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Article

Rugose Coral Biogeography of the Western Palaeotethys During the Mississippian

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Abstract: The Mississippian was an epoch of strong earth system changes, both tectonic and climatic. During the Mississippian, the marine faunas experienced a recovery after the late Devonian mass extinctions, and the rugose corals are a conspicuous example. This study tries to give a general view of the utility of rugose coral to reconstruct the palaeogeography in the Western Palaeotethys during the Mississippian. The methodology includes a database with the genera and species recorded in that area and time period, compiled using more than 700 articles and revisions of several collections in Europe. We worked with the six sub-provinces defined in previous studies for the Western Palaeotethys. A generic-level analysis was performed using paired group hierarchical clustering, building clusters for the Tournaisian, early Visean, late Visean and Serpukhovian. With that information, palaeomaps for those intervals have been illustrated and discussed. The rugose corals have some deficits for the reconstruction of the biogeography because of their strong palaeoecologic control and their insufficient and unequal record, but they provide important information that improves the knowledge on the palaeogeography of the studied region.

Keywords: rugosans; database; Mississippian; palaeogeography; Dice; Simpson; palaeomaps

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1. Introduction

Palaeogeographic analyses are essential for understanding Earth's history. Palaeogeography describes the distribution of continents and oceans and is applied in palaeoclimatology, resource explorations and plate tectonic reconstructions. The methodologies used to reconstruct the planetary palaeogeography are diverse. Some reconstructions are based on tectonic data [1–3]; some have been based on palaeomagnetic information [4–6]; others use sedimentological evidence [7–9]; finally, some are based on palaeontological distributions [10–14]. The most complete palaeogeographic studies comprise mixtures of several types of information [15–17]. Large compendiums of palaeogeographic maps also use diverse types of data [18–20], but the necessity to build global maps produces an absence of details in precise times and geographic areas. For instance, the most cited maps, those of Scotese [21] (palaeomaps 61 to 64) show the Rheic Ocean closed during the late Mississippian. They also show as continental zones many of the areas in the Western Palaeotethys where rugose corals and other marine invertebrates are recorded. In addition, the information given by foraminifers places the closing of the Rheic Ocean later in the Bashkirian. Some mostly accurate maps, such as those of Domeier and Torsvik [22], locate a part of southwestern Laurentia (Florida, Georgia, Alabama) between northern Africa and the Iberian plate. The coral assemblages from Iberia and northern Africa show many similarities, but show conspicuous differences from those from southeastern North America.

The Mississippian was an epoch of strong earth system changes. The Variscan orogeny was highly active because of the convergence of Laurussia and Gondwana, affecting several terrains located in between and changing the distribution of seas and land masses [23,24].

Additionally, variations in the climate produced the transition from Devonian greenhouse to Permo-Carboniferous icehouse conditions [25,26]. This was not a lineal progression, as several cooling and warming times happened during the Mississippian [27]. Several episodes of glaciation, sea-level changes and variations in the seawater temperature and CO^2 concentration have been recorded [28,29]. During the Mississippian, the marine faunas experienced a recovery after the late Devonian mass extinctions (Kellwasser and Hagenberg) [30]. The rugose corals are a notable example: they evolved slowly to reach a high diversity during the late Visean and suffered significant extinctions during the Serpukhovian and Bashkirian [31,32].

A strong faunal provincialism resulted from tectonic and climatic changes during that time. Bambach [33] showed the provincialism affecting different groups of invertebrates such as rugosans, tabulates, bivalvs, ammonoids, brachiopods and bryozoans. Fedorowski [34] distinguished three super-provinces for the rugose coral faunas during the Mississippian: the North American super-province, the Palaeotethyan super-province and the Australian super-province. The Palaeotethyan super-province is divided into three provinces: the Western Palaeotethys, comprising Europe, North Africa and Nova Scotia; the Central Palaeotethys, comprising the Ural Mountains and Middle Asia; and the eastern Palaeotethys, comprising China, southeast Asia and Japan. Somerville et al. [35] proposed four sub-provinces in the most Western Palaeotethys: the Atlantic sub-province, the West peri-Gondwanan sub-province, the Mediterranean sub-province and the Saharan sub-province. Rodríguez-Castro et al. [36] proposed two additional sub-provinces, the Central European sub-province and the Eastern European sub-province (Figure 1).

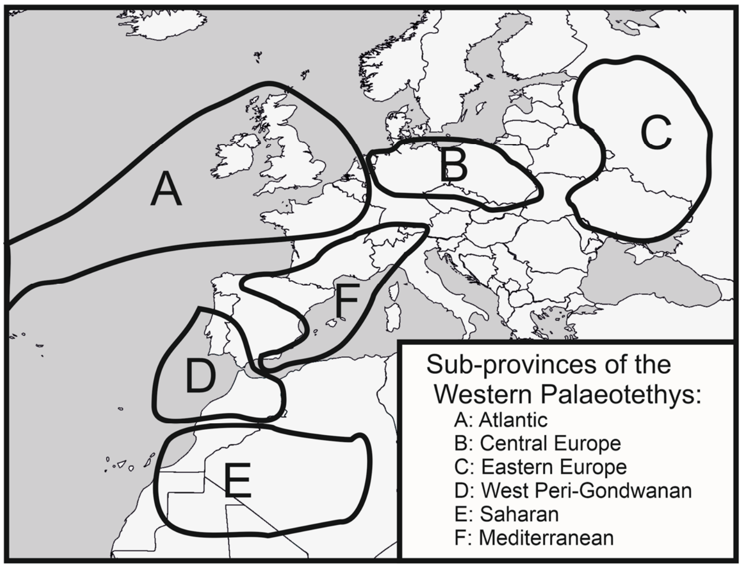

Figure 1. Distribution of the sub-provinces of the Western Palaeotethys in a recent map.

The communication between the super-provinces in the early Tournaisian was partially restricted [34] because of low sea levels and the cold climate [26]. During the late Tournaisian, the conditions improved, and there was better communication generating the "Avins event", produced by a rise in the sea level [37]. A global warming and a general transgression in the late Visean allowed easier migrations between different provinces and super-provinces, and the differences between the rugose coral assemblages diminished [34].

The variations of the rugose coral assemblages in the different sub-provinces of the Western Palaeotethys during the Mississippian provide useful information on the communication between them. The selection of the Western Palaeotethys is based on the abundance of rich rugose coral assemblages, which have been studied since the XIX century. Many papers have addressed this matter previously. Some of them are quite old [38,39]; they provide useful and interesting data, but the knowledge on rugose corals has improved in recent years. Some others are dedicated to local or regional areas such as North Africa [35,40], the Asian Gondwana margin [41], the British Isles [42], SW Spain [43], Belgium and surrounding areas [44,45], etc. Finally, other studies include only a part of the Mississippian, mainly the late Visean [46,47]. The present study aims to analyse the entire Mississippian in the Western Palaeotethys.

2. Materials and Methods

2.1. Sub-Provinces

The areas used for comparison are the four sub-provinces defined by Somerville et al. [35] and the two additional ones proposed by Rodríguez-Castro et al. [48] (Figure 1: A, Atlantic; G, West Perigondwanan; M, Mediterranian; C, central European; E, eastern European; and S, Saharan). The Atlantic sub-province comprises N. France, Belgium, the United Kingdom and Ireland. The West peri-Gondwanan sub-province comprises SW Spain and the Moroccan Meseta. The Mediterranean sub-province includes numerous outcrops in the Western Palaeotethys and along the eastern and southern borders of the French Massif Central and the Iberian Massif: Nötsch and the Carnic Alps in Austria, South France, the Pyrenees, the Cantabrian Mountains, the Betic Cordillera, the Rif and the Balearic Islands. The Saharan sub-province comprises the outcrops southern from the Atlas Mountains: Béchar, Regann, Ahnet-Mouydir and Tindouf. The Central Europe sub-province includes the Rhenohercynian, the Saxothuringian and the Moldanubian domains in Germany, the Sudetes, Upper Silesian Basin, Lublin Basin, and its southeastwards prolongation in Ukraine. The Eastern European sub-province includes Moscow Basin, Donets Basin and Voronezh.

Smaller areas would diminish the reliability of the results because of the scarcity and even the absence of coral records in some areas for particular time intervals. For instance, the absence of Tournaisian corals in SW Spain [49], the Moroccan Meseta [50] and Austria [36] or the absence of Serpukhovian corals in areas like Belgium [51] and the Rhenohercynian domain in Germany [52]. Although the coral record from the Balkans has also been compiled, it has not been included in the analysis. This region, comprised in the Brunovistulian and Moesian terranes [53], could be included in the Mediterranean sub-province or in an additional sub-province (eastern Mediterranean), together with the Istanbul Zone in north Turkiye. However, the data from the Balkans [54–56] are not entirely reliable since the figures and descriptions are of low quality.

2.2. Database

In order to ensure a robust comparison of rugose coral faunas, we began by selecting the appropriate time intervals. If the selection comprises very short intervals, such as the coral zones proposed by Poty [45], the number of genera and species will be small, and the comparison may lack statistical significance. However, if the intervals are too large, (such as the entire Mississippian), the comparison may lack accuracy. Consequently, we selected four intervals: the Tournaisian, the early Visean, the late Visean and the Serpukhovian. We built a database with the records of genera and species for each time interval considered. The database was made using about 700 papers, chapters of books and abstracts. Although the coral record data came from many different sources, most of the data were derived from the following papers and monographies: In the Atlantic Sub-province [57–63], in the Central Europe sub-province [64–69], in the Eastern Europe sub-province [31,70–76], in the West Peri-Gondwanan sub-province [77–80], in the Mediterranean sub-province [81–85] and in the Saharan sub-province [86–89]. In addition, we examined several collections from institutions in Europe (Table 1).

The database comprises 64 genera and 128 species for the Tournaisian, 56 genera and 148 species for the early Visean, 79 genera and 293 species for the late Visean, 78 genera and 151 species for the Serpukhovian (Tables 2–5 and Supplementary Tables S1–S4).

Table 1. Collections visited and revised by the authors. IRGC: Isabel Rodríguez-Castro; SRG: Sergio Rodríguez.

Institution	Checked by
British Natural History Museum, London	IRGC
British Geological Survey, Keyworth	IRGC
Institute of Geology, Adam Mickiewicz University, Poznan	IRGC
Institute for Earth Sciences at the Karl-Franzens-Universität, Graz	SRG
Vserossiskiy Nauchno-issledovatelskiy Geological Institut, S. Petersburg	SRG
Museum National d'Histoire Naturelle, Paris	SRG
Geol.-Palaont. Institut, Eberhard Karls Universität, Tübingen	SRG
Museum für Naturkunde, Berlin	SRG
Leiden University, Leiden	SRG
Geomuseum der Universität Münster, Münster	SRG
Division of the Geologic Patrimony, Rabat	SRG
Área de Paleontología, Universidad Complutense, Madrid	IRGC, SRG

Table 2. Distribution of genera in the Tournaisian.

Genera	Atlantic	C. Europe	E. Europe	Sahara
Allotropiophyllum	x			
Amplexizaphrentis		x		
Amplexocarinia	x	x		
Amplexus	x		x	x
Amygdalophyllum	x	x		
Arctophyllum			x	
Aulina	x			
Aulokoninckophyllum	x		x	
Axophyllum	x			
Batybalva		x		
Bifossularia	x	x		
Calmiussiphyllum	x		x	
Campophyllum	x	x	x	
Caninophyllum	x	x	x	
Caninia	x	x	x	x
Carruthersella	x	x		
Claviphyllum		x		
Clisiophyllum	x	x		
Commutia		x		
Conilophyllum	x	x	x	
Corphalia			x	
Corwenia	x			
Cravenia	x			
Cryptophyllum	x			
Cyathaxonia	x	x		

Table 2. *Cont.*

Genera	Atlantic	C. Europe	E. Europe	Sahara
Cyathyoclisia	x	x	x	
Delepinella	x			
Dorlodotia	x		x	
Drewerelasma	x	x		
Eostrotion	x	x		
Fasciculophyllum	x			
Hapsiphyllum	x	x		
Hebukophyllum		x		
Heterostrotion	x			
Howthia	x			
Kabakovitchiella		x		
Keyserlingophyllum	x	x	x	
Kizilia	x			
Koninckophyllum	x			
Laccophyllum		x		
Lophophyllidium	x	x		
Lophophyllum	x	x		
Lublinophyllum			x	
Melanophyllum	x			
Merlewoodia	x		x	
Nominoephyllum	x			
Palaeosmilia	x	x		
Pentaphyllum	x	x		
Proheterolasma	x		x	
Rhopalolasma	x	x		
Rotiphyllum	x	x	x	
Rylstonia	x	x		x
Saleelasma	x	x		
Semenoffia	x			
Siphonophyllia	x	x	x	x
Sochkineophyllum		x		
Solenodendron	x			x
Sychnoelasma	x	x	x	x
Syringaxon	x	x		
Thuriantha		x		
Ufimia	x	x		
Uralinia	x		x	
Zaphrentites	x	x	x	
Zaphriphyllum				x

Table 3. Distribution of genera in the early Visean.

Genera	Atlantic	C. Europe	E. Europe	W. Peri-G.	Sahara
Allotropiophyllum	x				
Amplexizaphrentis	x				
Amplexocarinia					x
Amplexus	x	x	x		
Amygdalophyllum	x	x	x		x
Aulina	x				
Auloclisia	x	x			x
Aulokoninckophyllum	x		x		x
Axoclisia	x		x	x	x
Axophyllum	x	x	x		x
Bifossularia	x	x	x		x
Bradyphyllum		x			
Calmiussiphyllum			x		
Calophyllum		x			
Campophyllum	x	x	x		
Caninia	x	x	x		x
Caninophyllum	x		x		
Carruthersella	x	x			
Clinophyllum		x			
Clisiophyllum	x	x	x		
Corphalia	x				
Cravenia	x			x	x
Cyathaxonia	x	x	x	x	
Cyathoclisia	x	x	x		x
Dibunophyllum	x	x			
Diphyphyllum	x		x		
Dorlodotia	x	x	x		
Drewerelasma		x			
Eolithiostrotionella			x		
Fasciculophyllum	x				
Haplolasma	x		x		x
Hettonia		x			
Koninckophyllum	x	x	x		x
Laccophyllum		x			
Lithostrotion	x	x			x
Merlewoodia	x				x
Palaeosmilia	x	x	x		x
Pentaphyllum	x	x			x
Proheterolasma	x				
Pseudouralinia		x			
Richrathina		x			

Table 3. *Cont.*

Genera	Atlantic	C. Europe	E. Europe	W. Peri-G.	Sahara
Rotiphyllum	x	x			
Rylstonia	x	x			x
Siphonodendron	x	x	x		x
Siphonophyllia	x	x	x	x	x
Solenodendron	x	x			x
Spirophyllum		x			
Sychnoelasma	x	x	x	x	x
Syringaxon		x			
Ufimia		x			
Uralinia		x	x		
Vassiljukia			x		
Verneuilites			x		
Zaphriphyllum					x
Zaphrentites	x	x	x		x
Zaphrentoides		x			x

Table 4. Distribution of genera in the late Visean.

Genera	Atlantic	C. Europe	E. Europe	W. Peri-G.	Saharan	Mediterranean
Actinocyathus	x	x	x			x
Allotropiophyllum.	x	x	x			
Amplexizaphrentis	x	x	x	x	x	x
Amplexocarinia	x	x		x	x	x
Amplexus	x	x	x	x		x
Amygdalophyllum	x	x	x	x	x	
Arachnolasma	x	x	x	x	x	x
Auloclisia	x	x	x	x	x	
Aulokoninckophyllum	x		x	x	x	x
Aulophyllum	x	x	x	x	x	
Axoclisia	x	x	x	x	x	
Axophyllum	x	x	x	x	x	x
Bifossularia	x	x	x	x		
Biphyllum		x				
Bothrophyllum	x	x	x	x		
Bradyphyllum	x	x		x		x
Calophyllum		x				
Campophyllum		x				
Caninia	x	x	x	x	x	
Caninophyllum	x		x	x	x	
Carruthersella	x	x			x	
Ceriodotia						

Table 4. *Cont.*

Genera	**Atlantic**	**C. Europe**	**E. Europe**	**W. Peri-G.**	**Saharan**	**Mediterranean**
Claviphyllum	x	x	x	x		
Clisiophyllum	x	x	x	x	x	x
Corwenia	x		x	x		
Cravenia	x			x		
Cryptophyllum		x	x			
Cyathaxonia	x	x	x	x		x
Dibunophyllum	x	x	x	x	x	x
Diphyphyllum	x	x	x	x	x	x
Enniskillenia	x		x	x		
Espielia				x	x	
Gangamophyllum	x	x	x	x	x	x
Guadiatia	x					
Haplolasma	x	x	x	x	x	x
Kizilia	x	x	x	x	x	x
Koninckinaotum		x	x			
Koninckophyllum	x	x	x	x	x	x
"Koninckophyllum" (colonial)	x		x			
Lithostrotion	x	x	x	x	x	x
Lonsdaleia	x	x	x		x	x
Lophophyllidium					x	
Lublinophyllum	x	x				
Melanophyllidium						x
Merlewoodia	x					
Mirka		x				
Morenaphyllum				x		
Neoclisiophyllum	x	x		x		
Neokoninckophyllum		x	x			
Nemistium	x	x	x	x		x
Nervophyllum		x	x			
Orionastraea	x	x	x			
Palaeosmilia	x	x	x	x	x	x
Palastraea	x	x	x	x		x
Pareynia	x			x	x	x
Pentaphyllum	x	x				x
Pseudocaninia		x				
Pseudoclaviphyllum			x			
Pseudozaphrentoides'	x	x	x	x	x	x
Rotiphyllum	x	x		x		x
Rozkowskia		x				
Rylstonia	x	x	x	x	x	

Table 4. *Cont.*

Genera	Atlantic	C. Europe	E. Europe	W. Peri-G.	Saharan	Mediterranean
Saharaphrentis					x	
Semenoffia				x		x
Siphonodendron	x	x	x	x	x	x
Siphonophyllia	x	x	x	x	x	x
Slimoniphyllum	x	x				
Solenodendron	x	x	x	x	x	x
Spirophyllum	x	x	x	x		
Tachylasma		x	x			
Tchernowiphyllum			x			
Thysanophyllum	x			x		
Tizraia			x	x	x	
Turbinatocaninia		x	x		x	
Ufimia	x	x	x	x		
Viseaulina	x					
Zakowia		x				
Zaphrentites	x	x	x	x	x	x
Zaphrufimia				x		

Table 5. Distribution of the genera in the Serpukhovian.

Genera	Atlantic	C. Europe	E. Europe	W. Peri-G.	Saharan	Mediterranean
Actinocyathus	x		x		x	x
Adamanophyllum			x			
Amplexizaphrentis	x		x			
Amplexocarinia				x		x
Amplexus	x		x	x		
Amygdalophyllum				x	x	
Antiphyllites		x				
Antiphyllum		x				
Arachnolasma		x	x	x	x	
Aulina	x		x		x	x
Auloclisia			x	x		
Aulokoninckophyllum		x	x	x	x	
Aulophyllum	x		x	x	x	
Axophyllum	x	x	x	x	x	x
Barytichisma			x			
Bothrophyllum		x	x		x	
Caninia	x	x	x			x
Caninophyllum			x		x	
Caninostrotion						x
Carruthersella					x	

Table 5. *Cont.*

Genera	Atlantic	C. Europe	E. Europe	W. Peri-G.	Saharan	Mediterranean
Claviphyllum		x	x			
Clisiophyllum	x	x	x	x	x	x
Corwenia			x	x		
Cyathaxonia		x	x	x		x
Diaschophyllum					x	
Dibunophyllum	x	x	x	x	x	x
Diphyphyllum	x	x	x	x	x	x
Effigies		x				
Eostrotion			x			
Fasciculophyllum		x				
Gangamophyllum		x	x		x	x
Guadiatia				x		
Haplolasma				x	x	x
Hapsiphyllum			x			
Kazachiphyllum			x			
Kizilia			x	x	x	x
Koninckophyllum	x	x	x		x	x
Lithostrotion	x	x	x	x	x	x
Lonsdaleia	x		x		x	x
Lophophyllidium		x				
Lublinophyllum		x				x
Lytvophyllum			x			
Melanophyllidium						x
Mirka		x				
Morenaphyllum				x		
Neokoninckophyllum		x	x			
Nemistium					x	x
Nervophyllum		x	x			
Nina			x			
Ostravaia		x				
Palaeosmilia	x	x	x	x	x	x
Palastraea	x			x	x	x
Pareynia				x	x	
Plerophyllum						x
Pseudoaulina	x				x	
Pseudozaphrentoides′		x		x	x	x
Rotiphyllum		x		x		x
Rylstonia			x			
Schoenophyllum			x			
Serraphyllum						x
Silesamplus		x				

Table 5. *Cont.*

Genera	Atlantic	C. Europe	E. Europe	W. Peri-G.	Saharan	Mediterranean
Siphonodendron	x	x	x	x	x	x
Siphonophyllia		x	x	x	x	x
Slimoniphyllum		x	x			
Solenodendron					x	
Spirophyllum		x				
Tachylasma		x	x			
Thysanophyllum	x					
Tizraia				x	x	
Turbinatocaninia	x	x	x			
Ufimia		x	x			x
Variaxon			x			
Vojnimitor						x
Vojnovskytes						x
Zakowia			x			
Zaphrentites	x	x	x	x		x
Zaphriphyllum			x			
Zaphrufimia		x	x			x

The coral genera and species described and/or figured in the bibliography have been carefully examined. Unfortunately, in many cases, especially in old papers, the low quality of the figures obstructs a precise identification. Moreover, in some cases, the classification is questionable because of the absence of figuration, description or both. The identifications of the corals from the collections have been examined maintaining a homogeneous criterion. In many cases, pictures of the specimens and the thin sections studied in the museums were taken in order to have a significant catalogue of Carboniferous corals.

2.3. Taxonomic Units

Some attempts to compare the species assemblages have been made in areas with homogeneous identifications and well-known assemblages [43,46]. However, we chose the generic assemblages for the overall comparison of the Western Palaeotethys. The main reason is that a high number of the specific identifications, about 40%, are in open nomenclature (sp., cf., aff., ?, etc.). Additionally, we try to avoid the problems caused by the different taxonomic criteria, preservation, and reliability of the data. This was already highlighted by Bambach [33], who analysed biogeographic distributions of several groups of invertebrates at the generic level. The authors who studied the corals in different times and geographic areas have also used different criteria for the identification of the corals. All the identifications of the specimens studied in different laboratories were homogenized. In addition, the old papers with low quality illustrations were interpreted with the same criteria. However, we accepted the identifications in most papers by recent authors, although the criteria were not always the same. Some authors are clearly splitters, and some other are clearly lumpers. This introduces a methodological problem that we will discuss in some particular cases.

2.4. Clusters

The palaeobiogeographical analyses have been performed using PAST [90]. The study uses paired group (UPGMA) hierarchical clustering. We examined several indices (Raup-Crick, Simpson, Dice, Jaccard), but we used only the Dice and Simpson indices because they produced better results in initial tests. Simpson is less influenced by differences in sample size or insufficient sampling [91] and reflects spatial turnover over nestedness [92]. This characteristic can lead it to consider areas with a small number of taxa as identical or almost identical to other areas, as long as the taxa present in the less diverse area are also found in the others. This problem should be less prevalent because the sub-provinces are large areas, but in some sub-provinces for several time intervals, the coral records are scarce (Tables 2–5). To address this limitation, we used both Simpson and Dice indices, providing a more nuanced comparison that takes into account both the presence and absence of taxa. A total of 1000 bootstrap resamples have been performed on the analysis to test the stability of the resulting clusters. The branches with a bootstrap value lower than 50% are unstable and are not considered well supported.

3. Results

3.1. Clusters

The comparisons between the sub-provinces are illustrated in Figures 2–5 and are completed with Table 6. Figure 2 shows the hierarchical cluster of the Tournaisian using Dice and Simpson indices. Only four sub-provinces are represented there, since the Mediterranean and the West Peri-Gondwanan sub-provinces do not present a rugose coral record during the Tournaisian. Both clusters have stable branches, with bootstrap values higher than 60%. Both clusters and similarity indices indicate that the Saharan and East European sub-provinces are more similar to each other than to the others. Central Europe is more closely related to the Atlantic sub-province than to the Saharan or East European sub-provinces. However, the Atlantic sub-province's relationships vary depending on the analysis: with the Dice index, it aligns more with Central Europe, while the Simpson index shows a closer connection to the Saharan or East European sub-provinces.

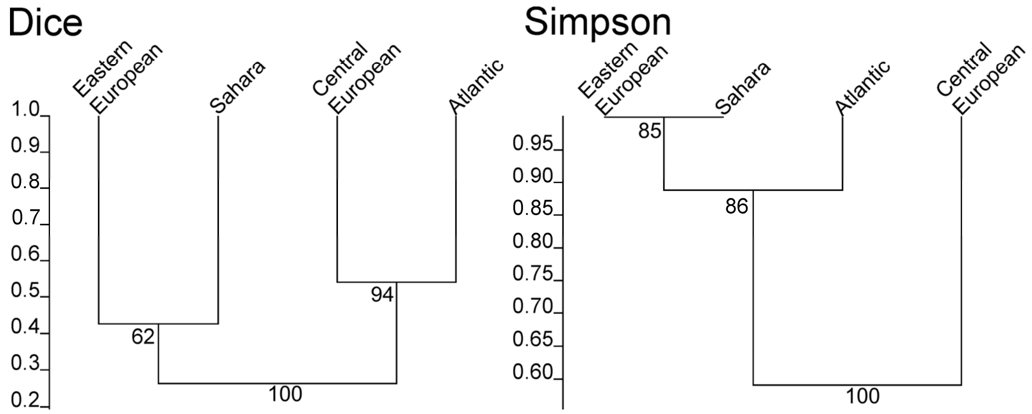

Figure 2. Hierarchical clusters of the sub-provinces during the Tournaisian.

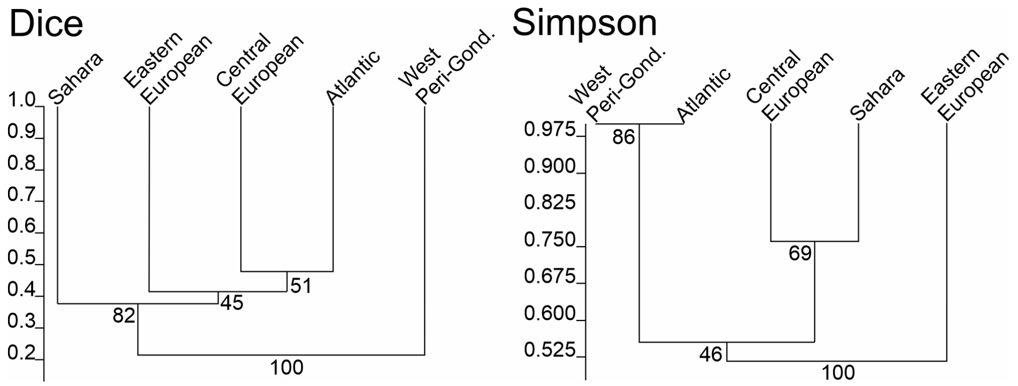

Figure 3. Hierarchical cluster of the sub-provinces during the Early Visean.

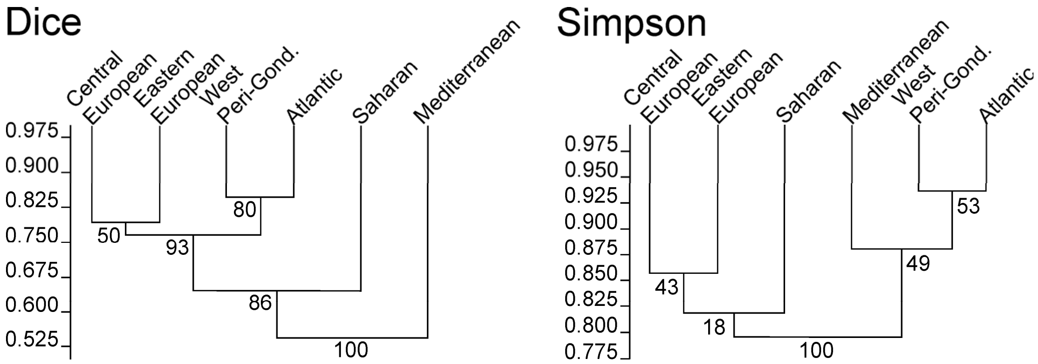

Figure 4. Hierarchical cluster of the sub-provinces during the Late Visean.

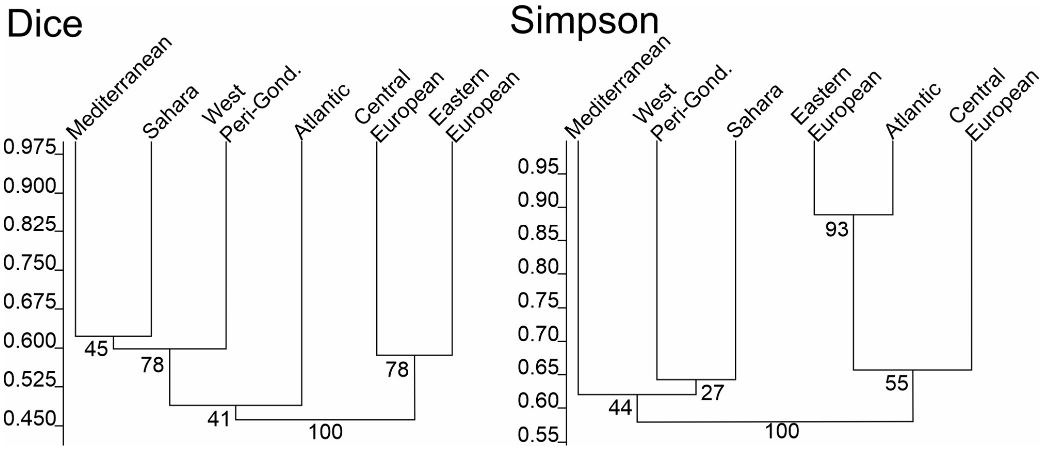

Figure 5. Hierarchical cluster of the sub-provinces during the Serpukhovian.

Table 6. Pairwise comparison between the different sub-provinces, rounded to the third decimal place.

Tournaisian					
DICE	**Atlantic**	**C. Europe**	**E. Europe**	**Sahara**	
Atlantic	1	0.548	0.394	0.182	
C. Europe	0.548	1	0.32	0.154	
E. Europe	0.394	0.32	1	0.476	
Sahara	0.182	0.154	0.476	1	
SIMPSON	**Atlantic**	**C. Europe**	**E. Europe**	**Sahara**	
Atlantic	1	0.676	0.813	1	
C. Europe	0.676	1	0.5	0.6	
E. Europe	0.813	0.5	1	1	
Sahara	1	0.6	1	1	
Early Visean					
DICE	**Atlantic**	**C. Europe**	**E. Europe**	**West Peri-G.**	**Sahara**
Atlantic	1	0.476	0.426	0.278	0.372
C. Europe	0.476	1	0.417	0.162	0.409
E. Europe	0.426	0.417	1	0.190	0.357
West Peri-G.	0.278	0.162	0.190	1	0.235
Sahara	0.372	0.409	0.357	0.235	1

Table 6. *Cont.*

Tournaisian						
SIMPSON	**Atlantic**	**C. Europe**	**E. Europe**	**West Peri-G.**	**Sahara**	
Atlantic	1	0.484	0.625	1	0.667	
C. Europe	0.484	1	0.625	0.6	0.75	
E. Europe	0.625	0.625	1	0.4	0.417	
West Peri-G.	1	0.6	0.4	1	0.4	
Sahara	0.667	0.75	0.417	0.4	1	
Late Visean						
DICE	**Atlantic**	**C. Europe**	**E. Europe**	**West Peri-G.**	**Sahara**	**Mediterran.**
Atlantic	1	0.789	0.773	0.846	0.622	0.561
C. Europe	0.789	1	0.792	0.712	0.578	0.512
E. Europe	0.774	0.792	1	0.792	0.683	0.514
West Peri-G.	0.846	0.712	0.792	1	0.7	0.583
Sahara	0.622	0.578	0.683	0.7	1	0.552
Mediterranean	0.561	0.512	0.514	0.583	0.552	1
SIMPSON	**Atlantic**	**C. Europe**	**E. Europe**	**West Peri-G.**	**Sahara**	**Mediterran.**
Atlantic	1	0.789	0.837	0.936	0.848	0.92
C. Europe	0.789	1	0.857	0.787	0.788	0.84
E. Europe	0.837	0.857	1	0.809	0.848	0.76
West Peri-G.	0.936	0.787	0.809	1	0.848	0.84
Sahara	0.848	0.788	0.848	0.848	1	0.64
Mediterranean	0.92	0.84	0.76	0.84	0.64	1
Serpukovian						
DICE	**Atlantic**	**C. Europe**	**E. Europe**	**West Peri-G.**	**Sahara**	**Mediterran.**
Atlantic	1	0.436	0.508	0.478	0.490	0.533
C. Europe	0.436	1	0.585	0.462	0.441	0.438
E. Europe	0.508	0.585	1	0.466	0.474	0.417
West Peri-G.	0.478	0.462	0.466	1	0.610	0.509
Sahara	0.490	0.441	0.474	0.610	1	0.655
Mediterranean	0.533	0.438	0.417	0.509	0.655	1
SIMPSON	**Atlantic**	**C. Europe**	**E. Europe**	**West Peri-G.**	**Sahara**	**Mediterran.**
Atlantic	1	0.667	0.889	0.611	0.667	0.667
C. Europe	0.667	1	0.649	0.536	0.484	0.533
E. Europe	0.889	0.649	1	0.607	0.581	0.533
West Peri-G.	0.611	0.536	0.607	1	0.643	0.607
Sahara	0.667	0.484	0.581	0.643	1	0.633
Mediterranean	0.667	0.533	0.533	0.607	0.633	1

Figure 3 shows the hierarchical cluster of the early Visean with Dice and Simpson indices. For this time interval, the West Peri-Gondwanan sub-province is already represented, but the number of genera recorded is low, because only one locality in the Moroccan Meseta provided a coral assemblage, and it has low diversity [80]. In this case, the stability of the clusters is lower, because there are some relationships that present bootstraps lower than

50%. Additionally, the results are quite different between both clusters. The Simpson index shows a close similarity between the West Peri-Gondwanan and the Atlantic sub-provinces, while the Dice index indicates the closest relationship between the Central Europe and Atlantic sub-provinces.

Figure 4 shows the hierarchical cluster of the late Visean with Dice and Simpson indices. In this case, all the sub-provinces are represented by a relatively high number of genera. This is due to the general warming and marine transgression [93–95], which increased the surface of the shallow carbonate platforms and, consequently, increased the ecological niches favorable for rugose corals. In this case, the cluster made with the Dice index shows higher reliability (all bootstraps higher than 50%) than the cluster with the Simpson index, where most bootstraps are below 50%. However, they show similar results, with the highest similarities being between Eastern and Central Europe and between the Atlantic and West Peri-Gondwanan sub-provinces.

Figure 5 shows the hierarchical cluster of the Serpukhovian with Dice and Simpson indices. Again, the six sub-provinces are represented, despite the increase in tectonic activity [96,97] and the cooling of the climate [26] reducing the number of areas with coral records. In this case, both clusters differ significantly, and the reliability of the branches is irregular, with varied bootstrap values.

3.2. Maps

Based on the data provided by the clusters and a previous map [80], we built the palaeogeographic maps corresponding to the four time intervals considered in this study. The biogeographic sub-provinces are shown in all the maps, and the different areas with records of rugose corals are numbered. According to the relationships between sub-provinces shown in the clusters and according to the oceanic circulation systems, the main oceanic currents have been illustrated. The possible movements of the continents, the transgressions and regressions and the new lands emerging because of the tectonic movements have been reflected in the changes of the maps along the four time intervals studied. The analysis of those changes is included in the discussion section.

4. Discussion

There are many obstacles to doing a complete and reliable identification of the Mississippian coral faunas. Their knowledge is very irregular: the coral record of precise time intervals (mainly in the late Visean) in some sub-provinces contains numerous genera because there are good outcrops, and they have been studied in detail for decades. In contrast, the Tournaisian or Serpukhovian outcrops are scarce, or, in most cases, they do not contain coral assemblages. Therefore, some sub-provinces are excluded from the clusters or contain few genera due to the scarcity of outcrops, which biases the results.

An additional problem is the environmental influence on the coral assemblages. Carboniferous corals are strong palaeoenvironmental indicators and have proven their use in palaeoecological studies [98–100]. This introduces an additional difficulty when comparing assemblages that originated in diverse environments. However, this influence is mitigated when comparing sub-provinces that comprise diverse environments, as their effects on the assemblages tend to average out.

4.1. Tournaisian

During the Tournaisian and early Visean, some regions, such as SW Spain and the Moroccan Meseta were mostly uplifted areas [101,102]. Additionally, most areas included in the Mediterranean sub-province were part of deep seas, without a record of rugose corals [85,103]. Therefore, the West peri-Gondwanan and the Mediterranean sub-provinces are excluded in the clusters for the Tournaisian.

The clusters with Simpson and Dice indices have high reliability (bootstraps above 60% in all cases), but they present somewhat different results that can be explained by the problems previously highlighted. The East Europe Sub-province seems to be closely related with the Saharan sub-province (Figure 2). This is possible because the equatorial current could turn south-westwards when colliding against the continental mass of the Ukrainian Shield (Figure 6). However, the very close relationship shown by the Simpson index may also be related to the low number of rugose coral records in both sub-provinces. Such a low number of records may be due to the high input of siliciclastic sediments in those areas during the Tournaisian. The high similarity between the Atlantic and Central European sub-provinces (Figure 2; about 0.6) is related to the easy communication along the platforms located in the southern border of Laurussia (Figure 6).

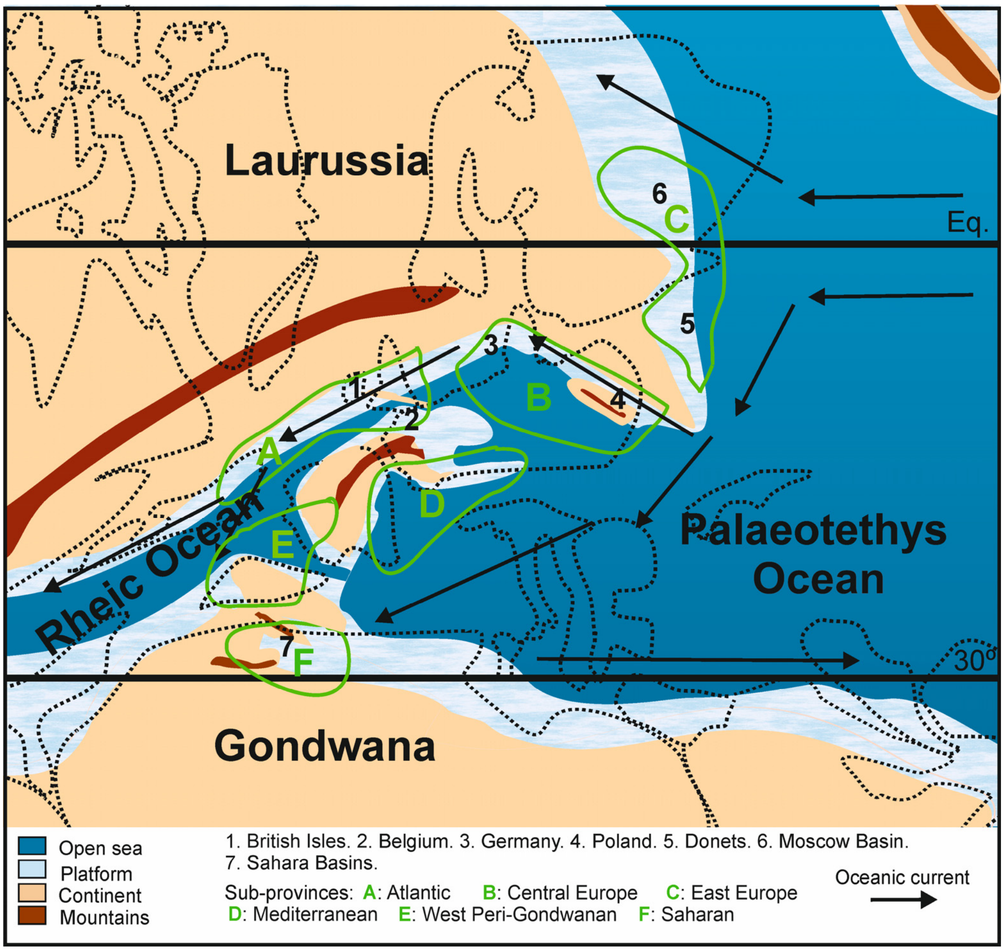

Figure 6. Palaeogeographic map of the Western Palaeotethys during the Tournaisian.

The pairwise comparison between the different sub-provinces (Table 6) shows a low similarity between them with the Dice index; all are below 0.5, except the relationship between the Atlantic and Central Europe. These low similarities are probably caused by an important level of endemism after the late Devonian extinctions and the low number of genera present in some of the areas. This is confirmed when analyzing the comparison with the Simpson index, which is less affected by the differences in the number of taxa among different sub-provinces.

4.2. Early Visean

The Mediterranean sub-province is also discarded here for the same reasons as in the Tournaisian. In contrast, the West Peri-Gondwanan sub-province is included because of the record of a low-diversity but significant assemblage in the Khenifra area (Moroccan Meseta) [80].

The results with the Dice and Simpson indices are very different (Figure 3). The reliability of the connections is not always high, because some bootstraps have values under 50% in both clusters. The Dice cluster shows similarities that fit with the previous knowledge [17,40], except for the low connection between the West Peri-Gondwanan sub-province and the rest. This is easily explained by its low number of taxa (five genera). All the genera present in this sub-province (*Axoclisia*, *Cravenia*, *Cyathaxonia*, *Siphonophyllia* and *Sychnoelasma*) are also recorded in the Atlantic sub-province, which explains the high similarity found by the Simpson index. The low number of genera in this sub-province could be explained by the low sea level, which isolated that area in an epicontinental zone (Figure 7) [102].

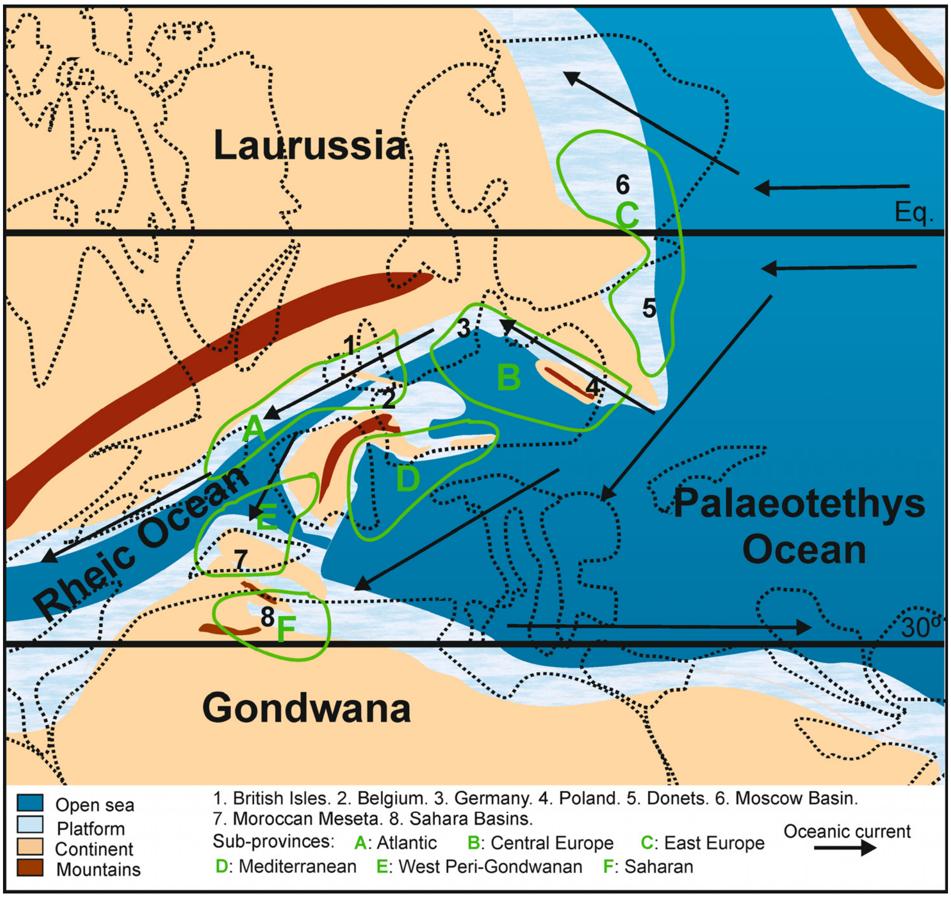

Figure 7. Palaeogeographic map of the Western Palaeotethys during the early Visean.

The main change in the palaeogeographic map from the Tournaisian to the early Visean is the light advance of Gondwana to Laurussia, with a little narrowing of the intermediate terrains.

The pairwise comparison between the different sub-provinces (Table 6) for the early Visean again shows lower values with the Dice index than with the Simpson index. None of the values are higher than 0.5 in the first case, but most are above that value in the second. The Simpson index shows a high similarity of the West Peri-Gondwanan with the Atlantic sub-province (Table 6), because all genera recorded in the Khenifra area are also present in South Wales [80,104]. However, the other relationships shown by this index are not consistent with the previous knowledge of other fossil groups [14].

4.3. Late Visean

The late Visean offers the most complete comparison between the six sub-provinces because all of them contain abundant rugose corals (a total of 79 genera and 293 species), with the assemblages in each of them being quite diverse (Table 4, 340 to 58 genera). This diversity is attributed to the already mentioned marine transgression, which not only facilitated communication between different basins through the extension of the marine areas but also led to the occupation of many new marine niches in the inundated low-lying areas of the continents, now transformed into epi-continental seas.

In this case, the results with the Simpson and Dice indices are similar [47]. All the connections shown by the Dice index are well supported, with bootstrap values of 50% or higher. However, several connections with the Simpson index have bootstraps lower than 50. Both indices show a high similarity between the Atlantic and West Peri-Gondwanan sub-provinces, which were connected along the northwestern coast of the Ibero-Armorican Massif or the southeastern part of the Rheic Ocean. Both analyses also group the Central European and Eastern European sub-provinces together, although with slightly lower support values.

Other connections are less evident, because the Simpson and Dice indices show different results. The Simpson index shows a connection of the West Peri-Gondwanan and Atlantic sub-provinces with the Mediterranean sub-province, and the Central and Eastern European sub-provinces with the Saharan sub-province, although with low bootstrap supports. The Dice index joins the Central and Eastern European sub-provinces with the West Peri-Gondwanan and Atlantic sub-provinces (Figure 4). This fits with the previous knowledge that supports the continuity of the Atlantic basins and platforms in Germany and Poland along the south border of Laurussia (Figure 8).

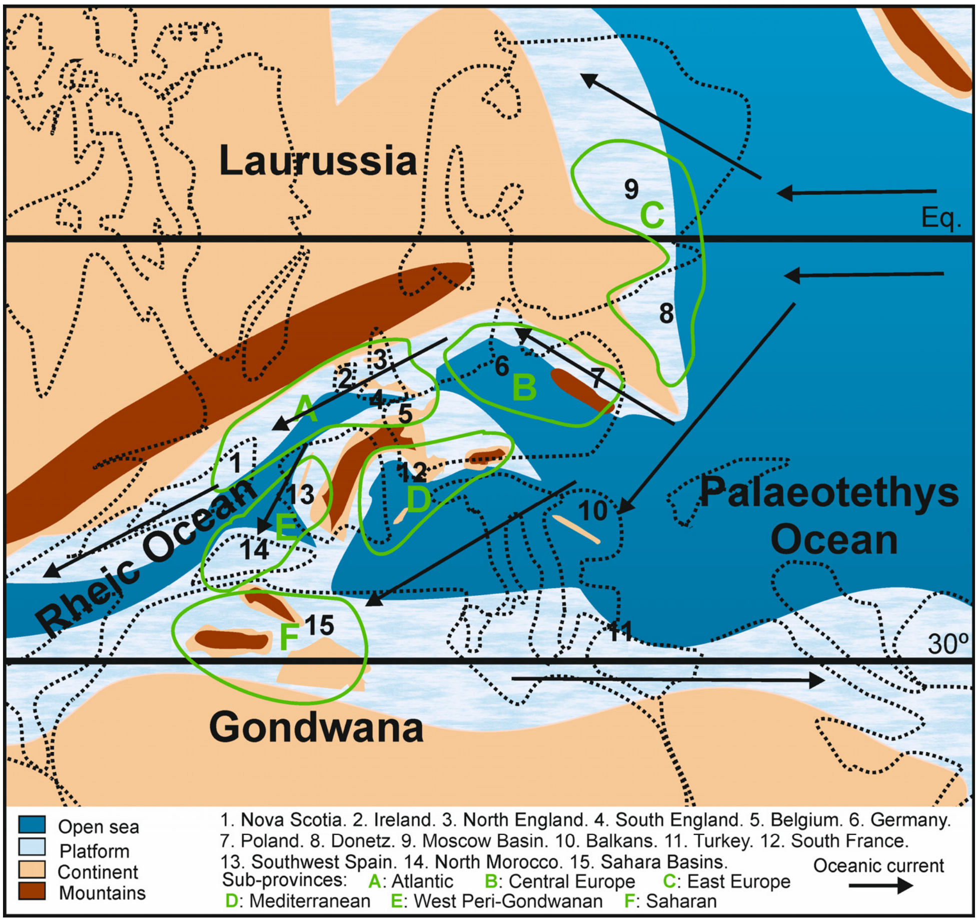

Figure 8. Palaeogeographic map of the Western Palaeotethys during the late Visean.

In any case, the similarities are high (see the pairwise comparison, Table 6), greater than those in the equivalent tables for the Tournaisian and the Early Visean.

During the Visean, the advance of Gondwana is more intense and the narrowing of the Rheic Ocean is evident, as well as the lifting of new continental areas or widening of other previously lifted regions.

4.4. Serpukhovian

The Serpukhovian also allows for a complete comparison of the six sub-provinces. The number of genera in most sub-provinces is lower, as some areas were affected by the input of siliciclastic sediments due to the active tectonics, and an increasing number of genera became extinct in some of the sub-provinces. However, the total number of genera remains high because several areas served as refuges for rugose corals [105], and the progressive isolation of some areas promoted the appearance of new genera [32].

The results obtained with the Dice and Simpson indices differ significantly. Several of the connections show low reliability (bootstraps lower than 50%). Both clusters show a grouping of the Mediterranean, the West Peri-Gondwanan and the Saharan sub-provinces, but the order of these connections varies (Figure 5). The closer relationship of the Saharan sub-province with the Mediterranean and the West Peri-Gondwanan may be due to the approach of Gondwana to the northern terranes (Figure 9). The separation of the West Peri-Gondwanan and the Atlantic sub-provinces may be related to the early stages of the closure of the Rheic Ocean, which will be complete later in the Bashkirian [14].

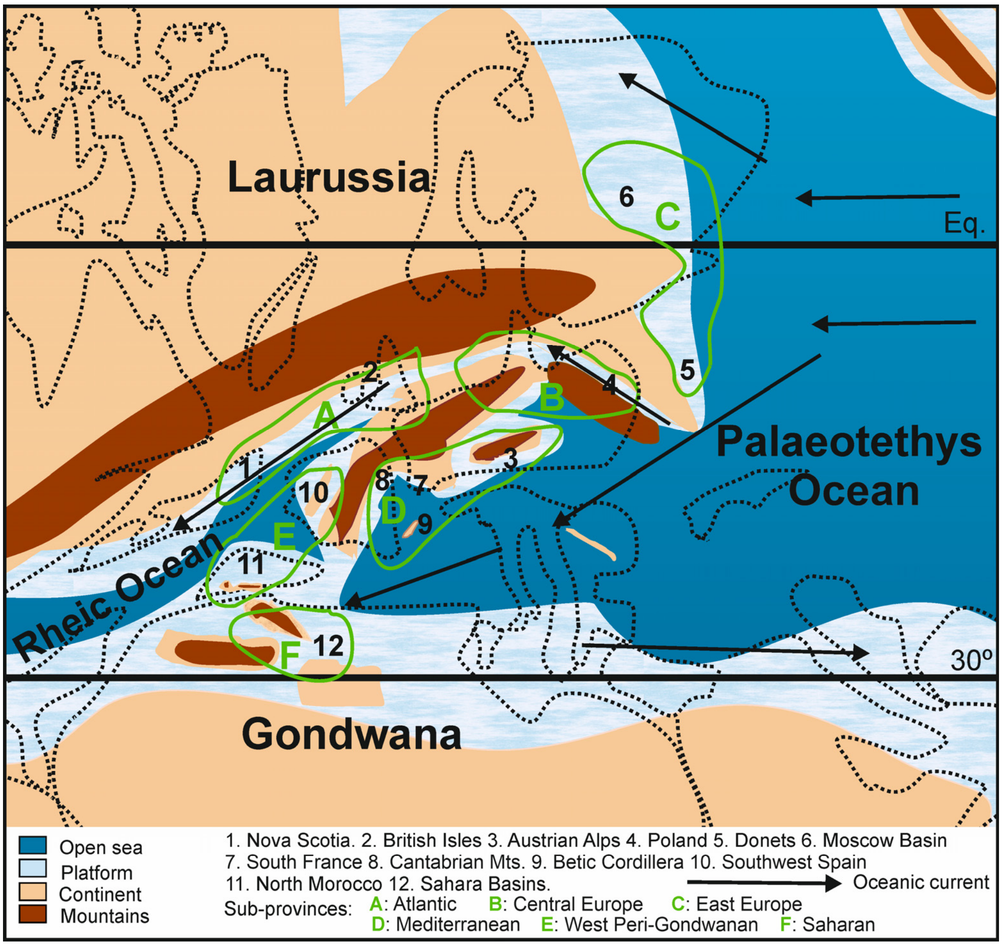

Figure 9. Palaeogeographic map of the Western Palaeotethys during the Serpukhovian.

The Dice index shows a close relationship between the Central and Eastern Europe sub-provinces, with a high level of confidence (bootstrap 70%) despite significant tectonic activity in those areas that closed some connection routes. The Simpson index cluster shows a very close connection between the Eastern Europe and the Atlantic sub-provinces that cannot be explained by palaeogeography (Figure 9), as the Central Europe sub-province should show intermediate features. The Dice index provides a more logical result, with a close connection between the Central and Eastern Europe sub-provinces and a weaker connection to the other sub-provinces (Figure 5).

In the Serpukhovian, the extension of lifted continental areas is larger, and the narrowing of the marine realms is evident. The lifted regions are more extensive, and the cordilleras are producing more terrigenous material that makes the development of corals more difficult.

4.5. Final Considerations

This is the first attempt to analyse the rugose coral biogeography in the Western Palaeotethys throughout the complete Mississippian. One of the main problems in these comparisons is that during the late Tournaisian and early Visean, some genera became widely distributed in the Palaeotethys. This trend was even stronger during the late Visean, when a high percentage of genera are present in five or six sub-provinces (Table 2). Moreover, their absence in some sub-provinces may be a result of deficient outcrops or incomplete records, because they also occur in other areas of the Palaeotethys and even in other seas. Consequently, their utility in biogeographical studies is limited. Some of these genera are *Amplexizaphrentis*, *Amygdalophyllum*, *Arachnolasma*, *Auloclisia*, *Aulokoninckophyllum*, *Aulophyllum*, *Axoclisia*, *Axophyllum*, *Caninia*, *Clisiophyllum*, *Cyathaxonia*, *Dibunophyllum*, etc.

The clusters generated using the distribution of rugose coral genera throughout the Mississippian provide valuable insights, despite several factors that may reduce the validity of the results. In most cases, the relationships shown between the different sub-provinces align well with previous data from other fossil groups [14] and with palaeomagnetic [3,16] and tectonic [3] data.

However, there are some cases that do not fit with the previous data or with the expected position of the terranes. This is more frequent in the clusters built with the Simpson index and, in several cases, with the relationships of the Central Europe sub-province. This could be related to the many new genera defined in that area, which has been studied in detail during many years with a splitter perspective, resulting in a high number of endemic taxa.

This study could be extended to include an additional sub-province comprising the Balkans and northern Turkiye. However, until we have more complete knowledge of the assemblages from that region, we have excluded it from our analysis.

Some of the more global reconstructions of the Mississippian depict the Rheic Ocean already closed and Gondwana merged with Laurussia at the middle Visean [20]. Our data do not align with that reconstruction, as there are epicontinental seas containing rugose corals in several areas, and rugose coral assemblages still exist in the Atlantic sub-province during the Serpukhovian. This indicates that the Rheic Ocean was still open at that time, as already postulated by several authors [3,14].

5. Conclusions

This is the first attempt to statistically analyse the rugose coral biogeography in the Western Palaeotethys throughout the complete Mississippian, from the Tournaisian to the Serpukhovian.

The databases compiling rugose coral species and genera present in the Western Palaeotethys during the Mississippian provide a substantial foundation for future research on rugose corals in that region.

The clusters built with the Simpson and Dice indices allow for a more complete view of the relationships between the sub-provinces defined in the Western Palaeotethys.

The results are not always satisfactory due to the uneven knowledge across different geographic areas, as some of them are well-known and others have been insufficiently studied. Additionally, many genera are widely distributed (some of them being regionally cosmopolitan), making them of low value in biogeographical comparisons.

The relationships between different areas and the information on marine areas during the Mississippian provided by the rugose coral assemblages allow for the presentation of a set of palaeographic maps of the Western Palaeotethys that show the evolution of the seas during that time.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/geosciences14110282/s1: Tables S1–S4. Four excel tables, representing for each stage (Tournaisian, early Visean, late Visean and Serpukhovian) the distribution of the Mississippian rugose coral species through the subprovinces.

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Data Availability Statement: Some or all data, models or code that support the findings of this study are available from the corresponding author upon reasonable request.

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