| Senckenbergiana lethaea | **80** | (2) | 555 – 566 | 6 Text-figs, 1 Tab. | Frankfurt am Main, 29.12.2000 |
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# Progress in mid Palaeozoic palaeoceanographical studies from Ostracoda - from local to global importance (a review)

With 6 Text-figures and 1 Table

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Lecture given at the occasion of the 13th International Symposium on Ostracoda, University of Greenwich, Chatham/Kent (UK), 28th-31st July, 1997 (ISO97).

## Abstract

A review is given of some thirty years research effort on the palaeoecology of marine Palaeozoic ostracods. From papers presented to relevant International Symposia on Ostracoda (ISO), the progress in this field is shown – step-by-step.

From various localities in the northern Eifel region characterised by ecologically important macrofossils (stromatoporids, corals, crinoids, brachiopods and pelecypods), distribution patterns of Middle Devonian ostracod faunas were calculated and compared with data given for Recent ostracods (ISO70).

Encouraged by the far-reaching conformity, a palaeoecological model of general validity was drafted in which the distribution of marine Palaeozoic ostracods is controlled by water energy (correlated with sedimentation). Three ecotypes had been distinguished: (1) the diverse, shallow-water Eifelian Ecotype, dominated by diverse, thick-shelled and sculptured ostracod assemblages, indicative of high-energy environments; (2) the rather monotonous Thuringian Ecotype, consisting of thin-shelled species with smooth but often delicately spinose valves, characteristic of low-energy environments; and (3) the Entomozoacean Ecotype, exclusively formed by (hemi)pelagic finger-print ostracods. At certain positions (e. g. the deeper slope) mixed faunas may have occurred. Subsequently, the first approach of local applicability was expanded to the Variscan belt and the model, considered from the beginning to be energy-related, was extended from local to global importance, applicable from Ordovician to Triassic (with some reservation also to Jurassic); entomozoaceans are restricted to the upper Palaeozoic (ISO76).

The Thuringian Ecotype, first applied to the basinal settings, was subsequently found to be generally indicative of calm-water conditions (considered to be roughly independent of the palaeogeography) and is, therefore, not exclusively basinal. Logically, a method was presented to classify distinctive biotopes in the low-energy realm in more detail. Specifically biotope indicative forms, i. e., rare specimens of erratic species migrated from adjacent (e. g. shallow-water) environments, are considered to be indicators of distinct positions with respect to (relative) depth and distance from the sediment sources (ISO89).

The method of erratic species was applied to event stratigraphy (Hangenberg Event, near the Devonian-Carboniferous boundary) (ISO94).

Subsequently, so-called Subecotypes (mixed assemblages of the Eifelian and the Thuringian ecotypes) are shown to be useful to distinguish ultra-, normal- and relatively shallow-basinal environments as well as peribiohermal- and epineritic-shallow water environments. In biostratigraphy, the very complex Eifelian Ecotype plays a rather modest part (only of regional or even local value). In contrast, the Thuringian Ecotype (first considered to be endemic) is delivering a biostratigraphy comparable with the entomozoid zonation and is of global importance (ISO97).

Key words: Ostracoda, palaeoecology, palaeoceanography, mid Palaeozoic, Europe.

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## Kurzfassung

[Fortschritte in mittelpaläozoischen paläoozeanographischen Ostracoden-Untersuchungen – von lokaler bis globaler Bedeutung (ein Rückblick).] — Untersuchungen in drei Jahrzenten zur Paläökologie mariner paläozoischer Ostracoden werden summiert, die Fortschritte anhand von Vorträgen des Verfassers, gehalten auf einschlägigen Tagungen („International Symposia on Ostracoda", ISO), belegt – Schritt für Schritt.

Verteilungsmuster mitteldevonischer Ostracoden-Faunen, entnommen an durch ökologische Charakterformen (Stromatoporiden, Korallen, Crinoiden, Brachiopoden und Muscheln) gekennzeichneten Lokalitäten der nördlichen Eifel, werden mit entsprechenden Beispielen rezenter Ostracoden verglichen (ISO70).

Ermutigt durch die weitgehende Übereinstimmung von fossilem und rezentem Bild, wird das paläökologische Modell der Verbreitung mariner paläozoischer Ostracoden skizziert, wonach der Wasserbewegung nach Art und Stärke (korreliert mit der Sedimentation) die Bedeutung des "ausschlaggebenden Umwelt-Faktors" zukommt. Drei Ökotypen werden unterschieden: (1) der Eifeler Flachwasser-Ökotyp, dominiert von diversen Ostracoden-Vergesellschaftungen, dickschalig und mannigfalig skulptiert und damit Hochenergie-Bedingungen anzeigend; (2) der eher monotone Thüringer Ökotyp, aus dünnschaligen, vornehmlich glatten, aber häufig zart und bizarr bestachelten Arten bestehend und damit charakteristisch für niedrig-energetige Milieus; und (3) der Entomozoen-Ökotyp, ausschließlich (hemi)pelagische „Fingerprint"-Ostracoden; an bevorzugten Stellen (z. B. tieferer Kontinental-Abhang, Slope) können „Mischfaunen" auftreten. Folglich wird das erste Konzept lokaler Anwendbarkeit auf die Variszische Geosynklinale ausgedehnt, wonach das von Anfang energiebezogene Modell nunmehr weltweit anwendbar vom Ordovizium bis in die Trias (mit Einschränkungen sogar bis in den Jura) ist; die Entomozoen bleiben auf das Jung-Paläozoikum beschränkt (ISO76).

Der zunächst im Becken festgestellte Thüringer Ökotyp war inzwischen als generelles Indiz für Stillwasser-Verhältnisse erkannt worden (d. h. in erster Näherung unabhängig von jeglicher Paläogeographie), ist somit nicht ausschließlich basinal. Konsequenterweise wurde nach Möglichkeiten der Untergliederung im niedrig-energetischen Bereiche gesucht und die Methode der „specifically biotope indicative forms" entwickelt, wonach seltene Vertreter „erratischer Spezies" Hinweise auf benachbarte Biotope, z. B. flach(er)es Wasser, geben und damit Anhaltspunkte für bestimmte Postionen zur Paläo-Küste sind (ISO89).

Die Methode der „erratischen Spezies" wird bei event-stratigraphischen Untersuchungen (Hangenberg-Event, nahe der Devon/Karbon-Grenze) angewendet (ISO94).

Hieran schließt an die Methode der „Subökotypen" („Mischfaunen" des Eifeler und Thüringer Ökotyps) zur Unterscheidung von ultra-, normal- und verhältnismäßig flacher basinaler als auch peribiohermaler und epineritischer Bereiche. Während der sehr komplexe Eifeler Ökotyp stratigraphisch eine eher untergeordnete Rolle (von nur regionaler oder gar lokaler Bedeutung) spielt, eröffnet der (ursprünglich für endemisch gehaltene) Thüringer Ökotyp eine im Paläozoikum weltweit anwendbare Biostratigraphie, durchaus vergleichbar der (allerdings nur im Oberdevon und Unterkarbon gültigen) Entomozoen-Chronologie (ISO97).

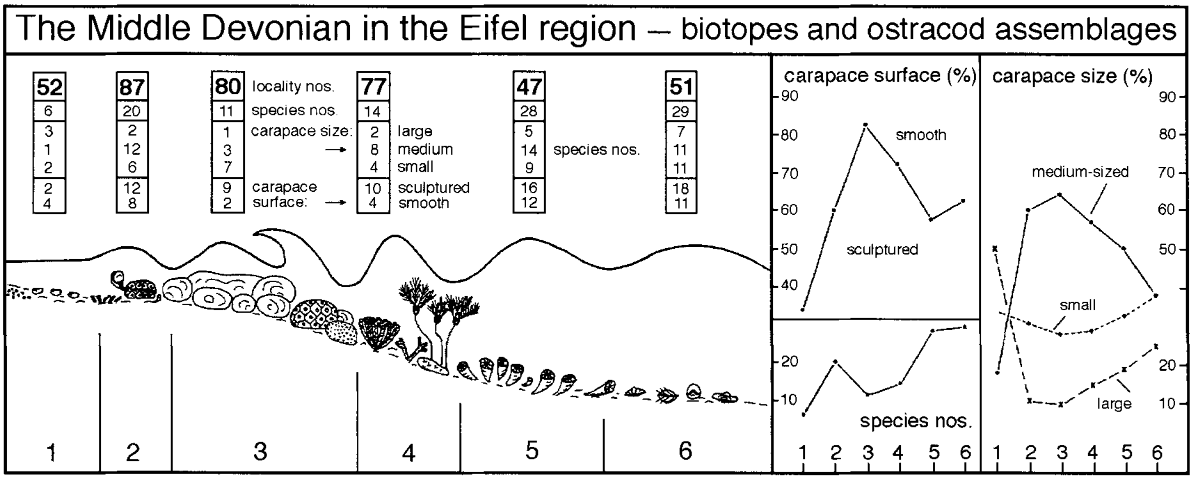
## Introduction

In the early sixties, while ostracod work was concentrated on the classic fields of taxonomy and biostratigraphy, a new direction was generally coming into fashion: studies in (palaeo)ecology. For ostracods, however, this new field was like an uncharted region, i. e., for Palaeozoic ostracods there was no previous. At that moment, the Napoli Symposium (ISO64) fortunately happened, conclusively influencing work on fossil ostracods. Consequently, the present author, who was dealing with Middle Devonian ostracods of the Eifel Mountains (Becker 1964, 1965), made first use of the new field (Becker 1969a, 1969b). A palaeoecological model, clearly energy-related in concept, was proposed on the occasion of the Pau Symposium (ISO70; Becker 1971). Later, several different ostracod ecotypes were distinguished (Becker in Bandel & Becker 1975; subsequently quoted as Becker 1975; emended Becker & Bless 1990 [non Lethiers & Crasquin 1987]) and the model, first applied to the shallow-water environments of the Middle Devonian sea in the Eifel region, was expanded to the Variscan belt (Adamczak 1976, Becker 1981a, 1981b, 1982a, 1982b). Subsequently, this model, which was considered from the beginning to be energy-related, was tested repeatedly and consequently improved, as demonstrated in Aberystwyth (ISO89; Becker & Bless 1990), in Prague (ISO94; Becker & Blumenstengel 1995a) and, also, in Chatham (ISO97; this paper). Finally, the model, now applicable from Ordovician to Triassic (? Jurassic), was extended from local to global applicability in scale.

The present paper will review thirty years of research effort to interpret the ecology of marine, Palaeozoic ostracods, showing progress, step-by-step with the examples of papers presented by Becker (1970 to 1997) on the occasion of relevant International Ostracod Symposia. The few opinions contributed by contemporaries will be discussed, and last of all, near the end of a researcher's life span, the primary idea that water energy (correlated with sedimentation and together with salinity and climate) was the controlling factor in (Palaeozoic) ostracod distribution is clearly demonstrated.

## First steps in palaeoecology

Following Wedekind (1924), a facies scheme for the Middle Devonian sea based on ecologically important macrofossils was developed by Struve (1961, 1963a-b) in the Eifel region.



Text-fig. 1. The Middle Devonian sea of the Eifel region. Left: Biotopes reconstructed by STRUVE (1961, 1963a-b) using ecologically important macrofossils, indicative of distinctive shallow-water conditions; one representative (water-energy controlled) ostracod fauna was selected for each biotope. Right: Composition of the selected ostracod faunas relative to number of species, ornamentation and carapace size (for details see the text). (1) lagoon, (2) back-reef, (3) reef-core, (4) fore-reef, (5) zone of solitary corals, (6) zone of brachiopods. – After (BECKER 1971).

In detail, six shallow-water, nearshore biotopes were distinguished (lagoon, back-reef, reef-core, fore-reef, and offreef) by means of indicator forms (stromatoporids and tabulate corals, crinoids, rugose corals, brachiopods and pelecypods), found to be controlled by water energy (low to high; calm or turbulent to laminar agitated). The ostracod faunas obtained from various localities in the northern Eifel region were put in this facies scheme and analysed by means of functional morphology; text-fig. 1 shows one representative fauna selected from each biotope (text-fig. 1, left: faunal indicators vs water energy; text-fig. 1, right: composition of selected faunas relative to carapace morphology).

In the lagoon (biotope 1), only six, primarily large and smooth species, but abundant, were adapted to the calm and extremely shallow water; in this extreme biotope, extraordinary ecological stress factors (variation in salinity and temperature) have additionally occurred. Against that, the back-reef area (biotope 2) was rich in sculptured and medium-sized ostracods (12 from 20); some of the species occur in appreciable numbers, others are represented only by rare, individual occurrences. In the stromatoporid bioherm (biotope 3) exposed to maximum water turbulence, comparatively few (11), without exception solidly built species were found, represented by relatively few individuals. In the fore-reef biostrome (biotope 4), the number of species (14) increased slightly, with an increase of smooth and large specimens. The off-shore faunas, living in at best laminar agitated waters rich in solitary corals and brachiopods (biotopes 5-6), show a marked increase in species (some 30) as well as in large and small, smooth forms; some (pachydomellid and bairdiid) species are extremely numerous, palaeocopine species in contrast are often rare in numbers of individuals.

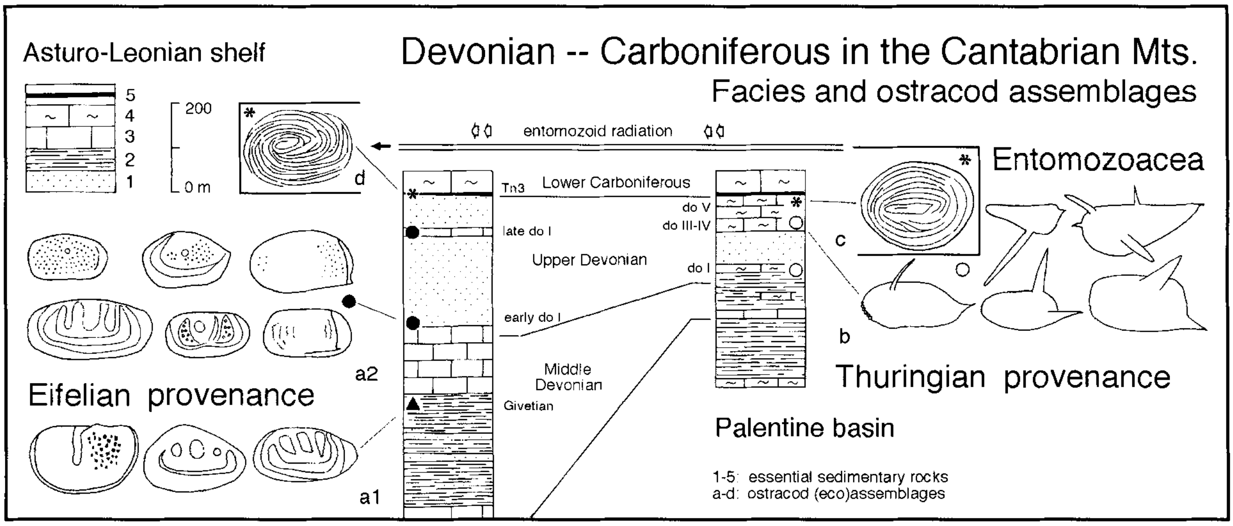
In summary, extreme values (shown by maxima, minima, turning points of the graphs) are clearly located in the turbulent agitated waters of the reef-core (biotope 3) and calm waters of the offshore brachiopod-zone (biotope 6) respectively; the lagoonal conditions are shown to be exceptional (extreme biotope). Comparable graphs (BECKER 1971: text-fig. 5B), calculated for the total (23) ostracod faunas known from the area in consideration, show similar trends; extreme values appear clearly for the same biotopes, but are even more pronounced.

The resulting patterns (showing compositions of assemblages relative to number of species, sculpture and carapace size) were compared with data given for Recent ostracods at the Napoli Symposium. Strikingly, a far-reaching conformity was observed concerning Recent Mediterranean ostracod faunas described as nearshore and offshore assemblages by PURI et al. (1965) or assemblages of the outer sublittoral zone by ASCOLI (1965). According to NEALE (1965), the distribution of Recent ostracods is mainly controlled by salinity and climate, which he called the primary factors. In the Devonian example, both of these parameters are believed (with the exception of the extreme biotope, the lagoon) to have been normal (salinity) and relatively constant in time and space (i. e. the total area studied). All remaining factors (intensity of light and oxygen content, food supply and predators, perhaps pH values) had only a mild and local influence on the distribution patterns.

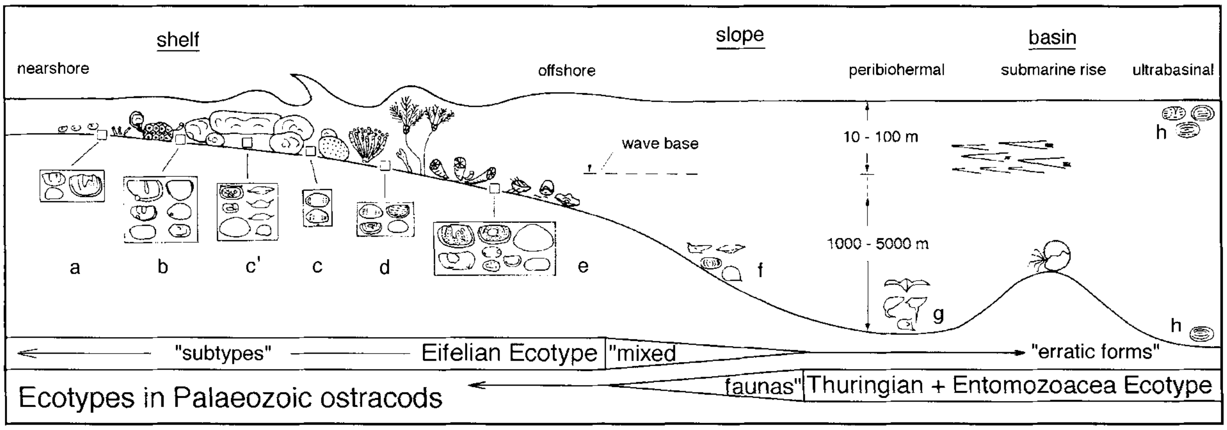
"These first results are encouraging and certainly substantiate the hope for improved results after more detailed studies have been carried out" (BECKER 1971: 814). Consequently, water energy (correlated with sedimentation) as the controlling factor was considered to be the central theme concerning the distribution of marine, Palaeozoic ostracod assemblages. This idea, first presented by BECKER (1969a, 1969b), runs like a thread through the research and, therefore, the present paper.

## Ostracod Ecotypes – from Variscan to global usability

With respect to Devonian ostracod assemblages in Central Europe, three ecotypes were distinguished by BECKER (1975): (1) the diverse, shallow-water Eifelian Ecotype, dominated by



Text-fig. 2. Biofacies characters (▲, ● = neritic, o = basinal, * = pelagic) in the Devonian-Carboniferous sequence of the Cantabrian Mountains (northern Spain); each facies is characterised by a specially adapted ostracod assemblage: epineritic shelf with benthic assemblages of Eifelian provenance (Eifelian Ecotype of text-fig. 3), basin with nectobenthic communities of Thuringian provenance (Thuringian Ecotype of text-fig. 3), and the pelagic realm with entomozoids (Entomozoacean Ecotype of text-fig. 3). Explanations. Sediment: (1) sand- and siltstones, (2) mud- and marlstones, (3) limestones, (4) nodular limestones, (5) black shales. Relationships are shown to ostracod faunas from the Middle Devonian of the Rheinische Schiefergebirge and Polish Mittelgebirge (a1), the Upper Devonian of Belgium and the Bergisches Land (a2) and the Upper Devonian of Thuringia (b); the entomozoids spread from east to west (c, d). – After BECKER (1982b).



Text-fig. 3. Distribution of ostracod ecotypes in the Variscan geosyncline (Rhenohercynicum, Saxothuringicum). Eifelian Ecotype (BECKER 1975) characteristic of high-energy environments (cf. text-fig. 1), with distinct subtypes for lagoon (a), back-reef (b), reef-core (c), fore-reef (d) and offreef (e). Mixed faunas (BECKER 1975) in nearshore, calm-water niches (c') or peribiohermal sediments (f, deeper slope). Thuringian Ecotype (BECKER 1975) indicative of low-energy environments (g); Entomozoacean Ecotype (BECKER 1975) in pelagic, (ultra)basinal sediments (h). Erratic forms, rare and specifically biotope-indicative (BECKER & BLESS 1990), are indicators for distinct positions with respect to (relative) depth (e. g. submarine rise sensu RABIEN 1956) and shore-line (see also text-fig. 4). – After BECKER (1981b)

thick-shelled and sculptured ostracod assemblages; (2) the rather monotonous Thuringian Ecotype, consisting of thin-shelled species with smooth, but often delicately spinose valves; and (3) the Entomozoacean Ecotype, exclusively formed by (hemi)pelagic (Late Palaeozoic) finger-print ostracods. Mixed faunas had occurred at distinct positions, e. g. the deeper slope (mixed faunas sensu BECKER 1982b) or in restricted marine areas (mixed marine ostracod assemblages, BLESS et al. 1988, BECKER & BLESS 1990).

The Eifelian (shallow-water) Ecotype consists of thick-shelled, frequently heavily lobed and ornamented ostracods; various sub-assemblages (as reported in section 2 above) are indicative of shallow-water environments.

The Thuringian Ecotype, first considered to be characteristic of the Thuringian sea, was applied by BECKER (1975) to assemblages of rather thin-shelled, often smooth ostracods, frequently possessing long spines. Although BECKER's model is principally morphologically defined, most of the typical taxa are podocopids.

By means of the following figures, the history of the adaptation of the energy-related ecotypes to the Variscan belt is sketched. In the southern Cantabrian Mountains (northern

Spain), ostracods of Ardenno-Rhenish provenance (Eifelian Ecotype; text-fig. 2, left) are distributed in the Asturo-Leonian shallow-water facies (e. g. BECKER et al. 1979). In the Palentine area, ostracod assemblages of clearly Thuringian provenance (Thuringian Ecotype; text-fig. 2, right) have been detected (BECKER 1981a, 1982a). At first surprising, not only for Spanish geologists, however, the basinal facies (see also text-fig. 4/1) was ultimately demonstrated by the entomozoids spreading from east to west in the Lower Carboniferous (see text-fig. 2).

To return to the controlling factor water energy, the Eifelian Ecotype is indicative of nearshore (but not necessarily marine), high-energy environments. In contrast, the Thuringian Ecotype is characteristic of marine, low-energy environments (to some extent, see below) independent of water depth and position in relation to the palaeo-coast line. In any case, the Thuringian Ecotype is not exclusively basinal.

First considered to be of only regional importance (Eifel region, Thuringia, Carnic Alps), ecotypes have later proved to be useful in the Upper Devonian to Lower Carboniferous of the Variscan belt. Currently, this model (see text-fig. 3) is applicable worldwide from Ordovician to Triassic (? Jurassic); the Entomozoacean Ecotype, however, remains restricted to the upper Palaeozoic (Upper Devonian to Lower Carboniferous, the lower Namurian included).

## Adoption of concept and terminology

The term Thüringischer Typ (see table 1) was informally mentioned by ZAGORA (1968: 11) for peculiar ostracod assemblages found while picking out conodonts. Originally the generally silicified assemblages were considered to be endemic of the Lower to Upper Devonian and the Lower Carboniferous of the Saalfeld basinal area (BLUMENSTENGEL 1965a). Later on, such silicified faunas (BECKER & BLESS 1974: text-figs 16-18) were detected in the hercynic magnafacies (Harz region, Moravian Karst).

Consequently, the term Thuringian Ecotype was subsequently applied by BECKER (1975) to basinal ostracod assemblages occurring in the calcareous-argillaceous, hemipelagic facies sensu ERBEN (1962) (Thüringisches Schiefergebirge, Harz region, Moravian Karst, Carnic Alps); later, however, refined (BECKER 1981a, 1981b, 1982b) to characterise in general ostracod assemblages found in low-energy environments of the Variscan belt. The relevant observations were made in Asturias (BECKER 1978) and in the Montagne Noire (BECKER 1982a), where in both areas, forms of clearly Thuringian aspect occur in shallow-water niches (text-fig. 3, c'). Consequently, the Thuringian Ecotype was shown to be clearly energy-related and indicative of calm water conditions.

Tab. 1. Chronology of terms. Compilation of relevant studies and those quoted in the present paper on the ecology of Palaeozoic ostracods, given in chronological order and showing the original spelling of terms (concerning facies or faunas, associations, assemblages respectively). For the facies scheme see text-fig. 3. Symbols: *Term established, {matter not studied in detail}, [comments by the present writer].

| FACIES/FAUNAS<br>AUTHOR(S) | neritic | | | hemi-pelagic | pelagic |
|---|---|---|---|---|---|
| | nearshore<br>küstenbeeinflußt | offshore<br>offen-marin | slope<br>peribiohermal | basin/submarine rise<br>basinal/Tiefschwelle | abyssal plain<br>ultrabasinal |
| Zagora (1968) | | | | Thüringischer Typ [endemic) | |
| Becker (1969 a-b) | Lagune/Rück-/Zentral-/Vorriff/offreef | | | | |
| Bless (1970) | *Carbonita/Geisina/Lingula/*Muschel/Biostr./Product. | | | | |
| Becker (1971) | lagoon/back-/central-/fore-reef/offreef | | | | |
| Polenova (1971) | beyrichiid-type | | | aparchitid-healdiid-type | |
| Becker (1973) | | | *peribiohermal | | |
| Becker and Bless (1974) | benthonic faunas | | | silicified faunas | pelagic (entomozoan) faunas |
| Becker (1975) | *Eifeler Ökotyp | | *Mischfauna | *Thüringer Ökotyp | *Entomozoen-Ökotyp |
| Becker et al. (1976) | | benthos below wave base | | | |
| Becker and Sánchez d. P. (1977) | | B. unterhalb d. Wellenbasis | | | |
| Requadt et al. (1977) | | B. d. tieferen Wassers | | | |
| Becker (1978) | B. d. sehr flachen Wassers | | | | |
| Becker and Boll (1979) | B. d. geschützten Wassers | | | | |
| Feist and Groos-Uffenorde (1979) | Eifeler Ökotyp (beyrichiid complex) | | | Thüringer Ökotyp | Entomozoen-Ökotyp |
| Olempska (1979) | Eifeler Ökotyp | | mixed association | Thuringer Ökotyp | Entomozoacean Ökotyp |
| Becker (1980) | protected lagunär/protected marin | | | | |
| Becker (1981b) | Stillwasser-Nische | | | Becken/Tiefschwellen | Beckentiefstes |
| Lethiers (1981) | Province à *Serinida* | | Province à *Graphiadactyllis* | Province à *hypsela/Rectonaria* | |
| Becker (1982a) | {*high-energy environments} | | | *low-energy environments [+ shallow-water n.] | |
| Bless (1983) | non-marine/near-shore | shallow off-shore | | | |
| Dreesen et al. (1985) | paraparch./kirkbyids/het. palaeocopines/bairdiaceans | | | Thuringian-type | |
| Becker and Bless (1987) | | | | | Fauna d. Epipelagial |
| Lethiers and Crasquin (1987) | | | | milieux profond [paléo-milieu froid, rareté de *Bairdia*] | |
| Becker (1987) | | | | Thüringer Ökotyp [stable basinal cond., rich in *Bairdia*] | |
| Becker (1988b) | | | | Thüringer Ökotyp [low oxygen concentration] | |
| Wang (1988) | Smooth-podocopid Association | | | Spinose-podocopid Association | |
| Bless et al. (1988) | | *mixed marine ostracod assemblage | | | |
| Berdan (1990) | Eifeler ecotype | | mixed association | Thuringian ecotype | |
| Becker and Bless (1990) | {Eifelian Ecoassemblages/subas.} | | | Thuringian Ecoassemblages [spec. biotope ind. f.] | |
| Lethiers and Feist (1991) | | | | l'ecotype de Thuringe [psychrosph.] | |
| Wang and Becker (1991) | Eifelian Ecotype | | | Thuringian Ecotype [thermosph.] | Entomoz. Ecot. |
| Becker and Blumenstengel (1995a) | | | | Thuringian Ecotype [lowstand sea-level] | |
| Casier and Devleeschouwer (1995) | l'ecotye de l'Eifel | | | | myodocopid ostracods |
| Casier (1997) | l'ecotye de l'Eifel | | | | *Myodocopid ecotype |
| Becker and Blumenstengel (1997) | Eifelian Ecotype/Subecot. Ee Ep | | Mixed f./Subecot. M | Thuringian Ecotype/Subecotypes Tf Tn Tu | |
| Casier and Lethiers (1998) | l'ecotye de l'Eifel | | | | l'ecotype à Myodocopida |

Actually, the Thuringian Ecotype is easier to understand than the highly complex shallow-water assemblages of the Eifelian Ecotype that are exposed to various and variable ecological stress (see BECKER 1971, BLESS et al. 1988). Assemblages of Thuringian provenience were subsequently detected in the Holy Cross Mountains (OLEMPSKA 1979), Pyrenees (DELVOLVÉ & LETHIERS 1986) and Montagne Noire (FEIST & GROOS-UFFENORDE 1979, LETHIERS & FEIST 1991), in Serbia (SPASSOV & BLUMENSTENGEL 1976) and the Moravian Karst region (DVOR˘AK et al. 1986), in North Africa (BECKER 1987) and South China (WANG 1988) and generally considered to be of basinal origin. At least, the term Thuringian Ecotype was generally adopted (see BECKER & BLESS 1990, WANG & BECKER 1991, LETHIERS & FEIST 1991).

There were, however, some other opinions. According to KOZUR (1991: 25, 30) "the term Thuringian for this ecotype cannot be used, because this term is preoccupied by the Thuringian stage (= Zechstein) of Upper Permian ... in the Permian, Thuringian Ecotype would mean Zechstein ecotype". Moreover, KOZUR (1991: 30) found that "unfortunately, both Eifelian and Thuringian are stratigraphic stages, so both terms can be misinterpreted). And finally (KOZUR 1991: 25), "the term paleopsychrospheric ostracod faunas is introduced for ... Silurian to Triassic (lower Liassic) ostracod faunas. General morphological characters and distribution patterns of these paleopsychrospheric ostracod faunas show similarities to the Tertiary – Recent psychrospheric ostracod faunas". BECKER (written comm., 1985; pers. comm., EOM89; see also BECKER 1993: 20-23) has replied to KOZUR's inconsistencies.

The idea of psychrospheric Thuringian ostracods was also adopted by LETHIERS (e. g. LETHIERS & CRASQUIN 1987: 415): "The analogy with actual psychrospheric ostracodes, the comparison with actual species of a same habitus and the facies analysis suggest a deep, calm, cold and oxygen deficient palaeobiotope with a high amount of dissolved silica". For the problems involved see BECKER (in BECKER et al. 1993: 61, 62, by extract, transl. G.B.): "Occasional attempts to compare (or even to equate) the mainly Palaeozoic Thuringian Ecotype with modern psychrospheric ostracod assemblages sensu BENSON (e. g. in BENSON & SYLVESTER-BRADLEY 1971: 65) have failed (OLEMPSKA 1979, MCKENZIE 1982, BECKER 1987, BECKER & WANG 1992; WHATLEY, pers. comm., EOM89); the origin of the faunas and the physical properties are too different". And BENSON (1975: 70), "in the past ... the thermosphere may have constituted most of the world-ocean, watermass system". In a recent paper, MAY (1997: 303, transl. G.B.) has discussed the factors influencing Frasnian-Famennian events: "In the whole space under consideration, there is no indication of continental glaciation (BOUCOT & GRAY 1982, BOUCOT 1988, BECKER & HOUSE 1994)".

Finally, the idea of estimating absolute values of water depth by means of ostracod studies, will (as already pointed out by LIEBAU 1980) remain an utopian dream. The attempt to calculate palaeo-depth by means of absolute and relative frequency of *Bairdia*, i. e. from numbers of species and specimens respectively (LETHIERS & CRASQUIN 1987, LETHIERS & FEIST 1991; see the discussion in BECKER et al. 1993: 62), seems little better than numerology. The same seems (in the opinion of the present writer) to be true for the recently expressed idea to "propose some data to determine absolute values of oxygen rate in Upper Palaeozoic neritic environments" (LETHIERS & WHATLEY 1995: 199); the starting point of this study is blased by ignoring the classic Rhenish localities. Referring to LETHIERS & WHATLEY (1995: text-fig. 1), the present writer (BECKER, pers. comm., ISO97) told one of the authors: "I have never understood that the Rheinische Spiriferen-Sandstein was poor in oxygen content".

Compared with the Thuringian Ecotype, the Eifelian Ecotype, characteristic of the arenaceous-calcareous facies sensu ERBEN (1962), has developed conceptually in the shadow of the former ecoassemblage. Recently, however, faunas of the Eifelian Ecotype are increasingly mentioned in the literature (e. g. CASIER 1997, CASIER & DEVLEESCHOUWER 1995, CASIER & PREAT 1996, CASIER & LETHIERS 1997, CASIER et al. 1998). Despite its stratigraphic name (see above), the term Eifelian Ecotype seems to be adopted. The Entomozoacean Ecotype, including large cypridinaceans and spread out in the argillaceous, hemipelagic facies sensu ERBEN (1962), was adapted to Myodocopid Ecotype (e. g. CASIER 1998). The mixed faunas (sensu BECKER 1975, sensu BLESS et al. 1988) are of special problematic nature and, although summarised in table 1, not furtherly considered in the present paper.

## Further development - the specifically biotope-indicative forms

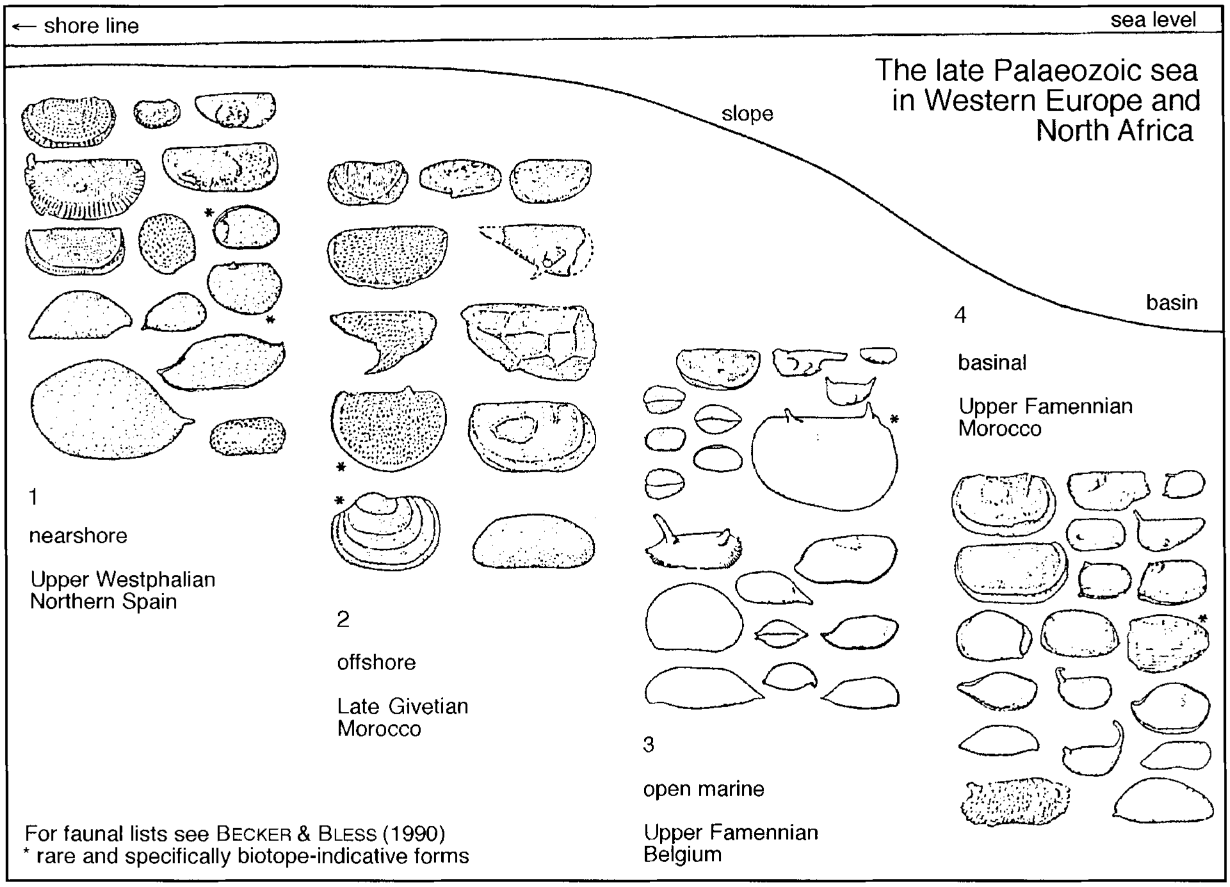
On the occasion of the Aberystwyth Symposium (ISO89), BECKER & BLESS (1990) presented a method to classify biotopes in the low-energy realm in more detail, probably with respect to the palaeo-shoreline. Specifically biotope indicative forms, i. e., rare specimens of erratic species migrated from an adjacent (e. g. shallow-water) environment, give information on palaeo-depth and shoreline.

Herein, text-fig. 4 gives an impression of an assumed facies series (Fazieskette sensu LIEBAU 1980) showing nearshore to basinal assemblages belonging to the Thuringian Ecotype; the particular, specifically biotope indicative forms are marked by an asterisk (*). Note that *Bairdia* species have been a common element in Palaeozoic assemblages, even in the basinal position.

In Prague (ISO94), BECKER & BLUMENSTENGEL (1994, 1995a) applied the method of erratic species to event stratigraphy (Hangenberg Event, near the Devonian-Carboniferous boundary). In the Sauerland area (Rheinisches Schiefergebirge), the ostracod fauna of principally Thuringian aspect recovered from the Upper Devonian *Imitoceras* limestones (Stockum level) yielded some shallow-water specimens (*Mauryella* sp., *Shichaella* sp.), considered (together with signs of sediment interruption and reworking) to be clearly indicative of water shallowing. And the typical shallow-water species (*Schweyerina reichsteini*), found in an assemblage of Thuringian aspect from the lower Famennian of the Harz region (BECKER & BLUMENSTENGEL 1995b), was interpreted as having lived in a less deep biotope, namely on the top or at the flank of a submarine rise (sensu RABIEN 1956).

## Subecotypes, the new palaeoecological tool

Now (ISO97), so-called Subecotypes (of both ecotypes) are considered to be useful to distinguish ultra-, normal- and relatively shallow-basinal environments as well as peribioher-



Text-fig. 4. Selected Thuringian Ecotype assemblages indicative of different low-energy environments from (1) nearshore, (2) offshore, (3) open marine to (4) basinal (facies series, Fazieskette sensu LIEBAU 1980); (*) specifically biotope-indicative forms (sensu BECKER & BLESS 1990) are indicators of different water depths and distances from palaeo-coasts. Note the abundant *Bairdia* species. – After BECKER & BLESS (1990).

mal- and epineritic-shallow water environments. This study (see text-fig. 5) was started in the Upper Devonian of the Rheinische and Thüringische Schiefergebirge by BECKER & BLUMENSTENGEL (1997) and will be expanded in time and space.

While the concept of erratic forms is based on rare specimens of (even a single) characteristic species, the new instrument of subecotypes works with mixed assemblages consisting of (more-or-less) numerous species from both realms. It is believed to complete, amplify and confirm the model drafted in the sixties.

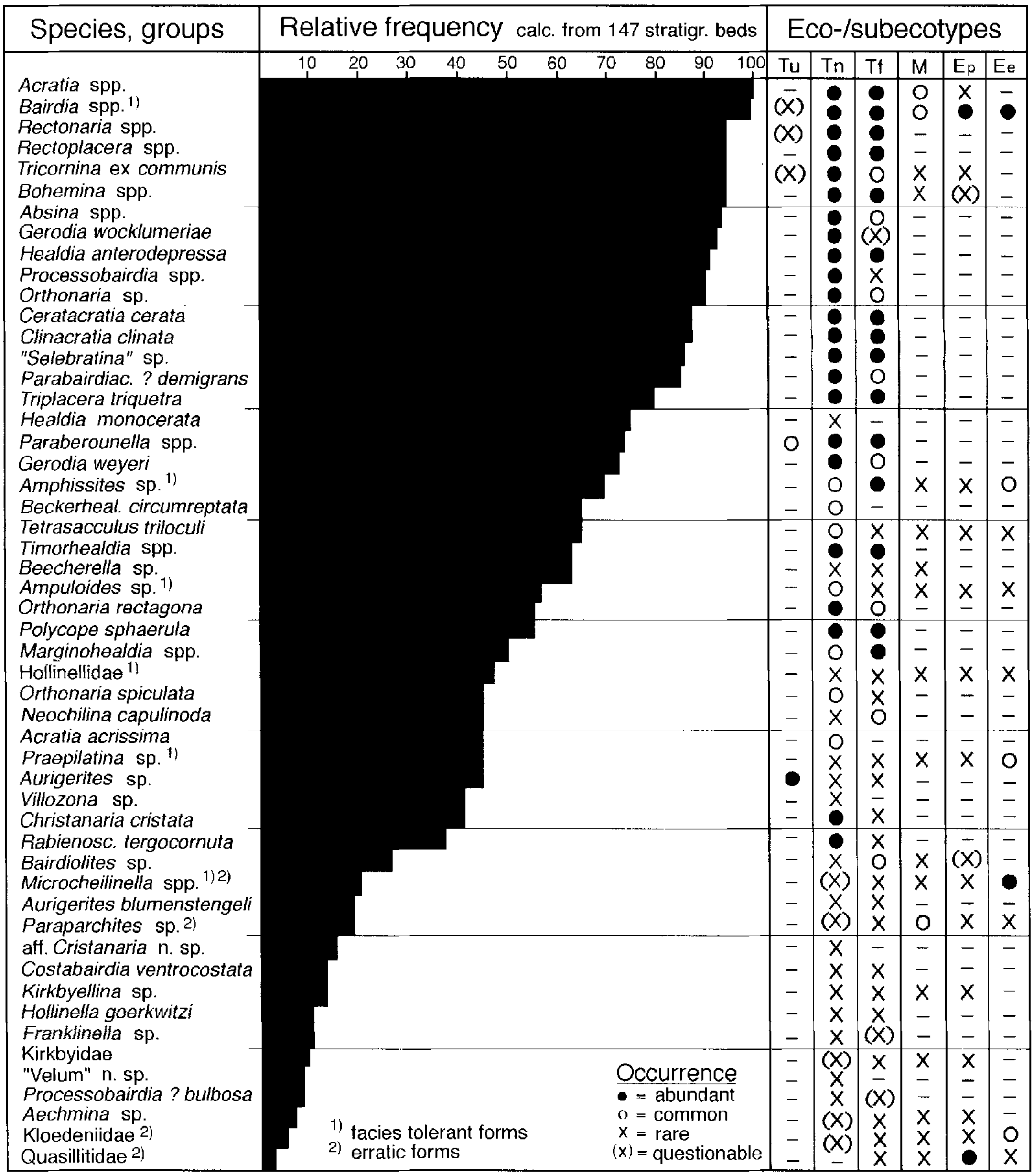
For the shallow-water realm (Eifelian Ecotype sensu BECKER 1975), the mixed faunas (sensu BECKER 1975) and subassemblages (sensu BECKER 1982b) already fit in the concept discussed here. With respect to (hemi)pelagic environments, first examples concerning the applicability of subecotypes in palaeozoogeographical studies can be given as follows.

*Villozona* GRÜNDEL, 1965 (sensu lato) is only known from basinal environments (Thuringia, Morocco, South China), mostly with small numbers of individuals – marking the basin proper (Subecotype Tn). Up to now, however, no species of the *Villozona villosa* group (sensu BECKER 1997) have been found in hemipelagic deposits (Subecotype Tf). Therefore, no evidence of the group (as well as of processobairdiids) is known from Upper Devonian to Lower Carboniferous assemblages recorded from the Sauerland area (BECKER 1988a, 1989, 1991; BECKER in BECKER et al. 1993, BECKER in press) which are considered to have lived at the top or flank of submarine rises (Tiefschwellen sensu RABIEN 1956). This pattern seems logical when recently COEN (1996: 57) described the site where *Villozona villosa villosa* occurs in Oujiachong (Hunan, South China; Lower Carboniferous) to be localised on a relatively deep marine shelf, while in adjoining Malabian (where contemporary samples are free of *Villozona* species), the general impression prevails of a shallower depositional environment (COEN 1996: 58).

COEN's report (1996) of *V. villosa villosa* from South China, however, confirms not only BECKER's concept of Palaeozoic ecotypes and, in particular, of specifically biotope-indicative forms, it also gives (by means of additional references, see below) cosmopolitan evidence of BLUMENSTENGEL's biostratigraphic scale.

## Prospects for the future – Thuringian ostracod zonation

In biostratigraphy, the very complex Eifelian Ecotype plays a rather modest part (only of regional or even local interest). For the Lower Devonian of the Cantabrian Mountains (Ge-



| Species, groups | Tu | Tn | Tf | M | Ep | Ee |
|---|---|---|---|---|---|---|
| *Acratia* spp. | – | ● | ● | ○ | X | – |
| *Bairdia* spp.[1] | (X) | ● | ● | ○ | ● | ● |
| *Rectonaria* spp. | (X) | ● | ● | – | – | – |
| *Rectoplacera* spp. | – | ● | ● | – | – | – |
| *Tricornina* ex *communis* | (X) | ● | ○ | X | X | – |
| *Bohemina* spp. | – | ● | ● | X | (X) | – |
| *Absina* spp. | – | ● | ○ | – | – | – |
| *Gerodia wocklumeriae* | – | ● | (X) | – | – | – |
| *Healdia anterodepressa* | – | ● | ● | – | – | – |
| *Processobairdia* spp. | – | ● | X | – | – | – |
| *Orthonaria* sp. | – | ● | ○ | – | – | – |
| *Ceratacratia cerata* | – | ● | ● | – | – | – |
| *Clinacratia clinata* | – | ● | ● | – | – | – |
| *"Selebratina"* sp. | – | ● | ● | – | – | – |
| *Parabairdiac. ? demigrans* | – | ● | ○ | – | – | – |
| *Triplacera triquetra* | – | ● | ● | – | – | – |
| *Healdia monocerata* | – | X | – | – | – | – |
| *Paraberounella* spp. | ○ | ● | ● | – | – | – |
| *Gerodia weyeri* | – | ● | ○ | – | – | – |
| *Amphissites* sp.[1] | – | ○ | ● | X | X | ○ |
| *Beckerheal. circumreptata* | – | ○ | – | – | – | – |
| *Tetrasacculus triloculi* | – | ○ | X | X | X | X |
| *Timorhealdia* spp. | – | ● | ● | – | – | – |
| *Beecherella* sp. | – | X | X | X | – | – |
| *Ampuloides* sp.[1] | – | ○ | X | X | X | X |
| *Orthonaria rectagona* | – | ● | ○ | – | – | – |
| *Polycope sphaerula* | – | ● | ● | – | – | – |
| *Marginohealdia* spp. | – | ○ | ● | – | – | – |
| Hollinellidae[1] | – | X | X | X | X | X |
| *Orthonaria spiculata* | – | ○ | X | – | – | – |
| *Neochilina capulinoda* | – | X | ○ | – | – | – |
| *Acratia acrissima* | – | ○ | – | – | – | – |
| *Praepilatina* sp.[1] | – | X | X | X | X | ○ |
| *Aurigerites* sp. | ● | X | X | – | – | – |
| *Villozona* sp. | – | X | – | – | – | – |
| *Christanaria cristata* | – | ● | X | – | – | – |
| *Rabienosc. tergocornuta* | – | ● | X | – | – | – |
| *Bairdiolites* sp. | – | X | ○ | X | (X) | – |
| *Microcheilinella* spp.[1][2] | – | (X) | X | X | X | ● |
| *Aurigerites blumenstengeli* | – | X | X | – | – | – |
| *Paraparchites* sp.[2] | – | (X) | X | ○ | X | X |
| aff. *Cristanaria* n. sp. | – | X | – | – | – | – |
| *Costabairdia ventrocostata* | – | X | X | – | – | – |
| *Kirkbyellina* sp. | – | X | X | X | X | – |
| *Hollinella goerkwitzi* | – | X | X | – | – | – |
| *Franklinella* sp. | – | X | (X) | – | – | – |
| Kirkbyidae | – | (X) | X | X | X | – |
| "Velum" n. sp. | – | X | – | – | – | – |
| *Processobairdia ? bulbosa* | – | X | (X) | – | – | – |
| *Aechmina* sp. | – | (X) | X | X | X | – |
| Kloedeniidae[2] | – | (X) | X | X | X | ○ |
| Quasillitidae[2] | – | – | X | X | ● | X |

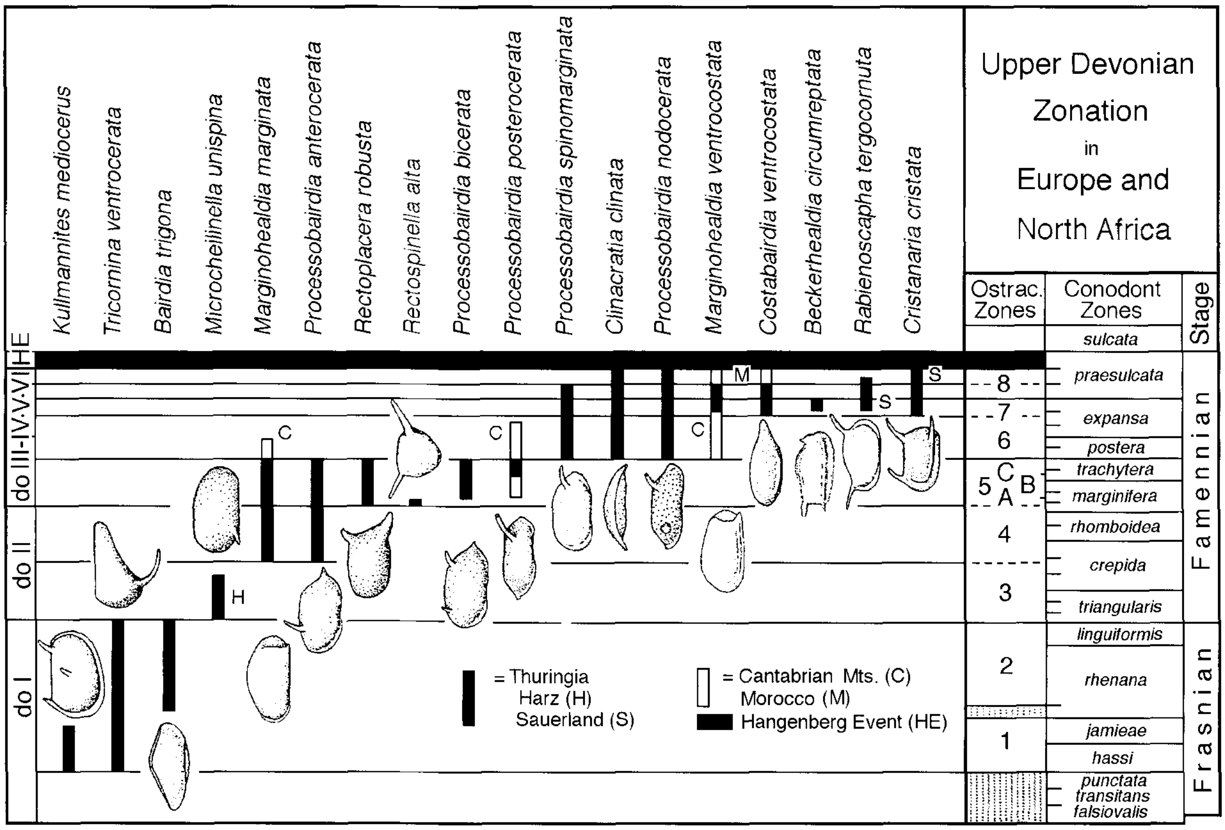
● = abundant
○ = common
X = rare
(X) = questionable

Text-fig. 5. Ecotypes in Palaeozoic ostracod assemblages from Central and Western Europe. Relative frequencies of selected species calculated from 147 stratigraphical beds. Explanation of abbreviations: T = Thuringian Ecotype (with subecotypes: u = ultrabasinal, n = basinal, f = submarine rise), M = mixed faunas, E = Eifelian Ecotype (with subecotypes: p = peribiohermal, e = epineritic). – After BECKER & BLUMENSTENGEL (1997).

dinnian to Upper Emsian) and the Middle Devonian (Eifelian to Givetian) of the Eifel Mountains, BECKER (1996) has summarised the present state of knowledge. All the so-called zonations (e. g. LETHIERS 1974) based on shallow-water forms are rather doubtful; only species of *Polyzygia* (*P. insculpta* line; GOODAY & BECKER 1979; BECKER 1995) seem to be useful.

In contrast, the Thuringian Ecotype is believed to deliver a biostratigraphy comparable with the entomozoid zonation and may be applicable world-wide. The peculiar Thuringian nectobenthic forms were considered to be endemic (BLUMENSTENGEL 1965a). Therefore the biostratigraphy proposed by BLUMENSTENGEL (1965b, 1979, 1981) was believed to be only of regional (Thuringian) interest. Later, BECKER (1982a, 1987) extended (with some caution) the Thuringian concept to the Upper Devonian of the southern Cantabrian Mountains (Palentine basin) and to North Africa (Tafilalt, Ben Zireg). Now, the global importance can be demonstrated (WANG & BECKER 1991; COEN 1996, see above). Text-fig. 6 presented herein, summarises stratigraphical data from Thuringia and northern Spain.

For the moment, BLUMENSTENGEL's concept of a zonation based on Upper Devonian to Lower Carboniferous, nectobenthic forms seems to be the weakest link in the chain of ideas



Text-fig. 6. Selected markers of the Thuringian Ecotype; stratigraphy based on nectobenthic (Thuringian) ostracods applicable world-wide in Upper Devonian and Lower Carboniferous strata. – After BECKER & BLUMENSTENGEL (1997).

discussed in the present paper. However, there is global circumstantial evidence known from the relevant literature (e. g. GREEN 1963; MÜLLER-STEFFEN 1965; BUSHMINA 1975, 1977; SPASSOV & BLUMENSTENGEL 1976; BECKER 1977, 1981a, 1982a, 1987, 1988a, 1991; SHI 1982; DVOŘAK et al. 1986; BARTZSCH & WEYER 1986; BUSHMINA et al. 1987; OLEMPSKA 1979; KUWANO 1987; WANG 1988; WANG & BECKER 1991; BECKER et al. 1993; COEN 1996) as well as from personal observations (concerning unpublished material from Morocco and Vietnam) that further investigations will stabilise the biostratigraphical concept of nectobenthic ostracods, finally expected to be comparable with the entomozoid zonation (RABIEN 1954).

## Conclusions

The present paper gives evidence of the beneficial circumstances some 30 years ago that made it possible to do deal with a formerly vague problem, namely the palaeoecology of Palaeozoic ostracods. Of course, the concept of uniformitarianism (see the review in NEALE 1983) has been respected and the old pioneers in Recent research (e. g. REMANE 1933, 1963; ELOFSON 1941; HARTMANN 1963; OERTLI 1963) have been consulted. However, the coincidence of two requirements accidentally happening in the early sixties – the fundamental, biofacies investigations of STRUVE (1961, 1963a-b) concerning the Middle Devonian sea of the Eifel region, and the research on Recent ostracods demonstrated at the 1st International Symposium on Ostracoda in Napoli (ISO64) – opened the possibility of tackling the difficult problem with considerable success. With respect to Palaeozoic ostracod distributions, the idea of a water-energy related model (BECKER 1969a, 1969b, 1971) was born, subsequently followed and developed by the concepts of facies-related ecotypes (BECKER 1975), specifically biotope-indicative forms (BECKER & BLESS 1990) and distinctive subecotypes (BECKER & BLUMENSTENGEL 1997).

In addition to the new ideas mentioned above, the model discussed herein was continuously faced with Recent (sometimes, at the first sight, contradictory) data provided by various authors. In this way, it became possible to improve and amplify BECKER's original model by repeated tests. While sorting out unclear opinions, the paradigm was shown to be always plausible. The review given herein shows how reasonable results, even in a complex field, can be obtained by simple, practical and easily understood methods. Originated from the Eifel region (BECKER 1969a, 1969b, 1971) and later extended to the Variscan belt (BECKER 1981b, 1982b), the energy-related model for Palaeozoic marine ostracod distribution patterns is currently working worldwide and is applicable from the Lower Palaeozoic (Ordovician) to the Triassic (probably Jurassic).

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