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Global Campanian (Upper Cretaceous) ostracod palaeobiogeography

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Abstract

The distribution of 218 Campanian marine ostracod genera from 38 geographical areas was used for a quantitative palaeobiogeographical analysis. The data were analysed using multivariate statistical methods, ordination methods and parsimony analysis of endemism. These methods resulted in distinct geographical area groupings of the studied regions. With these groupings, seven palaeobiogeographical units based on Campanian ostracod occurrences are distinguished. The composition of the area groupings and the distribution of the palaeobiogeographical units are discussed. Their development and spatial distribution are broadly controlled by Campanian palaeoclimates, partly modified by palaeogeographical conditions.

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1. Introduction

For the palaeobiogeographical interpretation of Campanian (Upper Cretaceous) marine ostracods, the distribution of 218 genera from 38 selected areas was analysed. Therefore, a dataset was compiled based on published literature and own unpublished

data from Kuwait, Mozambique and Ivory Coast. As this palaeobiogeographical analysis deals with large, heterogeneous datasets whose variations are usually multidimensional, it requires some kind of statistical treatment. The raw data were quantitatively analysed by subjecting them to phenetic analyses using multivariate statistical and ordination methods and, moreover, to parsimony analysis of endemism (PAE). The results achieved using these methods are supposed to be little affected by errors or inconsistencies due to inadequate sampling, incompleteness of documentation, imperfect temporal placement of some localities

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or even by incorrect identifications. They are thus more reliable than the use of a small number of selected taxa and trying to assess their biogeographical history. The general difficulties of palaeobiogeographical work and the advantages and problems of phenetic and ordination methods and PAE were discussed at some length by several authors (e.g. Rosen, 1988, 1992; Rosen and Smith, 1988; Shi, 1993; Liu, 1995; Shi and Archbold, 1996; Bengtson and Kakabadze, 1999; Lieberman, 2000). For more background information on the methodology, the reader is referred to the above studies.

2. Methods

2.1. Dataset

A raw dataset from 38 operational geographical units (OGUs) was compiled for Campanian ostracods (Fig. 1, Table 1). An OGU is a geological entity, such as a marginal basin or an epicontinental seaway. OGUs are as extensive as possible to embrace fossil communities from a wide palaeoenvironmental range, such as various substrates and water depths, provided that only one basin is involved. Thus, an OGU may

represent a fauna from one locality or a composite record of several assemblages from the same basin (Shi and Archbold, 1996). This procedure was designed to minimise the potential effect of local ecology on large-scale palaeobiogeographical studies (e.g. Rosen, 1988; Shi and Archbold, 1996).

More general palaeobiogeographical data and information on the geographical distribution of selected ostracod groups in the Cretaceous are presented by Tambareau (1982a,b), Babinot and Colin (1988, 1992), Fauth (2002) and Puckett (2002).

Generally, species might give more detailed palaeobiogeographical information than genera. However, for fossil and extant molluscs, Hallam (1969) emphasised that genera are more reliable than species for biogeographical plotting. Also, Ekman (1967) has shown that genera most clearly define biogeographical provinces and subprovinces in modern seas. In our study of ostracods, we insist on the genus as the basic taxonomic unit because (1) evaluation of published taxonomic information is critical for the quality of the data and cannot always be carried out at the desired species level and (2) the data were in a few cases compiled from stratigraphical or more general geological studies which provided no descriptions or illustrations of fossils. Therefore, generic assignment

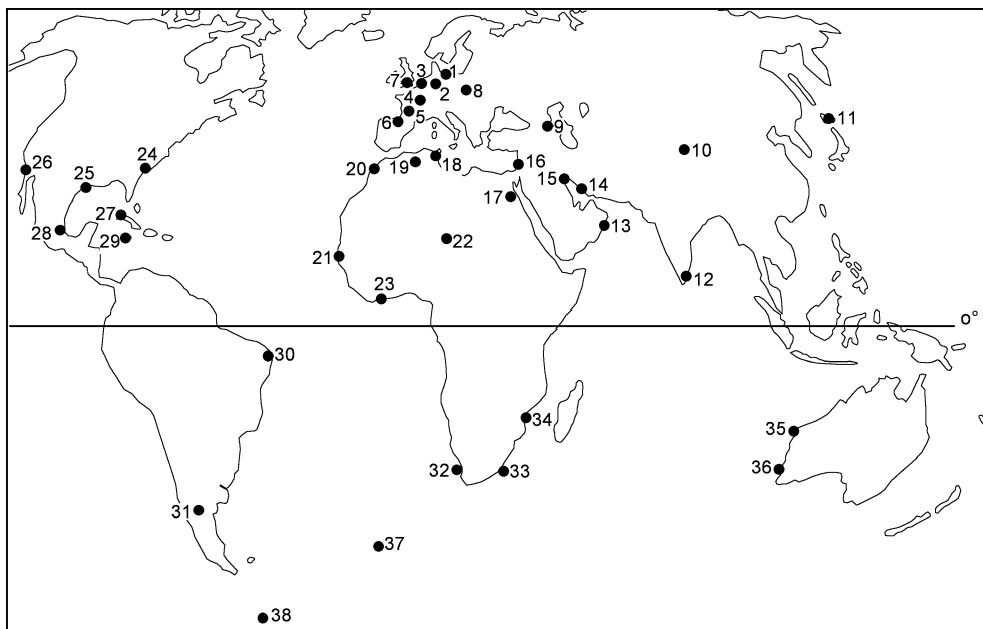


Fig. 1. Location of the 38 OGUs analysed for this study. For numbering of the OGUs, see Table 1.

Table 1
OGUs, geographical regions and sources from which ostracod faunas were compiled

No.	OGU	Region	Data source
1	Rügen	NE Germany	Herrig et al., 1997
2	NW Germany	NW Germany	Clarke, 1982, 1983; Schwarzkopf, 1991
3	Netherlands/ Belgium	S Netherlands/ NE Belgium	Bonnema, 1940, 1941; Deroo, 1966; Felder et al., 1985; Robaszynski et al., 1985; Bless and Robaszynski, 1988; Bless, 1988a,b, 1989, 1991; Bless et al., 1990; Bless and Felder, 1989; Felder and Bless, 1989
4	Paris Basin	N France	Damotte, 1964a,b, 1966, 1971; Babinot et al., 1983, 1985
5	Aquitaine Basin	SW France	Colin, 1973a,b; Babinot et al., 1983, 1985; Colin and Damotte, 1985; Damotte and Odin, 2001; Andreu, 2001; Andreu and Odin, 2001
6	Vasco-Cantabrian Bs.	N Spain	Zarraga and Rodriguez Lazaro, 1990; Rodriguez Lazaro and Zarraga, 1992
7	S England	British Isles	Kaye, 1964; Neale, 1978; Lord and Bown, 1987
8	Poland	Poland	Szczechura, 1964, 1965
9	Russia	C Asia	Andreev, 1999; Andreev and Mandelstam, 1971
10	Tarim Basin	China	Yang et al., 1995
11	Hokkaido	N Japan	Ishizaki, 1992
12	India	India	Sastry et al., 1972; Sugumaran et al., 1997
13	Oman	Arabian Peninsula	Athersuch, 1988, 1994; Babinot and Bourdillon de Grissac, 1989; Platel et al., 1994
14	Iran	Persian Gulf	Grosdidier, 1973
15	Kuwait/ Saudi Arabia	Persian Gulf	Al-Furaih, 1980, 1985, 1986, 1993; JP Colin, unpublished data
16	Israel+ Sinai	Israel	Honigstein, 1984; Honigstein et al., 1985; El-Nady, 2002
17	Eastern Desert	Egypt	van den Bold, 1964; Ismail, 1992
18	N Tunisia	Tunisia	Donze et al., 1982; Peypouquet et al., 1986; Abdallah et al., 1995; Said-Benzarti, 1998

Table 1 (continued)

No.	OGU	Region	Data source
19	N Algeria	Algeria	Grékoff, 1968; Bellion et al., 1973; Vivière, 1985; Braccini, 1994
20	Morocco	Morocco	Andreu and Tronchetti, 1994; Andreu, 1996, 2002
21	Senegal	W Africa	Apostolescu, 1961, 1963; Babinot et al., 1988
22	Lake Chad Basin	Niger, W Africa	Colin and Hochuli, 1992
23	Ghana/ Ivory Coast	Gulf of Guinea	Khan, 1970; Kogbe and Me'hes, 1986; JP Colin unpublished data
24	E Georgia/ S Carolina	SE USA	Gohn, 2001; Swain, 2001
25	Gulf Coast/ USA	SE USA	Hazel and Paulson, 1964; Crane, 1965; Hazel and Brouwers, 1982; Puckett, 1992, 1995a,b, 1996
26	California	W USA	Holden, 1964
27	Cuba	Cuba	van den Bold, 1946; Ljübmova and Sanchez-Arango, 1974
28	NE Mexico	Mexico	Caus et al., 2002
29	Jamaica	Jamaica	Hazel and Kamiya, 1993
30	Potiguar Basin	NE Brazil	Delicio et al., 2000; Viviers et al., 2000
31	Chubut Basin	Argentina	Rossi de Garcia and Proserpio, 1980
32	Orange Basin	W South frica	Dingle, 1969, 1971, 1981, 1982, 1996
33	E South Africa	South Africa	Dingle, 1969, 1971, 1981, 1982, 1996
34	Mozambique	Mozambique	JP Colin, unpublished data
35	Carnarvon Basin	W Australia	Bate, 1972
36	Perth Basin	W Australia	Neale, 1975
37	ODP Site 689	Southern Ocean	Majoran and Widmark, 1998
38	James Ross Basin	Antarctic Peninsula	Fauth et al., 2003

for the considered ostracods is much more reliable, straightforward and less confusing. Moreover, ostracod species have a tendency for endemism and this taxonomic level might thus have only limited validity. In compiling the raw data, a list of genera is provided for each OGU and, wherever necessary, revised from the original literature in terms of modern taxonomy, in which we have tried to use the most recent determinations. In any case, minor changes in the faunal list should not seriously alter the overall pattern. The raw

dataset is available at request by the corresponding author.

A total of 218 Campanian ostracod genera were encountered from the 38 OGUs. The various OGUs have been studied to different extents, and in some cases, the data situation is poor (Table 2). This may be due to (1) low sampling, (2) the lack of study or (3) the lack or scarcity of suitable environments for ostracods leading to primarily low diversity faunas. In

Table 2

N =total number of Campanian ostracod genera, n =total number of endemic genera present in the 38 OGUs and percent endemicity for each OGU

No.	OGU	N	n	Endemicity
1	Rügen	69	23	33
2	NW Germany	49	4	8
3	Netherlands/Belgium	54	2	4
4	Paris Basin	24	0	0
5	Aquitaine Basin	44	5	11
6	Vasco-Cantabria	25	3	12
7	S England	29	0	0
8	Poland	18	0	0
9	Russia (C Asia)	17	1	6
10	Tarim Basin	9	0	0
11	Japan	9	2	22
12	India	28	3	11
13	Oman	20	4	2
14	Iran	11	0	0
15	Kuwait	15	0	0
16	Israel and Sinai	21	3	14
17	Eastern Desert	17	0	0
18	N Tunisia	32	1	3
19	Algeria	29	1	3
20	Morocco	24	1	4
21	Senegal	13	0	0
22	Lake Chad Basin	20	0	0
23	Ghana/Ivory Coast	14	0	0
24	E Georgia	21	2	1
25	US Gulf Coast	47	5	11
26	California	20	2	10
27	Cuba	22	0	0
28	Mexico	13	0	0
29	Jamaica	16	1	6
30	Potiguar basin	21	0	0
31	Chubut	14	3	21
32	Orange Basin	19	1	5
33	E South Africa	32	2	6
34	Mozambique	15	0	0
35	Carnarvon Basin	31	7	23
36	Perth Basin	36	7	19
37	ODP Site 689	9	1	11
38	James Ross Basin	12	1	8

Numbering of OGUs is according to Table 1.

order to achieve a more or less homogenous and comparable dataset, only regions were taken into account for the quantitative methods where at least 10 genera are present. Therefore, the three OGUs Tarim Basin (China), Hokkaido (Japan) and ODP Site 689 (Southern Ocean) were excluded from the calculation. In the case of the latter two of these OGUs, this low diversity is combined with high to relatively high rates of endemicity (see Table 2). This would disturb the dataset and lead to an outgrouping of these areas. All analyses were carried out on an IBM-compatible PC using PAST software package version 0.87b (Hammer et al., 2001).

2.2. Endemicity

The study of endemics has proved to be a useful tool in biogeography. For ostracods, a number of studies have highlighted that extended spatial isolation is essential for the generation of endemic taxa (e.g. Larwood and Whatley, 1993; Boomer and Whatley, 1996). Consequently, by measuring endemicity, it is possible to allude to the degree and duration of geographic isolation of a fauna. Herein, endemicity is measured as a percentage: percentage endemism= $n/N \times 100$, with N the total number of taxa in a given OGU and n the number of taxa restricted to that particular region (Table 2).

2.3. Multivariate statistics

The use and methodology of multivariate analyses for palaeobiogeographical interpretations have been discussed and applied to different faunas in a number of studies (e.g. Rosen, 1988, 1992; Smith, 1992; Shi and Archbold, 1996; Liu et al., 1998; Geraads, 1998; Shen and Shi, 2000). An overview on the various multivariate methods, their mathematical background and the use of different similarity coefficients and clustering methods were provided by Cheetham and Hazel (1969), Shi (1993), Liu (1995) and Harper (1999), among others.

From the raw data, a secondary data matrix was developed, consisting of presence/absence (i.e. 1/0) data of all genera from the 35 remaining OGUs. From this dataset, a similarity matrix was constructed to formulate the Jaccard ("coefficient of community") coefficient of similarity between samples. This was

chosen because it is a widely used binary similarity coefficient that has demonstrated its suitability in a number of studies (e.g. Cheetham and Hazel, 1969; Shi, 1993 and references therein). Shi (1993) tested 39 binary coefficients and rated their overall suitability as similarity measures between samples. He concluded that none of these coefficients meets all the tested criteria perfectly. However, the Jaccard coefficient is among those that perform better than others, and Shi (1993) strongly recommended its usage. Based on the Jaccard coefficient, a cluster analysis was carried out and a dendrogram was constructed based on an unweighted pair-group method using arithmetic average (UPGMA). There are a number of clustering techniques, which are distinguished by the manner of defining intercluster distances. An overview on these and the advantages and disadvantages of the different methods are given by Shi (1993).

2.4. Ordination

To complement the multivariate statistical methods and as a cross-checking tool for the congruency and rigour of the different methods used, the dataset was also analysed with ordination methods. The two methods used were principal coordinate analysis (PCO) and nonmetrical multidimensional scaling (NMDS). Ordination is a method to simplify high-dimensional datasets. The samples are ordered along a line or placed in a low-dimensional space in such a way that distances between them are preserved as far as possible. In our study, each OGU is a data point in a high-dimensional space, with a number of variables equal to the number of taxa present. Ordination means projection of this complicated dataset onto a low-dimensional space, be it 3D space, a plane—as in our study—or a line. As we used the Jaccard coefficient for the statistical methods, we also used this index for the ordination methods. For more information on ordination methods and their application, the reader is referred to Shi (1993), Jongman et al. (1995), Shi and Archbold (1996), Etter (1999) and references in these studies.

2.5. Parsimony analysis of endemism

Parsimony analysis of endemism (PAE) has become an important method in historical biogeog-

raphy. It was introduced by Rosen and Smith (1988) and subsequently discussed and tested in a number of studies (e.g. Rosen, 1988, 1992; Smith, 1992; Geraads, 1998; Waggoner, 1999; Glasby and Alvarez, 1999). PAE is a 'cladistic' method that treats the taxa of a given locality or region as its 'taxonomic' characters and groups areas (analogous to taxa in phylogenetic analysis) by their shared taxa (analogous to characters). Presence of a taxon in a given area is therefore equivalent to a derived or advanced character state in a given taxon and absence to a primitive character state. The method is used to construct monophyletic groups consisting of areas sharing one or more taxa. PAE is not 'cladistic biogeography' (e.g. Humphries and Parenti, 1986; Lieberman, 2000). In opposition to the latter concept, it does not depend on a robust phylogenetic hypothesis for the group of organisms being used (Waggoner, 1999). This is an advantage in palaeontology as in many cases the phylogeny of fossil groups is not as sound as it is for extant taxa. Cladistic biogeography applies the criterion of parsimony to the synapomorphies among different taxa in order to obtain relationships between the taxa, and area cladograms are derived from superimposing geographical distributions of these phylogenies (Rosen, 1988). In PAE, parsimony is applied to shared ('synapomorphic') taxa of different sample localities and produces area cladograms of sample localities directly from geographical distributions (Rosen, 1988).

For PAE, the taxa were coded for their absence (0) or presence (1) in each OGU in a data matrix. As the method is based on shared characters, taxa found in a single OGU (equivalent to autapomorphies) are not useful for assessing relationships. The same applies for any taxon common to all OGUs (cf. plesiomorphy). These taxa were therefore excluded from the original matrix, and the calculation of the PAE was based on a modified matrix of 134 genera. The cladogram was rooted in an ancestor or ancestral association with all taxa absent, assumed to be the most primitive state.

3. Area groupings

With UPGMA, the OGUs are broadly grouped in three large clusters (I–III) (Fig. 2). Cluster I comprises

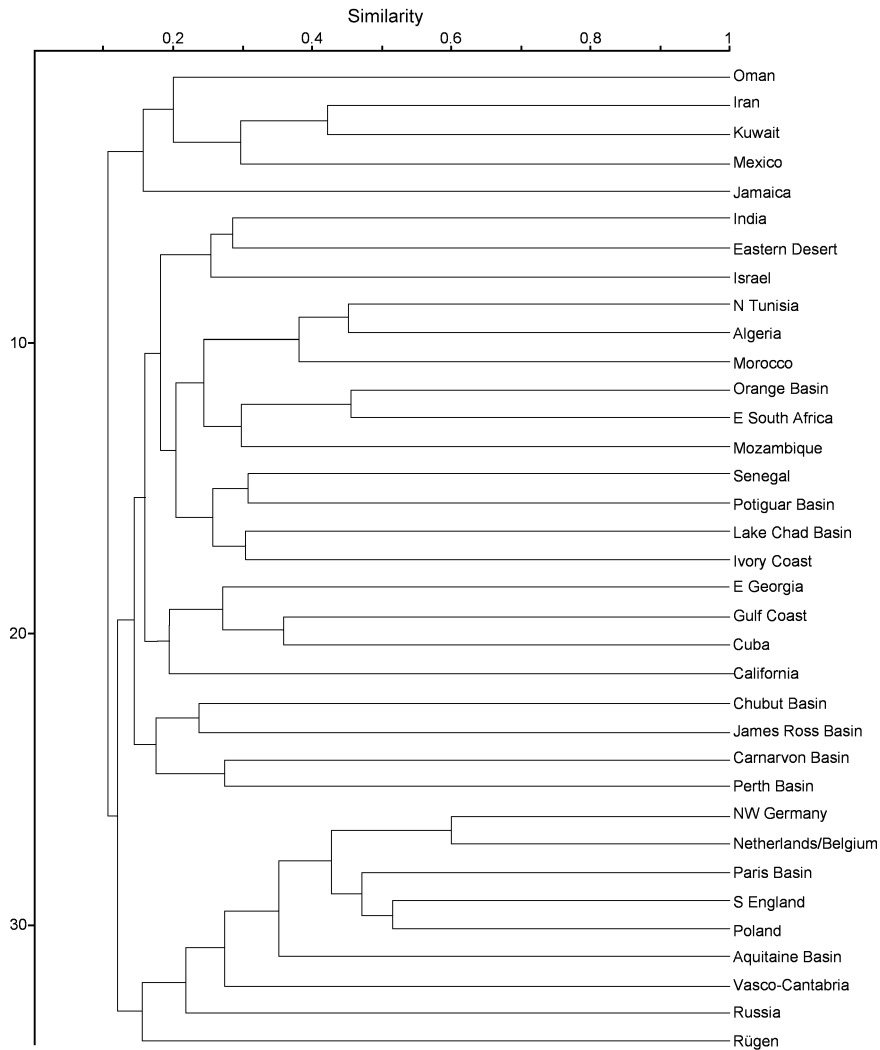


Fig. 2. Dendrogram resulting from the cluster analysis based on the Jaccard coefficient using an unweighted pair-group method with arithmetic averaging (UPGMA).

the Middle East OGUs Oman, Kuwait, Iran along with the Central American/Caribbean Mexico and Jamaica. This cluster is well separated from the other groupings. Clusters II and III contain the remaining OGUs, in which the latter includes all nine European OGUs, including the Russian locality. Cluster II has a more heterogeneous composition and allows subdivision in a number of smaller groupings. The first of these subdivisions (IIa) is represented by the three OGUs India, Eastern Desert and Israel. Cluster IIb is further subdivided in three smaller clusters: (IIb1) with the northern African OGUs Tunisia, Algeria and

Morocco, (IIb2) with the southern African OGUs Orange Basin, eastern South Africa and Mozambique and (IIb3) with the western Central African OGUs Senegal, Lake Chad Basin and Ghana/Ivory Coast that group with the northeastern Brazilian Potiguar Basin. In Cluster IIc, the North American OGUs eastern Georgia, California and the US Gulf Coast are grouped along with Cuba, in which the latter two show the greatest similarities. Somewhat separated from the other clusters that form larger cluster II is the grouping made up of the four southern South Hemisphere OGUs Chubut Basin and James Ross Basin

and the two Australian OGU's Carnarvon Basin and Perth Basin (cluster IId).

Overall, the area groupings produced by the two ordination methods are similar to those achieved by UPGMA. However, there are slight deviations between these two and the statistical method, and, moreover, there are also slight divergences between PCO (Fig. 3) and NMDS (Fig. 4). A group that was created by both methods comprises the European OGU's, herewith reproducing cluster III of the UPGMA. In contrast to the former, the North American OGU's show different behaviour as they form two small and relatively separated groups with ordination methods. Eastern Georgia and California plot between the northern African and the Southern Hemisphere OGU's, whereas the US Gulf Coast and Cuba show more affinities to the European areas. As it was the outcome of the UPGMA, the northern German OGU Rügen seems to be somewhat distant from the other European OGU's. A second grouping

created by both methods reproduces cluster I of the UPGMA. However, unlike NMDS, the PCO excludes Jamaica from this group (Fig. 3).

The smaller clusters that are included in cluster II by UPGMA are largely reproduced by ordination. However, especially the southern African OGU's are slightly more unstable with these methods and, in some details, show different behaviour. A relatively stable group with both methods is made up of the three Central western African OGU's and the Potiguar Basin. Another relatively stable group is formed by the southern South Hemisphere OGU's. The James Ross Basin is most closely related to the Argentinean Chubut Basin with UPGMA and PAE and, moreover, are very close with PCO and NMDS. Both basins have affinities to the two Australian basins that always group together. The same is true for the three North African OGU's N Tunisia, Algeria and Morocco that are closely related. India shows some relations to Israel and the Eastern Desert.

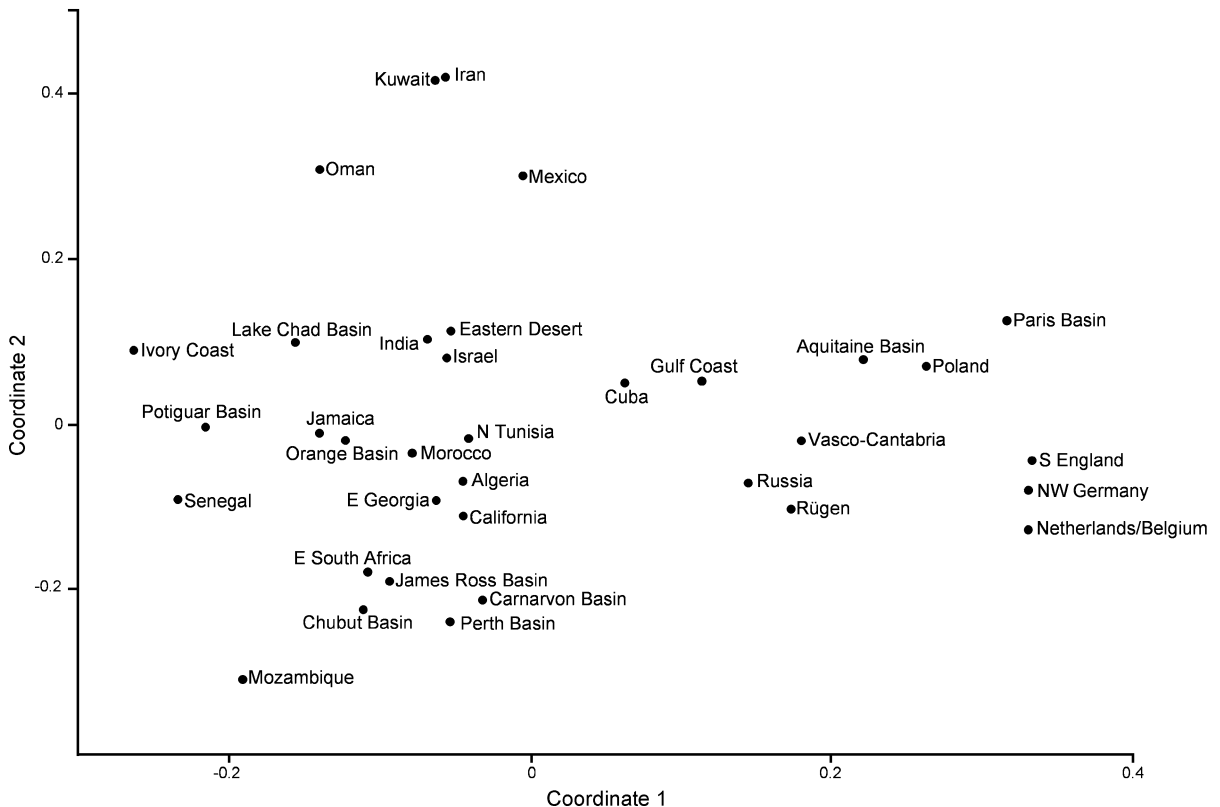


Fig. 3. Two-dimensional plot for the first two principal axes resulting from the principal coordinate analysis (PCO).

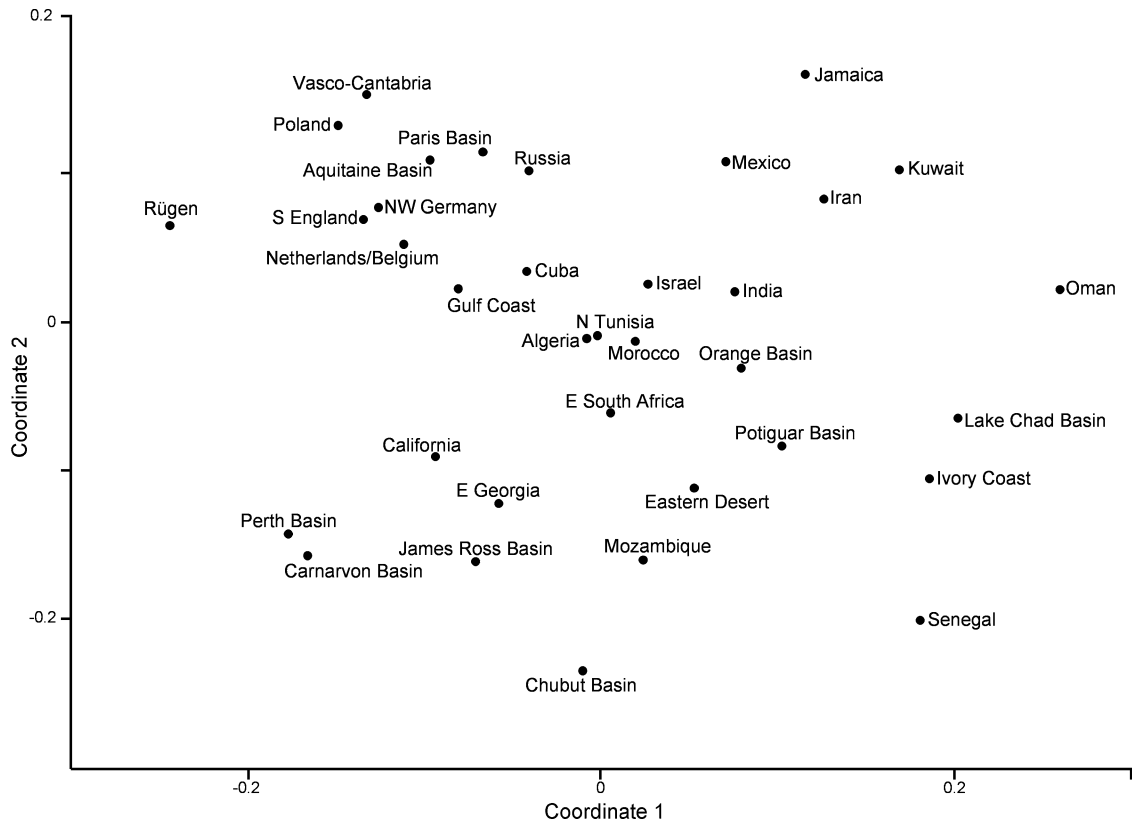


Fig. 4. Two-dimensional plot for the first two principal axes resulting from nonmetrical multidimensional scaling (NMDS).

PAE produces seven distinct area groupings that can be further subdivided into smaller groups. Even though based on a very divergent basic approach and founded on a varying dataset, the resulting area groupings achieved with PAE are very similar to those described above for the other methods (Fig. 5). In its general overall pattern of grouping together areas, the results of this method seem to be very close to those of the UPGMA. There are only a number of slight differences. With PAE, (1) Jamaica is grouped with Senegal and the Potiguar Basin, in this case reproducing the result of the PCO; (2) India groups with the southern African OGU and not with Israel and the Eastern Desert as with all other methods; and (3) James Ross Basin and the Chubut Basin form a group that is somewhat separated from the other Southern Hemisphere areas. However, although there are variations in a number of details, all methods result in a more or less similar overall pattern. Altogether, the groupings produced with the four

methods applied to the dataset seem to be relatively stable. There are only some slight variations that may be due to the different methodological approaches used.

4. Palaeobiogeographical interpretation

Biogeographical relationships between different regions are often treated using a qualitative approach. They are discussed in terms of affinities and exchange of specific taxa, rather than of overall similarities of assemblages present in these regions. Also, biogeographical provinces are often defined by single or only a few taxa. Ostracods are organisms that are sensitive to ecological conditions. Consequently, in many cases, the distribution of anyone of them does not allow more than the recognition of its own 'province'. Taking whole faunas into account enables detection of areas of greater similarity that are less likely to have

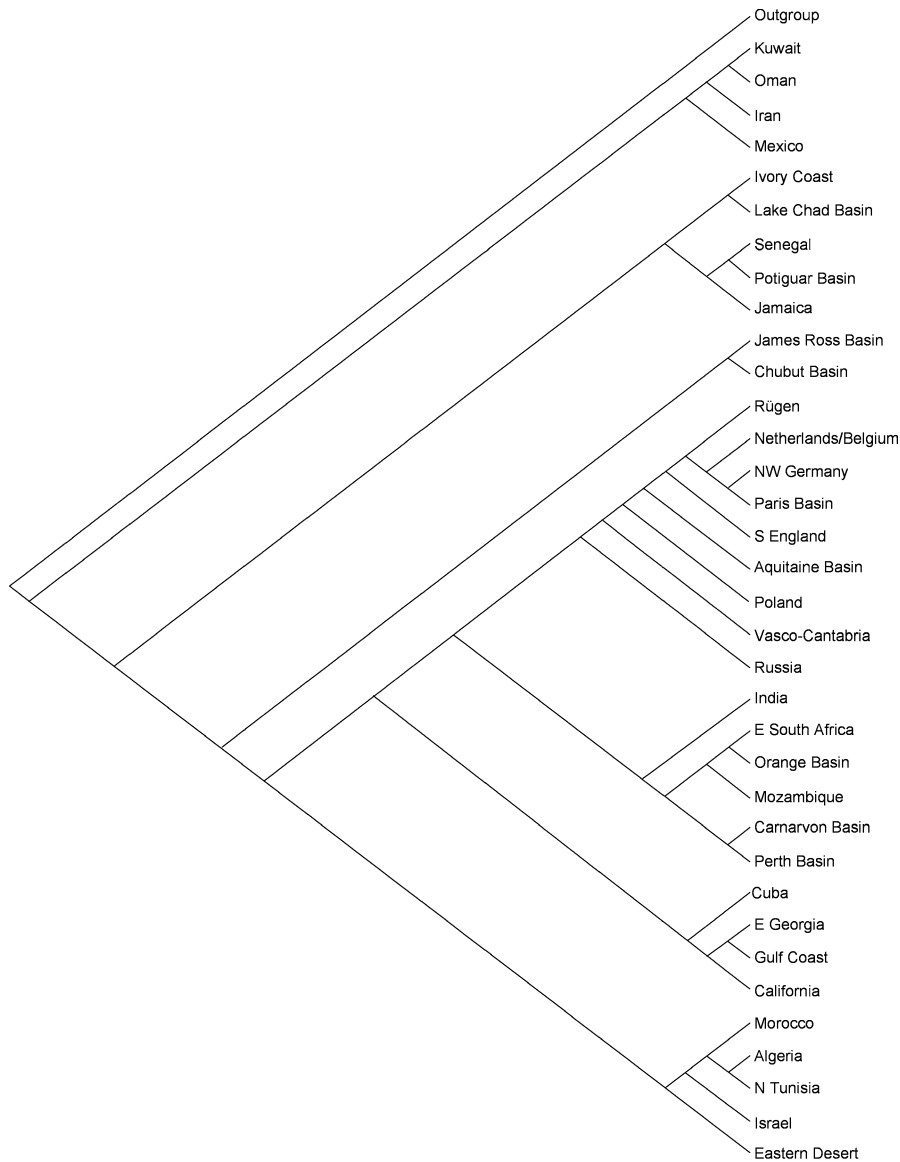


Fig. 5. Cladogram showing the one of three possible most parsimonious trees resulting from the parsimony analysis of endemicity (PAE).

purely ecological significance (Geraads, 1998). Such areas are represented by the distinct area groupings that were produced by the methods used in this study.

The area groupings were plotted on a palaeogeographical map for the Campanian that also comprised the location of the 35 OGU's calculated (Fig. 6). This resulted in seven distinct palaeobiogeographical units (PBUs) for Campanian ostracods. The term PBU is used herein as a neutral term that is solely based on

the area groupings that came out of the methods applied in this study. This terminology was chosen because it does not imply any ranking as would be indicated by terms like realm, province or subprovince, which are used in divergent manner by different authors (Westermann, 2000a,b and references therein). It also avoids confusion with the large number of names introduced into the literature by different authors for different palaeobiogeographical

units, based on different fossil groups and established for different geological times. However, in the discussion of the PBUs recognised with Campanian ostracods, a correlation with units already established is attempted. Qualitative faunal composition in the different areas as well as local environmental conditions and facies development are also taken into account. The following seven PBUs could be distinguished:

(1) A northern warm temperate or Boreal European PBU, including the mid-European OGUs Rügen, NW Germany, Netherlands/Belgium, southern England, Paris Basin, Aquitaine Basin, Vasco-Cantabria, Poland and the Russian OGU, which form a stable group with all methods. This PBU is part of the North European Province (e.g. Kauffman, 1973) of the Boreal Realm (e.g. Westermann, 2000b). The slightly greater statistical distance of Rügen from the other OGUs is most probably substantiated in the very high diversity of the Rügen fauna that is combined with a very high endemicity of 33%. There are a number of uncertainties connected with this fauna because the material from Rügen is not autochthonous but derived from a glacial erratic lump that was embedded in early Pleistocene till (Herrig et al., 1997). It represents the only sample of Campanian age known from the Isle of Rügen. The material for that study was sampled in the 1950s, and in the mean time, the outcrop was totally destroyed by coastal erosion. It could not have been restudied and the authors depended on written communications of the original finder. Herrig et al. (1997) attempted an interpretation of the geographical origin of this material. With regards to the possible distribution of Campanian sediments in the area and in consideration of the direction of the ice movement, they concluded an original deposition in the east or northeast of Rügen, between the isles of Bornholm in the north and Usedom/Wolin in the east. However, in comparing their ostracod and foraminifer fauna to those of adjacent areas, Herrig et al. (1997) pointed out that there are greater affinities to western European faunas of northwest Germany and the Netherlands than to that of Poland.

Within the Boreal European PBU, two principal types of ostracod assemblages can be distinguished. The first assemblage is represented by a shallow-water, high-energy fauna, restricted to the “tuffeau” bioclastic carbonate facies, that occurs at the margins

of the Aquitaine Basin (Babinot and Colin, 1983). This assemblage contains various genera of the Trachyleberididae and Hemicytheridae, for example, *Dumontina*, *Kikliocythere*, *Limburgina*, *Mauritsina*, *Mosaeleberis* and *Spinoleberis*. This is a typically “ancestral” Tethyan association, known to occur from the Cenomanian of the northern margin of the Tethys. Northward migration of Tethyan taxa was related to warm water currents and the opening of a seaway between the Tethyan and Boreal realms and could have started in the Santonian (Bless et al., 1990; Bless, 1991). The second assemblage is present in the deeper water, chalky facies of northern Europe (England, Belgium, Netherlands, Germany and Poland) and the deep environments of the central Aquitaine Basin and northern Spain (Vasco-Cantabrian region). This fauna is characterised by a high diversity of Bythocytheridae and the common presence of, for example, *Trachyleberidea*, *Pterygocythere*, *Alatacythere*, *Phacorhabdotus*, *Imhotepia* and *Cytherelloidea*. According to Clarke (1982), the presence of the latter genus clearly suggests warm water temperatures.

(2) An arid to warm temperate northern American PBU including eastern Georgia, the US Gulf Coast and California. With UPGMA and PAE, these three OGUs form a distinct group that has affinities to the European warm temperate faunas, as well as to the Tethyan subtropical PBU discussed below. The correspondence of these two PBUs is also reflected by the qualitative composition of the faunas, in which warm temperate European elements (e.g. *Trachyleberidea*, *Curfsina*, *Limburgina*, *Pterygocythere* and *Neocythere*) occur along with typical Tethyan taxa (e.g. *Physocythere*, *Brachyocythere*, *Veenia*). This might be the consequence of (a) their location close to the boundary of the arid and warm temperate climate belts and (b) their position at the eastern border of the North Atlantic Ocean that represented a commensurate barrier for faunal migration of the European, as well as for the Tethyan North African faunas. Remarkably, there are no affinities to the adjacent tropical faunas of Mexico and Jamaica, which had a relatively close palaeogeographical position. However, it has to be stressed that the ostracod faunas described from the Campanian of Mexico and Jamaica derive from Tethyan carbonate facies with larger foraminifera and rudists (Dilley,

1973). According to Babinot and Colin (1988), the fauna shows a certain endemism marked by the presence of the genera *Fissocarinocythere*, *Ascetoleberis*, *Escharacytheridea* and *Antibythocypris*. This PBU might extend as far north as off eastern Canada (Ascoli, 1975).

(3) An arid, subtropical Tethyan PBU that, in addition to Israel, Egypt, Tunisia, Algeria and Morocco, also comprises India. The first five OGUs of this PBU lie within the Mediterranean Province (e.g. Kauffman, 1973) or the Mahgreb–Near East Subprovince of the Afro-Arabian Bioprovince (Babinot and Colin, 1992) of the Tethyan Realm (e.g. Westermann, 2000b).

In shallow platform environments, the fauna contains typical “West African” elements, as illustrated by the occurrences of *Brachycythere*, *Buntonia*, *Cophinia*, *Ovocytheridea* and *Veenia*. In marked contrast to this are faunas from outer-neritic environments, where an assemblage with *Aphrikanocythere*, *Doricysthereis*, *Kefiella*, *Megommatocythere*, *Ordonyia* and *Paleocosta* developed. Unfortunately, data from India are meagre and somewhat problematic. The presence of the important genus *Brachycythere* should, however, be mentioned. Jain (1977) reported a fauna from the lower Maastrichtian of South India that has great similarity to the Maastrichtian of Holland. In particular, the occurrence of the genera *Curfsina*, *Dumontina*, *Limburgina* and maybe *Mauritsina* indicates strong affinities with the Boreal European PBU (McKenzie, 1982; Babinot and Colin, 1992). These faunal affinities are somewhat contradictory to the proposed geographical position of India during this period.

(4) A tropical West African–northern South American PBU, composed of Senegal, Lake Chad Basin, Ghana/Ivory Coast, Potiguar Basin and probably Jamaica, as the latter is included with PCO and PAE in this group. With regards to the qualitative composition of the faunas, this PBU apparently also includes Liberia, Cameroon, Nigeria, Gabon and the Congo (Grékoff, 1951; Khan, 1970; Kogbe and Me’hes, 1986; JPC unpublished data). The most diagnostic taxa for this PBU are *Brachycythere*, *Buntonia*, *Nigeria*, *Ovocytheridea*, *Protobuntonia*, *Reticulocosta* and *Soudanella*. To some extent, the Lake Chad Basin shows affinities with the shallow water subtropical Tethyan PBU as indicated

by the presence of *Hermanites*, *Veenidea* and *Tethysobuntonia*.

(5) A tropical Arabian PBU that includes Oman, Iran, Kuwait and Saudi Arabia. These areas show affinities to the Central American OGU Mexico with all methods and to Jamaica with UPGMA and NMDS. This PBU is related to the tropical PBU described before (4) above. Characteristic genera of this PBU are *Brachycythere*, which is represented by several species, *Nucleolina*, *Foveoleberis*, *Paragrenocythere* and *Kaesleria*. The latter two genera are strictly restricted to this area during the Campanian (Al-Furaih, 1980, 1986).

(6) An arid, subtropical South African PBU comprising the three OGUs Orange Basin, eastern South Africa and Mozambique. Data from the Maastrichtian of Madagascar are in perfect agreement with the faunal composition of this PBU (Babinot et al., 1996; JPC, work in progress). These OGUs show a somewhat unstable behaviour that might be a consequence of (a) their palaeogeographic position near the borders of the southern arid and warm temperate climate belts on the one hand and (b) on the northern coast of the Southern and Indian oceans on the other. The flooding of the Walvis Ridge–Rio Grande Rise barrier allowed faunal exchange along the western margin of the African continent from late Cenomanian times onwards. This led to the establishment of a widely distributed Pan-Gondwanian fauna by Coniacian times at the latest (Dingle, 1988). Consequently, there are some affinities to the other Southern Hemisphere localities as reflected by the presence of, for example, *Apateloschizocythere* and *Rayneria*. However, affinities to the arid northern African OGUs seem to be closer, which is underscored by the frequent occurrence of, for example, *Brachycythere* and *Buntonia*.

Characteristic genera of this PBU are *Australileberis*, *Dutoitella*, *Haughtonileberis*, *Agulhasina*, *Unicapella*, *Pondoina* and *Gibberleberis*. Most of these genera are endemic to this PBU. The common presence of *Brachycythere*, a typical Pan-Gondwanian genus (sensu Dingle, 1988), clearly differentiates this province from the following Austral PBU.

(7) A southern warm temperate or Austral PBU including the Chubut Basin and the James Ross Basin

and, in western Australia, the Carnarvon and Perth basins. Data from the Southwest Pacific indicate that these faunas (including, for example, *Pennyella* and *Parahemingwayella*) belong to this PBU (Boomer et al., 1995). The Austral PBU lies within the Austral Bioprovince of Babinot and Colin (1992) or the Transitional Realm of Huber (1992). For the Cretaceous southern high-latitude regions, a number of biogeographical province names were introduced and used by various authors: (1) Palaeoaustral Element used by Fleming (1962) and Stevens (1980) based on faunal and floral endemism of Early Cretaceous shallow marine and terrestrial organisms; (2) Weddellian Province used by Zinsmeister (1982) and Macellari (1985) based on faunal endemism of Late Cretaceous molluscs (bivalves, gastropods, ammonites); (3) Austral Province used by Fleming (1967) and Kauffman (1973) based on faunal endemism of Early Cretaceous bivalves and gastropods, and Scheibnerova (1971, 1973), Sliter (1976) and Krashennikov and Basov (1983, 1986) based on the low diversity and absence of tropical species among Early Cretaceous benthic and planktonic foraminifera; (4) Austral Realm used by Huber (1992) based on endemism, low diversity and absence of tropical species of benthic and planktonic Late Cretaceous foraminifers. The term Austral Realm was also used by Babinot and Colin (1992) for Late Cretaceous ostracod distributions. All the above studies are founded on qualitative methods to compare and differentiate faunas. Consequently, the definitions of these biogeographical units are based on such approaches. According to Westermann (2000b), the term Austral Realm is the valid and preferred name for the southern high-latitude Mesozoic biogeographical unit.

The most characteristic ostracod genera for the Austral PBU are *Majungaella* and *Rostrocytheridea*. In comparison to the South African PBU, the most apparent difference is the absence of *Brachycythere* and *Haughtonileberis*. The genus *Bertlesiana* has up to now only been reported from the Chubut Basin and is most probably restricted to that basin. The assemblage at Hamilton Point is mainly composed of species of *Rostrocytheridea*, *Mandelstamia*, *Majungaella* and *Cytherelloidea*, whereas species of *Cytherella*, *Bairdia*, *Argilloecia*, *Paracypris*, *Eocytheropteron* and *Cytheropteron* are less frequent. The generic composition of the fauna indicates normal

marine salinity. Although the genus *Cytheropteron* can have a wide bathymetric range, typical deep water genera are absent from the assemblage. The abundance of *Majungaella*, which had a typically tropical distribution in the Cretaceous (Whatley et al., 2001), as well as the occurrence of *Cytherelloidea* indicate relatively warm water temperatures. This supports the idea of warm climates in high-latitude regions in the Late Cretaceous (e.g. Barron et al., 1995; Huber, 1998; MacLeod et al., 2001). The two Australian OGUs are characterised by relatively high degrees of endemism of 25% and 19%, respectively (Table 2). Typical endemic genera for these basins are *Eorotundacythere*, *Hystrichocythere*, *Paramunseyella*, *Premunseyella*, *Scepticocythereis*, *Toolongella*, *Hemingwayella* and *Verseyella*. In discussing the generic composition of these ostracod faunas, Neale (1976) pointed to the mixture of cosmopolitan and endemic genera in this region. He entitled this “an Australian Upper Cretaceous paradox” and, assuming that ocean currents are the main controlling factor in ostracod migration and dispersal, he proposed a model for the distribution of Australian Cretaceous ostracods. The faunal affinities between assemblages in different regions of this PBU may be, on the one hand, related to seafloor spreading and subsidence between Antarctica, Australia and New Zealand and the northward drift of South America from the Antarctica Peninsula, and, on the other, to a global sea-level rise during the middle Campanian, which provided new routes for shallow marine communication between the Indian, Pacific and South Atlantic ocean basins (Huber and Watkins, 1992). Species of *Majungaella* are considered good examples for the faunal exchange during the Cretaceous in this region (Ballent et al., 1998).

The main factors controlling marine ostracod distributions are salinity, composition of seawater, bathymetry, temperature, the substrate, hydrodynamics and nutrients (Whatley, 1983). According to most authors, recent benthic ostracods are unable to migrate over long distances without stable ecological conditions (see discussions in Babinot and Colin, 1992; Fauth, 2002). For that reason, migration of such organisms requires a great number of generations. However, in consideration of a mean species duration in ostracods of around 4.8 Ma (Lethiers, 1988), there was time enough for migration over

wide distances. In addition, iterative adaptation to small environmental changes by means of allopatric speciation may take place along the migration pathway (Whatley, 1983; Whatley and Ayress, 1988). Ostracods can therefore migrate latitudinally when temperature and other ecological parameters remain stable within certain limits and continental margins can function as migration pathways (Babinot and Colin, 1992).

The ostracod PBUs are broadly ordered parallel to the palaeolatitudes, and it appears that their development and distribution were largely controlled by palaeoclimate, partly modified by Campanian palaeogeographies. This becomes evident in particular when the resulting ostracod provinces are compared to the extensions of the Late Cretaceous climate zones (Fig. 6). Late Cretaceous climates were generally warm and the global sea level much higher than today. This led to relatively low-temperature gradients between polar and equatorial regions (Huber et al., 1995). However, also in Late Cretaceous times, differences in regional climates existed

that allows the differentiation of climate zones. Humid areas occurred around the equator and in the mid-latitudes. Arid climate conditions were distributed north- and southward of the equator to 30° latitude (Dullo et al., 1996). These are bordered by warm temperate zones to the north and the south. Only directly in the vicinity of the poles cooler but still temperate climates existed (e.g. Ditchfield et al., 1994). On the basis of geochemical data, for example, Huber et al. (1995), Huber (1998) and Dingle and Lavelle (2000) proposed a warm climate for the Turonian–Campanian with a temperature optimum around early-mid-Campanian times for southern high-latitude regions. This is strengthened by sedimentological (Dingle and Lavelle, 1998) and palaeobotanical (Francis, 1999; Francis and Poole, 2002) studies. A warm climate for the Campanian of Antarctica is also confirmed by the composition of the ostracod fauna from the James Ross Basin (Fauth et al., 2003). In particular, the presence of *Cytherelloidea* and *Majungaella* suggests warm water temperatures, and Whatley et al. (2001) stated that

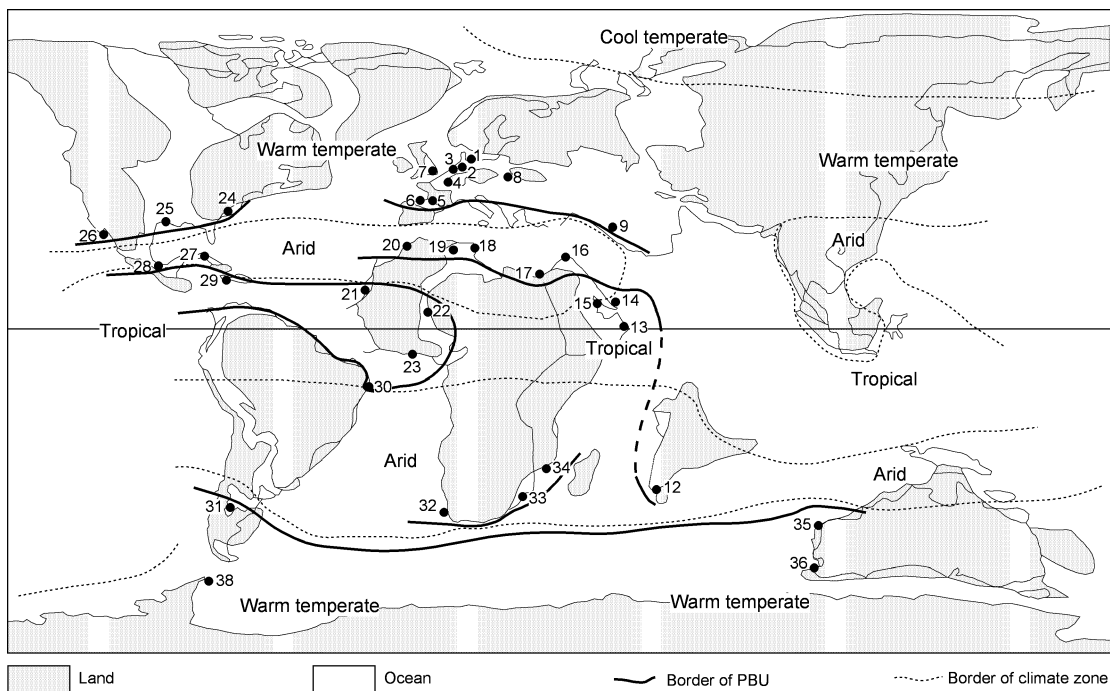


Fig. 6. Palaeogeographical map for the Campanian including extension of climate zones during the Late Cretaceous, location of the 35 OGUs calculated and ostracod PBUs resulting from the different methods applied in this study. Reconstruction of climate zones is based on Scotese (2002), and palaeogeographical reconstruction is based on Barron et al. (1981), Barron (1987), Funnell (1990) and Scotese (2002).

“the occurrence of *Majungaella* in the Mesozoic is unequivocally tropical”.

5. Conclusions

As statistics, ordination and ‘cladistic’ methods are much less sensitive to inadequate sampling, unsure dating of localities or even taxonomical uncertainties; they are much more reliable for palaeobiogeographic interpretations than the use of selected taxa. In particular, when the dataset is analysed by different methods based on divergent methodological approach, these statistics are complementary and may function as a cross-check for the stability of the results. The analyses of ostracod faunas reveal that seven marine biotic geographical units defined by the occurrences of genera of that fossil group appear to have existed during the Campanian (Upper Cretaceous). These are (1) a northern warm temperate or Boreal European PBU, (2) an arid to warm temperate northern American PBU, (3) an arid, subtropical Tethyan PBU, (4) a tropical West African–northern South American PBU, (5) a tropical Arabian PBU, (6) an arid, subtropical South African PBU and (7) a southern warm temperate PBU. The distribution of these palaeobiogeographic units shown by ostracods appears to be mainly controlled by latitude-related thermal gradients, i.e. the development of climate belts evident at that time. Slight divergences in the distribution of palaeogeographic units and Campanian climate zones may be due to additional factors such as palaeogeographies, geographic distances and ocean circulation patterns, which might have functioned as biogeographical barriers or provided possible migration routes for ostracod exchange between different areas. The Campanian ostracod faunas from James Ross Island (Antarctic Peninsula) are part of a southern warm temperate or Austral biogeographic unit. The greatest similarities exist with southern Argentinean faunas from the Chubut Basin, whereas affinities with the two Australian basins that are also part of this unit are less strong.

6. Uncited reference

Whatley et al., 1988

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.palaeo.2004.07.020](https://doi.org/10.1016/j.palaeo.2004.07.020).

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