Soviet specialists and Western European workers such as Coen, Crasquin & Lethiers) claims that the Bairdiacean carapace exhibits enough criteria for a sound and useful specific identification permitting long-distance and even intercontinental correlation. The other group (including a.o. Bless, Groos-Uffenorde, Jones & Sohn) suggests that distinctive carapace features are generally lacking in Bairdiacean ostracodes. Since accurately identifiable ostracode taxa form the basis for a meaningful biostratigraphic zonation and correlation, universally accepted criteria for identification of such taxa are needed.

BIOSTRATIGRAPHY

Actually, three groups of marine ostracodes are frequently used in late Devonian and early Dinantian stratigraphy. These are the Entomozoaceans with their characteristic fingerprint-like ornamentation; the "Thuringian-type" ostracodes including many forms with a rather spinous carapace; and a wide range of benthic ostracodes occurring in marine shelf deposits varying from open marine to brackish or hypersaline lagoonal facies. Often, these ostracode assemblages are treated separately in the literature. Therefore, the same procedure is followed here.

ENTOMOZOACEAN OSTRACODES

A zonation with entomozocean ostracodes was established by Rabien (1954) in the hercynian Upper

Devonian of the eastern part of the Rhenish Schiefergebirge, Germany. The early Upper Devonian (do I, *Manticoceras* stage) had been subdivided into eleven entomozocean zones (Rabien, 1970) characterized by *Ungerella*, *Bertillonella* and *Entomoprimitia* species. In contrary to this subdivision the entomozocean zonation of the late Upper Devonian (do II - VI, *Cheiloceras* to *Wocklumeria* stage) is less detailed. The zonation in the late Upper Devonian was named by Rabien (1954) after typical entomozocean genera and subgenera. Meanwhile this zonation was slightly modified and named after entomozocean species (synopsis in Buggisch, Rabien & Hühner, 1978 : 109). Only the *sigmoidale* Zone (Raith, 1968) and the *hemisphaerica-dichotoma* Zone are total range zones. The extinction of the typical early Upper Devonian (do I) *Entomoprimitia* species lies within the lower *sigmoidale* Zone slightly above the recently proposed top of the Frasnian. The first occurrence of the typical early Famennian *Entomozoe* species of the *serratostrinata-nehdensis* group within the upper *sigmoidale* Zone is above the recently proposed base of the Famennian. This remarkable change within the entomozocean faunas coincides with the boundary of the *Manticoceras/Cheiloceras* stage, whereas the Frasnian/Famennian boundary at the base of the Middle *Palmatolepis triangularis* Zone lies most probably within the *splendens* Zone. The first occurrence of the late Upper Devonian *Richterina* species, mainly *Richterina (Richterina) striatula* and a few *Richterina (Fossirichterina)* marks the base of the Upper *serratostrinata-nehdensis* Zone (= *serratostrinata/intercostata* Zone *sensu* Rabien, 1970). The late Famennian zonation of Rabien (1954) was enlarged by the *hemisphaerica/dichotoma* Interregnum of Rabien (1960) (supported e.g. by Groos-Uffenorde & Uffenorde, 1974 and Bless & Groos-Uffenorde, 1984 : 26 but doubted in Thuringia by Bartzsch & Weyer, 1980 : 41-42).

Because of the lack of favourable sections besides the Stockum trenches/Rhenish Schiefergebirge the recently proposed Devonian-Carboniferous boundary between *Siphonodella praesulcata* and *Si. sulcata* cannot be exactly correlated by entomozocean ostracodes. But the conodont boundary seems to be near the base of the *laticornis* Zone of the Rhenish Schiefergebirge (see Groos-Uffenorde, 1984 and Bless & Groos-Uffenorde, 1984). The Lower Carboniferous entomozocean assemblages contain new entomozocean species but no remarkable change took place. Even the typical early Upper Devonian genus *Ungerella* occurs again in the lowermost Carboniferous of the Rhenish Schiefergebirge and Southwest England.

Even if their pelagic mode of life is questioned (Gooday, 1983 : 758-760) Entomozoacea have a worldwide distribution within (hemi)pelagic sediments and rich entomozocean faunas have not been reported from nearshore facies or shallow water deposits.

Upper Devonian entomozocean ostracodes have

L. Carb.	SDS	Amm. Z.	"Stages "	RABIEN 1954		Entomozoacean Zones		Conodont Zones				
Upper Devonian	Famennian	cd I					<i>latior</i>		<i>sulcata</i>			
		do VI	Wocklum	Jüngere <i>Maternella</i> -Zeit			<i>hemisphaerica/latior</i> Interregnum		<i>praesulcata</i>			
		do V	Dasberg	tdo + tw		U	<i>hemisphaerica</i>	U	<i>expansa</i>			
		do IV	Hemberg	Ältere <i>Maternella</i> -Zeit bzw. Jüngere <i>Fossirichterina</i> -Zeit		L	<i>-dichotoma</i>	U	<i>postera</i>			
		do III		Ältere <i>Fossirichterina</i> -Zeit			<i>intercostata</i>	U	<i>trachytera</i>			
		do II	Nehden	α β	<i>Entomozoe</i> -Zeit				U	Uppermost		
	post							L	<i>serratostrata</i> <i>-nehdensis</i>	U	<i>marginifera</i>	
	Frasnian	do I	δ	Adorf	tn				U	<i>rhomboidea</i>		
					tao 5				L	<i>sigmoidale</i>	U	<i>crepida</i>
					tao 4					<i>splendens</i>	U	<i>triangularis</i>
					tao 3					<i>reichi/splendens</i> Int.	M	Uppermost
					tao 2					<i>reichi</i>	L	Upper
tao 1									<i>schmidti</i>	sarteneri	gigas	
tam					<i>volki</i>	Lower						
					<i>materni</i>							
						<i>barrandei</i>						
						<i>cicatricosa / barrandei</i> Interregnum						
						<i>cicatricosa</i>						

Figure 1. - Zonation with Upper Devonian entomozoacean ostracodes of Rabien 1954 and Buggisch, Rabien & Hühner (1978 : 109) compared with the conodont zonation of Ziegler & Sandberg (1984 : 180).

The base of the *intercostata* Zone (lower coarsely dashed line) is drawn after unpublished results of A. Rabien (letter of April 1985).

often been found as external and internal moulds in shales (e.g. Rabien, 1954, 1970; Müller-Steffen, 1966; Gooday, 1974, 1978). Because of the abundance of the so-called fingerprint ostracodes the facies had formerly been called "Cypridinenschiefer". But nevertheless Entomozoacea have been described from limestones (e.g. Rabien, 1954; Langer, 1973; Olempska, 1979) and especially the two Kellwasser Limestone horizons (Frasnian) may be distinguished by their different entomozoacean ostracodes. Occasionally silicified or pyritized Entomozoacea have been etched from limestones (e.g. Blumenstengel, 1965; Tschigova, 1977; Becker, 1977, 1982; Olempska, 1979). In weathered nodular (cephalopod) limestones the Entomozoacea may be preserved as external and internal moulds, but little attention has been paid to them.

The occurrences of Upper Devonian and Lower Carboniferous entomozoacean ostracodes have been summarized by Groos-Uffenorde (1984 : 213). Despite the undisputed stratigraphical value of the Entomozoacea only a few continuous entomozoacea-bearing sequences have been described and unfortunately many

of the rich Entomozoacean faunas have been reported from isolated localities (e.g. North America, Spain, France, Belgium, Poland, USSR). But current investigations of Wang Shang-qi will prove the great abundance of entomozoacean faunas and a complete record of the German Upper Devonian entomozoacean zonation in South China.

At the moment no complete sequence with a great abundance of Entomozoacea seems to be available to correlate exactly with the recently proposed (but not yet decided) boundaries of the Famennian defined by conodonts (SDS boundaries see fig. 1). This is not only partly due to the unfavourable facies conditions and missing favourable sections but also due to the lack of detailed investigations. It is necessary to look for additional boundary sections containing at least conodonts and Entomozoacea to promote detailed stratigraphical studies at the same time by different specialists.

THURINGIAN-TYPE OSTRACODES

These ostracode assemblages are characterized

by many (mainly Podocopid) taxa with a spinous carapace. Typical representatives are a.o. *Orthonaria*, *Rectonaria*, *Rectoplacera*, *Processobairdia*, *Ceratacratia*, *Tricornina* and *Saalfeldella*. Presumably, these preferred rather calm offshore waters, which may have been relatively deep (Bandel & Becker, 1975; Blumenstengel, 1975). Accompanying fossils are conodonts, cephalopods (and sometimes crinoids). Thuringian-type ostracodes are frequently recovered as silicified specimens from (nodular) limestones (e.g. Blumenstengel, 1965; Becker, 1982). But these also occur (often as poorly identifiable impressions) in marly or silicified shales (e.g. Sanchez de Posada, 1973; Jordan & Bless, 1970). They may occur together with Entomozoaceans (Bless, 1983) or with ostracodes of the deeper offshore shelf (Dreesen *et al.*, 1985).

Thuringian-type ostracodes have been described from many places throughout the world. However, biostratigraphic zonations of Upper Devonian strata based on these microfossils have only been proposed for Thuringia in the German Democratic Republic (Blumenstengel, 1965) and for the Cantabrian Mountains in Northern Spain (Becker, 1982). In both cases, the age of the ostracode assemblages was checked by conodonts.

The original ostracode zonation for the late Devonian of Thuringia is partly based on assemblages and not always on the ranges of individual species (Blumenstengel, 1965). Later studies revealed that the range of many species is longer than had been accepted before (Blumenstengel, 1979). The late Devonian ostracode assemblages of Northern Spain are roughly comparable to those of Thuringia (Becker, 1982). But detailed correlations (based on Thuringian-type ostracodes) between these two areas are only possible for the late Frasnian (do I), but not for the Famennian (do II - do VI). Noteworthy is the observation in Becker (1982) that many species appear later in the Cantabrian Mountains than in Thuringia, although exceptions are known where the reverse is true. This matches a similar trend observed by Bless, Bouckaert & Paproth (1986) for Carboniferous Thuringian-type ostracodes and Kulm-type trilobites. The latter authors noticed that for example rectonariid ostracodes disappear later in the Paleotethys realm (in the Namurian) than in Northern Europe (in the Viséan). The same happens with the Kulm-type trilobite genus *Archaeogonus*, ranging until late Viséan in Northwestern Europe and into the Westphalian of Spain (Gandl, 1977, 1980).

Summarizing these observations we must conclude that the distribution of Thuringian-type ostracode assemblages is strongly controlled by the paleo-environment. They may serve for detailed correlations within a basin (cf. Becker, 1982), but should be treated with care when long-distance correlations are envisaged.

MARINE SHELF OSTRACODE ASSEMBLAGES

Relatively thick-shelled, benthic ostracodes predominate in the marine shelf deposits of the Devonian and Carboniferous. Attempts have been made to define these assemblages with the term "Eifelian type" for the Devonian (Bandel & Becker, 1975; Gooday & Becker, 1979) and with the term "assemblages with Bairdiacea and Paraparchitacea" for the Dinantian (Crasquin, 1984b). This doesn't imply a stratigraphic value for the same. As already indicated by Becker (1982), Eifelian type assemblages also occur in the (Upper) Carboniferous, their main characteristics being the relatively large number of Palaeocopids, Platycopids and Metacopids. Also Bairdiacean-Paraparchitacean assemblages are not restricted to the Dinantian. For example Sohn (1975) described similar associations from the Lower Permian of the USA. Maybe, Eifelian type assemblages indicate more turbulent (high energy) subtidal to intertidal environments, whereas Bairdiaceans and Paraparchitaceans preferred a rather quiet (low energy) facies? Whatever may be the correct solution, there is no doubt that marine shelf ostracode assemblages underwent drastic changes in their composition near the Devonian-Carboniferous boundary (Tschigova, 1977; Lethiers *et al.*, 1986). However, it is extremely difficult to define this boundary by using some worldwide occurring marker species.

Apparently, the first and last occurrences of any species differ from area to area, and often even from location to location, because of variations in the depositional environment (Bless & Groos-Uffenorde, 1984). Frequently, the marine shelf ostracode assemblages exhibit a high degree of endemism. This may be exemplified by the study of Lethiers (1981) on the Late Devonian of Western Canada. About 82% (61 species) of the 74 species (Entomozoaceans excluded) listed by that author for the Famennian-Strunian of Western Canada is restricted to that area (Lethiers, 1981, table 14 and remarks on species distribution in text). Twelve of these 61 species (16%) show affinities with species elsewhere (Lethiers, 1981, fig. 66) of about the same age. These might be considered as belonging to species groups.

However, detailed comparison between the stratigraphic ranges of those species also recognized outside Western Canada (13 out of 74 species, or 18%) and of the 12 species groups shows significant differences (Figs. 2 and 3). Usually, these ostracodes appear earlier and/or disappear earlier in Western Canada than in other regions. Also remarkable is the fact that seven species disappearing at the end of the Famennian or during the (early) Strunian in Western Canada only seem to appear somewhere in the basal Dinantian elsewhere. Seven more species disappearing during the Famennian-Strunian in Western Canada range from the Famennian into the Dinantian elsewhere. This suggests that a certain number of species (according to

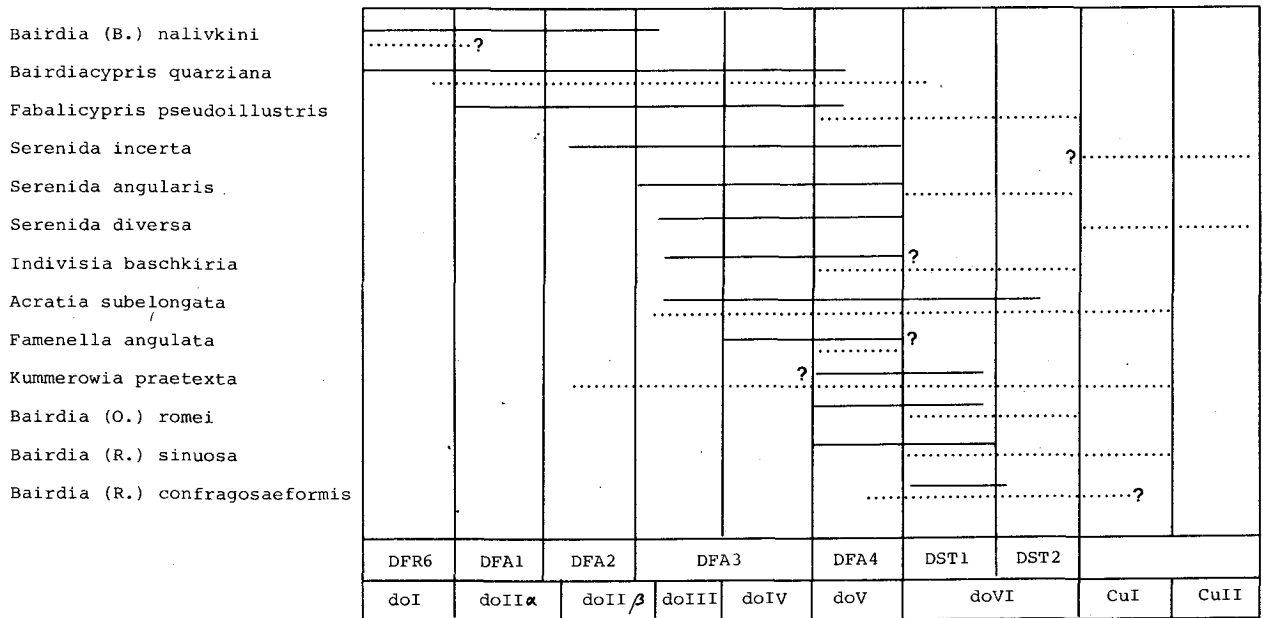


Figure 2. - Stratigraphic ranges of ostracode species in Western Canada (full lines, upper zonation) and elsewhere (stippled lines, lower zonation) from Lethiers, 1981.

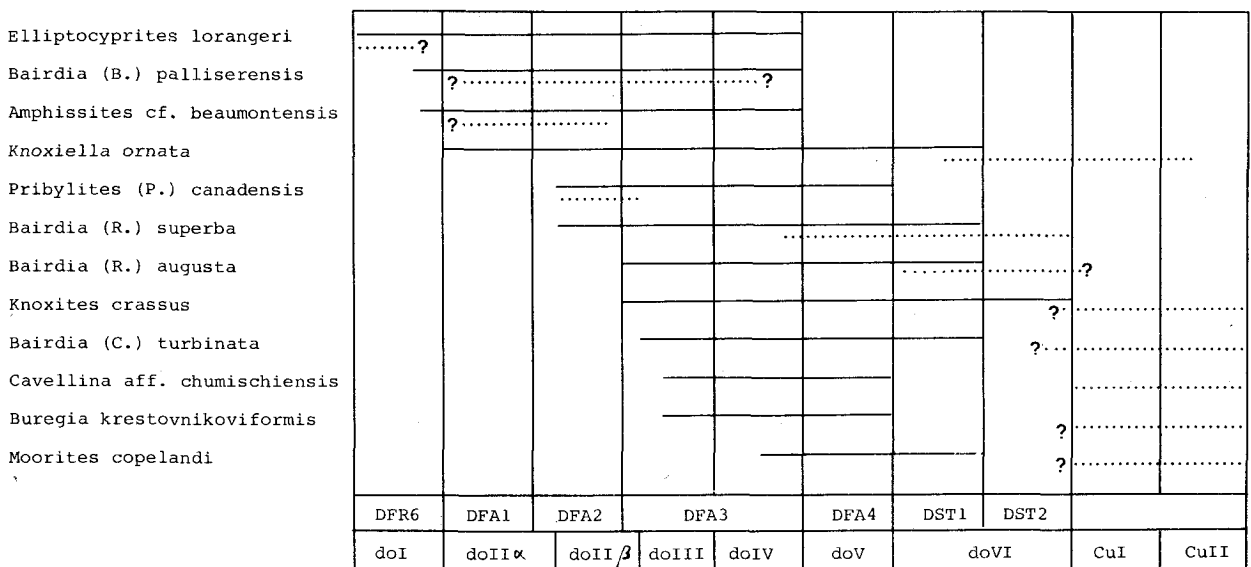


Figure 3. - Stratigraphic ranges of ostracodes in Western Canada (full lines, upper zonation) compared with those of closely related species (belonging to same species group ?) elsewhere (stippled lines, lower zonation) after Lethiers, 1981.

the Canadian example some 20 % or 14 out of 74) crosses the Devonian–Carboniferous boundary, albeit not in the same area because of changes in the regional environment.

These observations are not new, nor are these restricted to Western Canada. Similar remarks have been published on the distribution of the genus *Cryptophyllus*. The top of the epibole of *Cryptophyllus* more or less matches the top of the Strunian in Canada, Northwestern Europe and the Russian Platform, whereas rare specimens range into the Middle Tournaisian of Northwestern Europe (Crasquin, 1984a). However, *Cryptophyllus* is a common element in the Dinantian (Tournaisian and Visean) assemblages of Australia, Iran and North Africa (Bless, Bouckaert & Paproth, 1986). Maybe, there is a general trend in these heterochronic appearances and disappearances insofar as these seem to be earlier in northern paleolatitudes and later in more southern paleolatitudes, thus matching the northward shift of the Euramerican Old Red Continent?

The conclusion might be that at least long-distance correlations of Late Devonian strata based on marine shelf ostracode assemblages should be confirmed by those based on other fossil groups.

PALEOECOLOGY – PALEOBIOGEOGRAPHY

The relation between Devonian–Carboniferous ostracode assemblages and the sedimentary facies has been discussed by many authors, e.g. Bandel & Becker (1975), Lethiers (1981), Bless (1983) and Crasquin (1984a). Their publications have yielded the widely recognized distinction between Entomozocean assemblages, Thuringian type assemblages and marine shelf assemblages. Within the complex group of marine shelf assemblages several smaller entities may be distinguished characterizing the quiet (deep ?) offshore shelf (comprising a.o. the assemblages with Bairdiacea and Paraparchitacea sensu Crasquin 1984a), the more turbulent (shallow) nearshore shelf (comprising a.o. the Eifelian type assemblages sensu Bandel & Becker, 1975) and the brackish-water (deltaic, estuarine) and hypersaline (lagoon) environments. Brackish-water and hypersaline deposits are marked by the occurrence of rather monotonous ostracode assemblages, including only one or a few species. Some species of *Cryptophyllus* and *Beyrichiopsis*, and some Paraparchitacea and Kloedenellacea seem to have favoured brackish-water environments during the late Devonian and Dinantian (e.g. Robinson, 1978; Bless, 1983; Dewey, 1983; Crasquin, 1984b).

Recognition of these assemblages and their dependence on sedimentary facies is a must for a reliable reconstruction of paleobiogeographic maps and of possible migration routes. This has been emphasized also by Robinson (1978) and by Sohn & Jones (1984) in advocating that like should be compared only with

like. This field is still rather unexplored, pioneers being Lethiers (1983) for the late Devonian and Crasquin (1984a) for the Dinantian ostracodes. Analysis of the ostracode provinces proposed by these authors and of the existent literature stresses the importance of comparing like only with like. For example, the distribution of *Graphiadactyllis* may point to a special environment rather than to provincialism. Indeed, *Graphiadactyllis* assemblages are characteristic for the Lower Tournaisian deposits of the Appalachians in North America where Lethiers (1983) and Crasquin (1984a) created a *Graphiadactyllis* province. But these occur also in the Upper Tournaisian of Northwestern Europe (20–60 % Quasillitacea in the ostracode assemblage of Rügen; cf. Blumenstengel, 1975; Gründel, 1975), and in the Chesterian of Illinois (Cooper, 1941).

Similar observations might be made for *Serenida*. This genus characterizes the (Famennian) *Serenida* province roughly covering North America (except for the Appalachians), the Russian Platform and Western Siberia (Lethiers, 1983). However, the two species claimed to have the most widespread distribution within this province (*S. incerta* and *S. diversa*) may not occur simultaneously in Western Canada and Western Siberia. In Canada, these are restricted to the Upper Famennian (disappearing at the base of the Strunian) whereas these are perhaps limited to the basal Dinantian in Siberia (Lethiers, 1981).

Also the appearance of the Paraparchitacean genera *Shishaella* and *Shivaella* is not synchronic in Western Canada, Northwestern Europe, the Russian Platform and Siberia. In Canada, these only appear at the end of the Lower Tournaisian (Crasquin, 1984a) whereas these are absent in the Strunian of that area (Lethiers, 1981). In the other areas *Shishaella* and *Shivaella* appear in the early Strunian (e.g. Tschigova 1977; Becker & Bless, 1974; Barskov *et al.*, 1984) or maybe even in the Upper Famennian of France.

The above examples suggest that the contents of the Famennian and Dinantian ostracode provinces and also the boundaries between the same were highly flexible because of heterochronic changes in the regional or even local environments. This doesn't detract any merit from the work realized by Lethiers (1983) and Crasquin (1984a). Their papers will serve as a basis for further research and discussions.

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