OnLine Journal of Earth Sciences 1 (2): 113-118, 2007

Quantitative Biogeography of the Upper Aalenian-Lower Bajocian Ammonites (Western Tethys): Application of the Multivariate Methods

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Abstract: In order to quantify the biogeographic dynamics of ammonites faunas of Upper Aalenian-Lower Bajocian, 9 areas located in Western Tethys were analyzed by the multivariate method (Principal coordinate analysis and calculating similarity index and distance). The results obtained reveal the following facts: -the stability and resemblance during the time of faunas of the Betic Cordillera, Iberian Cordillera, central High Atlas and the Lusitanian basin,-the fluctuation starting from the Laeviuscula zone of Dorset-Somerset, the basin of South-east of France and the folded Middle Atlas. This fluctuation is controlled by several factors: paleotemperature, eustatism, paleogeography, and trophic conditions,-the isolation of faunas of Beni Snassen and Umbria-Marche Apennines.

Key words: Biogeography, ammonites, upper aalenian-lower bajocian, multivariate method

INTRODUCTION

During the Upper Aalenian-Lower Bajocian interval Western, Tethys and Northwestern European are marked by important tectonic and eustatic events (Distension is accentuated, facies of open sea seem to extend towards the West and faunal connections become easier) (Elmi, 1993). These paleogeographic changes resulting from the break up of Pangea had an important effect on the communities and the renewal of the ammonite fauna. Accordingly, we considered it useful to quantify the relations between faunas resulting from various areas. This quantification of biogeographic dynamics is based on a phenetic approach, which takes account neither of the ecological constraints nor of the historical atavism (Dommergues and Marchand, 1988). It uses only the multivariate method to recognize associations of taxa (genera or families) which make it possible to allot an area to a given paleobiogeographic entity. In the case of our study, the multivariate method (Principal coordinate analysis and the calculation of similarity and distance indices) seems quite appropriate to the quality of the gathered data.

MATERIALS AND METHODS

The data used in this research come from 9 areas divided in Western Europe and North Africa (Fig. 1). Dorset-Somerset (Callomon and Chandler, 1990), the Lusitanian basin (Fernandez-Lopez *et al*., 1988; Rocha *et al*., 1990; Henriques, 1992, 2000) the Iberian Cordillera (Fernandez-Lopez, 1985; Linares *et al*., 1988 and Goy and Ureta, 1990), the Betic Cordillera (Sandoval, 1983; Sandoval, 1990; Linares and Sandoval, 1990; Linares and Sandoval, 1993; Sandoval *et al*., 1999 and Sandoval *et al*., 2001), the South-east of France basin (Caloo, 1970, 1971; Pavia, 1983 and Sadki, 1984), the Umbria-Marche Apennines (Cresta, 1988; Cresta and Galacz, 1990 and Cresta *et al*., 1995), Beni Snassen (Ouahhabi, 1994), the Folded Middle Atlas (Benshili, 1989, 1990 and Benshili and Elmi, 1994) and the central High Atlas (Sadki, 1992, 1994, 1996). These various areas have been selected for their relatively precise biostratigraphic data.

Working of the faunal lists: As we use data coming from different authors, we are thus obliged to homogenize to maximum the faunal lists from a taxonomic viewpoint. First, certain suspect data have been corrected by a revision of the material preserved at the universities of: Coimbra (Portugal), Granada (Spain) and Lyon (France) or simply by an analysis of the figurations. Then, dubious categories (cf, gr., aff. and sp.) were removed and the faunal lists have been consigned in two types of matrices:

- Matrix representing the taxonomic composition in term of genera number per family for each area;

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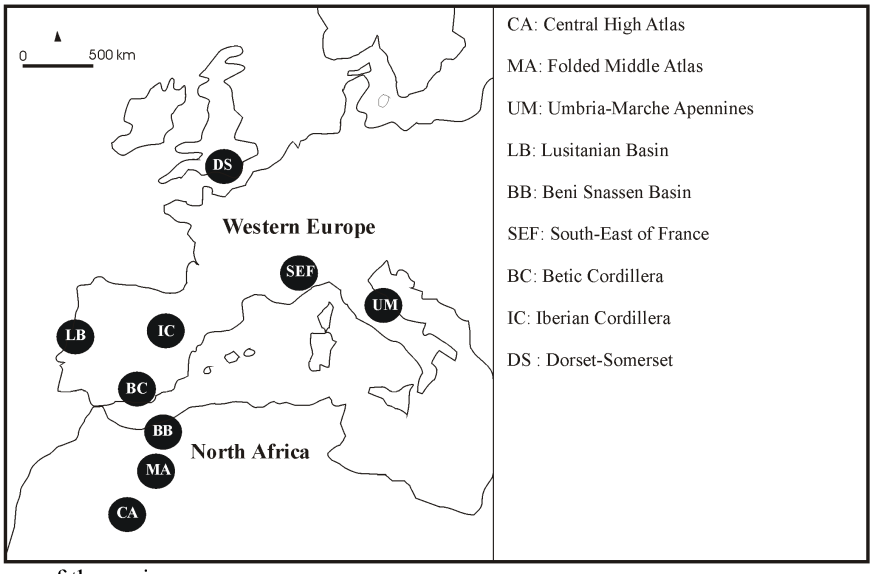

Fig. 1: Location map of the main areas

- Binary matrix (Presence/Absence), i.e. number Tables expressing the presence, or the absence of a taxon in an area, coded by 1 (certified presence) or 0 (probable absence).

Let us note that, microconch-macroconch dimorphism suggested by certain authors was not retained in this analysis. Each dimorphus couple has been regarded as two distinct taxonomic entities.

Data processing

Quantitative data processing (abundance): For the analysis of abundance data, we used the software PAST-Palaeontological Statistics, ver. 1.30 (Hammer *et al*., 2004). The matrix obtained in term of genera number per family for each area (Table 1) has been treated by using principal coordinate analysis and hierarchical ascendant classification. The latter is the result of distance measurement based here on the Bray-Curtis's coefficient. It makes possible to gather the areas according to their proximity in taxonomic term of composition. However, it is important to stress that the choice of the algorithm calculation of distances depends on the type of the elaborated matrix. In our case, the matrix manufactured starting from 12 families and 9 areas hardly adapts to the use of distance index (Chord, Manhattan and Pickford) often employed by certain authors for more important data (Moyne and *al*., 2004).

Qualitative data processing (binary): Contrary to the preceding method, we chose, for the qualitative data analysis (binary), the software BG-Index worm.1.1 ß (Escarguel, 2001). The aim was to compare the degree of resemblance or dissimilarity between each couple of lists generated by the data base. This degree has been calculated by the index of similarity (coefficients of

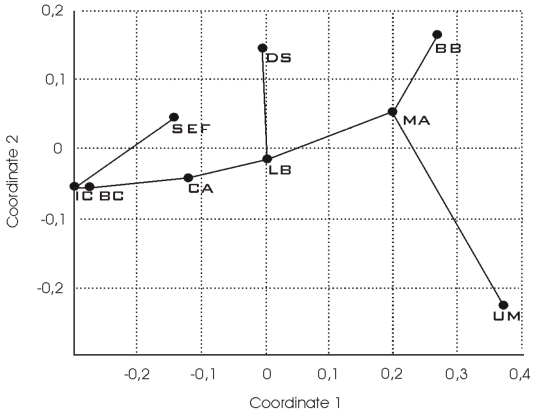

Fig. 2: Principal coordinates analysis of the distance matrix of Bray-Curtis calculated for Table 1

Simpson, Jaccard, Dice and Braun-Blanquet) or of distance (Bray-Curtis coefficient) from a chronological viewpoint, by carrying out calculations interval by interval. The results of these calculations have been represented in a phenogram pattern, which will be transformed thereafter into Venns's Diagram, or "Hierarchical Diagram of Association".

RESULTS AND DISCUSSION

Quantitative comparison of the intrafamily taxonomic richness between areas: The results obtained by the program PAST-PAlaeontological STatistics from the genera abundances matrix (all confused chronological intervals) are presented as plane graphs (principal coordinate analysis) and trees of which the length of the branches is proportional to the distance between the taxonomic composition with the various areas.

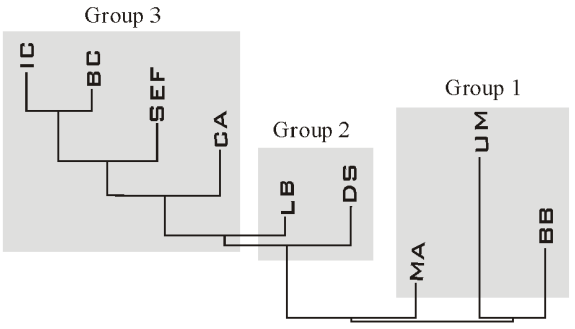

Fig. 3: Phenogram (tree of "Neighbor-Joining") allowing the visualization of the proximity relations between areas recorded in the distance matrix of Bray-Curtis calculated for Table 1

Thus, from this intrafamily genera richness, three principal groups come out (Fig. 2 and 3). A first group made up of three areas: Umbria-Marche Apennines basin (UM), Beni Snassen (BB) and folded Middle Atlas (MA). It is more or less isolated on the hierarchical ascendant classification. A second intermediate group: Dorset-Somerset (DS) and Lusitanian Basin (LB) showing an intrafamily genera composition relatively nearby. Finally, four remaining areas: Iberian cordillera (IC), Betic Cordillera (BC), South-east of France (SEF) and central High Atlas (CA) form the third group. This group marked by the prevalence of three families (*Graphoceratidae*, *Sonniniidae* and *Stephanoceratidae*) has an intrafamily genera richness extremely similar. This taxonomic organization does not correspond to any obvious geographical gradient, as well latitudinal as longitudinal. Its significance is thus ecological and/or physiographical.

Qualitative comparison of the taxonomic composition between areas: From the similarity and distance matrix obtained with 5 indexes, we have analyzed here the similarity of faunas by comparing the 9 areas for each Upper Aalenian-Lower Bajocian interval (Fig. 4). Let us note that only identical values of Jaccard index, Dice and of Bray-Curtis have been further presented and discussed. The very affected values of Simpson index and Braun-Blanquet are not taken into account.

Interval 1: Concavum zone: During this interval, general topology shows that faunas of the Betic Cordillera (BC) and Iberian Cordillera (IC) are the most nearly similar and share 22 genera (57 %). The distance separating this fauna and that from the three areas: Beni Snassen (BB), folded Middle Atlas (MA) and the Umbria-Marche Apennines basin (UM) is maximum, which corresponds to a little marked faunal isolation in the domain of Western Tethys.

Interval 2: Discites zone: From this period, general topology starts to change by the bringing together of the folded Middle Atlas (MA) and those of the Dorset-Somerset (DS) faunas. These two areas marked by primarily condensed deposits have 8 genera (*Euhoploceras*, *Docidoceras*, *Toxolioceras*, *Braunsina*, *Bradfordia*, *Fontannesia*, *Haplopleuroceras* and *Trilobiticeras*). For the other areas, the similarity gradient is the same one.

Interval 3: Laeviuscula zone: During this period, a new similarity gradient is indicated. It's characterized especially by:

- The large ressemblance between the Iberian Cordillera (IC) and the Central High Atlas (CA) faunas. This resemblance is related to the presence of 26 genera common to the both areas (70 %).
- The fauna distance of Dorset-Somerset (DS) compared to those of the South-east of France (SEF).
- The bringing together of faunas of the folded Middle Atlas (MA) of those of the South-east of France (SEF). We could record 8 genera in commun (*Bradfordia*, *Emileia*, *Euhoploceras*, *Gerzenites*, *Pelekodites*, *Sonninia*, *Trilobiticera* and *Witchellia*).

Interval 4: Propinquans zone: During this interval, the modification of general topology is accentuated. Thus, we have distinguished:

- A great ressemblance enters faunas of the central High-Atlas (CA) and those of the Betic Cordillera (BC). The two areas share 19 genera in commun runs (54%).
- A fauna distance of the South-East of France (SEF) compared to those of the folded Middle Atlas (MA). The South-east basin of France (SEF) presents at this period an intermediate similarity between the Iberian Cordillera (IC) and the Lusitanian Basin (LB).
- A fauna distance of Dorset-Somerset (DS) towards the South. They form with faunas of the Umbria-Marche Apennines (UM) a new node. The total number of genera is 7 (*Emileia*, *Kumatostephanus*, *Labyrinthoceras*, *Otoites*, *Papilliceras*, *Skirroceras* and *Stephanoceras*).

Interval 5: Humphriesianum zone: During the Humphriesianum zone, inferred topology differs appreciably. The bringing together, between faunas of the central High Atlas (CA) and the folded Middle Atlas (MA) on the one hand and faunas of the Lusitanian basin (LB) and the Umbria-Marche Apennines (UM) on the other hand, is related to the

Table 1: Matrix of genera belonging to different families and divided into 9 areas

Family	DS	LB	IC	BC	SEF	UM	BB	MA	CA
Hammatoceratidae	1	3	3	5	3	3	1	3	4
Graphoceratidae	6	6	11	10	10	1	4	4	5
Erycitidae	2	3	7	7	1	3	1	2	5
Sonniniidae	11	11	12	11	9	5	6	7	13
Strigoceratidae	2	3	4	4	3	3	2	1	4
Lissoceratidae	1	1	1	2	1	0	1	1	1
Oppeliidae	5	5	10	8	9	1	4	4	6
Otoitidae	5	6	6	6	5	4	3	4	6
Sphaeroceratidae	4	3	4	4	3	1	3	2	3
Stephanoceratidae	8	7	16	15	12	5	5	7	11
Perisphinctidae	0	0	2	0	1	0	0	0	0
Incertae sedis	0	1	0	1	0	0	0	0	1

Table 2: Values of Pielou's criterion calculated for each chronological interval
Index: Simpson (**S**), Braun-Blanquet (**BB**), Jaccard (**J**), Dice (**D**), Bray-Curtis (**BC**)

	Q1/Qmax					
	S	BB	J	D	BC	----------Q/Qmax----------
Humphriesianum	0,4267	0,4853	0,4744	0,4744	0,4744	
Propinquans	0,4725	0,5128	0,5275	0,5275	0,5275	
Laeviuscula	0,5385	0,4707	0,5018	0,5018	0,5018	0,3921 < Q/Qmax < 0,6060
Discites	0,5476	0,5421	0,5659	0,5659	0,5659	
Concavum	0,4908	0,4963	0,5238	0,5238	0,5238	

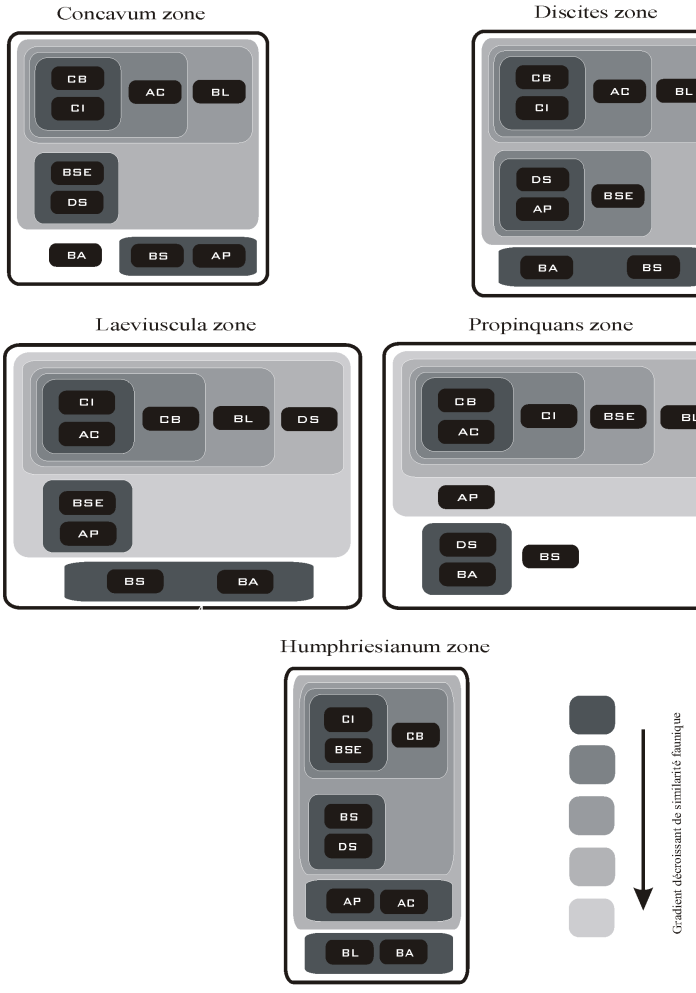

Fig. 4: Hierarchical diagrams of associations between area by chronological intervals

quality of the faunal register. With regard to the other areas, the faunal distances show light modifications.

Criterion test of Pielou: The obtained values of Pielou's criterion (Q / Qmax) show that matrix (DS-LB-CI-BC-SEF-UM-BB-MA-CA) (Table 1) is completely disordered (ungraded matrix) (Table 2). Therefore, the order of the analyzed areas on this matrix does not follow any geographical or chronological sequence.

CONCLUSION

During Upper Lias-Dogger, the Western Europe and North Africa paleogeographic diagram corresponds to a continental shelf carrying an archipelago surrounded by more important continental masses (Contini, 1990). This new situation generated the installation of several paleobiogeographic units which we tried to analyze from the viewpoint of their faunal similarity through the nine areas considered. The whole of the data subjected to treatment for each interval shows during Upper Aalenian -Lower Bajocien the following facts:

- The great stability in time of faunas of the Betic Cordillera, Iberian, central High Atals and the Lusitanian basin.
- The fauna fluctuation (displacement) of Dorset-Somerset of South - east of France basin and the folded Middle Atlas. This fluctuation , well underlined starting from the zone with Laeviuscula , is related to coincidence between the rise in paleotemperatures according to a North-South gradient , the eustatic variations, the paleobiogeography, the trophic substances and finally the facility of the faunal connections between the areas.
- The fauna isolation generally of Beni Snassen and the Umbria-Marche Apennines.

ACKNOWLEDGEMENT

The authors thank Pr. M.H. Henriques (Portugal) and Pr . J. Sandoval (Spain) who helped us to revise a part of fauna . Dr. G. Escarguel (France) for his judicious remarks is concerning the data processing of the database. We are grateful to F. Hadji (Department of Earth Sciences , University of Tlemcen, Algeria) for the correction of the English text.

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