UNIVERSIDAD COMPLUTENSE DE MADRID
FACULTAD DE CIENCIAS GEOLÓGICAS

TESIS DOCTORAL

Paleobiogeografía y evolución de los corales rugosos en el Paleo-Tetis Occidental durante el Misisípico

Rugose Coral Palaeobiogeography and Evolution in the Western Palaeotethys during the Mississippian

MEMORIA PARA OPTAR AL GRADO DE DOCTOR

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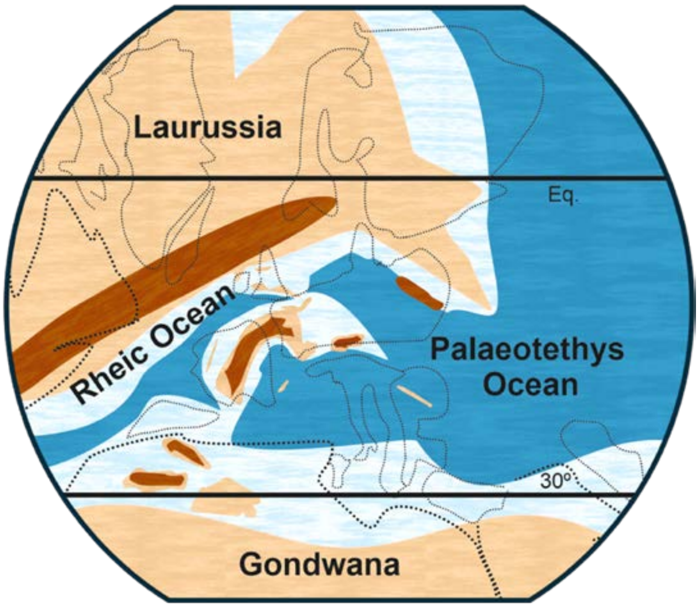

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ABSTRACT

The Western Palaeotethys bioprovince includes the current regions of North Africa, Europe and Nova Scotia. During the Mississippian period it suffered climate changes, sea level variations, and significant tectonic changes due to the approach of Gondwana toward Laurussia, in the context of the Variscan orogeny. These environmental changes affect the evolution and distribution of marine faunas such as rugose corals.

The main objective of this study is to improve the current understanding of Mississippian rugose coral evolution and distribution in the Western Palaeotethys, and their interrelation with palaeogeography. To that aim, our goals include building a database on Mississippian rugose coral distribution throughout the Western Palaeotethys and to test the utility of rugose corals for quantitative palaeogeographical studies, using the information provided by them to refine palaeobiogeographical and palaeogeographical reconstructions.

Our methods include examining collections and extensive bibliographic research to build the database, which is currently based on more than 700 sources. Palaeobiogeographical analyses were conducted comparing rugose coral faunas with cluster analysis. We compare several similarity indices, and worked at different scales: first in a small, well-studied area (El Guadiato Area), then performing regional comparisons, and finally studying the whole Western Palaeotethys. We also studied the dispersion of particular taxa (*Lonsdaleia* and *Actinocyathus*) and the evolutionary trends and changes in diversity of the Mississippian rugose corals.

Our results support the proposal of two additional biogeographical sub-provinces for the Western Palaeotethys, adding the Central European and the Eastern European sub-provinces to the already defined Atlantic, West Peri-Gondwanan, Mediterranean and Saharan sub-provinces.

There are limitations to the availability and homogeneity of the coral records in the Western Palaeotethys. However, our analyses have found rugose corals useful for palaeogeographical studies. They offered insights into the connectivity between units and basins both in the El Guadiato Area, and in larger scale comparisons. The changes in the similarity between regions through the Mississippian also provided information about the development of geographical barriers. The increase both in diversity and in similarity during the late Visean correlates with a marine transgression that creates extensive epicontinental seas and favours the dispersion of rugose corals. The Serpukhovian extinction and endemism align with the increased isolation of the sub-provinces due to the Variscan orogeny.

This information was used to refine our palaeogeographical maps for the Tournaisian, early Visean, late Visean and Serpukhovian stages, depicting the approach of Gondwana towards Laurussia and the uplift of the Iberian, Armorican and Welsh-Anglo-Brabant massifs.

These results improve the knowledge of the Western Palaeotethys and offer a more detailed understanding of the rugose coral evolution during the Mississippian. Future research should focus on improving the database with more sampling efforts targeting understudied regions and extending it to the Pennsylvanian.

RESUMEN

La bioprovincia del Paleo-Tetis Occidental engloba el Norte de África, Europa y Nueva Escocia. Durante el Misisípico se vio afectada por cambios climáticos, variaciones del nivel del mar y por la actividad tectónica causada por el acercamiento de Gondwana a Laurussia, en plena orogenia Varisca. Estos cambios ambientales determinaron la evolución y distribución de las faunas marinas, destacando entre ellas los corales rugosos.

El principal objetivo de este estudio es mejorar el conocimiento actual de la evolución y distribución de los corales rugosos misisípicos en el Paleo-Tetis Occidental, y cómo se relacionan con la paleogeografía de este océano. En este contexto se enmarcan objetivos más concretos, que incluyen desarrollar una base de datos de la distribución en el Paleo-Tetis Occidental de los corales rugosos del Misisípico y evaluar la utilidad de los corales rugosos en estudios paleogeográficos cuantitativos, con el fin de incorporar esta información a mapas y reconstrucciones paleobiogeográficos y paleogeográficos.

Nuestros métodos incluyen la revisión de colecciones y la recopilación de bibliografía para construir la base de datos, que actualmente se basa en más de 700 referencias. Los análisis paleobiogeográficos se han realizado comparando las asociaciones de corales rugosos con análisis clúster. Se han utilizado varios índices de similaridad y se ha trabajado a diferentes escalas: primero en un área pequeña y bien estudiada (El Guadiato), después llevando a cabo comparaciones regionales, y finalmente analizando todo el Paleo-Tetis Occidental. También se han estudiado la dispersión y migración de

taxones específicos (*Lonsdaleia* y *Actinocyathus*) y los patrones evolutivos y cambios en la diversidad de los corales rugosos durante el Misisípico.

Los resultados obtenidos apoyan la propuesta de dos nuevas subprovincias biogeográficas para el Paleo-Tetis Occidental. Se añaden de este modo las subprovincias de Europa Central y de Europa del Este a las definidas anteriormente: las subprovincias Atlántica, del Oeste de Gondwana, Mediterránea y Sahariana.

Estos estudios se encuentran con limitaciones en la disponibilidad y homogeneidad de la información sobre los corales rugosos en el Paleo-Tetis Occidental. Pese a estas dificultades, los resultados apoyan la utilidad de los corales rugosos para estudios paleogeográficos. Los análisis basados en estas faunas han aportado evidencias sobre la conectividad entre diferentes cuencas y unidades paleogeográficas, tanto en el Área de El Guadiato como en comparaciones a mayor escala. Las semejanzas entre las diferentes regiones han variado a lo largo del Misisípico, sufriendo cambios que revelan la formación de barreras geográficas. El aumento en diversidad y semejanzas durante el Viseense tardío se corresponde con una transgresión marina que favorece la dispersión de los corales rugosos aumentando la conectividad entre regiones y creando nuevos mares epicontinentales. Las extinciones del Serpukhoviense y el aumento del endemismo durante este piso coinciden con el mayor aislamiento de las subprovincias causado por la orogenia Varisca.

La información obtenida en estos estudios se ha utilizado para refinar mapas paleogeográficos del Tournaisiense, el Viseense temprano, el Viseense tardío y el Serpukhoviense. Estos representan el acercamiento de Gondwana a Laurussia y el levantamiento de los macizos Ibérico, Armoricano y Galés-Anglo-Brabante.

Estos resultados mejoran el estado del conocimiento del Paleo-Tetis Occidental, y ofrecen nuevos detalles sobre la evolución de los corales rugosos durante el Misisípico. Para avanzar en este campo, futuras investigaciones deberían ampliar la base de datos con un muestreo más completo en regiones poco estudiadas, y extender su alcance al Pensilvánico, para englobar así todo el Carbonífero.

1 INTRODUCTION:

1.1 CONTEXT AND STATE OF THE ART

The Order Rugosa (Phylum Cnidaria, Class Anthozoa) comprises sessile marine organisms with a calcite skeleton. They first appeared in the Ordovician and inhabited the oceans until their extinction at the end of the Permian (Hill, 1981). Their study faces difficulties and methodological challenges in the identification of species and cladistic analyses, due to phenomena such as parallel, iterative and convergent evolution (Fedorowski, 1989), and homeomorphism and intraspecific variations (Webb, 1993, 1994). Despite the difficulties, extensive literature examines the evolution of rugose corals, with many articles focusing on specific taxa, such as particular families (e.g. (Nelson, 1959; Poty, 1984; Kossovaya, 1993, 1998; X.-D. Wang, 1994; Chen et al., 1997; Poty & Hecker, 2003; Hecker, 2010; Rodríguez & Somerville, 2014). Other studies explore how the evolution of rugose corals relates to environmental variations (Sando, 1989; Rodríguez & Somerville, 2010). The details of the literature on the evolution of rugose corals will be more thoroughly covered in chapter six.

Rugose corals, being highly sensitive to environmental changes in marine ecosystems, have repeatedly proven their value in palaeoecological and palaeoenvironmental analyses (Hill, 1938; Vuillemin, 1990; Kullmann, 1997; Somerville & Rodríguez, 2007; Aretz, 2010). This sensitivity makes their evolutionary development and distribution patterns especially relevant during times marked by significant Earth system changes, such as those of the Mississippian.

The Mississippian epoch (358.9–323.2 Ma) is divided into the Tournaisian, Visean, and Serpukhovian stages. It was marked by dynamic tectonic activity and climatic fluctuations. The Variscan orogeny was in full force, driven by the convergence of Laurussia and Gondwana, which reshaped the distribution of seas and landmasses (Franke, 2000; Blakey, 2003). During this time, climatic variations caused a shift from Devonian greenhouse conditions to the Permo-Carboniferous icehouse state (Buggisch et al., 2008; Montañez & Poulsen, 2013). However, this transition was not linear: the Mississippian experienced multiple episodes of cooling and warming (Yao et al., 2020), alongside glaciation events, sea-level changes, and fluctuations in seawater temperature and CO^2 concentration (Fielding et al., 2008; Isbell et al., 2012). It is worth mentioning the major transgressive events that took place in the late Visean, extending shallow water platforms and creating new marine niches (Ramsbottom, 1973; Ross & Ross, 1985; Somerville, 2008).

In marine ecosystems, this epoch was crucial for faunal recovery following the late Devonian mass extinctions (Kellwasser and Hangenberg events) (Becker et al., 2016). Among the marine taxa recovering from these extinctions were rugose corals, which underwent a gradual diversification, reaching a notable diversity by the late Visean, before facing significant extinctions in the Serpukhovian and Bashkirian (Fedorowski, 2022). The environmental changes during the Mississippian also induced pronounced faunal provincialism, influencing various invertebrate groups such as rugosans, tabulates, bivalves, ammonoids, brachiopods, and bryozoans (Bambach 1990). Fedorowski (2023) divided rugose coral faunas into three major palaeobiogeographical superprovinces: the North American, Palaeotethyan, and Australian superprovinces. He also described how low sea levels and a cold climate partially restricted the communication between these superprovinces during the early Tournaisian. The ecological conditions improved during the late Tournaisian, and a rise in sea level caused a worldwide spread of corals (Poty, 2007). The following drop in sea level fostered the development of more endemic faunas during the early Visean (Poty, 2007). The late Visean was characterised by global warming and a marine transgression, allowing easier communication and migration between the superprovinces, diminishing the differences between rugose coral faunas (Fedorowski, 2023).

The Palaeotethyan superprovince, of particular interest to this research, is further subdivided into three regions: the Western Palaeotethys (Europe, North Africa, and Nova Scotia), the Central Palaeotethys (Ural Mountains and Middle Asia), and the Eastern Palaeotethys (China, Southeast Asia, and Japan). The Western Palaeotethys, directly affected by the convergence of Laurussia and Gondwana, can provide through palaeogeographical analysis valuable insights into how these changes shaped marine biodiversity during the Mississippian. This serves as an example of how palaeogeography is crucial for understanding both Earth's evolution and the history of life. The discipline studies the distribution of landmasses and oceans in the past and its changes through time, and it has numerous applications, including plate tectonic reconstructions, palaeoclimatology, resource exploration and palaeobiogeographical studies.

The scale, scope and focus of palaeogeography research can vary. Some palaeogeographical analysis and reconstructions are conducted at a global scale (Torsvik et al., 2002; Golonka, 2007; Scotese, 2021), while others are more regional and focus on particular areas. These can range from specific microplates (Robardet, 2003), countries (Schönlaub, 1997a) or regions (Yanev, 2000), to entire continents (Paproth, 1991, 2006; Cocks, 2000) or palaeo-continents (Blakey, 2008). The time constraints of these studies can also range from specific periods of time to the evolution of the palaeogeography along different geological periods and eras. Golonka (2002) published maps of the entire Phanerozoic, Torsvik et al. (2002) explores palaeogeography of the world and the North Atlantic from the Silurian until recent times, Blakey (2008) focused on Gondwana during its entire 500my of existence, Cocks (2000) studied the Early Palaeozoic and Paproth (1991, 2006) centres her publications on the Carboniferous.

The methodology employed by different studies also varies. Two common and reliable tools for palaeogeographical research are palaeomagnetic data (Tait et al., 1994; Torsvik & Rehnström, 2001; Pastor-Galán et al., 2014) and tectonic information (Stampfli et al., 2002; Gutiérrez-Alonso et al., 2004; Domeier & Torsvik, 2014). Sedimentological data can also be useful for palaeogeographical reconstructions (Rau & Tongiorgi, 1981; Walkden, 1987; Golonka, 2002), and some analyses use the palaeontological record and the distributions of fossil taxa (Hill, 1981; Paproth & Streel, 1985; Herbig, 1989; Debrenne et al., 1999; Webb, 2002; W. Cao et al., 2017; Davydov & Cózar, 2019).

Carboniferous rugose corals have also been used in palaeogeographical studies, in addition to their palaeoecological significance. Despite their sessile lifestyle, their life cycle includes a free-swimming larval stage called planula (Hill, 1981). This stage allows them to migrate using favourable currents, enabling them to spread and colonize new domains and regions. As a result, rugose corals can serve as indicators in palaeobiogeographical and palaeogeographical analyses. Some examples from the Carboniferous are the studies by Fedorowski (1981), Rodríguez et al. (1986), Aretz (2002, 2011), García-Bellido & Rodríguez (2005), Somerville et al. (2012) and Denayer (2015, 2016).

It is also common to combine different types of data to achieve more comprehensive and complete results (Harper et al., 1996; Torsvik & Cocks, 2004; Paproth, 2006). Global compendiums, such as those by Mckerrow & Scotese (1990), Torsvik et al. (2002), Cocks & Torsvik (2006) or Scotese (2021), usually adopt this mixed approach. However, the large scale of global reconstructions often leads to a lack of details and inaccuracies in smaller areas or specific time periods. Notable examples are the maps of

Scotese (2021), which are widely used and among the most cited palaeogeographical reconstructions. These maps show the Rheic Ocean as already closed during the late Mississippian and uplifted as continental land by the Variscan orogeny. However, they overlook fossil evidence suggesting that the Rheic Ocean remained open until the Pennsylvanian. Mississippian rugose corals and other marine fossils are found in regions that once belonged to the Rheic Ocean, such as Nova Scotia, the British Isles, Southwestern Spain, and North Morocco. Furthermore, studies on foraminifers (Davydov & Cózar, 2019) indicate that the Rheic Ocean did not fully close until the Bashkirian. Domeier & Torsvik (2014) early Carboniferous map does not share this mistake, but it still has some issues regarding the details around the Western Palaeotethys and the Rheic Ocean. Specifically, it places Florida and its neighbouring states (SE USA) between the Iberian plate and North Africa. However, palaeontological evidence does not support this placement: rugose coral faunas in Spain and Morocco share many similarities, while the assemblages from the southeastern United States show clear differences (Lord et al., 2011; Rodríguez & Kopaska-Merkel, 2014). This highlights how, even though global maps are useful and necessary tools and compendiums of our palaeogeographical knowledge, they benefit from detailed regional studies that offer new insights and can afford to be more precise.

Within this palaeogeographical context, the Western Palaeotethys and the Rheic Ocean emerge as key regions for studying the impacts of tectonic and climatic changes on marine biodiversity. The eastern region of the Rheic Ocean shares many faunal similarities with the Western Palaeotethys, since there was not a significant barrier between them. For this reason, and to simplify the language, in this thesis we use “Western Palaeotethys” to include both the strict Western Palaeotethys and adjacent regions from the eastern Rheic Ocean (Nova Scotia, the British Isles, Southwestern Spain and North Morocco).

This palaeobioprovince was situated in equatorial and subtropical regions during the Mississippian (Torsvik et al., 2024). It comprises Nova Scotia, Europe (from the British Isles to Türkiye, and from the Moscow Basin to Southwestern Spain) and North Africa (from Morocco to Libya). Somerville et al. (2013) proposed four palaeobiogeographical sub-provinces for the western half of the Western Palaeotethys: the Atlantic Sub-province (Nova Scotia, the British Isles, and Belgium), the West Peri-Gondwanan Sub-province (southwestern Spain and northern Morocco, from the coast to the South Atlas Fault), the Mediterranean Sub-province (southern France, the Pyrenees and Cantabrian Mountains, the Baetic Cordillera, the Riff and the Balearic Islands) and the Saharan Sub-province (southern Morocco, Algeria, and the Carboniferous basins in northern Mauritania, Mali and western Libya).

There are some palaeogeographical studies in the Western Palaeotethys that focus on specific areas, such as the British Isles (Somerville, 2008), Belgium (Poty, 1980, 1989), North Africa (Legrand-Blain et al., 1989; Somerville et al., 2013), or Türkiye (Denayer, 2015). While these studies have explored key regions within the Western Palaeotethys, Aretz (2011) offers another relevant contribution to its palaeobiogeography. This analysis focuses on the late Visean and covers several regions of Western Europe and North Africa, using rugose corals as palaeogeographical indicators. Although this study offers valuable insights into coral distributions across these regions, it is restricted to seven areas in Western Europe, North Africa and Nova Scotia, omitting completely Central and Eastern Europe. Moreover, being an abstract from a symposium, it lacks detailed methodology and an extended dataset, limiting its reproducibility.

A more comprehensive study of the palaeogeography of the Western Palaeotethys is offered by Vai (2003). This study covers the Pennsylvanian and early Permian periods, providing a detailed and thorough analysis of the palaeogeographical evolution of the region. It remains one of the most detailed reconstructions of the Western Palaeotethys, and there is not a comparable study for the Mississipian. However, the research group on the Carboniferous at the Complutense University of Madrid is actively working on reconstructing the distribution of landmasses, epicontinental platforms, and open marine areas in the Western Palaeotethys during the Mississippian, using palaeontological evidence. This ongoing project has already produced several published studies (Somerville et al., 2012; Cózar et al., 2014; Rodríguez et al., 2020a; Rodríguez et al., 2020b).

1.2 OBJECTIVES AND STRUCTURE

The present thesis is a part of this broader project, and it is focused on using rugose corals and quantitative methods to improve our understanding of the palaeogeography of the Western Palaeotethys during the Mississippian stages. Previous analyses often rely on corals from extensive stratigraphical intervals, and few of them incorporate quantitative methods. These studies also face the problem of the uneven knowledge of rugose coral faunas across different regions. Some areas of the Western Palaeotethys have been studied in detail during decades (Poty, 1985; Mitchell, 1989;

Denayer et al., 2011; Rodríguez et al., 2016) and even since the XIX century (e. g. Dana, 1846; Michelin, 1847; F. McCoy, 1851). Therefore, their assemblages are well known, while others have been neglected and the information on their faunas is scarce or outdated.

Therefore, our main objectives are:

1) **Building an extensive database on Mississippian rugose corals**, documenting their geographical distributions throughout the stages of the Mississippian. This involves compiling all the relevant literature and examining collections from different institutions, ensuring a comprehensive, accurate and up to date database.
2) **Testing the utility of rugose corals for quantitative palaeogeographical studies**, by using various similarity indices, comparing areas of different sizes, focusing on specific genera and evaluating the influence of additional variables on the results.
3) **Conducting palaeogeographical and palaeobiogeographical analysis and reconstructions** for the Tournaisian, early Visean, late Visean and Serpukhovian stages. This results in updating previous palaeogeographical maps of the Western Palaeotethys to incorporate the results and insights obtained from rugose corals.
4) **Improving the current understanding of rugose coral evolution during the Mississippian**, with a focus on the factors driving diversity changes. This involves studying speciation patterns and evolutionary trends in well-studied coral families and comparing the changes in diversity and habit to the variations in climatic conditions.

To achieve these objectives, the early and late Visean will be treated as different stages due to their climatic and sea-level differences. This thesis is divided in six different phases, each represented by an article featured as a chapter. The sequence presented here follows the order of their development rather than their publication dates:

First, we focused on a well-studied small region, to test the robustness of the methodological and statistical tools. El Guadiato Area, situated in the suture zone between the Ossa Morena and Centroiberian domains of the Iberian Massif, presents an ideal scenario for this purpose. Its coral faunas have been thoroughly studied for more than 30 years (Rodríguez et al., 2016), so the distribution of species in the different outcrops is well known and complete, allowing for precise comparisons. We focused on the late Visean, as this stage is present across all tectonic units in El Guadiato Area. These analyses are presented in the second chapter of the thesis: “Palaeogeographic significance of rugose corals: El Guadiato Area (Southwestern Spain) as a case study”.

Then we focused on a couple of genera which were widespread during the Mississippian: *Lonsdaleia* and *Actinocyathus*. As the study includes only two genera, the sample size is too small for quantitative methods, and we employ qualitative analysis: we examine their evolution and dispersion patterns to draw conclusions about the communication between different marine areas. This study conforms the third chapter of the thesis: “Origin and evolution of the genera *Lonsdaleia* and *Actinocyathus*: Insights for the Mississippian palaeogeography from the western Palaeotethys”.

For the third analysis we described a new collection from Nötsch (Austria), which improved the known assemblage from the area. Incorporating the new taxa to our database, we compared the Austrian genera with the corals from carbonate platforms in Central and Eastern Europe. This offers a preview into the connections between different basins during the Mississippian, although this analysis groups the late Visean and Serpukhovian stages, since many of the corals appear on reworked facies that mix Visean and Serpukhovian material. These results are in chapter four: “The palaeobiogeographic significance of the Nötsch area (Austria) during the Middle and Late Mississippian based on rugose corals”.

Following these initial comparisons, we proceeded with a more detailed study of the late Visean coral assemblages. These analyses are performed at the genus level to avoid inaccuracies introduced by the many species left in open nomenclature in most areas. This analysis compares both the Western Palaeotethys sub-provinces and palaeogeographical units defined by related terranes and basins. The combination of favourable climatic conditions, marine transgressions, and the consequent high rugose corals diversity during the late Visean makes it an ideal scenario for such in-depth analyses. These findings are presented in chapter five: “The palaeobiogeography of the western Palaeotethys during the late Visean based on rugose corals”.

After carefully studying the late Visean, we expanded our study to encompass all stages of the Mississippian. In this larger-scale analysis, we focused on the Tournaisian, early Visean, late Visean, and Serpukhovian stages, comparing coral assemblages across sub-provinces rather than more specific palaeogeographical units. This choice reflects the broader larger scale of the study, as well as the lower diversity of rugose corals during the earlier and later Mississippian stages, which would make finer-scale comparisons less statistically robust. This study forms the basis of chapter six: “Rugose Coral Biogeography of the Western Palaeotethys During the Mississippian”. Although there is some overlap with the previous chapter in its treatment of the late Visean, this study presents only a summary of those results and frames them in the context of the entire Mississippian, comparing them to earlier and later stages.

Finally, we focused on the evolution of rugose corals during the Mississippian, exploring key speciation patterns, the apparition and spread of new habits and the impact of environmental changes on coral diversity. This analysis concludes the publications of the thesis and is discussed in the seventh chapter: “Some facts on the evolution of rugose corals during the Mississippian”.

To bring everything together and conclude the thesis, we include an integrating discussion in chapter eight, where we examine updates to the articles, synthesise our findings, and suggest future research avenues. Finally, we close the thesis in chapter nine with the conclusions.

2 PALAEOGEOGRAPHIC SIGNIFICANCE OF RUGOSE CORALS: EL GUADIATO AREA (SOUTHWESTERN SPAIN) AS A CASE STUDY

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RESEARCH PAPER

Palaeogeographic significance of rugose corals: El Guadiato Area (Southwestern Spain) as a case study

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Abstract

Carboniferous rugose corals are useful for palaeoecological, palaeoenvironmental and palaeogeographic studies. However, most analyses are qualitative and/or comprise corals from long stratigraphical intervals, and detailed palaeogeographic studies in the Carboniferous from western Palaeotethys are scarce. This report presents a quantitative analysis of the late Visean coral assemblages from the El Guadiato Area (Southwestern Spain), which has been thoroughly studied during the last 30 years. This case study aims to check the utility of rugose corals in detailed palaeogeographic studies, reconstructing tectonic movements in the suture zone between the Ossa Morena and Centroiberian domains in the Iberian Massif. Sixty-one rugose coral species from the El Guadiato Area were included in the analyses. Moreover, two other late Visean rugose coral faunas have been added as an external reference: Los Santos de Maimona (Southwestern Spain) and Kingscourt (Ireland). The presence/absence datasets have been treated with paired group (UPGMA) Hierarchical Clustering and a Detrended Correspondence Analysis. The results of this study support previous observations about the palaeogeography of the El Guadiato Area, backing the hypothesis that the strike slip faults of the area produced large lateral displacements. The results of analyses conducted at this level of detail appear to be conditioned by palaeoenvironmental differences, but the results of the comparison with Los Santos de Maimona and with Kingscourt's faunas look promising for future larger comparisons between different basins.

Keywords Mississippian · Visean · Biogeography · Cluster analysis

Resumen

Los corales rugosos del Carbonífero han probado su utilidad para estudios paleoecológicos, paleoambientales y paleogeográficos. Sin embargo, la mayor parte de los análisis empleando estos corales son cualitativos, o comprenden intervalos estratigráficos largos. Este trabajo presenta un análisis cuantitativo de las asociaciones de corales rugosos del Viseense tardío en el Área de El Guadiato (Sureste de España), estudiadas exhaustivamente durante los últimos treinta años. El objetivo es poner a prueba la utilidad de los corales rugosos en análisis paleogeográficos detallados, resolviendo los movimientos tectónicos del Área de El Guadiato, situada en la zona de sutura entre el dominio Centroibérico y el de Ossa Morena, en el Macizo Ibérico. Los análisis incluyen sesenta y una especies de corales rugosos de dicha área, además de dos faunas de corales rugosos del Viseense tardío que se utilizan como referencias externas: Los Santos de Maimona (Sureste de España) y Kingscourt (Irlanda). Los sets de datos de presencia/ausencia se han tratado con análisis clúster jerárquicos y análisis de correspondencia sin tendencia. Los resultados de este estudio coinciden con las observaciones y publicaciones previas sobre el Área de El Guadiato, apoyando la hipótesis de que las fallas tipo *strike-slip* del área produjeron grandes desplazamientos

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laterales. Los análisis a la escala y nivel de detalle de este trabajo parecen condicionados por las diferencias paleoambientales, pero los resultados de las comparaciones con las faunas de Los Santos de Maimona y Kingscourt parecen prometedores ante futuras comparaciones a mayor escala y entre diferentes cuencas.

Palabras clave Misisípico · Viseense · biogeografía · análisis clúster

1 Introduction

Detailed palaeogeographic studies in the Carboniferous from the western Palaeotethys are scarce. The most comprehensive study is that of Vai (2003) made on Pennsylvanian and early Permian data. However, there is not a comparable study for the Mississippian palaeogeography. The research group on Carboniferous of the Complutense University (Madrid) is undertaking a project to reconstruct the distribution of land masses, epicontinetal platforms and open sea areas in the western Palaeotethys during the Mississippian using palaeontological data. Some results were presented previously (Cózar et al., 2014; Rodríguez et al., 2020; Somerville et al., 2012). A more comprehensive study is being accomplished with quantitative data of the coral assemblages. The present paper is a first case study to check the utility of rugose corals in the reconstruction of tectonic movements in the El Guadiato Area, the suture zone between the Ossa Morena and Centroiberian domains of the Iberian Massif.

Carboniferous rugose corals have a high value in palaeoecological and palaeoenvironmental studies (Aretz, 2010; Hill, 1938–41; Kullmann 1997; Somerville and Rodríguez, 2007; Vuillemin 1990). They are also useful for biogeographic analyses (Aretz 2002, 2011; Denayer, 2015, 2016; Fedorowski, 1981; García-Bellido & Rodríguez, 2005; Hill, 1973; Rodríguez et al., 1986; Somerville et al., 2012). However, most analyses are qualitative and/or comprise corals from quite extensive stratigraphical intervals.

Another problem posed by most previous analyses is the uneven knowledge on different outcrops and regions. Corals from some regions have been studied in great detail, while some others show a scarcity of data. This report presents a quantitative analysis of the coral assemblages in a limited stratigraphic interval (upper Visean) and a well-studied small region (El Guadiato Area, Southwestern Spain). Rugose corals of the El Guadiato Area have been studied in detail during the last 30 years, and Rodríguez et al., (2016) synthesised the findings in those studies some years ago. Therefore, the knowledge of the composition and the age of the assemblages is quite complete. However, no previous studies on the palaeogeography of that area have been attempted except for that of Armendáriz et al., (2008), based on isotope variations in brachiopod shells.

2 Geological setting

The El Guadiato Area (Córdoba Province, SW Spain) is in a region between the Ossa Morena and the Centroiberian zones (Chacón et al., 1974; Delgado-Quesada et al., 1977), which has also been called the Lusitan-Marianic Zone (San José et al., 2004). Carboniferous rocks ranging in age from Visean to Moscovian occur in the region. The Mississippian rocks are mainly marine, whereas the Pennsylvanian rocks are continental. Rugose and tabulate corals are common in the Visean from the El Guadiato Area and several previous papers describe them (Rodríguez, 2004; Rodríguez & Falces, 1996; Rodríguez & Said, 2009; Rodríguez & Somerville, 2014; Rodríguez et al., 2001a, 2001b, 2002, 2004, 2006, 2016).

The studied region is along the El Guadiato Valley that runs from NW to SE for over 50 km and is bounded by ridges composed of Precambrian to Devonian rocks (Fig. 1). The Mississippian rocks from the El Guadiato Area have been divided into three tectonostratigraphic units separated by major faults (Cózar & Rodríguez, 1999a). Those are the Fresnedoso Unit, Visean in age and composed mainly of siliciclastic rocks; the Sierra del Castillo Unit, composed mainly of Visean limestones, and the San Antonio-La Juliana Unit, composed of both siliciclastic rocks and limestones, which are mostly Serpukhovian in age, but containing Visean limestone olistoliths. The corals used for the present analysis belong to the Sierra del Castillo Unit and to the olistoliths in the San Antonio-La Juliana Unit (Figs. 1 and 2).

The time interval covered by the Sierra del Castillo Unit and the olistoliths in the San Antonio-La Juliana Unit is relatively short, comprising only the Asbian and early Brigantian subages (Cózar & Rodríguez, 1999; Rodríguez & Somerville, 2007). Marine lower Visean or Tournaisian rocks have not been recorded in Sierra Morena, and the first marine sediments in the area relate to the late Visean transgression. Sedimentation during the Visean took place in a syntectonic environment, and tectonic movements affected the original platforms, which implies that the carbonate platforms where the corals lived have rarely been preserved. The corals in the El Guadiato Area often occur in debris flows and olistoliths, and consequently they are not in original position. The main exception to that is the Sierra del Castillo Block, where a large part of a shallow water platform is preserved.

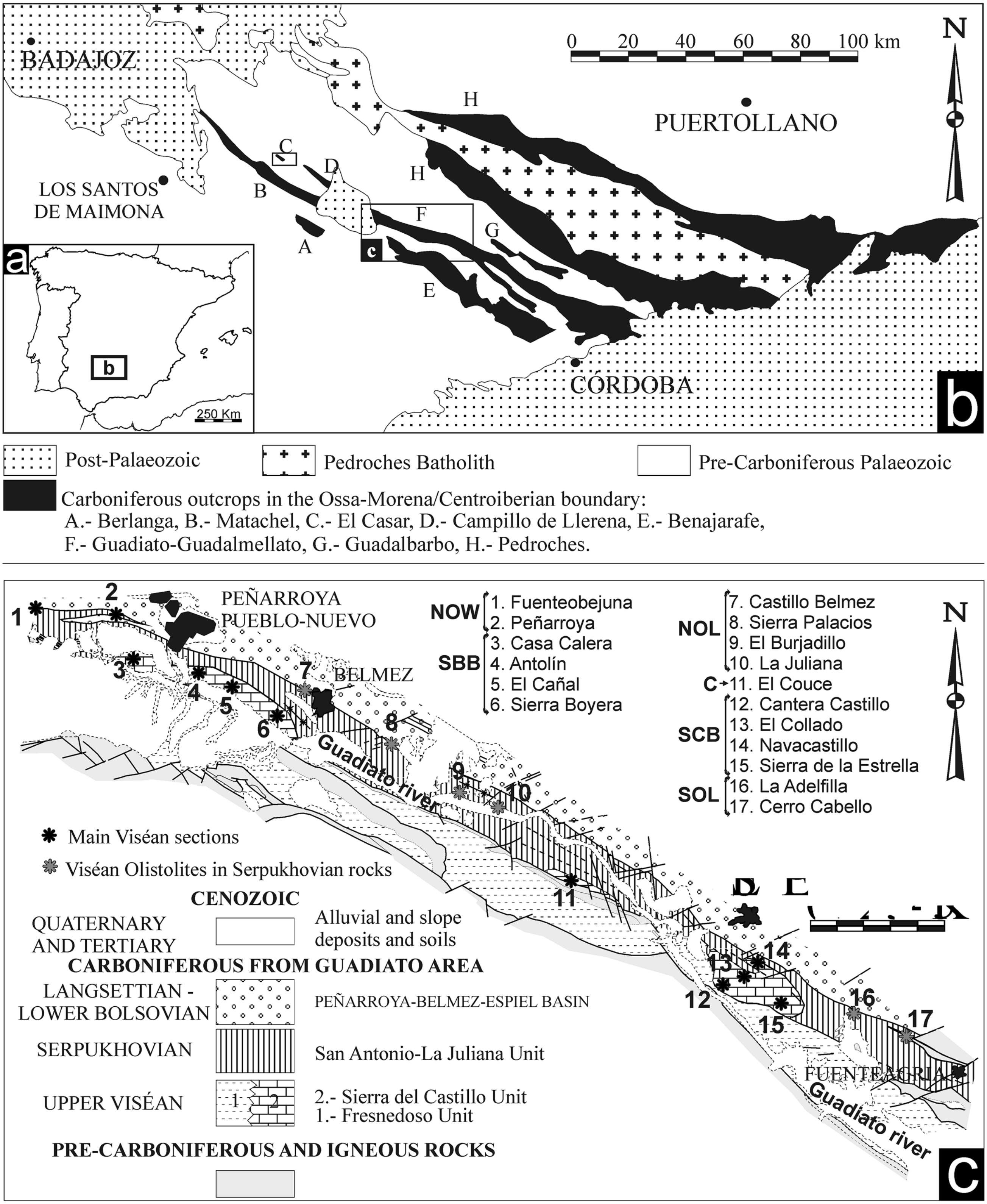

Fig. 1 Location maps of the El Guadiato Area and the studied outcrops. **a** Location of the El Guadiato Area and Los Santos de Maimona in Spain. **b** Regional map and location of the El Guadiato Area Carboniferous outcrops in SW Spain. Modified from Rodríguez et al., (2016). **c** Location of the studied outcrops (excluding El Casar) in the El Guadiato Area. Modified from Cózar & Rodríguez (1999)

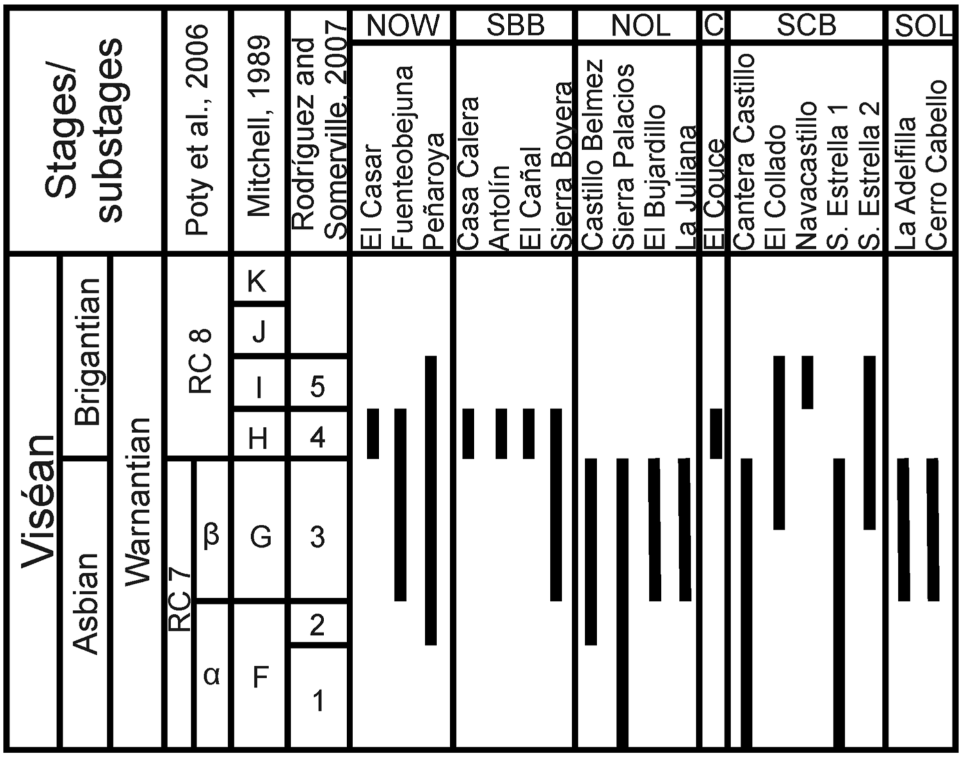

Fig. 2 Stratigraphic range of the studied outcrops from the El Guadiato Area. NOW: Northwestern outcrops. SBB: Sierra Boyera Block. NOL: Northern Olistoliths. C: El Couce outcrop. SCB: Sierra del Castillo Block. SOL: Southern olistoliths. (Rodríguez et al., 2016)

As the region was tectonically active during the Variscan Orogeny, faults and thrusts often separate the outcrops from one another. The area has suffered erosion, but little sedimentation during the Mesozoic and Cenozoic eras and, therefore, no significant thickness of sediments accumulated over the Mississippian rocks.

3 Data and methods

This research includes 19 outcrops from the El Guadiato Area (Fig. 1). The individual localities have been grouped in the six sectors proposed in Rodríguez et al., (2016): Northwestern Outcrops (NOW; El Casar, Fuenteobejuna, Peñarroya), Sierra Boyera Block (SBB; Casa de la Calera, Antolín, El Cañal, Sierra Boyera), Northern Olistoliths (NOL; Castillo Belmez, Sierra Palacios, El Bujardillo, La Juliana), El Couce outcrop (C; El Couce), Sierra del Castillo Block (SCB: Cantera Castillo, El Collado, Navacastillo) and Southern olistoliths (SOL: La Adelfilla, Cerro Cabello). Most of these sectors comprise outcrops that are fairly close together and in continuous rock bodies, without big faults or modern sediments separating them, with the Northwestern Outcrops being the main exception. The situation of Fuenteobejuna and Peñarroya, surrounded by Cenozoic sediments and limited by faults (Cózar et al., 2007; Rodríguez et al., 2016), and El Casar, roughly 50 km northwest of the rest of the outcrops, raises whether they should be grouped in one sector. However, the analyses conducted with the individual localities systematically show high similarities between El Casar, Fuenteobejuna and Peñarroya, so their classification as members of the Northwestern Outcrops has been maintained in this study.

This approach, grouping the localities, reduces the incompleteness of the individual localities, which can be affected by selective preservation, small sample sizes and poor outcropping conditions. All analyses have been applied to the composite sectors and to the individual localities, but the small sample size and low diversity of some localities produced hardly useful results, which are not included in this report.

Since the aim of this research is to carry out a detailed analysis of a particular area, rather than a big comparison of large biogeographic regions, the results might be influenced by other factors apart from distance. Two other faunas have been included as a reference to avoid drawing wrong interpretations: the rugose corals from Los Santos de Maimona Basin (late Visean, also in Ossa Morena) and from Kingscourt (late Visean, Ireland). These two locations have sizes and ages similar to the El Guadiato Area. If the differences and similarities found between the sectors within the El Guadiato Area are due to their palaeogeographic placement, Los Santos de Maimona and Kingscourt are expected to show even larger differences.

The analyses include over 1000 specimens from the El Guadiato Area, assigned to sixty-one species representing 36 genera of rugose corals (Table S1). This species inventory is based on Rodríguez et al., (2016) and unpublished data. Los Santos de Maimona's inventory has been compiled with data from Rodríguez & Falces (1992, 1994) and unpublished data, and it comprises 33 species of rugose corals, representing 20 different genera. Kingscourt species inventory has been compiled with data from Somerville (1997); the 35 species included here belong to 19 genera of rugose corals of Asbian and Brigantian ages. Most species in open nomenclature haven been left out of the analysis. However, they are included whenever it is evident that they do not belong to species found in other localities.

Two different datasets of presence and absence of species have been used. The first one includes all outcrops and localities and all rugose coral species. The second one is an attempt at lowering the environmental influence over the analyses. To that aim, it excludes the El Couce and both the Sierra la Estrella outcrops, which Rodríguez et al., (2016) describe as deeper water facies, while most the El Guadiato Area localities comprise shallow water ramp facies. It also excludes undissepimented corals since they are typical from deep water or turbid water facies (Hill, 1938–41, Kullmann, 1997) and their distribution might be more indicative of environmental differences than of palaeogeographic distances.

An attempt at narrowing down the age of the studied faunas was also made. To this aim, exclusively Brigantian outcrops and corals were removed from the analyses, so the comparison only comprised the late Asbian, present in all composite sectors from the El Guadiato Area. However, this approach implied removing some of the more prolific outcrops of the El Guadiato Area, such as El Cañal and Antolín, and the number of species remaining in some sectors was too low to produce stable clusters. The difference between late Asbian and early Brigantian faunas is small, and only one species found in the El Guadiato Area (*Palastrea regia*) and one found in Kingscourt (*Koninckophyllum volgense*) appear after the Asbian (despite a few more of them being absent in Kingscourt's Asbian faunas). Therefore, the analyses without Brigantian faunas were not useful enough to justify the significance loss and are not included in this report.

This study uses paired-group (UPGMA) Hierarchical Clustering and a Detrended Correspondence Analysis (DCA). Hierarchical Clustering requires a similarity index. Several authors have proposed and evaluated multiple indices, arriving at different conclusions (Hubálek, 1982; McCoy & Heck, 1987; Raup & Crick, 1979;Rodríguez, 1986;Schmachtenberg, 2008; Shi, 1993). This study compares Dice, Jaccard, Simpson and Raup-Crick indices, which have different strong points and shortcomings. Dice and Jaccard indices are widely recommended and used in biogeography, but they are strongly affected by differences in sample size (Hammer & Harper, 2006). The Simpson index, which is also very commonly used, is immune to those differences, and it is less affected by absence of taxa (Hammer & Harper, 2006), but it indicates the same similarity for cases that clearly represent different realities and processes (Raup & Crick, 1979). Raup-Crick ensures that widespread data do not have a disproportionate influence on measurement of similarity (Raup & Crick, 1979), but gives slightly different results every time it is used.

Cluster analysis will produce clusters whether there are real groups with meaningful differences or not. To validate a cluster it is important to test its stability. The cluster should not disappear if the data set suffers minor changes (Henning, 2007). To test stability, 100 bootstrap resamples have been performed on every cluster analysis, and only clusters with bootstrap values higher than 50% have been considered stable.

From the ordination methods available, we have chosen the Detrended Correspondence Analysis because it minimises an arch effect typical in other ordination methods (Hill & Gauch, 1980) and has been widely used and recommended in palaeobiogeography.

All analyses have been performed using Paleontological statistics (PAST 4).

4 Results

4.1 Cluster analysis

Figure 3 represents the different clusters produced by the analyses that include all considered outcrops and corals (both dissepimented and undissepimented).

Analyses using Jaccard and Dice similarity indices yielded almost identical results. The clusters display the same branches and nexus, with only slight differences in the similarity index. Since those analyses turn out redundant, only the one using Jaccard has been included in Figs. 3 and 4.

All analyses group together the Northern and Southern olistoliths; all similarity indices support the likeness between the coral faunas found in those sectors, regardless of the dataset. The Northwestern outcrops are also similar to the Northern and Southern olistoliths in all clusters, though the extent of that similarity and the stability of the cluster vary.

Bootstrapped cluster analyses based on Jaccard and Dice indices find five clusters with support values higher than 50%. Two of them are the aforementioned grouping of the Northwestern Outcrops and the Northern and Southern olistoliths. The clusters that join Los Santos de Maimona and the Sierra del Castillo Block, and those sectors and Kingscourt, also present high stability. The fifth cluster groups all outcrops except El Couce together.

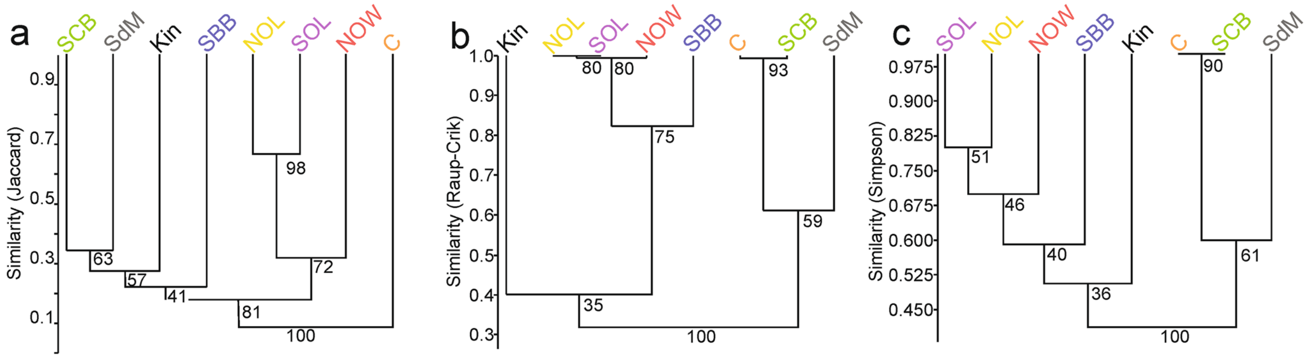

Fig. 3 Paired Group (UPGMA) Hierarchical Cluster analyses, including all outcrops and all rugose coral species. Different clusters correspond to different similarity indices: **a** Jaccard, **b** Raup-Crick, **c** Simpson. NOW: Northwestern outcrops; SBB: Sierra Boyera Block; NOL: Northern Olistoliths; C: El Couce Outcrop; SCB: Sierra del Castillo Block; SOL: Southern Olistoliths; SdM: Los Santos de Maimona; Brt: Britain

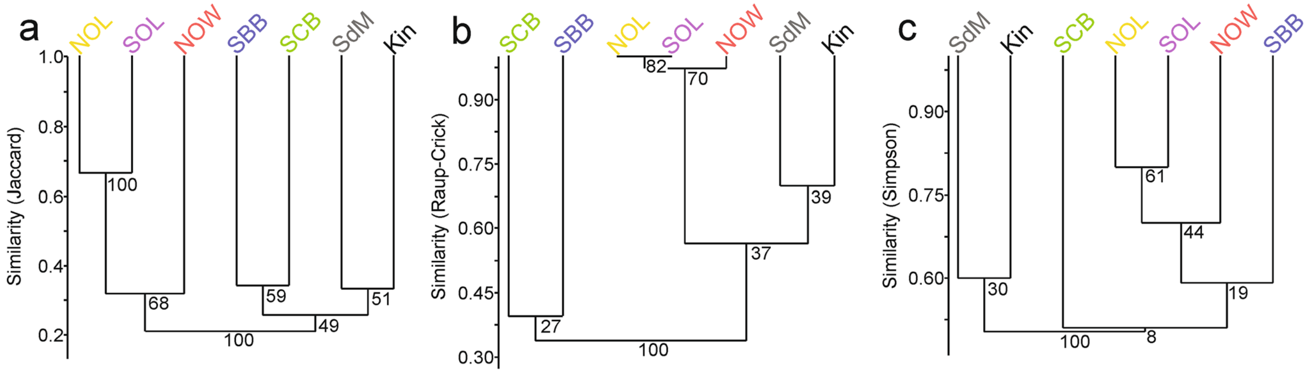

Fig. 4 Paired Group (UPGMA) Hierarchical Cluster analyses, after removing deeper water environments and undissepimented rugose corals. Different clusters correspond to different similarity indices: **a** Jaccard, **b** Raup-Crick, **c** Simpson. Abbreviations as in Fig. 3

Most clusters identified by Raup-Crick index present bootstrap values higher than 50%. The only exception is the cluster that groups Kin with some of the Spanish outcrops. The Nortern Olistoliths, the Southern Olistoliths and the Northwestern Outcrops are closely related, and they are grouped with the Sierra Boyera Block, while El Couce, the Sierra del Castillo Block and Los Santos de Maimona are grouped together. El Couce and the Sierra del Castillo Block show a strong relationship.

Simpson index only finds three clusters with support values higher than 50%, and those coincide with three of Raup-Crick's clusters. They are the grouping of the Northern and the Southern Olistoliths, the strong likeness between El Couce and the Sierra del Castillo Block, and the similarities of the latter group with Los Santos de Maimona.

After removing outcrops characterized by deeper water facies and undissepimented corals from the analyses (Fig. 4), Jaccard and Dice indices find two clusters with bootstrap values higher than 50% besides those that define the relationships between the Northern olistoliths, the Southern olistoliths and the Northwestern outcrops: they group the Sierra Boyera Block and the Sierra del Castillo Block in a cluster with a support value of 59%, and Los Santos de Maimona and Kingnscourt in another one, with a support value of 51%. The relationships between those clusters are not resolved since the cluster that defines them has low stability.

Raup-Crick index still maintains the clusters grouping the Northern Olistoliths, the Southern Olistoliths and the Northwestern Outcrops, but it shows lower bootstrap values for the cluster joining the Sierra Boyera Block and the Sierra del Castillo Block (27%). It also does not resolve the relationship of Los Santos de Maimona with the El Guadiato Area's localities and Kingnscourt.

Simpson index only finds one cluster with high stability: the relationship between the Northern Olistoliths and the Southern Olistoliths. Other clusters, despite not being very stable, agree with previous analyses, such as the link between the Northwestern Outcrops and the Northern and Southern Olistoliths and the grouping of Kingscourt and Los Santos de Maimona.

4.2 Detrended correspondence analysis

The first Detrended Correspondence Analysis (Fig. 5a), containing all localities and including also undissepimented corals, clearly differenciates two groups along Axis 1: Kingnscourt, Los Santos de Maimona, El Couce and the Sierra del Castillo Block on one side, and the Northern Olistoliths, the Sierra Boyera Block, the Southern Olistoliths and the Nortwestern Outcrops on the other. Axis 2, however, further divides this second group: the Northern Olistoliths, the Southern Olistoliths and the Nortwestern Outcrops are still close, while the Sierra Boyera Block does not belong clearly to any group.

Kingnscourt is still clearly different from the Spanish outcrops when the analyses do not include the deeper localities and the undissepimented corals (Fig. 5b). Los Santos de Maimona is also different to the sectors from the El Guadiato Area, since it is further away from the Sierra del Castillo Block. The El Guadiato Area's sectors are grouped in the lower end of Axis 1. The Southern Olistoliths and the Northern Olistoliths are still close, and there is no evident groups among the other sectors.

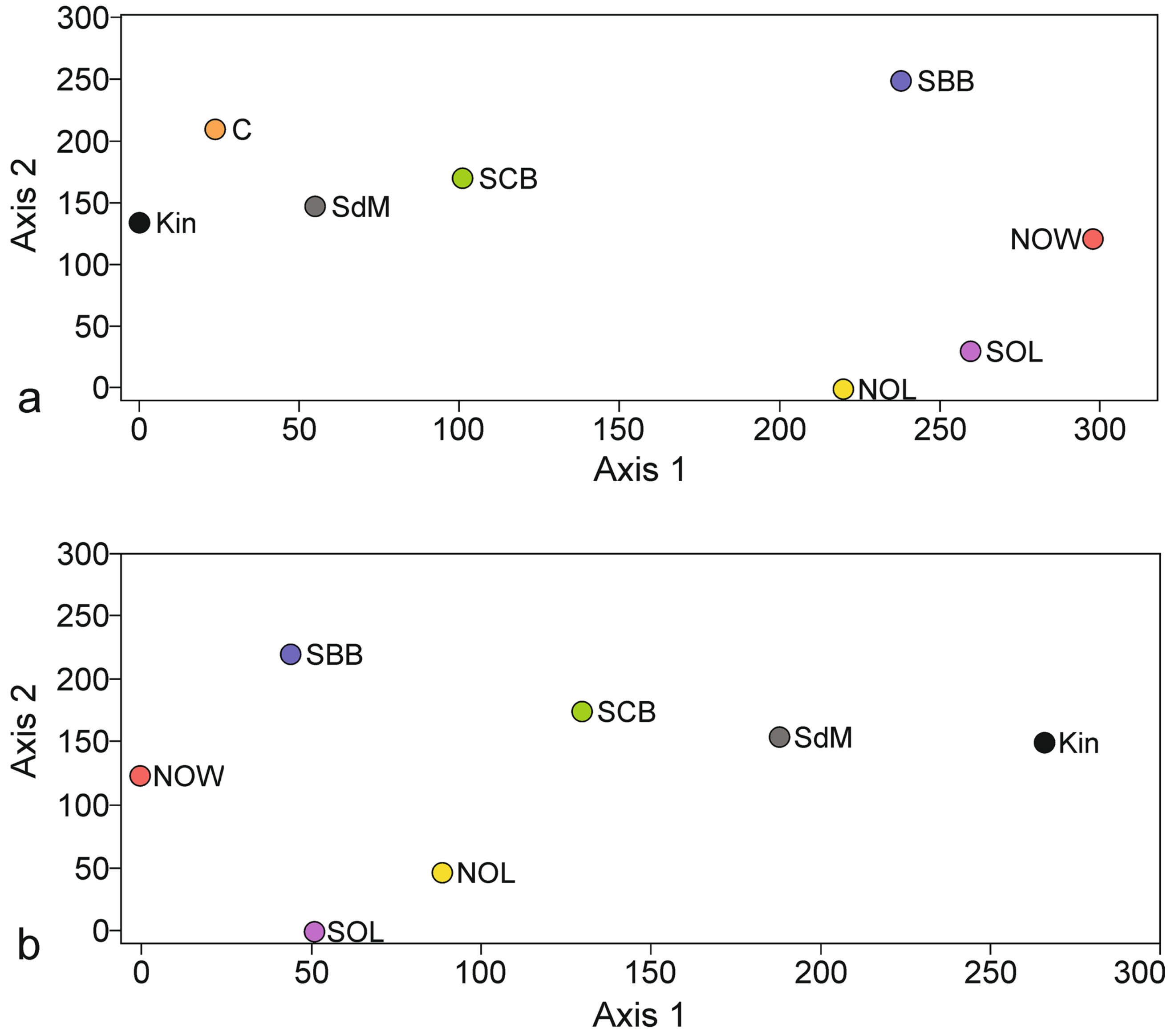

Fig. 5 Detrended Correspondence Analyses: **a** All outcrops and all rugose coral species; **b** Shallow water outcrops, undissepimented rugose corals not included. Abbreviations as in Fig. 3

5 Discussion

Palaeogeographical reconstructions of the Visean outcrops from the El Guadiato Area have to deal with two main questions. First, the uncertain relationships of the Northwestern Outcrops, which are limited by faults and surrounded by Cenozoic sediments (Cozar et al., 2007; Rodríguez et al., 2016), but have been traditionally assigned to the San Antonio-La Juliana Unit. Secondly, the strike-slip faults that separate the San Antonio-La Juliana Unit (Northern Olistoliths and Southern Olistoliths) and the Sierra del Castillo Unit (Sierra Boyera Block and Sierra del Castillo Block) Cózar & Rodríguez, 1999; Silva and Pereira, 2004; Wagner, 1999, 2004). Wagner (1999, 2004) estimated that these faults could have laterally displaced the units 100 to 200 km. If the current placement of the outcrops indicated the original distance between the localities, or if the faults only displaced both units a small distance, a high similarity between the Southern Olistoliths and the Sierra del Castillo Block could be expected. Meanwhile, the Northern Olistoliths and the Northwestern Outcrops should have more in common with the Sierra Boyera Block, and El Couce would show characteristics intermediate between those groups.

5.1 First dataset and the El Couce question

El Couce, however, presents some difficulties. Only the analyses applied to all outcrops include it (Figs. 3 and 5b), but the results regarding this locality change drastically when using different indices. Its small diversity clearly impacts Jaccard and Dice indices' assessment of its ties to other outcrops (Fig. 3a). Despite that all the species found in El Couce are also found in the Sierra del Castillo Block (and some of them in Santos de Maimona and Kingscourt), Jaccard index places it as the most different outcrop of the analysis. It finds closer ties between El Couce and the Northwestern Outcrops and the olistoliths from the El Guadiato Area, which also have lower sample sizes than the Sierra del Castillo and Sierra Boyera blocks, Los Santos de Maimona and Kingscourt. However, Raup-Crick (Fig. 3b), Simpson (Fig. 3c), and the Detrended Correspondence Analysis (Fig. 5a) find higher similarities between El Couce and the Sierra del Castillo Block. This is to be expected, since El Couce represents a deeper water distal shelf or slope and the Sierra del Castillo Block contains the Sierra de la Estrella outcrops, which are the result of the sedimentation in deeper-water environments than the rest of the El Guadiato Area's localities (Somerville & Rodríguez, 2007).

Los Santos de Maimona's fauna also presents ties with El Couce and the Sierra Castillo Block in most analyses. This again can be explained because of the high diversity of undissepimented corals (13 species out of 33 in Los Santos de Maimona), which are scarce in other the El Guadiato Area's localities but make up most of El Cource's rugose corals (6 out of 8 species) and a quarter of the Sierra Castillo Block (11 out of 41 species).

Environmental factors clearly determine the relationships between the aforementioned sectors. This could imply that the similarity between the Northern and Southern olistoliths and the Northwestern Outcrops found by the same analyses is influenced by all of them representing faunas from shallow water platforms, if the analyses performed without the deeper water outcrops would not support that similarity.

5.2 Second dataset

Removing the undissepimented corals from the El Guadiato Area, Los Santos de Maimona and Kingscourt, and the deeper-water outcrops from the El Guadiato Area lowers the impact of environmental influence without dramatically reducing the sample size. The Sierra Boyera Block and Los Santos de Maimona suffer a relatively large sample size reduction, but both are still among the most diverse sectors of the study. It is important to note that subtler differences in depositional environment can affect the faunas. The difference between waters above and under the normal wave base, or the effect of subaerial exposure or its absence, result in different coral associations (Somerville & Rodríguez, 2007), and those differences can be present in these analyses. This approach means entirely removing El Couce from the subsequent analyses. However, this doesn't hinder the palaeogeographical reconstruction, since the links between El Couce and other outcrops are clearly determined by both its small sample size (especially when using Jaccard index) and its environment, and cannot be used to assess a real palaeogeographical relationship.

Once the analyses focus on shallow-water outcrops and species, Kingscourt and los Santos de Maimona are systematically found to be different from the El Guadiato Area's localities by cluster analyses (Fig. 4), although the clusters are often not stable. The Detrended Correspondence Analysis (Fig. 5b) also places them close to each other, but it appears to differentiate more clearly Kingscourt from the Spanish faunas.

The Northern and Southern olistoliths maintain their clear similarity in all these analyses, as well as their proximity to the Northwestern Outcrops, so the likeness between these sectors is evident even when reducing environmental influence.

The relationships between this group, the Sierra Boyera Block, the Sierra del Castillo Block and Los Santos de Maimona and Kingscourt are not well resolved by the cluster analyses, though Jaccard and Simpson indices group the blocks from the Sierra del Castillo Unit together. Through most analyses, the Sierra Boyera Block is more similar to the Northwestern Outcrops and the olistoliths than the Sierra del Castillo Block.

The performed cluster analyses often find that the sectors from the El Guadiato Area have bigger differences between themselves than with Santos de Maimona, therefore it might be premature to assume that similarities found between the different outcrops from the El Guadiato Area are only due to palaeogeographic placement. However, it is important to note that those differences are never on stable clusters and that the relationship with Los Santos de Maimona is never fully resolved. The Detrended Correspondence Analysis, on the other hand, clearly differentiates Los Santos de Maimona from most outcrops from El Guadiato Area, and still maintains the main groupings and relationships between them found by most cluster analyses.

5.3 Clarifications and remarks

Every analysis supports a clear similarity between the coral faunas of the Northern and Southern olistoliths and evident differences between them and the outcrops found in the Sierra del Castillo Unit, despite their current placement next to each other. These differences support a large movement along the strike-slip faults that would place the original location of the olistoliths further away from the Sierra Boyera and Sierra del Castillo blocks, in accordance with the estimations of Wagner (1999, 2004). Moreover, since the fault movements mean that the San Antonio-La Juliana Unit was further south (Simancas et al., 2001; Silva & Pereira, 2004; Wagner, 2004) and the Northwestern Outcrops show clear similarities with the olistoliths, the latter appear to be part of the San Antonio-La Juliana Unit.

The relationships between the localities from the San Antonio-La Juliana Unit and those from the Sierra del Castillo Unit are harder to establish. The solution most coherent with the regional tectonics and with our results would place the sectors in the following order, from northwest to southeast: Sierra Boyera Block, El Couce, Sierra del Castillo Block, Northwestern Outcrops, Northern Olistoliths and Southern Olistoliths.

However, Jaccard and Dice indices of similarity (Fig. 4a) and the Detrended Correspondence Analysis (Fig. 5b) place the Northwestern Outcrops between the olistoliths and the Sierra Boyera Block, with more ties to the latter than to the Sierra del Castillo Block. Rodríguez et al., (2016) already pointed that the Sierra Boyera Block and the Northwestern Outcrops share a few species that are not present in the rest of the outcrops. Further examination of the data, however, has reduced those species to two rugose coral (*Amplexocarinia* sp. and *Amygdalophylloides anticuum*) and one tabulate coral (*Multithecopora* sp. B), which is not included in this study. Both rugose coral species are endemic to the El Guadiato Area (Rodríguez & Saíd, 2009 plus unpublished data), so their presence in only two sectors appeared promising to establish the similarities and the distance between them. Rodríguez et al., (2016) concluded that the San Antonio-La Juliana Unit (not including the Northwestern Outcrops) was originally further northwest, positioning the sectors in the following order, from northwest to southeast: Northern Olistoliths, Southern Olistoliths, Northwestern Outcrops, Sierra Boyera Block, El Couce, Sierra del Castillo Block. This is coherent with the similarities and differences found in this study by Jaccard and Dice similarity indices and the Detrended Correspondence Analysis, but not with the previous tectonic studies of the region (Simancas et al., 2001, 2004; Silva & Pereira, 2004; Wagner, 2004). The direction of the fault movements, as shown in different tectonic studies, means that the Sierra del Castillo Block should present more similarities with the outcrops from the San Antonio-La Juliana Unit than the Sierra Boyera Block. However, all analyses show the opposite. The larger differences between the Sierra del Castillo Block and the San Antonio-La Juliana Unit, and the absence in the Sierra del Castillo Block of the endemic species shared between the Northwestern Outcrops and the Sierra Boyera Block, cannot be explained by palaeogeography alone. It strongly suggests that something else than placement and distance is influencing the results, most likely differences in environment, as suggested by the evident variation between the first set of analyses (Figs. 3 and 5a) and the second (Figs. 4 and 5b).

It is also possible that a stratigraphic signal is affecting the results. This study comprises a small slice of time, but it includes the transition from Asbian to Brigantian, and some localities are exclusively Asbian, while others are younger the limit between the two. The dataset that was meant to prove or discard this signal did not provide useful results. However, the small number of species restricted to one of these substages present in the analyses means that the effect of the age is likely negligible.

6 Conclusions

Statistical comparisons of the rugose coral faunas from the El Guadiato Area (Southwestern Spain) show clear similarities between the Northwestern Outcrops, the Northern Olistoliths and the Southern Olistoliths, consistent through all different analyses. These similarities place the Northwestern Outcrops as part of the San Antonio-La Juliana Unit and support large lateral displacements produced by the strike-slip faults that limit the San Antonio-La Juliana and Sierra del Castillo units. A palaeogeographical reconstruction coherent with local tectonics and the conducted analysis would place the analysed sectors in the following order, from northwest to southeast: Sierra Boyera Block, El Couce, Sierra del Castillo Block, Northwestern Outcrops, Northern Olistoliths and Southern Olistoliths.

This quantitative approach to the study of the rugose coral fauna of the El Guadiato Area has proven helpful to confirm qualitative comparisons and reduce subjective biases. A good understanding of the geology and tectonics of the area allows inferring palaeogeographical implications from the results of the cluster analyses and the Detrended Correspondence Analysis, but the results of all analyses conducted at this level of detail appear strongly conditioned by environmental differences. However, the results of the comparison with Los Santos de Maimona and with Kingscourt's faunas appear more controlled by palaeogeographical distance, which seems promising for future larger comparisons between different basins.

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Declaration

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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3 ORIGIN AND EVOLUTION OF THE GENERA *LONSDALEIA* AND *ACTINOCYATHUS*: INSIGHTS FOR THE MISSISSIPPIAN PALAEOGEOGRAPHY FROM THE WESTERN PALAEOTETHYS

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Biopalaeogeography

Origin and evolution of the genera *Lonsdaleia* and *Actinocyathus*: Insights for the Mississippian palaeogeography from the western Palaeotethys

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Abstract Representatives of the subfamily Lonsdaleiinae Chapman, 1893 are common in the Mississippian of the western Palaeotethys. A general analysis of the origin, distribution and evolution of that subfamily has been undertaken. The most probable hypothesis for the origin of the genus *Lonsdaleia* McCoy, 1849 is to acquire colonialism via the genus *Axophyllum* Milne Edwards and Haime, 1851. *Actinocyathus* d'Orbigny, 1849 would be a descendant of *Lonsdaleia* by increasing integration in the colonies. The first occurrences of *Lonsdaleia* have been recorded in the lower Visean from northern Britain and northern Tianshan Mountains of northwestern China, but the diversification and migration to the whole Palaeotethys only happened in the late Visean. Three hypotheses are proposed on that matter. The Serpukhovian was also a period of migrations and diversification for these genera. Both *Lonsdaleia* and *Actinocyathus* have been recorded in Bashkirian refuges, the Sverdrup Basin in northern Laurasia and the Tindouf Basin in northern Africa, respectively. The division of the western Palaeotethys into six subprovinces based on the distribution of corals is proposed.

Keywords Carboniferous, Palaeotethys, Biogeography, Evolution, Rugosa

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1. Introduction

The subfamily Lonsdaleiinae Chapman, 1893 comprises colonial corals of the family Axophyllidae (Hill, 1981). The genera *Lonsdaleia*, *Actinocyathus* and *Serraphyllum* are included in that subfamily. The first two genera are abundant and almost cosmopolitan. The third one has been recorded only in the Montagne Noire up to now (Poty and Hecker, 2003). Some other genera have been also included in the subfamily, but they have been regarded as synonyms of the cited ones (Hill, 1981).

The Lonsdaleiinae have been cited in most areas of the world in the upper Visean and the Serpukhovian (see references below), and more rarely in the Bashkirian. However, their distribution is quite irregular for several reasons: The knowledge of the Mississippian coral record shows strong variations in different geographical areas. In addition, the name *Lonsdaleia* has been used for Pennsylvanian corals that belong to other families such as Petalaxidae or Waagenophyllidae (Dobrolyubova, 1936; Douglas, 1936; Easton, 1960; De Groot, 1963). Moreover, some citations may not be consistent, either because the identification is not clear, or because the age of the occurrence is doubtful (Grosch, 1912; Hudson, 1958). An extensive revision of the occurrences of the genera *Lonsdaleia* and *Actinocyathus* in different regions of the world provides new data that are useful to present a general view of the origin, evolution and migrations of these two genera.

The taxonomic position of the two involved genera, *Lonsdaleia* McCoy, 1849 and *Actinocyathus* d'Orbigny (1849), has been matter of discussion for a long time. Martin (1809) described and figured corals with the names *Erismatolithus Madreporites (duplicatus)* and *Erismatolithus Madreporites (floriformis)*. Both were later described and figured under different names (see Smith, 1915 for a complete review of the older literature). McCoy (1849) defined the genus *Lonsdaleia* for fasciculate corals having a complex axial structure and lonsdaleoid dissepiments. d'Orbigny (1849) introduced the genus *Actinocyathus* for corals having massive (cerioid) habit, complex axial structure and lonsdaleoid dissepiments. McCoy (1851) established the species *L. duplicata* as the genotype of *Lonsdaleia* and used the name *Strombodes* for the massive corals with identical inner features. Milne-Edwards and Haime (1850—54) included both massive and fasciculate forms in a single genus that they called *Lithostrotion* (in 1850) and later *Lonsdaleia* (in 1851 and 1854). Fromentel (1861) introduced the name *Stylidophyllum* for the massive forms. This proposal was not much followed, because most authors in the subsequent years used the name *Lonsdaleia* for both massive and fasciculate corals (Thomson and Nicholson, 1876; Vaughan, 1905; Garwood, 1912; etc.), but some authors used that name (Chi, 1931; Gorsky, 1935).

Lang *et al.* (1940) stated that the name *Actinocyathus* is available. Kato (1966) demonstrated that it has priority over *Stylidophyllum* Fromentel (1861) that was used for cerioid Lonsdaleiinae by some authors (Gorsky, 1935; Dobrolyubova, 1936, 1958; Yamagiwa, 1961), either as a subgenus of *Lonsdaleia* or as a generic name. Kato (1966) proposed that *Actinocyathus* should substitute *Stylidophyllum* if the latter could be considered as a separate genus. Thus, Sando (1975) postulated it as a subgenus of *Lonsdaleia*. Hill (1981) proposed the use of *Actinocyathus* as a separate genus from *Lonsdaleia*. Subsequently, some authors considered it as a subgenus (Poty, 1981; Sando, 1983; Poty and Hecker, 2003; Hecker, 2012) and others as a genus (Mitchell, 1989; Wang, 1989; Rodríguez *et al.*, 2013a). The differentiation of genera based on different habits is a common feature in Paleozoic corals (e.g. *Lithostrotion* Fleming, 1828, *Siphonodendron* McCoy, 1849), but there are different opinions between the specialists on rugose corals on that matter (Hill, 1938—41, 1981; Fedorowski, 1978, 1981, 1984; Poty, 1981, 2010). In the case of *Lonsdaleia* and *Actinocyathus*, as there is no consensus, and since it is a matter of subjectivity, we will use both names as separate genera, because it simplifies the terminology.

2. Discussion

The Lonsdaleiinae from the Tindouf Basin in Morocco provide important information for the understanding of the Visean and Serpukhovian palaeogeography of the western Palaeotethys, because they complete the view of the evolution of these corals in the context of Europe and North Africa. In order to analyse the distribution of the Lonsdaleiinae, it is necessary first to revise the origin and evolution of the genus *Lonsdaleia* s.l. (including the genera/subgenera *Lonsdaleia* and *Actinocyathus*).

2.1. Lonsdaleia origin and diversification

Several hypotheses have been proposed in order to explain the origin of the genus *Lonsdaleia*. Thomson (1883) suggested that *Thysanophyllum* (a massive genus similar to *Lonsdaleia*, but without or with reduced axial structure) could be the ancestor of *Lonsdaleia*. Carruthers in Garwood (1912) followed that hypothesis by comparing the neanic stages of *Lonsdaleia* and *Thysanophyllum*. Smith (1915), in his monograph on *Lonsdaleia*, supported it, showing the early neanic stages of these genera in his plate XVII. Vaughan (1905) proposed a different hypothesis when he suggested that *Lonsdaleia* was derived from the solitary genus *Clisiophyllum* by development of colonialism and lonsdaleoid dissepiments. Only a year later, Matley and Vaughan (1906) changed his hypothesis and proposed the genus *Carcinophyllum* as the ancestor of *Lonsdaleia*. The advantage of this genus for the ancestry is its lonsdaleoid dissepimentarium, and thus requiring only the development of colonialism for the appearance of the new genus.

Hill (1938—41) suggested that the relationship between *Lonsdaleia* and *Thysanophyllum* could be inverse, with the first being the ancestor of the latter. That hypothesis was followed by Vassiljuk (1960) and other authors, but they did not explain the ancestry of *Lonsdaleia*. Poty (1981) suggested that *Axophyllum* should be the ancestor of *Lonsdaleia*, following the hypothesis of Matley and Vaughan (1906), as Semenoff-Tian-Chansky (1974) demonstrated that *Carcinophyllum* is a synonym of *Axophyllum*. That hypothesis has been followed later by most authors (Poty and Hecker, 2003; Poty, 2010; Rodríguez and Somerville, 2010; Somerville and Rodríguez, 2010). Smith (1915) also suggested that the massive forms of *Lonsdaleia* derived from the fasciculate ones. He used the name *Lonsdaleia*, but now the name *Actinocyathus* is accepted for massive forms, either as a separate genus, or as a subgenus. Also, the consideration of *Lonsdaleia* as an ancestor of *Actinocyathus* is agreed by most authors (Hecker, 1997; Poty and Hecker, 2003; etc.).

An important question for the analysis of the distribution of the genera *Lonsdaleia* and *Actinocyathus* is when and where they appeared. The oldest *Lonsdaleia* species is *L. praenuntia* Smith (1915). The type specimens were collected by Vaughan (1911) in the lower Visean from Arnside, NW England. This species shows a reduced axial structure that resembles that of Cysto*lonsdaleia* Fomichev, 1953 or *Dorlodotia* Salée, 1920. In fact, this species was not included in the biostratigraphical chart of Mitchell (1989), who considered the first appearance of *Lonsdaleia* to be much higher, in his zone H (Brigantian). The doubts on the identification of the specimens of Vaughan (1911) as *Lonsdaleia* are due to the absence of buddings that demonstrate its coloniality. Thus, they could also be regarded as representatives of *Axophyllum*. Poty (1980, 1981) suggested that this species could be the ancestor of the genus *Dorlodotia*. Hecker (2011, p. 47) indicated that *"studies of variability in Dorlodotia suggest that Lonsdaleia praenuntia is also a Dorlodotia*". We can't agree with this statement, because even if the axial structure of *L. praenuntia* is "*loosely constructed and asymmetrical* ..." as pointed out by Smith (1915, p. 243), the structure of the tabularium is typical of *Lonsdaleia* and, as noted by Smith (1915, p. 243), "*the central column exhibits no marked difference from the same structure in L. duplicata*." Fig. 1 shows the similitudes and differences: a complex axial structure and concave periaxial tabulae in *L. praenuntia* and simple axial structure and periaxial tabulae elevated towards it in *Dorlodotia briarti*. Consequently, *Lonsdaleia praenuntia* must be regarded as an early representative of that genus.

It is a common fact in many rugose corals that colonial taxa descend from solitary corals (Fedorowski, 1978; Poty, 2010; Rodríguez and Somerville, 2010; Denayer and Webb, 2015). In many cases, there are some intermediate stages of gregarism and of solitary corals developing offsets in the calice without further growth of a true colony. It has been called quasi-colonialism (Fedorowski, 1978) or protocolonialism (Somerville and Rodríguez, 2010). As stated above, *Lonsdaleia* probably derived from a solitary species of *Axophyllum*, a genus which shares most inner features with it. A case of a gregarious and quasi-colonial axophyllid (*Howthia* Somerville and Rodríguez, 2010) was

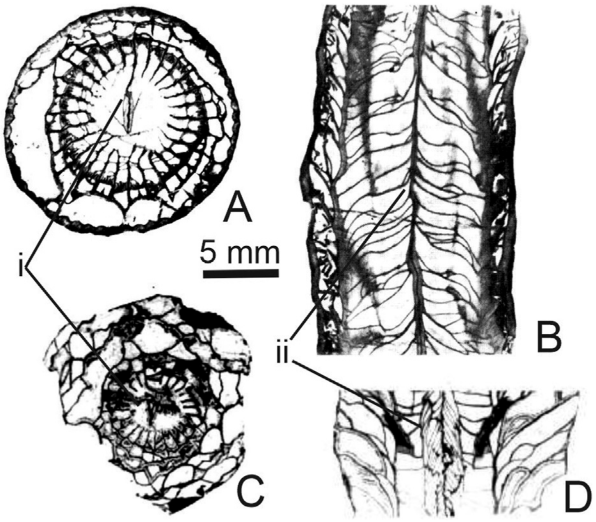

Fig. 1 Comparison between *Dorlodotia briarti* (A, B, transverse and longitudinal sections; figures taken from Poty, 1981) and *Lonsdaleia praenuntia* (C, D, transverse and longitudinal sections; figures taken from Smith, 1915). The main differences are (i) that the axial structure is more complex in *L. praenuntia*; it is joined to the counter septum in *D. briarti* and to the cardinal septum in *L. praenuntia*, and (ii) the periaxial tabulae are concave and more or less horizontal in *L. praenuntia*, but in *D. briarti* there are no axial and periaxial series of tabulae and they are elevated towards the medial plate.

described in the upper Tournaisian from Howth (Ireland). It could be an example of the way for the appearance of *Lonsdaleia* from *Axophyllum*. And it could be the ancestor of all the Lonsdaleiinae if they are not polyphyletic.

The main difficulty to accept *L. praenuntia* as the ancestor of the late Visean species of *Lonsdaleia* is the total absence of the genus in the middle Visean. However, several species have been recorded in the upper Visean of the same domain (the Alston block of northern Britain) (Smith, 1915). This could be due to two different reasons (1) *L. praenuntia* is not the ancestor of the late Visean species, and they evolved quickly during the Asbian transgression. The development of that species could be an early attempt to develop colonialism in the family, without descendants, or it could be an *Axophyllum*. (2) The presence of several species in the same area indicates a previous diversification during the middle Visean that is not recorded, or they evolved quickly during the late Visean.

However, the development of colonialism could have occurred more than one time in the Axophyllidae and *Lonsdaleia* could be polyphyletic. In many species of *Lonsdaleia*, the axial structure is closer to that of the genus *Dibunophyllum* than to that of *Axophyllum*. In *Dibunophyllum* and many species of *Lonsdaleia*, the axial structure is composed of a median lamella, a small number of radial lamellae and tabulae inclined to the periphery. The lamellae are usually anastomosed or winding. On the contrary, in *Axophyllum*, the axial structure is composed of thickened, more irregular and anastomosing radial lamellae, crossed by a median plate. This was the reason why Smith (1915) also suggested the possibility of that genus as the ancestor of *Lonsdaleia*. He rejected that possibility, but the similarities are conspicuous, because in many species of the *Lonsdaleia duplicata* and *Actinocyathus floriformis* groups, the axial structure is mainly dibunophylloid. We checked many specimens of *Lonsdaleia* from different provenances (Tindouf, Betic Cordillera, Britain, Carnic Alps, Moscow Basin, etc.) and all of them show a consistent homogeneity in the microstructure that fit with the Axophyllidae family (lamellar wall, tabulae, dissepiments and septal stereoplasm), but not with *Dibunophyllum* (granulo-fibrous mesoplasm and fibrous stereoplasm).

Actinocyathus and *Lonsdaleia* can be divided into several groups of species, with different features, and probably with different ecological constraints that conditioned their palaeogeographic distribution. Hecker (1997, 2010) gave a complete view of the species groups of *Actinocyathus*; the species group of *A. floriformis* Martin with short minor septa and the species group of *A. crassiconus* with long minor septa (Fig. 2). As she explained in detail their geographic and ecological distribution, we will not develop this matter here. Some species belonging to the *A. floriformis* group are *A. borealis*, *A. bronni* and *A. rossica* (Hecker, 1997). Typical representatives of the *A. crassiconus* group are *A. gorskyi*, *A. latevesiculosus*, *A. mariae*, *A. sarytschevae*, and *A. subtilis*.

In *Lonsdaleia*, the type species *Lonsdaleia duplicata* and most species show a dibunophylloid axial structure and thin structures and lived mainly in stable carbonate platforms. Some of the species included in this group are *L. alstonensis* Smith (1915), *L. arctica* Gorsky (1935), *L. caledonia* Smith (1915), *L. crassigemmata* Dobrolyubova (1958), *L. duplicata* Martin (1809), *L. grandicaspia* Degtiarev (1965), *L. majiobaensis* Fan (1978), *L. melmerbiensis* Smith (1915), *L. multiseptata* Dobrolyubova (1958), *L. permanoseptata* Vassiljuk (1960), *L. siblyi* Smith (1915), *L. singularis* Dobrolyubova (1958), and others. In contrast, some other species that we will name the *Lonsdaleia corbarensis* group, show smaller corallites, thick structures and more irregular axophylloid axial structure. The species that we include in this group are *L. agapoviensis* Kachanov, 1964, *L. corbariensis* Semenoff-Tian-Chansky and Ovtracht (1965), *Lonsdaleia carnica* Rodríguez et al., 2019, *L. redondensis* Poty and Hecker

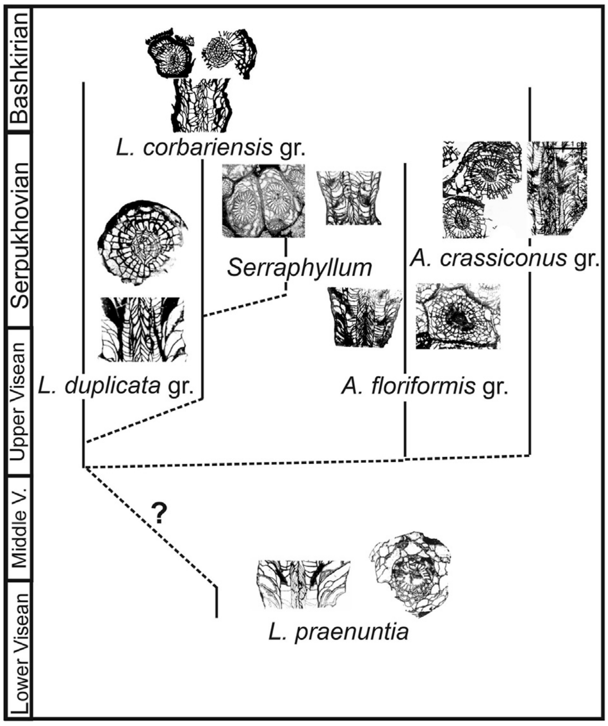

Fig. 2 Inferred phylogenetic relationships between the different species groups in Lonsdaleiinae. Abbreviations: *A.* = *Actinocyathus*; *L.* = *Lonsdaleia*; gr. = Group.

(2003), *L. reutheri* Boll (1985), *L. taveli* Altmark (1963) and *L. tichyi* Dobrolyubova (1958). Most of these species lived in more unstable environments, associated to microbial communities, and their geographical distribution differs greatly from those of the *Lonsdaleia duplicata* group. Poty and Hecker (2003) demonstrated the presence of a biform tabularium and periaxial cones in several species of *Lonsdaleia*. We checked all our specimens and many in the literature to analyse the presence of these features in the mentioned groups. In many cases we couldn't find proofs of their presence because the published figures don't show these features, but they seem to be present in several species of both groups of *Lonsdaleia* and in *Actinocyathus* (Table 1).

2.2. *Lonsdaleia and Actinocyathus distribution*

Any palaeogeographic analysis needs to take into account the plate tectonics, and the areas to be compared should be consistent with the different terranes that are known in each period of geological history. We tried to follow this axiom in the analysis of the distribution of the genera *Lonsdaleia* and *Actinocyathus*, but sometimes, the record itself or the studies in some areas are scarce. For example, in Germany, three palaeogeographic domains are recognised for the Carboniferous: the Rhenohercynian, the Saxothuringian and the Moldanubian, from north to south (Weyer, 2000), but records in those domains are very scarce and in most cases they occur in allochthonous blocks or in reworked facies (olistostromes or culm). Thus, for this study, these three domains will be amalgamated as one single area (Germany). The same has been done with other areas, such as the three main Austrian outcrops yielding Mississippian corals (Carnic Alps, Nötsch and the Greywacke Zone; Hubmann, 2002) that will be considered as one unit. We also use the name Poland for several palaeogeographic units in that country (Sudetes, Upper Silesian Basin, Lublin Basin, and also the prolongation southeastwards

Table 1 Comparison of biometric data for species of *Lonsdaleia* and *Actinocyathus* mentioned in this paper. Abbreviations: N = Number of major septa; Dt = Diameter of tabularium; Das/Dt = Ratio of diameter of axial structure to tabularium diameter; RL = Number of radial lamellae; B.T. = Biform tabularium; ? = Not determined.

Species	N	Dt	Das/Dt	RL	B.T.	Minor septa
Lonsdaleia						
L. duplicata Martin	25–27	4.5–6	1/3–1/2	10–20	Present	Short
L. agapoviensis Kachanov	25–27	9.0–11.0	1/4	5–10	No	None
L. alstonensis Smith	26–28	4.0–5.0	1/2	15–30	?	Short
L. arctica Gorsky	22–24	3.0–5.0	1/3–1/2	20–30	?	Short
L. caledonia Smith	28–30	7.0–9.0	1/2	15–25	No	Long
L. corbariensis Semenoff-Tian-Chansky	20–25	5.0–7.0	1/2	15–20	?	Long
L. crassigemmata Vassiljuk	25–30	7.0–9.0	1/5–1/4	6–10	No	Short
L. grandicaspia Degtiarev	30–35	10.0–12.0	1/3–1/2	25–30	?	Long
L. majiobaensis Fan	36–37	10.0–12.0	1/4	20–25	Present	Short
L. melmerbiensis Smith	26–28	6.0–8.0	1/3	5–10	Present	Short
L. multiseptata Dobrolyubova	27–28	9.0–10	1/3	15–25	Present	Long
L. permanoseptata Vassiljuk	18–21	5.0–7.0	1/3	13–15	?	Short
L. praenuntia Smith	26–28	5,0–6,0	1/3	5–10	?	None
L. *redondensis* Poty and Hecker	15–18	3–4.2	1/3	5–10	Present	Long
L. *reutheri* Boll	24	7.0–10.0	1/3	5–10	Present	Short
L. *siblyi* Smith	22–24	5.5–6.5	1/3–1/2	10–15	No	Short
L. singularis Dobrolyubova	27–29	9.0–10.0	1/3–1/2	15–25	?	Short
L. taveli Altmark	27–28	6.0–9.0	1/3	8–10	?	Long
L. tichyi Dobrolyubova	20–23	5.0–7.0	1/3	5–10	?	None
L. carnica Rodríguez	22–25	4.3–5.2	1/4–1/3	5–20	No	Long
Actinocyathus						
A. borealis (Dobrolyubova)	19–23	5.0–6.5	1/4–1/2	10–20	Present	Short
A. bronni (Milne-Edwards and Haime)	30–34	7.0–10.0	1/3	10–15	No	Short
A. crassiconus (McCoy)	22–27	4.8–6.5	1/2	15–30	Present	Long
A. floriformis (Martin)	20–25	4.0–6.0	1/3	5–10	Present	Short
A. gorskyi (Dobrolyubova)	26–33	5–7.5	1/2	15–24	Present	Long
A. latevesiculosus (Dobrolyubova)	22–27	6–8.5	1/3	7–12	Present	Long
A. mariae Rodríguez *et al.*	23–28	6–9	1/3–1/2	10–30	Present	Long
A. rossicus (Stuckenberg)	19–24	5.0–6.0	1/3–1/2	15–25	No	Short
A. sarytschevae (Dobrolyubova)	34–40	7.5–10.3	2/3	10–30	Present	Long
A. sp. A Hecker	21–26	4.8–6.5	1/3–1/2	8–20	Present	Long
A. subtilis (Dobrolyubova)	21–30	4–6.3	1/3–1/2	10–24	Present	Long

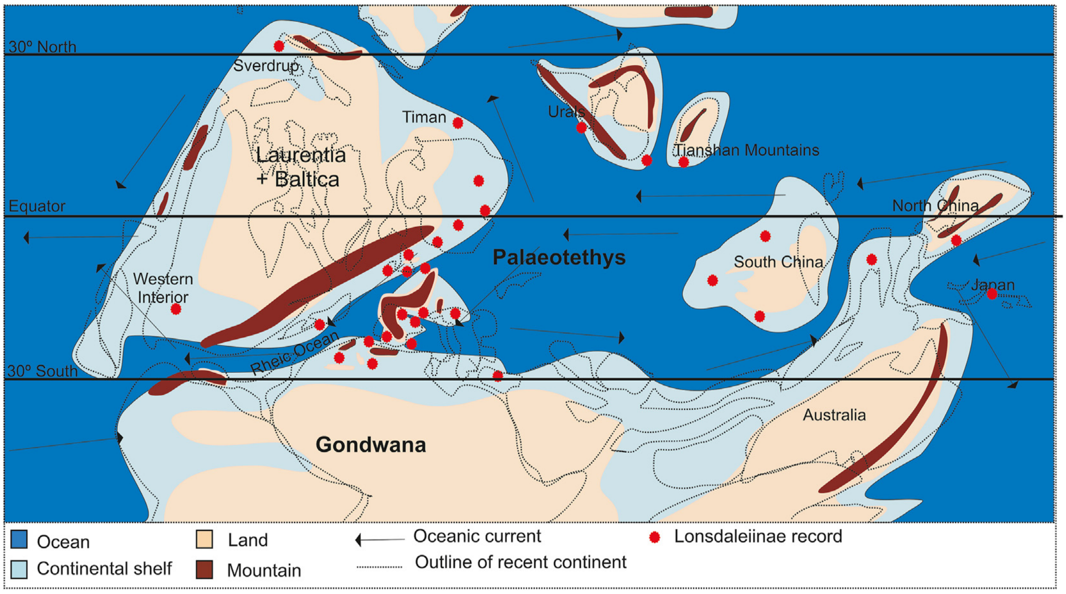

Fig. 3 Global palaeogeography during the late Mississippian with location of occurrences of the Lonsdaleiinae. The geographical areas that are not labelled are listed in Fig. 4 (modified from Webb, 2002 and Somerville *et al.*, 2020).

of it in Ukraine, the Lviv-Volynsk Basin). The same problem exists with the Balkans, where there are some important studies (Kolosvary, 1951; Kostic-Podgorska, 1957, 1958), but the knowledge is scarce and incomplete. In other cases, the palaeogeographic domains do not fit completely with the recent political divisions. In order to avoid unnecessary terminology, we will use a generic geographic name as an approximation. Thus, Scotland, northern England, NW England, Derbyshire and North Wales can all be included in northern Britain, with South Wales, Bristol district and Mendips in southern Britain. Although two distinct palaeogeographic regions can be distinguished in Belgium, the Campine and the Franco-Belgian basins, we will consider both under the common name of Belgium, because the data in the Campine Basin are relatively scarce (Poty, 1981; Aretz and Chevalier, 2007) and because the two genera involved are respectively in the Franco-Belgian Basin and in the Campine Basin (Poty, 1981; Denayer *et al.*, 2011). Finally, Turkey comprises several terranes that were clearly separated during the Mississippian; in at least four of them there are records of Mississippian corals. In the Istanbul-Zonguldak terrane, whose position in the Visean is not clear (Okay and Tüysüz, 1999), there is no record of *Lonsdaleia* or *Actinocyathus* and it will not be considered here as a separate unit. The Tauride block is related to the north border of Gondwana (Denayer, 2015).

If the oldest known occurrence of *Lonsdaleia* is that of *L. praenuntia* in the lower Visean from northwestern England, we can assume that the genus appeared in that area of the British Isles during the early Visean. The maximum development of *Lonsdaleia* occurred in the late Visean. The great transgression that took place in that period (Conil and Lys, 1977; Ramsbottom, 1979; Herbig, 1998) facilitated the distribution of the coral planulae transported by currents for large distances, because they easily found marine areas to attach themselves to. *Actinocyathus* first appeared also in the late Visean and quickly reached a large area of distribution.

We summarize the occurrences of both genera in Figs. 3 and 4. A general view of their distribution in the Palaeotethys is given in Fig. 3 and a more detailed one with data on each genus is presented in Fig. 4. Only data for the western Palaeotethys are included in the latter, because considering larger areas would impede a precise recognition of the details. Going from south to north and from west to east, the occurrences are as follows.

In the Tindouf Basin of southern Morocco (1), *Lonsdaleia* first occurs in the uppermost Visean, and reaches the maximum abundance and diversity during the Serpukhovian. *Actinocyathus* first occurs in the Serpukhovian, and is still recorded in the lower Bashkirian (Rodríguez et al., 2013a, 2013b). In the Béchar and Reggan areas of Algeria (2), the only record of *Lonsdaleia* is from the Serpukhovian and *Actinocyathus* hasn't been recorded there (Semenoff-Tian-Chansky, 1985). We included here the eastern Tafilalt (near Erfoud, eastern Morocco) where neither *Lonsdaleia* nor *Actinocyathus* have been recorded (Aretz *et al.*, 2013). The same situation happens in Jerada (3) and

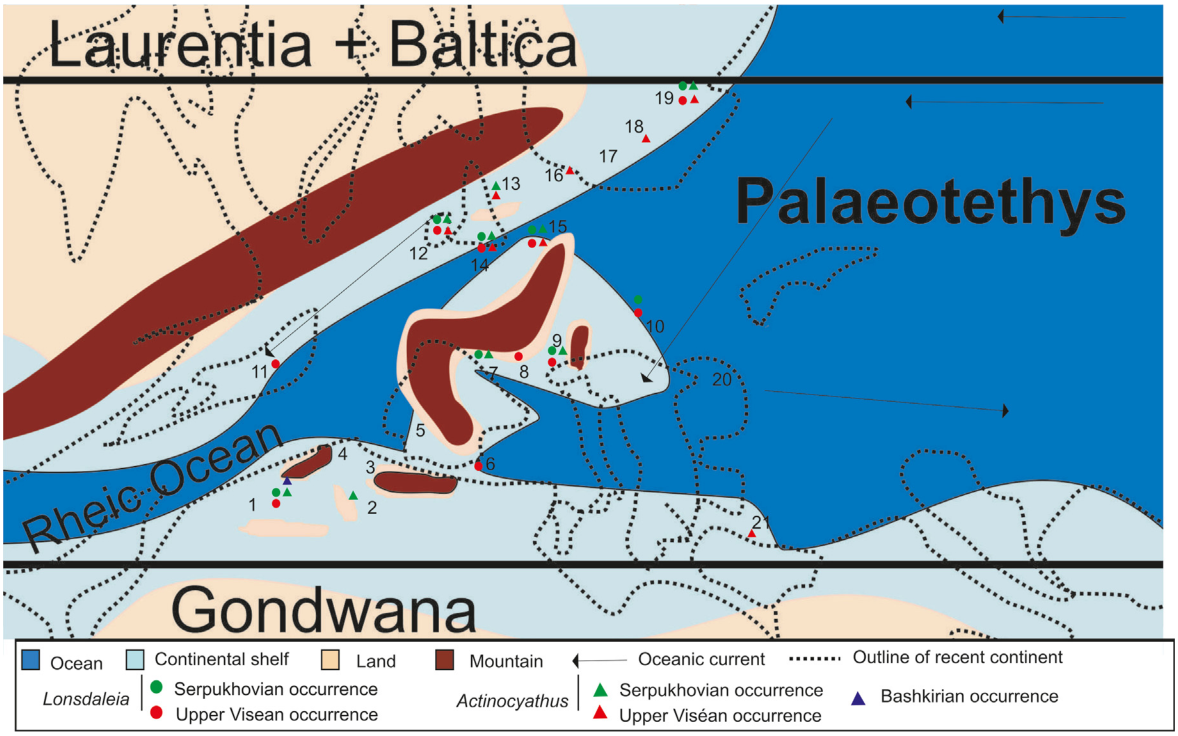

Fig. 4 Palaeogeography of the western Palaeotethys with location of occurrences of the Lonsdaleiinae in the Visean, Serpukhovian and Bashkirian (modified from Webb, 2002 and Somerville *et al.*, 2020). 1 — Tindouf Basin; 2 — Béchar-Reggan; 3 — Jerada; 4 — Azrou-Khenifra Basin; 5 — Ossa-Morena; 6 — Betic Cordillera; 7 — Cantabrian Mountains; 8 — Pyrenean Mountains; 9 — Montagne Noire; 10 — Carnic Alps (+Nötsch); 11 — Nova Scotia; 12 — Ireland; 13 — Northern Britain; 14 — Southern Britain; 15 — Southern Belgium; 16 — Germany; 17 — Poland; 18 — Donetz Basin; 19 — Moscow Basin; 20 — Balkans; 21 — Tauride.

the Azrou-Khenifra Basin (4) of northeastern and north central Morocco, respectively (Said *et al.*, 2007, 2013; Aretz, 2010). In the Guadiato area and the Los Santos de Maimona Basin (Ossa Morena, SW Spain) (5) both genera are also absent in the Visean and Serpukhovian rocks (Rodríguez and Falces, 1994; Rodríguez *et al.*, 2016). On the contrary, in the Betic Cordillera (S. Spain, 6), *Lonsdaleia* and *Actinocyathus* were recorded in the uppermost Visean and lowermost Serpukhovian (Herbig and Mamet, 1985).

In the Cantabrian Mountains of North Spain (7) both genera are absent in the Visean, but they have been recorded in the Serpukhovian (Boll, 1985). In the Pyrenean Mountains (8), Perret and Semenoff-Tian-Chansky (1971) recorded *L. duplicata*, and in the Hautes Corbières, a massif located somewhat further north, Semenoff-Tian-Chansky and Ovtracht (1965) recorded *L. corbariensis*, in both cases in the upper Visean. *Actinocyathus* was not recorded in that region. In the Montagne Noire of south central France (9), *Lonsdaleia* was recorded both in the upper Visean and in the Serpukhovian. On the contrary, *Actinocyathus* was only recorded in the Serpukhovian (Aretz and Herbig, 2003; Poty *et al.*, 2019). In addition, Poty and Hecker (2003) described there the subgenus *L. Serraphyllum*, with intermediate features between *Lonsdaleia* and *Actinocyathus* (Fig. 2). In the southern Austrian outcrops (Greywacke zone, Nötsch and Carnic Alps) (10), only the fasciculate genus *Lonsdaleia* has been recorded, both in the upper Visean from the Greywacke zone (Heritsch, 1933) and in the Serpukhovian of the Carnic Alps (Rodríguez *et al.*, 2019).

In Nova Scotia (11), *Lonsdaleia* has been also recorded in the upper Visean, but not in the Serpukhovian (Lewis, 1935; Poty, 2002). In Ireland (12), both genera, *Lonsdaleia* and *Actinocyathus* have been recorded (Caldwell and Charlesworth, 1962; Gallagher and Somerville, 1997; Somerville *et al.*, 2007), including transitional forms between them (Cózar and Somerville, 2005). A similar occurrence is recorded in the north of England and Scotland (northern Britain, 13), where both genera occur in the upper Visean, but only *Actinocyathus* has been verified in the Serpukhovian (Hill, 1938—41; Jackson, 1958; Mitchell, 1989; Riley, 1995). In southern Britain (14), the record is like that in Ireland, with the two genera occurring both in the upper Visean and Serpukhovian (Mitchell, 1989; Riley 1995). In southern Belgium (15) the detailed studies by Poty (1985, 1989) indicate the presence of *Actinocyathus* in the coral zone RC8, i.e., uppermost Visean. Poty *et al.* (2006) showed also the presence of *Lonsdaleia* in that zone. As stated previously, the record in Germany is scarce and derived mainly from allochthonous rocks. *Actinocyathus* has only been recorded in the Brigantian from the Rhenohercynian domain (16), and there is no record of *Lonsdaleia*. Similarly, only *Actinocyathus* has been recorded in the upper Visean from the Lublin Basin (Poland) (Khoa, 1977) (17) and its southeastern prolongation in the Lviv-Volynsk Basin (Ukraine) (Shul'ga and Ogar, 2009). The record in the Serpukhovian from Poland is very poor and composed mainly of undissepimented corals, and neither *Lonsdaleia* nor *Actinocyathus* have been reported there. Both *Lonsdaleia* and *Actinocyathus* have been recorded in the Donetz Basin (18) (Vassiljuk, 1960; Fedorowski, 2022). In the Moscow Basin (19), the Lonsdaleiinae flourished, with *Lonsdaleia* and *Actinocyathus*, both being present in the upper Visean and in the Serpukhovian (Dobrolyubova, 1958; Hecker, 1997, 2001, 2010; Somerville *et al.*, 2020).

None of the Lonsdaleiinae genera have been cited in the Balkans (20). As stated previously, the record there is scarce, and that region seems to be a mélange of terranes that were piled up against the Variscan Cordillera during the orogeny. The Tauride (21) represent a terrane closely related with northern Gondwana.

The Urals and Timan provided occurrences of *Lonsdaleia* and *Actinocyathus*, both in the upper Visean and Serpukhovian (Gorsky, 1949; Degtiarev, 1965; Sayutina, 1973; Kossovaya, 1996, 1997). Gorsky (1935, 1938) described several species of *Lonsdaleia* and *Actinocyathus* in the upper Visean from Novaya Zemlya, but only the latter in the Serpukhovian.

China and the surrounding areas have usually been divided into four or five areas regarded as different terranes with different sedimentation and coral assemblages during the Carboniferous (Wu and Zhao, 1979; Yang *et al.*, 1985; Wang, 1989): In Tianshan Mountains, Wang *et al.* (1994) cited *Lonsdaleia* in the lower Visean. It is a very important recording, because the only other mention to lower Visean *Lonsdaleia* is that of *L. praenuntia* in northern England. In the same region, *Lonsdaleia* has been recorded in the upper Visean (more precisely in the Jilin area, Yang *et al.*, 1985). In Kunlun Mountains, northwestern China, Wu *et al.* (1982) described *Lonsdaleia* in the upper Visean. *Lonsdaleia* and *Actinocyathus* have been mentioned and/or described in the upper Visean and Serpukhovian from Sichuan, Guizhou, and Hunan provinces of South China (Yu, 1937; Jia, 1977; Fan, 1978; Jiang, 1982; Wang *et al.*, 2006), but there are no mentions of these genera in North China.

Fontaine *et al.* (1991, 2003, 2005) cited or described *Lonsdaleia* and *Actinocyathus* in the upper Visean and Serpukhovian from Thailand and Malaysia.

In Japan, there are several citations and descriptions of both *Lonsdaleia* and *Actinocyathus* in the upper Visean and Serpukhovian from different areas, such as Akiyoshi terrane, Ichinotani Mountains, Fukuji, Onimaru and Omi Limestone (Kato, 1966; Niikawa, 1979; Kato *et al.*, 1987; Igo and Adachi, 2001).

The only citing in Australia of *Lonsdaleia* (Hill and Woods, 1964) seems to be a misinterpretation and consequently the Lonsdaleiinae are not present on that continent.

In North America, Webb (1987) described both *Lonsdaleia* and *Actinocyathus* from the upper Chesterian (Serpukhovian) in Oklahoma and Arkansas. Fedorowski *et al.* (2012) described *Lonsdaleia* in the Bashkirian from Sverdrup Basin (Arctic Canada).

2.3. Insights for the evolution of the subfamily Lonsdaleiinae from the western palaeotethys

Lonsdaleia and *Actinocyathus* are present in all continents except in Australia and South America during the Visean and Serpukhovian. So, they can be considered as cosmopolitan genera. The configuration of their occurrences can be used for illustrating the coral migration patterns in the late Mississippian. The major factors controlling those patterns are.

1) The coral reproductive cycle; being sessile epibenthic organisms, their only way for migration and colonization of new habitats is the transport of the larvae (planulae).
2) The oceanic regime of currents; applying what we know on the system of currents in our planet, Earth's rotation causes a main equatorial current that flows from east to west, and other currents flow polarwards towards high latitudes conditioned by the distribution of the land masses. We can apply actualism here, because the Earth's rotation did not change during its history.
3) The distribution of land masses; we have an approximate view of the position of continents because of the many studies that have been carried out from different perspectives (tectonic, palaeomagnetic, biogeographic, etc.). But still, there are different models and reconstructions that do not agree on this matter (see Golonka, 2002; Blakey, 2008; Metcalfe, 2013; Scotese, 2021). The main reason is that the Visean and Serpukhovian are synorogenic periods and the land masses were changing at that time.

In order to identify the migration paths of the studied genera, the first step is determining where they appeared. The main distribution of *Lonsdaleia* and *Actinocyathus* occurred during the late Visean, but there are at least two earlier records. The two places where *Lonsdaleia* has been mentioned in the early Visean are NW England and Tianshan Mountains (NW China). It is not possible that it migrated between the Tianshan terrane and the UK during the early Visean without leaving occurrences in geographically intermediate areas, many of which are quite well studied. This implies that either one or both of these references may not be correct or that the genus could be polyphyletic.

Consequently, three hypotheses can be proposed on the origin of the genus.

1. *Lonsdaleia praenuntia* appeared in Arnside, NW England, near the western end of the Palaeotethys in the early Visean. It had a certain period without main changes and without expanding its distribution. But in the late Visean a major transgression took place and *Lonsdaleia* developed some structural changes diverging in several species in the same geographical area (*L. alstonensis*, *L. caledonia*, *L. melmerbiensis*, *L. siblyi*, etc.). It also evolved into the massive forms of the genus *Actinocyathus* (Smith, 1915). Both genera, also favoured by the transgression, migrated quickly. Theoretically, the main current in the Rheic Ocean, which was near to its final closure, should flow south-westwards (Fig. 4). Thus, the planulae could reach quickly the Nova Scotia territory (Poty, 2002). This hypothesis is also supported by foraminiferal data (cf. Cózar and Somerville, 2021). In a different way, the planulae could use local currents in the shallow platforms that bordered the continent of Laurentia plus Baltica towards Scotland, southern England, Belgium, Poland, Donetz and the Russian Platform. The migration was very quick, and both genera reached the Urals, the Tianshan Mountains, North and South China, and Japan, along the northern margin of the Palaeotethys (Fig. 3). The maximum area of development was the Russian Platform (Hecker, 1997, 2010; Poty and Hecker, 2003). A notable diversification took place there, with the development of two evolutionary lines in *Actinocyathus* and the appearance of the species group of *L. corbariensis* in *Lonsdaleia*, adapted to less favourable environments, and related to microbial communities. That line is represented in the Russian Platform by *L. tichyi*.

In all the cited areas, *Lonsdaleia* and *Actinocyathus* flourished during the late Visean and Serpukhovian. The local absence of them can be due more to problems of preservation and the destruction of the original habitats during the Variscan Orogeny. But their presence illustrates the quick evolutive and ecologic success of both genera in so many and distant geographic areas.

Also, during the late Visean, a migration took place towards the southeast, probably from the Moscow or Donetz Basin. The migration in this way was represented mainly by the *L. corbariensis* group of species, which has been recorded in the southern terranes of Europe, and mainly in the border of the Armorica-Iberian Massif (Montagne Noire, Pyrenees, Cantabrian Mountains and Betic Cordillera). Most occurrences of these species are related to allochthonous blocks in flyschoid facies or in olistostromes and related to microbial communities (Boll, 1985; Herbig and Mamet, 1985; Aretz and Herbig, 2003; Poty and Hecker, 2003; Rodríguez *et al.*, 2019). But the migration towards southwest reached longer, far away to the epicontinental platforms in North Africa (Legrand-Blain *et al.*, 1989). There, the represented species group of *Lonsdaleia* is the *L. duplicata* group that reached the region during the late Visean and *Actinocyathus*, which reached the region during the Serpukhovian (Rodríguez *et al.*, 2013b and above). The stable conditions in that region, far from the main tectonic movements occurring in the northern part of the western Palaeotethys, allowed some representatives of the genus to survive into the lower Bashkirian. A possible way of migration along the southern border of the Palaeotethys is discarded, because neither *Lonsdaleia*, nor *Actinocyathus* have been recorded in eastern terranes such as the Tauride Alborz etc. The reasons could be excessive amounts of terrigenous material or too high latitudes (see Denayer, 2015).

An additional route of migration took place from the Russian Platform towards the north, reaching Timan (Kossovaya, 1997) and Novaya Zemlya (Gorsky, 1935, 1938). This migration was directed to the west and reached the Sverdrup Basin in northern Canada (Fig. 3), where *Lonsdaleia* has been recorded in the Bashkirian (Fedorowski and Bamber, 2012; Fedorowski *et al.*, 2012).

The occurrence of *Lonsdaleia* and *Actinocyathus* in the Midcontinent and Western Interior of USA (Webb, 1987) is less easy to explain. The northern route is discarded because these genera have not been recorded in the upper Visean and Serpukhovian in the Rockies. The southern route along the Rheic Ocean is also difficult to accept, because most palaeogeographic reconstructions close the Rheic Ocean before the Visean (Blakey, 2008; Cao *et al.*, 2017; Scotese, 2021). However, the coral data (as well as foraminiferal data; see Cózar and Somerville, 2021) show that the Rheic Ocean didn't close before the Bashkirian, because there are typical components of the western Palaeotethys assemblages in the Midcontinent and Western Interior domains (García-Bellido and Rodríguez, 2005; Rodriguez and Kopaska-Merkel, 2014). However, the percentage of western Palaeotethys species in North America is very low, indicating a low level of communication.

A particular case is that of the domains of southwestern Spain, the Jerada Basin and the Azrou-Khenifra Basin, where *Lonsdaleia* has not been recorded (localities 3—5, Fig. 4), despite the fact that there have been intense studies on the coral assemblages (Aretz, 2010; Said *et al.*, 2013; Rodríguez *et al.*, 2016). The explanation may be that both the Iberian Massif and the Anti-Atlas formed important barriers for this genus. On the other hand, these domains could be separated from Nova Scotia and Western European domains by a narrow but a deep remnant of the Rheic Ocean, before its final closing. It is remarkable, because in most other aspects, the assemblages of these areas have a high level of similarity with other domains from North Africa and Western Europe.

2. The second hypothesis only changes the origin of the genus to the northern Tianshan Mountains, if *Lonsdaleia praenuntia* is really an *Axophyllum*. From this area, it migrated to the east and southeast to the North China, South China and Japan terranes and at the same time to the west along the coastal platforms of the terranes bordering the northern Palaeotethys, and/or along the equator, taken advantage of the equatorial current and possible islands in the Palaeotethys, reaching first the Eastern European Platform and later (always in the late Visean) the Western European region and the northern Gondwana epicontinental seas. This second hypothesis has the advantage that it could explain better the late arrival to the latter and the scarcity of occurrences in the Midcontinent and Western Interior from North America. It also would explain better the absence in the basins of the South Iberian Massif and in the most northern basins of Gondwana and the refuge in Sverdrup, one of the most distant domains in which *Lonsdaleia* has been recorded.
3. The appearance of *Lonsdaleia* and *Actinocyathus* almost simultaneously in the whole Palaeotethys during the late Visean and two doubtful occurrences in the early Visean allow the validity of a third hypothesis: these genera could be polyphyletic, and originating in different regions at the same time (South China, northern Tianshan Mountains of northwestern China, Russian Platform, and northern Britain). The homogeneity of structures and microstructures reduces the possibilities of this last hypothesis, but it is not completely discarded. The appearance in different domains could be favoured by the creation of conducive environments for colonial corals associated with the Asbian transgression, which covered with epicontinental seas many previous coastal plains. It also explains the quick diversification. All the routes described in the first hypothesis are valid also in this one.

The distribution of the occurrences of *Lonsdaleia* and *Actinocyathus* in the western Palaeotethys (Fig. 4) confirm the proposal of Somerville *et al.* (2013) on their division into four palaeogeographical subprovinces that we augment to six: (1) The Atlantic Subprovince (West European countries and Nova Scotia) shows a consistent abundance of both genera in the Visean. In some areas of this subprovince, the Variscan Orogeny activity implied increase of terrigenous sediments and reduction of coral habitats, with the subsequent extinction of these genera during the Serpukhovian. (2) The Mediterranean Subprovince (Pyrenees, Montagne Noire, Betic cordillera, Rif, Balearic Islands, Nötsch, and Carnic Alps) shows similar occurrences of the *L. corbariensis* group in the upper Visean and/or the Serpukhovian. (3) The Saharan Subprovince (Béchar, Reggan, Ahnet-Mouydir, and Tindouf Basin) shows irregular occurrences of both genera, but it was a refuge for the genus *Actinocyathus* in the Bashkirian. (4) The West peri-Gondwanan Subprovince (SW Spain and Moroccan Meseta) shows a total absence of both genera. (5) The Eastern European Subprovince (Moscow Basin, Donetz Basin, and Voronezh) shows also abundance of both genera in the Visean and Serpukhovian. (6) Finally, the Central Europe Subprovince (Germany and Poland) shows an irregular record due to the effects of the Variscan Orogeny that produced a structural mélange of domains and occurrences, mainly in allochthonous facies.

3. Conclusions

The most likely ancestor of the genus *Lonsdaleia* is the solitary genus *Axophyllum*, which would acquire colonialism in favourable environments. *Actinocyathus* descends from *Lonsdaleia* by acquiring the massive habit by increasing the degree of integration in the colonies.

Two records of *Lonsdaleia* have been cited in the lower Visean from northern Britain and northern Tianshan Mountains of northwestern China. But none of these records have continuity in the middle Visean.

The diversification and migration of *Lonsdaleia* and *Actinocyathus* only occurred in the late Visean and continued during the Serpukhovian. Three hypotheses are proposed on the origin and migration of these genera: (1) Origin in northern Britain and first migration along the epicontinental seas bordering the Palaeotethys; (2) Origin in northern Tianshan Mountains and first migration using the equatorial current and later the epicontinental seas; (3) Simultaneous appearance in several domains of the Palaeotethys and migrations using the previously mentioned routes (polyphyletic hypothesis). In all cases, the migration was quick, because these two genera are recorded in the upper Visean from the whole Palaeotethys and North America.

Lonsdaleia and *Actinocyathus* became extinguished in most regions at the end of the Mississippian. However, *Lonsdaleia* has been recorded in the Bashkirian of the Sverdrup Basin in northern Laurasia and *Actinocyathus* has been recorded in the Bashkirian of the Tindouf Basin in northern Africa. They both could represent refuges in tropical areas far from the zones affected by the Variscan Orogeny during the early Pennsylvanian.

The western Palaeotethys is divided into six subprovinces with different distribution of the Lonsdaleiinae and other rugose corals.

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Authors' contributions

All the authors participate in the planning of the study, in the review of the taxa, in the design of the manuscript, and wrote parts of it. All authors read the manuscript and approved it.

Conflict of interest

The authors declare that they have not conflict of interest.

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4 THE PALAEOBIOGEOGRAPHIC SIGNIFICANCE OF THE NÖTSCH AREA (AUSTRIA) DURING THE MIDDLE AND LATE MISSISSIPPIAN BASED ON RUGOSE CORALS.

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Research Paper

The palaeobiogeographic significance of the Nötsch area (Austria) during the Middle and Late Mississippian based on rugose corals ☆

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ABSTRACT

The Carboniferous of Nötsch (South Austria) is composed of three formations: the Erlachgraben Formation, the Badstub Breccia, and the Nötsch Formation, that yielded abundant corals, several of them being new for that region. The assemblage is composed of 11 rugose coral species (*Siphonophyllia* sp., *Pseudozaphrentoides juddi*, *Lublinophyllum*? sp., *Dibunophyllum bipartitum*, *Arachnolasma cylindrica*, *Palaeosmilia murchisoni*, *Aulokoninckophyllum carinatum*, *Siphonodendron martini*, *Diphyphyllum furcatum*, *Solenodendron furcatum*, and *Solenodendron horsfieldi*), two tabulate species (*Multithecopora* sp. and *Palaeacis* sp.) and one heterocoral species (*Hexaphyllia mirabilis*). In addition, five rugosans that are not in our collection have been identified by previous authors (*Clisiophyllum* sp., *Pseudozaphrentoides* sp., *Caninia* sp., "*Palaeosmilia isae*", and *Lophophyllidium* sp.). The rugose and tabulate species are described and figured. A palaeobiogeographic analysis comparing the Mississippian assemblages from Nötsch and other Austrian outcrops with other domains in Central Europe has been performed using hierarchical clustering with Simpson and Dice similarity indices. The statistical comparison of the rugose coral assemblages at the genus level allows a better perception of the distribution of the shallow water carbonate platforms in that part of the Western Palaeotethys during the Visean and Serpukhovian. The results are incorporated in a schematic palaeogeographical map of the studied area for the late Visean.

1. Introduction

The Nötsch outcrops are located in South Austria, on the north hillside of the Gail Valley. The name is given by the Nötsch River, which crosses the outcropping area from north to south, and the Nötsch village, located to the south of the Carboniferous outcrops. The Carboniferous outcrops extend as an 8 km long and 2 km wide fault-bounded wedge (Fig. 1). They contain abundant coral fossils and consequently have been studied by palaeontologists since the first half of the twentieth century. However, the detailed stratigraphy was only studied at the end of the twentieth century (Schönlaub, 1985; Flügel and Schönlaub, 1990; Schraut, 1996; Kabon, 1997; Van Amerom and Kabon, 1999, 2000).

The Carboniferous of Nötsch is composed of three formations that are, in stratigraphic ascending order (Fig. 2): the Erlachgraben Fm., composed of greyish blackish shales, micaceous siltstones, sandstones and conglomerates rich in quartz grains; the Badstub Breccia, composed of subrounded and rounded clasts of amphibolites, gneisses, schists, mica-schists, quartz, quartzites, marbles and limestones embedded in a green tholeititic matrix; and the Nötsch Fm. with similar composition to the Erlachgraben Fm. (Hubmann et al., 2003).

The Badstub Breccia has a sedimentary origin (Schönlaub, 1985). Its age, based on plants, is Namurian A (Kabon, 1997), or Serpukhovian based on conodonts (Schönlaub, 1985). The limestone clasts contain abundant fossils that allowed their dating as latest Visean or probably early Serpukhovian (Hubmann et al., 2003), Early Serpukhovian (Vachard et al., 2018) or Late Serpukhovian (Krainer and Vachard, 2002). Megaplant fossils from the upper part of the Nötsch Fm. indicate an Alportian (earliest Bashkirian) age (Van Amerom and Kabon, 2000). Foraminifers and algae from

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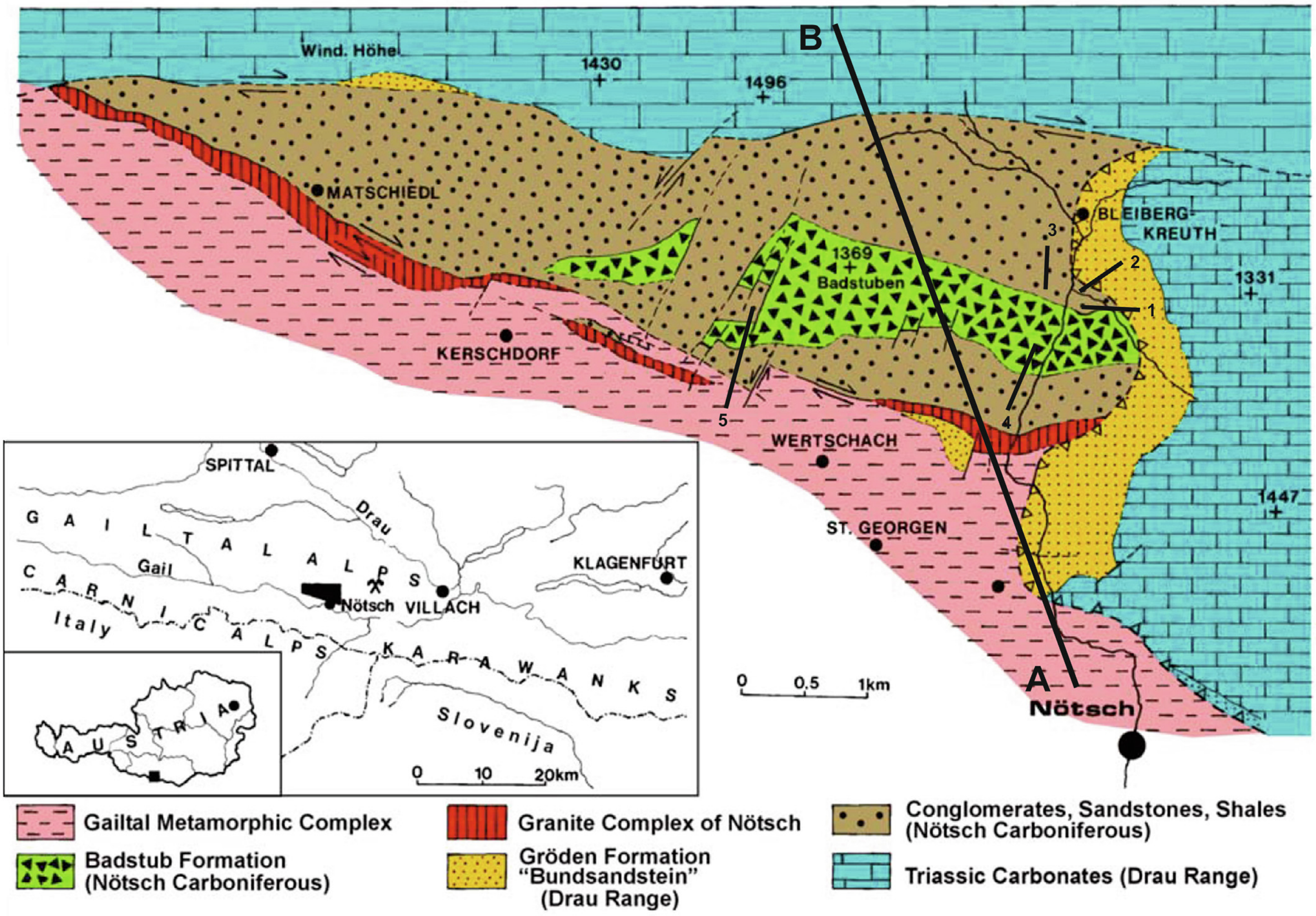

Fig. 1. Location of the outcrops (modified from Hubmann et al., 2003). The corals have been collected in the breccias of the Badstub Formation and in the conglomerates, sandstones and shales of the Erlachgraben and Nötsch formations (both having the same lithologies and represented with the same color). Sampling locality number: 1, Hermsberg (HEK); 2, Lerchgraben (LK); 3, Nötschgraben (EK, EL); 4, Jakomini Quarry (BZ); 5, Nötsch Formation (NÖ21). Section A-B is shown in Fig. 2.

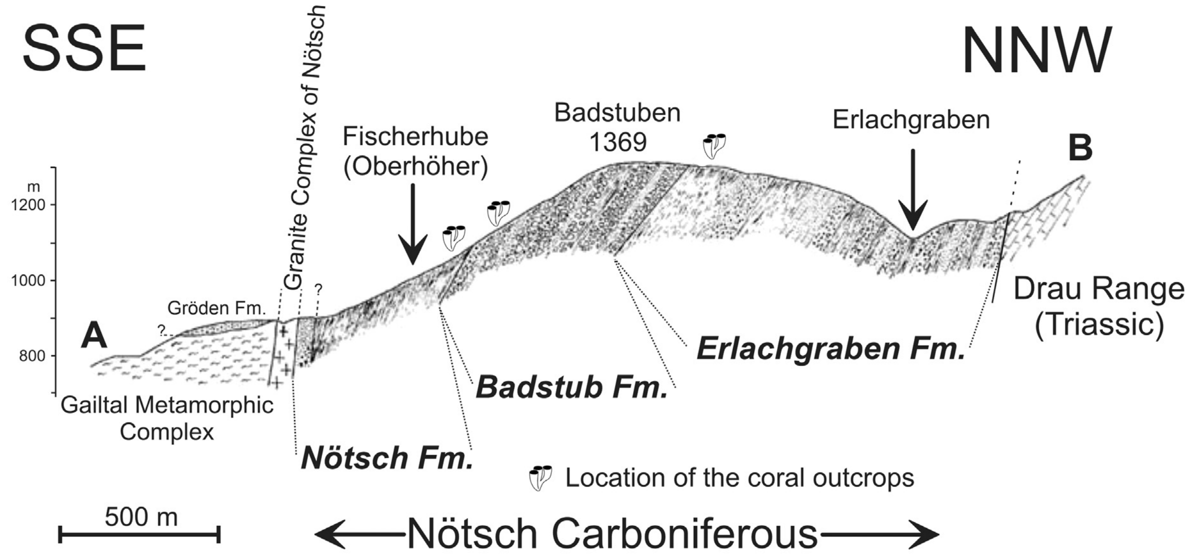

Fig. 2. Section along the A-B line in Fig. 1, showing the stratigraphy of the Nötsch area (Taken from Hubmann et al., 2003).

exotic limestone clasts of the Badstub Fm. indicate a Steshevian (lower Serpukhovian) age (Vachard et al., 2018). These authors suggested that the Erlachgraben, Badstub and Nötsch formations probably constitute a continuous lithostratigraphic group deposited from the latest Visean to the early Bashkirian and probably include a complete Serpukhovian succession.

Flügel and Schönlaub (1990) regarded the limestone clasts as exotic remains reworked from an extensive shallow water carbonate platform located north of the present day Southern Alps and adjacent to a land area. As that platform has been completely reworked in an accretionary wedge or dismantled in an active platform margin, the only relict is represented by the limestone boulders of the Badstub Breccia and the flysch deposits of the Hochwipfel Fm. located southwards in the Carnic Alps (Flügel and Schönlaub, 1990). Other outcrops in Austria that could contain relicts of such a carbonate shelf are the Greywacke zone and the Gurktal Nappe (Hubmann, 2002), but coral assemblages from these areas are poorly and badly preserved.

The abundant marine fauna from the Carboniferous of Nötsch has been described in many papers that have been compiled by Schraut (1999). Rugose and tabulate corals have been described in the papers by De Koninck (1873), Heritsch (1918, 1934), Kuntschnig (1926), Flügel (1965, 1972), and Flügel and Hubmann (1994). The identifications of taxa by these authors as well as those by ourselves are summarized in Table 1.

The corals from the Carboniferous of Nötsch are usually compressed and/or fragmented and a significant part of them cannot be properly identified. However, they are abundant and show a quite high diversity. One of us (H.K.) has sampled them over many years and compiled an excellent collection that allows an important contribution to the knowledge of the assemblage. Eight species of rugose corals and two species of tabulate corals that were not previously known in the area are shortly described hereafter (Table 1). The total assemblage from all localities in Nötsch (Table 2), including species described by previous authors which are accepted here as valid (Table 3), comprises 16 rugosan taxa.

The main interest of the coral assemblage from Nötsch is its location in an area of connection between the western European basins and platforms (Namur-Dinant, British Isles, Montagne Noire, Cantabrian Mountains, etc.) and the eastern European basins and platforms (Donets Basin, Lublin region, Holy Cross Mountains). The main aim of this paper is to compare the coral assemblages of Central Europe to analyse the palaeogeographical relationships of the different domains in that territory during the Visean and Serpukhovian.

2. Material and methods

2.1. Stratigraphy and coral sampling localities

Fossil coral remains are described from five localities of the Carboniferous of Nötsch. Three outcrops are situated in the uppermost part of the Erlachgraben Fm. Number one is located beside the road to Hermsberg (HEK; N46°37.177′, E13°37.039′). The corals of outcrop number two were found in the Lerchgraben (LK; N46°37.244′, E13°37.049′). Sampling locality number three is situated on the northern side of Jakomini Quarry in Nötschgraben (EK, EL; N46°37.214′, E13°36.657′). Megaplant fossils from the uppermost part of the Erlachgraben Fm. indicate an Arnsbergian age (Van Amerom and Kabon, 1999). The Badstub Fm. is most completely exposed in the Jakomini Quarry. The corals of the Badstub Fm. were collected in the year 1992 in a several metres thick dark shale ("Zwischenschiefer"), intercalated within the upper third of the Badstub Fm. (Outcrop number four: BZ; N46°37.112', E13°36.611'). Outcrop four no longer exists today because of the growth of the quarry. Coral outcrop number five (NÖ21; N46°37.092', E13°35.148') is located in the basal part of the Nötsch Fm. on the southern slope of mountain Badstuben (1,369 m).

2.2. Methodology

The corals have been sampled during many years of fieldwork in the Nötsch area by one of us (H.K.). This collection largely increases the known assemblage of rugose corals in that area. It comprises more than 100 fragments of solitary and colonial corals;

Table 1
Historical identifications of corals in Nötsch.

De Koninck (1873)	Frech (1894)	Heritsch (1918)	Kuntschnig (1926)	Heritsch (1934)	Flügel (1972)	**This paper**
Zaphrentis intermedia	*Zaphrentis intermedia*					
	Lonsdaleia rugosa			*Axophyllum expansum*	*Clisiophyllum?*	
	Syringopora	*Syringopora*				
		Caninia murchisoni	*Caninia murchisoni*	*Caninia juddi*	*Pseudozaphrentoides juddi*	*Pseudozaphrentoides juddi*
		Caninia compressum		*Caninia compressum*	*Pseudozaphrentoides* sp.	
				Caninia sp.	*Caninia* sp.	
		Cyathophyllum sp.	*Cyathophyllum carinthiaca*	*Palaeosmilia carinthiaca*	*Palaeosmilia murchisoni*	*Palaeosmilia murchisoni*
				Palaeosmilia isae	*"Palaeosmilia" isae*	
					Lophophyllidium sp.	
		Cyathaxonia rushiana				
				Koninckophyllum interruptum	*Arachnolasma cylindrica*	*Arachnolasma cylindrica*
						Dibunophyllum bipartitum
					Hexaphyllia mirabilis	*Hexaphyllia mirabilis*
						Aulokoninckophyllum sp.
						Diphyphyllum furcatum
						Siphonodendron martini
						Siphonophyllia sp.
						Solenodendron horsfieldi
						Solenodendron furcatum
						Multithecopora sp.
						Palaeacis sp.

Table 2
Distribution of identified taxa in the different outcrops.

Identified species \ localities	HEK	LK	EK, EL	BZ	NÖ
Arachnolasma cylindricum	1				1
Aulokoninckophyllum carinatum				1	
Dibunophyllum bipartitum	11		7	5	
Diphyphyllum furcatum	1				
Lublinophyllum? sp.	1				
Palaeosmilia murchisoni	2			4	
Pseudozaphrentoides juddi	2				
Siphonodendron martini	3				
Siphonophyllia sp.	2				
Solenodendron furcatum	1				1
Solenodendron horsfieldi	5	1			
Multithecopora sp.		1	1		
Palaeacis sp.				1	
Hexaphyllia sp.	1			1	

Table 3
Generic distribution of corals in the selected areas.

Genus	Austria	Poland	Moravia	Balkans	Donets	Germany	Belgium	S. France
Actinocyathus		x			x		x	x
Amygdalophyllum		x		x			x	
Arachnolasma	x	x			x		x	
Auloclisia				x				
Aulokoninckophyllum	x	x					x	x
Aulophyllum		x		x	x	x	x	
Axoclisia						x	x	
Axophyllum	x	x	x	x	x	x	x	x
Biphyllum		x						
Bothrophyllum		x		x		x	x	
Caninia	x	x	x	x	x	x	x	x
Caninophyllum							x	
Clisiophyllum	x	x		x	x	x	x	x
Corwenia		x			x			
Dibunophyllum	x	x	x	x	x	x	x	x
Diphyphyllum	x	x	x		x	x	x	x
Dorlodotia					x		x	
Gangamophyllum		x	x	x	x			x
Haplolasma		x				x	x	
Kizilia		x					x	x
Koninckonaotum		x						
Koninckophyllum	x	x	x	x	x	x	x	x
Lithostrotion		x		x	x	x	x	x
Lonsdaleia	x	x	x		x	x	x	
Lophophyllidium	x							x
Lublinophyllum	x?	x						
Melanophyllidium								x
Mirka		x						
Nervophyllum		x			x			
Orionastraea		x						
Palaeosmilia	x	x	x	x	x	x	x	x
Palastraea		x				x	x	
Pareynia							x	x
Pseudozaphrentoides	x	x	x	x	x	x	x	x
Rozkowskia		x						
Schoenophyllum					x			
Siphonodendron	x	x	x	x	x	x	x	x
Siphonophyllia	x	x		x		x	x	
Solenodendron	x				x	x	x	
Spirophyllum		x						
Heterophyllia		x	x		x	x		
Hexaphyllia	x	x			x	x		x
Aulopora		x						
Michelinia		x			x	x		
Multithecopora	x	x			x	x		
Palaeacis	x	x		x		x	x	
Syringopora	x	x	x	x	x	x	x	x

66 specimens were identified at generic level and 44 were identified at specific level. The best-preserved specimens have been sectioned; 70 thin sections 2.8 × 4.8 cm, 10 thin sections 5 × 5 cm and 2 thin sections 5 × 8 cm have been prepared and studied with an Olympus SZ61 binocular and a LEICA DLMP microscope. The pictures of the specimens were taken with an Olympus SP 500 UZ photo camera and a LEICA DFC420C camera. They were cleaned and handled with Photoshop and Photopaint software.

All palaeobiogeographic analyses have been performed using PAST 4 (Hammer et al., 2001). The study uses a paired group (UPGMA) Hierarchical Clustering. Hierarchical Clustering requires the use of a similarity index, for which many authors proposed different ones (Raup and Crick, 1979; Hubálek, 1982; Rodríguez, 1986; McCoy and Heck, 1987; Shi, 1993; Schmachtenberg, 2008). Several indices were used to analyse the biogeographical relationships of the selected domains. To test the stability of the resulting clusters, 1000 bootstrap resamplings have been performed on them. The branches with bootstrap values lower than 50% are not stable and should not be considered conclusive. In most cases the bootstrap supports were low and most indices were discarded for this reason. Finally, Simpson similarity index was selected because it is not strongly affected by differences in sample size or heterogeneous sampling effort (Hammer and Harper, 2006), because the bootstrap support is higher than all other indexes, and to better reflect the spatial turnover over the nestedness (Baselga, 2010). The Dice index has been also considered for comparison.

Any palaeobiogeographic analysis should take into account the plate tectonics, and the blocks to be compared should be consistent with structural units. We tried to follow this axiom in our palaeobiogeographic analysis, but in some cases the record itself or the studies in some areas are scarce. Three palaeogeographic domains are recognised in Germany for the Mississippian: the Rhenohercynian, the Saxothuringian, and the Moldanubian, from north to south (Weyer, 2000). However, records there are scarce and in the second and third domains, the corals always occur in allochthonous facies (olistostromes or Culm), probably coming from the first domain (Weyer, 2000). Thus, for this study, these three domains have been amalgamated as one single area (Germany). The same was done with the three main Austrian outcrops yielding Mississippian corals (Carnic Alps, Nötsch, and the Greywacke Zone; Hubmann, 2002) and several palaeogeographic units in Poland (Sudetes, Upper Silesian Basin, Lublin Basin and its southeastward prolongation in Ukraine, the Lviv-Volynsk Basin and Moravia in the Czech Republic have been grouped under the "Poland" name). The same problem exists in the Balkans, where there are some key studies (Kolosvary, 1954a; Kostic-Podgorska 1955, 1964), but the knowledge is scarce and incomplete. Thus, single localities were grouped in larger regions, mostly coinciding with countries to avoid different levels of knowledge of the palaeontological record.

As in the outcrops of Nötsch, and also in many other outcrops from central Europe, the corals occur in reworked sediments (breccias, conglomerates, olistoliths and flysch) and species are not identifiable in many cases. Since families are not detailed enough, the taxonomical level used for this comparison is the genus. When all or most regions contain well-preserved and well-known assemblages, the use of species is preferable (Rodríguez Castro and Rodríguez, 2022), but this is not the case for this study because even the best studied area (Belgium) has a high percentage of taxa left in open nomenclature (45%; Denayer et al., 2011). In an attempt at lowering the environmental influence over the analyses, our analyses exclude the undissepimented corals since they are typical of deep water or turbid water facies (Hill, 1938–41; Kullmann, 1997).

The main interest of the Nötsch outcrops from the point of view of the corals is the identification of an assemblage that lived on a carbonate platform that is not preserved. Similar cases are common in the Mississippian from Europe. The Variscan Orogeny destroyed several Visean and Serpukhovian carbonate platforms whose relicts are preserved in olistostromes and olistoliths or whose inhabitants were reworked into turbiditic sediments, usually Serpukhovian and Bashkirian in age. That is the case of the "Eder Gebiet" in Germany (Weyer, 2000), of the "Montagne Noire" in France (Aretz and Herbig, 2003), of the Malaguides (Herbig, 1986) and partly of the Guadiato Area in Spain (Rodríguez et al., 2016). The Asbian transgression favoured the development of wide carbonate platforms around the emerged regions, where corals flourished and diversified (Herbig, 1998). The succeeding Brigantian and Serpukhovian regression caused the erosion of the late Asbian shallow-water carbonates and their redeposition as debris-flows and conglomerates within the flysch succession. In some of these cases, the reworking processes produced fragmentation, compression and recrystallization of the corals. Consequently, in many cases the identification at species level is not possible and even in some instances, the corals are not identifiable at all.

As many taxa have been identified only at the generic level in Nötsch, but also in other countries in Central Europe, comparisons with assemblages of other regions were done at this level. The genus *Lublinophyllum*, which has been identified with doubts, has been included in the comparison as well as all the undetermined species of different genera. The palaeogeographical interest of the Austrian assemblages lies in their intermediate position between the well-known platforms from Western and Eastern Europe. The comparison of assemblages will be reduced to the current closest areas. A wider comparison of the Western Palaeotethys Mississippian corals is in preparation by one of us (I.R.-C.).

The comparison tries to find the palaeobiogeographic relation between shallow carbonate platforms during the late Visean and early Serpukhovian. Consequently, only corals regarded as living in shallow-water environments have been considered here in order to avoid interferences from ecologic relationships. The use of a broad stratigraphic range is due to the occurrence of many of the coral records in Serpukhovian and Bashkirian reworked facies (debris, olistoliths, olistostromes, flysch) in which there is a mixture of material from the Visean and the Serpukhovian. That problem was already pointed out by Schönlaub (1997) in his analysis of the Carboniferous biogeography of Austria. Theoretically, the biogeographic comparison should be made between assemblages of the same age. But the special situation of the outcrops in Central Europe, which suffered strongly from the Variscan Orogeny, means that in some areas only Serpukhovian assemblages have been preserved, in other areas only upper Visean assemblages have been preserved and, finally, some areas contain both. Because of that, both Visean and Serpukhovian assemblages have been taken into account here. It surely produces a reduction of the precision of the results, but we should keep in mind that presence of a genus in two areas in different times also indicates that there was a communication between those areas (the corals migrated earlier or later between them). So, the biostratigraphic value of the comparison is lower, but the global analysis of the geographic relationships remains valid.

An extensive bibliography has been consulted for analysing the assemblages from Central Europe. In some cases, synthetic papers have simplified the task. Excellent syntheses such as Weyer (2000) for Germany, Denayer et al. (2011) for Belgium, Fedorowski (1968, 1975, 1981) for Poland have been useful for our purposes. On the contrary, other areas needed the revision of a large number of papers. The information from Balkans was mainly obtained from Kolosvary (1954a, 1954b), Kostic-Podgorska (1954, 1955, 1960, 1964); the information from Moravia was obtained from Zukalová (1961, 1965); the information from Ukraine was extracted from Vassiljuk (1960, 1964); the information from Southern France was obtained from Semenoff-Tian-Chansky and Ovracht (1965), Perret and Semenoff-Tian-Chansky (1971), Aretz (2002), and Aretz and Herbig (2003). The results of the bibliographic analysis plus our own identifications of the corals are shown in Table 3.

There are some methodological problems to solve because of the different level of study in different regions. Some regions have been studied for a long time because of the presence of good outcrops and scientific tradition, like Belgium, Germany or Poland. Some other areas present few coral studies because the outcrops are not appropriate or because the corals are not well preserved, like in Balkans or Austria. In addition, the late Visean is a time of high temperatures, with an important transgression (Herbig, 1998), when migrations were easy for the coral planulae because most marine connections between different regions were open. In that contex, a high diversification took place, but also many of the genera reached a cosmopolitan distribution, or almost.

3. Results

The specimens from Nötsch are mostly fragmented (lacking the apexes or the calices), eroded (lacking partly or totally the dissepimentarium) and/or compressed, with their inner structures broken (Fig. 3). So, only 60% of the sectioned specimens have been identified at the generic level and only 50% of them have been identified at the species level, despite most of them belonging to well-known genera. Nevertheless, the assemblage is quite diverse, composed of 11 rugose coral species, two tabulate species and one heterocoral species. Three taxa of rugose corals (*Clisiophyllum*? sp., *Caninia*? sp. and *Lophophyllidium* sp.), not present in our collection but previously identified by Flügel (1972), and a tabulate (*Syringopora* sp.) identified by Heritsch (1918) have been also recorded in Nötsch. The species *Lonsdaleia carnica*, recorded in a boulder in the Hochpwipfel Fm. from the close Carnic Alps (Rodríguez et al., 2018), and the genus *Axophyllum*, recorded in the Greywacke zone in flysch facies, have been included in the Austrian assemblage for comparison with other areas. Only the rugose species have been included in the palaeobiogeographic analysis because, in some areas selected for comparison, the studies on tabulate corals and heterocorals are scarce or totally absent.

This paper is not a taxonomic review. The descriptions are given for the illustration of the coral identifications. Consequently, the descriptions of the identified species are complete but they do not contain detailed synonymies; references to papers where they can be found are included in the species remarks and the diagnosis are not included, but referred to well-known previous papers. The morphological terminology is based on Hill (1981) with some additions by Poty (1981) and Rodríguez (1984). The microstructural descriptions are based on the terminology proposed by Semenoff-Tian-Chansky (1974) and some refinements by Rodríguez (1984). The taxonomic classification follows Hill (1981) with some variations following later papers (Denayer et al., 2011; Rodríguez et al., 2016).

3.1. Systematic palaeontology

Phylum Cnidaria Hatschek, 1888
Class Anthozoa Ehrenberg, 1834.
Subclass Rugosa Milne-Edwards and Haime, 1850.
Order Stauriida Verrill, 1865.
Family Cyathopsidae Dybowski, 1873.
Genus ***Siphonophyllia*** Scouler in McCoy, 1844.
Siphonophyllia sp.
Fig. 3(A)

Material: Two incomplete and partly compressed specimens: HEK12C, HEK51, Hermsberg road, upper part of the Erchlachgraben Fm.

Description: Two cylindrical fragments of solitary corals, 15 mm in diameter. 30 major septa, not extending to the axis. The minors are irregular, sometimes short, sometimes reaching the border of the dissepimentarium, and thinner than the major septa. Some majors and minors are interrupted by lonsdaleoid dissepiments in the external part of the dissepimentarium. The major septa are thickened in the tabularium. A slightly shortened cardinal septum is visible in an inconspicuous fossula (Fig. 3(A), lower-central part) and other protosepta are not prominent. The dissepimentarium is wide, composed of 5 to 6 rows of intercepted and lonsdaleoid dissepiments irregularly distributed. Outer wall is simple and thick.

Remarks: The specimens show all diagnostic features of the genus *Siphonophyllia* (see Rodríguez et al., 2016), solitary corals having thickened septa in the tabularium, cardinal septum shortened in fossula, dissepimentarium wide, made of several rows of interseptal and lonsdaleoid dissepiments, and complete tabulae. The poor and incomplete preservation and the partly eroded external portion of the specimens impede a specific identification and the features do not fit with the most common Mississippian species of the genus. This genus has not been previously identified in Nötsch.

Genus ***Pseudozaphrentoides*** Stuckenberg, 1904.
Pseudozaphrentoides juddi Thomson, 1893.
Fig. 3(B, C)

Material: Two incomplete and compressed specimens: HEK31 and HEK40J, Hermsberg road, upper part of the Erchlachgraben Fm.

Diagnosis: See Semenoff-Tian-Chansky (1974: p. 193).

Description: Cylindrical fragments of solitary, strongly compressed coral. The reconstructed diameter is ca. 29 mm and the number of major septa is 40. The wall and dissepimentarium are partly eroded, but the wall is moderately thick and smooth and dissepiments are both regular and angular (Fig. 3(B)). The septa are short, leaving a large free zone in the central part of the tabularium. They are thin in the dissepimentarium and strongly thickened in the tabularium. The protosepta are not identifiable due to the strong compression. Features of the tabulae could not be identified in the two studied specimens.

Remarks: Preservation is very poor, but most features (septa and dissepiments) and dimensions (diameter and number of septa) fit well with the diagnostic characters given by Semenoff-Tian-Chansky (1974) and Poty (1981). This species has been previously cited and described in Nötsch by Heritsch (1934) and Flügel (1972).

Genus ***Lublinophyllum*** Khoa, 1977.
Lublinophyllum? sp.
Fig. 3(D)

Material: One fragment of corallite: HEK40L, Hermsberg road, upper part of the Erchlachgraben Fm.

Description: Fragment of a corallite, 15 mm in alar diameter, 9 mm in tabularium diameter and 34 septa. The wall is thick and festooned. The septa are short, thin and they are interrupted in the dissepimentarium by lonsdaleoid (transeptal) dissepiments of first and second order. None of the protosepta is conspicuous. The lonsdaleoid dissepiments are locally very large, leaving empty spaces in the dissepimentarium. The preserved portion is located at the calice, where three offsets are observed. That located at the right side (Fig. 3(D)), shows the cardinal septum already developed. They show a new wall covering a portion of the calice.

Remarks: The specimen from Nötsch is included in *Lublinophyllum* with question mark, because it shares most features with the specimens described by Khoa (1977), including the local large lonsdaleoid dissepiments but that genus shows lateral increase whereas our specimen shows an axial increase. The features are similar to those in *Siphonopyllia*, but the absence of thickened septa in the tabularium and the large lonsdaleoids leaving empty spaces in the dissepimentarium in that genus, plus the solitary habit are

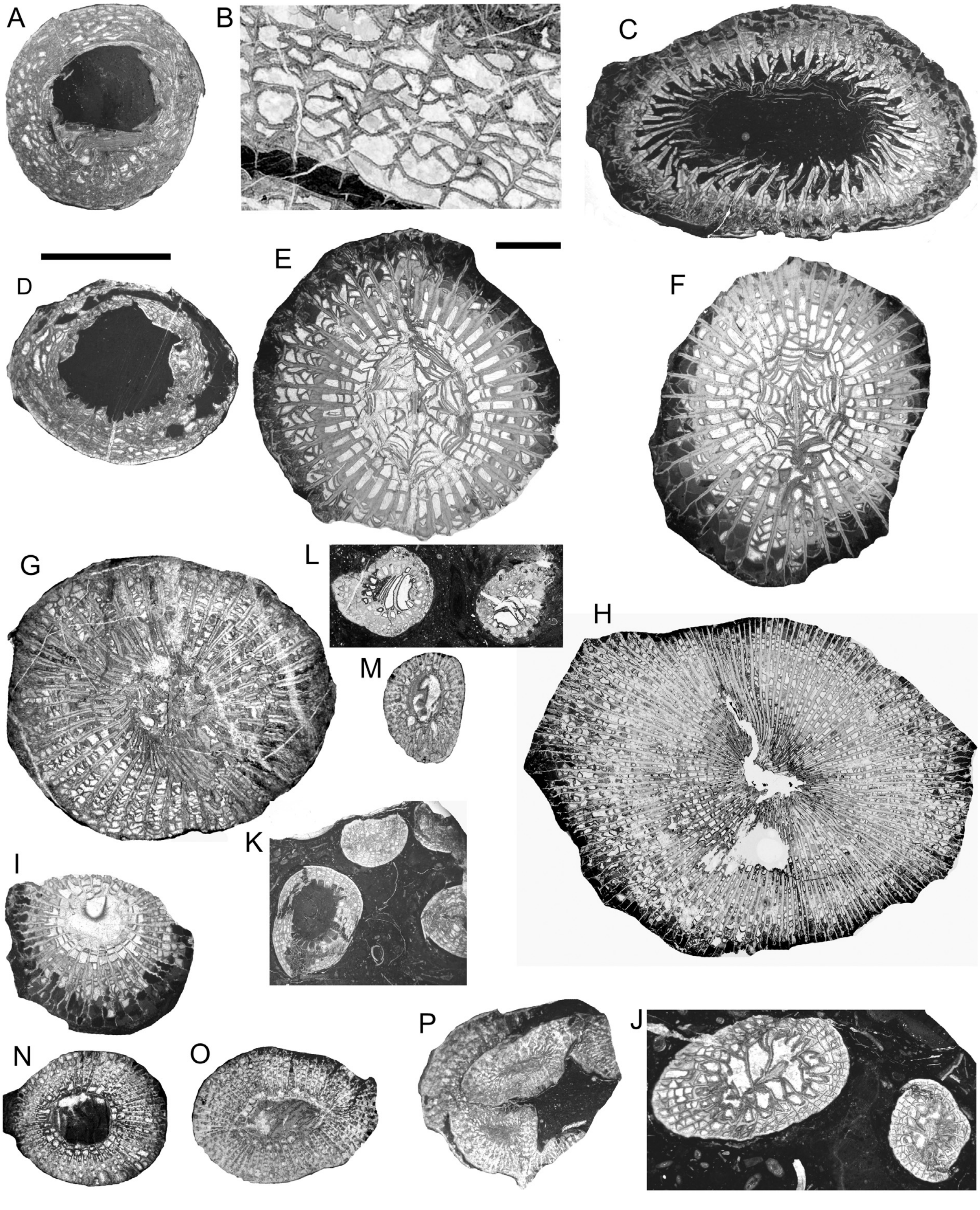

Fig. 3. Rugose corals from Nötsch. **A.** *Siphonophyllia* sp., specimen HEK51, transverse compressed and fragmented section. Note the lonsdaleoid dissepiments in the upper left side of the corallite. **B, C.** *Pseudozaphrentoides juddi*. B: specimen HEK 40 J, detail of the dissepimentarium; C: specimen HEK 31, transverse compressed section. **D.** *Lublinophyllum?* sp., specimen HEK 40L, transverse section showing calicular buddings. **E, F.** *Dibunophyllum bipartitum*. E: specimen BZ3A, transverse section; F: specimen HEK0, transverse section. **G.** *Arachnolasma cylindrical*, specimen HEK 7B, transverse section. **H.** *Palaeosmilia murchisoni*, specimen BZ4A, transverse section. **I.** *Aulokoninckophyllum carinatum*, specimen BZ25, transverse section. **J.** *Siphonodendron martini*, specimen HEK 30D, fragment of colony. **K.** *Diphyphyllum furcatum*, specimen HEK 12B, fragment of colony. **L, M.** *Solenodendron furcatum*. L: specimen NÖ 21-1B, transverse section of a part of the colony; M: specimen HEK 40 M, transverse section of corallite. **N-P.** *Solenodendron horsfieldi*. N: specimen HEK 20 M, transverse section of corallite; O: specimen HEK 40H, transverse section of corallite; P: specimen LK2A, transverse section showing offsetting. Scale bars: 10 mm (A, C-P), 2 mm (B).

too important differences. *Lublinophyllum* has not been cited previously in Nötsch.

Family Aulophyllidae Dybowski, 1873.
Subfamily Dibunophyllinae Wang, 1950.
Genus ***Dibunophyllum*** Thomson and Nicholson, 1876.
Dibunophyllum bipartitum (McCoy, 1849)
Fig. 3(E, F)

Material: 23 specimens in different stages of preservation: BZ1C, BZ3A, BZ7, BZ10, BZ20, Jakomini Quarry, upper Badstub Fm.; EK4, EL1, EL2, EL3A, EL4, EL6, EL10A, Nötschgraben, upper part of the Erchlachgraben Fm.; HEK0, HEK2, HEK8a, HEK9, HEK10, HEK11, HEK12, HEK14a, HEK15, HEK30D'and HEK45D, Hermsberg road, upper part of the Erchlachgraben Fm.

Diagnosis: See Poty (1981: p. 41).

Description: Eroded solitary corals that show commonly the wall and part of the dissepimentarium eroded. Some of them are also compressed. The best preserved specimens show an alar diameter comprised between 18 and 27 mm, a tabularium diameter comprised between 12 and 16 mm and an axial structure comprised between 5 and 7 mm. The number of septa varies between 41 and 54. The wall is thin and smooth. The dissepimentarium is composed of 3 to 5 rows of angulate to inosculate dissepiments, with the inner row thickened. The septa are long, reaching the axial structure. They are thin in the dissepimentarium, but thick in the tabularium. The axial structure is variable. It reaches 1/3 of the diameter and is composed of a median lamella, a small number of radial lamellae and tabulae inclined to the periphery. The lamellae are usually anastomosed or winding. The tabulae are incomplete, tent-shaped and divided in two series: axial and periaxial.

Remarks: This species is well known and very abundant in the upper Mississippian of the whole Palaeotethys. The specimens from Nötsch show similar features to the specimens described in other areas of the Western Palaeotethys, such as Belgium (Poty, 1981; Denayer et al., 2011), Spain (Rodríguez et al., 2001, 2016) and Morocco (Semenoff-Tian-Chansky, 1974; Said and Rodríguez, 2008; Aretz, 2012). Some specimens are very compressed and their structures are not well preserved. As the genus *Arachnolasma* is close to *Dibunophyllum* and it has been described previously in Nötsch (Flügel, 1972), two or three of the specimens assigned to *Dibunophyllum* whose structures are not well preserved could belong to *Arachnolasma*.

Genus ***Arachnolasma*** Grabau, 1922.
Arachnolasma cylindrica Grabau, 1922.
Fig. 3(G)

Material: two compressed specimens: HEK7B, Hermsberg road, upper part of the Erchlachgraben Fm.; NÖ21-1, Basal part of the Nötsch Fm.

Diagnosis: See Said and Rodríguez (2008: p. 29).

Description: Solitary corals partly compressed. The reconstructed alar diameter varies between 22 and 24 mm. 44–45 thick, long major septa that reach a small axial structure (ca. 1/5 of the alar diameter) without well-defined boundaries and having a thick axial lamella and a low number of radial lamellae. The dissepimentarium is partly eroded, composed of 6–8 rows of angular dissepiments. The septa show two phases of secretion. Minor septa are very short and discontinuous.

Remarks: The key differences between *Arachnolasma* and *Dibunophyllum* are a thick axial plate and a smaller axial structure without well-defined boundaries in *Arachnolasma*. As most dibunophylloid specimens from Nötsch are compressed, the details of the axial structure are not well preserved. However, most specimens that are quite well preserved show a well-defined axial structure and mostly thin axial plate. Therefore, most specimens have been included in *Dibunophyllum* although this genus was not previously cited in Nötsch. On the contrary, the only two specimens included in *Arachnolasma* show a thick axial plate, diffuse boundaries in their small axial structures and measurable features identical to *A. cylindrica*. This species has been previously cited in Nötsch by Flügel (1972).

Family Palaeosmiliidae Hill, 1940
Genus ***Palaeosmilia*** Milne-Edwards and Haime, 1848.
Palaeosmilia murchisoni Milne-Edwards and Haime, 1848.
Fig. 3(H)

Material: Six fragmented and variously compressed specimens: BZ4A, BZ6B, BZ8, BZ24, Jakomini Quarry, upper part of the Badstub Fm.; HEK8b, HEK38, Hermsberg road, upper part of the Erchlachgraben Fm.

Diagnosis: See Denayer et al. (2011: p. 161).

Description: Large fragments of trochoid solitary corals. The alar diameter varies from 25 to 50 mm; the tabularium diameter varies from 12 to 28 mm. The external wall, as well as considerable parts of the dissepimentarium, are eroded. The dissepimentarium is composed of 10 to 20 rows of dissepiments. The inner rows are made of interseptal, mainly regular, but sometimes angulose dissepiments. The innermost row may be slightly thickened. Major septa are very long, all reaching the axial zone. They are fibrous and straight in the tabularium, but trabecular and slightly to strongly sinuous in the dissepimentarium. Their number varies from 93 to 110. The cardinal septum is shortened in a long and narrow fossula, slightly expanded in the axial zone. The minor septa are also long, approximately reaching 1/2 length of the major septa.

Remarks: All specimens from Nötsch show the typical features of the species which is highly variable (Semenoff-Tian-Chansky, 1974: p. 160). The fragmentary stage of the specimens and erosion of their wall and external parts of the dissepimentarium impede a more detailed description.

Genus ***Aulokoninckophyllum*** Sando, 1976.
Aulokoninckophyllum carinatum Carruthers, 1909.
Fig. 3(I)

Material: One single portion of a solitary specimen: BZ25, Jakomini Quarry, upper part of the Badstub Fm.

Diagnosis: See Sando (1976: p. 432).

Description: Solitary aulate fragment of coral. The alar diameter is 15 mm, the tabularium diameter is 9 mm and the aulos diameter is 4 mm. The number of major septa is 25. The wall is mostly eroded, but some relicts preserved in the counter quadrants are thin and smooth. The septa are long, most of them reach an incomplete and irregular aulos, which occupies 1/4 of the corallite diameter. The septa are thin in the dissepimentarium, and strongly carinate. The carinae are formed of trabeculae. The major septa are thickened in the outer tabularium, slightly tapering and thinning axially and with fibrous microstructure. In the dissepimentarium, the septa are undulating and sinuous and in the tabularium only slightly undulating. In the dissepimentarium, the minor septa are of the same thickness as majors and may penetrate slightly into the tabularium. The dissepimentarium is partly eroded, composed of 6 to 7 rows of regular and angulate dissepiments. The inner rows are slightly thickened and closely spaced.

Remarks: The specimen from Nötsch shows all typical features of the species *A. carinatum*, (strong carinae and undulate septa in the dissepimentarium, irregular aulos and thickening of septa at the transition dissepimentarium/tabularium). *A. carinatum* has a large range of variability in size and number of septa; the specimen from Nötsch fits well with the lowest range of diameter and number of septa of the species.

Family Lithostrotionidae d'Orbigny, 1852.

Genus ***Siphonodendron*** McCoy, 1849.

Siphonodendron martini (Milne-Edwards and Haime, 1850)

Fig. 3(J)

Material: Three fragments of colonies: HEK20D, HEK30D and HEK30E, Hermsberg road, upper part of the Erchlachgraben Fm.

Diagnosis: See Poty (1981: p. 27).

Description: Fragments of fasciculate corals. The corallites are 6 to 9 mm in diameter, 4 to 6 mm in tabularium diameter and have a styliform columella. 22 to 27 major septa that are variable in length and may reach the columella. Minors length is ca. one half of that of the majors. The dissepimentarium is well developed, composed of two rows of regular dissepiments. Complete, conical tabulae.

Remarks. The specimens identified as *S. martini* from Nötsch show identical size and number of septa to those typical for the species, but only small fragments of colonies having 2 to 6 corallites have been recorded. It was not previously cited in Nötsch.

Subfamily Diphyphyllinae Dybowski, 1873.

Genus ***Diphyphyllum*** Lonsdale, 1845.

Diphyphyllum furcatum Hill, 1940

Fig. 3(K)

Material: One single fragment of a phaceloid colony with corallites compressed and broken: HEK12B, Hermsberg road, upper part of the Erchlachgraben Fm.

Diagnosis: See Poty (1981: p. 34).

Description: Fragment of a fasciculate coral with corallites lacking a columella. Corallites 6–7 mm in diameter and having 25–27 major septa that are quite short, leaving a wide axial zone. Minor septa are very short, reduced to the dissepimentarium and being absent in some loculi. The dissepimentarium is composed of 2–4 rows of interseptal dissepiments.

Remarks: The specimen from Nötsch shows a diameter and number of septa located in the higher part of the variability of the species, but the diameter is clearly smaller than *Diphyphyllum fasciculatum*. All the features are typical of the genus, except that its typical peripheral increase is not recorded in the small portion of the preserved colony. The absence of columella in all the preserved corallites discards the possibility of being a diphyphylloid *Siphonodendron*. The genus *Diphyphyllum* has not been previously recorded in Nötsch.

Genus ***Solenodendron*** Sando, 1976.

Solenodendron furcatum (Smith, 1925)

Fig. 3(L, M)

Material: Two fragments of colonies: HEK40M Hermsberg road, upper part of the Erchlachgraben Fm.; NÖ21-1B, Basal part of the Nötsch Fm.

Diagnosis: See Denayer et al. (2011: p. 172).

Description: Fragmentary fasciculate aulate corals in which the aulos is formed by union of deflected axial ends of majors. The alar diameter reaches 4.5 to 5 mm, the tabularium diameter 2.5 to 3.5 mm, and the aulos diameter 1.8 to 2.2 mm. 23 to 24 major septa. The major and minor septa are carinate. The dissepimentarium is regular.

Remarks: The recorded specimens are included in masses of broken solitary and colonial corals. In both cases, the corallites show all features typical of the identified genus and species. The alar diameter and number of septa fit well with the diagnostic features. The aulos is typically composed of the deflected axial ends of the septa and these are carinate. This species is first described in Nötsch.

Solenodendron horsfieldi Smith and Yü, 1943.

Fig. 3(N–P)

Material: 6 fragments of colonies and isolated corallites: HEK14A, HEK20D', HEK20M, HEK20N, HEK40H, Hermsberg road,

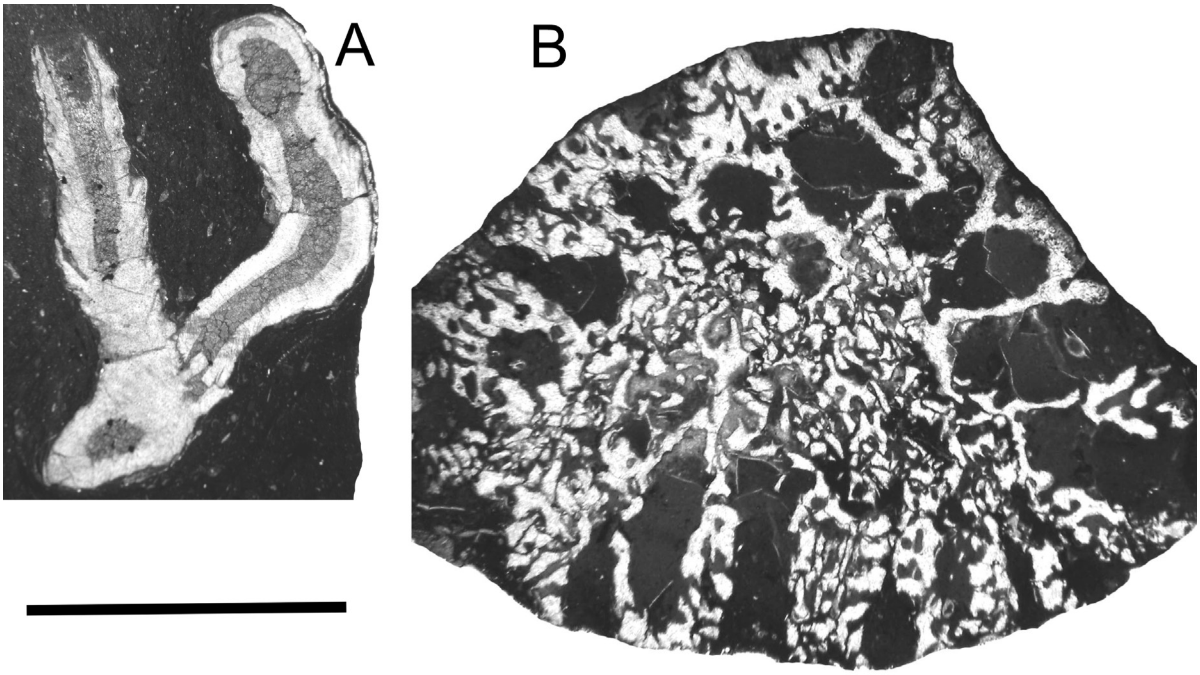

Fig. 4. Tabulate corals from Nötsch. **A.** *Multithecopora* sp., specimen LK2B, longitudinal section. **B.** *Palaeacis* sp., specimen BZ21, transverse section of the colony. Scale bar: 5 mm.

upper part of the Erchlachgraben Fm.; LK2A, Lerchgraben, upper part of the Erchlachgraben Fm.

Diagnosis: See Sando (1976: p. 426).

Description: Phaceloid *Solenodendron* with corallites 9–10 mm in alar diameter, 6–7 mm in tabularium diameter, 3.5–4 mm in aulos diameter, and 27–32 strongly carinate major septa. The aulos is composed of the deflected ends of the major septa. The minor septa are also carinate and penetrating slightly in the tabularium. The dissepimentarium is composed of 4 to 6 rows of interseptal, regular dissepiments. Increase calicular in the studied specimens (Fig. 3(P)).

Remarks: All the specimens fit well with the features (carinate septa, aulos composed of deflected ends of the major septa) and dimensions of the species. As well as most species described in this paper, it has not been previously described in Nötsch.

Order Tabulata Milne-Edwards and Haime, 1850.
Family Syringoporidae Fromentel, 1861.
Genus ***Multithecopora*** Yoh, 1927.
Multithecopora sp.
Fig. 4(A)

Material: two fragments of colonies: EL3B, Nötschgraben, upper part of the Erchlachgraben Fm.; LK2B, Lerchgraben, upper part of the Erchlachgraben Fm.

Description: Fasciculate colonies, formed of cylindrical corallites with well-defined wrinkled epitheca. Thick wall composed of layers of lamellar and fibrous microstructure. The lumen of the corallites is reduced to 2/5–1/3 of the diameter. Corallite diameter ca. 1.5 mm. Lumen diameter 0.5–0.6 mm. Connecting tubules have not been recorded. Tabulae thin, complete, horizontal to concave, in places absent. Lateral increase.

Remarks: The corallite and lumen diameters fit well with *Multithecopora* sp. C of Coronado and Rodríguez (2014) (Visean, SW Spain), but the fragments are too small for further comparison.

Family Palaeacidae Roemer, 1883.
Genus ***Palaeacis*** Haime in Milne-Edwards, 1860.
Palaeacis sp.
Fig. 4(B)

Material: One single specimen: BZ21, Jakomini Quarry, upper part of the Badstub Fm.

Description: fragment of colony, 16 mm in diameter. Corallite walls 0.5–1 mm thick. More than 20 corallites generally subcircular, but may be polygonal, and reach a maximum diameter of 3 mm. Corallite lumen ca. 1.5 mm. Calices deep, without tabulae. The corallite walls are penetrated by tubes 0.1–0.2 mm in diameter, which connect adjacent corallites. Absence of tabulae.

Remarks: Few species of *Palaeacis* have been nominally described. The specimen from Nötsch has smaller corallites than *P. axinoides*, *P. smythi* and *P. cuneiformis*, and a higher number of corallites than *P. smythi*. The existence of only a single, fragmentary specimen impedes further identification. This genus is first mentioned in Nötsch.

3.2. Quantitative palaeobiogeographic analysis

A brief previous palaeoecological analysis of the coral assemblage must be done. All the specimens are transported, broken and compressed. Consequently, they do not constitute a biocoenosis, but a taphocoenosis, coming from different locations and ages. The solitary dissepimented corals are by far the most abundant, with the species *Dibunophyllum bipartitum* being the most abundant. If we include the tabulate corals, the solitary specimens constitute 70.6% of the identified specimens. This percentage is probably lower if we consider all the unidentified fragments. In addition, no massive rugosans have been recorded. The assemblage is a mixture of the associations 1, 2 and 3 (Somerville and Rodríguez, 2007), which represent different areas of a shallow carbonate platform.

In order to check the direct relationships of the Austrian assemblages with the other regions, we built a paired table (Table 4) with the values of the Simpson similarity index. Some areas may have a low number of genera for reasons other than the original diversity of the assemblage. The lack of studies in some regions, or a poor fossil record with only reworked facies could introduce inaccuracies in the analyses. The effects of nestedness (Baselga, 2010, 2012), which could be caused by geographical barriers, and the effects of insufficient sampling are not distinguishable just looking at the numbers.

Fig. 5 represents the clustering produced by the analysis of the dataset that includes the rugose coral genera without inclusion of the tabulate corals and heterocorals, and also excluding the undissepimented corals. Results from both Simpson and Dice indices are shown. The Dice index is more affected by influences such as nestedness (Baselga, 2010), and by heterogeneous sample size (Hammer and Harper, 2006). The results were similar topographies, with only the Balkans occupying a different position. Since we want to focus on the spatial turnover (Baselga, 2010) over the nestedness, we only discuss here the results of the Simpson index-based clustering. Moreover, the Dice cluster shows lower bootstraps, with only one stable node.

The Simpson index-based clustering shows a close relationship between Germany and Belgium, in a very stable branch (90% bootstrap support). The proximity between these regions is easy to understand, because the Belgian platforms were prolonged eastwards. Most occurrences of dissepimented corals in Germany occur in reworked rocks and in calciturbidites, transported into deep settings, because the original platforms are mostly not preserved. Despite that, the coral assemblages show a close similarity with Belgium. The analysis also shows a close relationship between Poland and the Balkans. A bootstrap support of 56% (Fig. 5) indicates also the reliability of this relation. The aforementioned groups (Germany-Belgium and Poland-Balkans) seem to be more similar between them than to the Donets region, even though those branches of the cluster are not stable (31% bootstrap support; Fig. 5).

The differences between the Donets and Poland, despite the geographical proximity, might be associated with the existence

Table 4
Pairwise comparison of the selected regions based on the Simpson Similarity index.

	Austria	Poland	Balkans	Donets	Germany	Belgium	S. France
Austria	–	0.875	0.600	0.750	0.750	0.875	0.685
Poland	0.875	–	0.933	0.850	0.889	0.807	0.777
Balkans	0.600	0.933	–	0.733	0.800	0.866	0.666
Donetz	0.750	0.850	0.733	–	0.722	0.800	0.666
Germany	0.750	0.889	0.800	0.722	–	1.000	0.555
Belgium	0.875	0.807	0.866	0.800	1.000	–	0.777
S. France	0.687	0.777	0.666	0.666	0.555	0.777	–

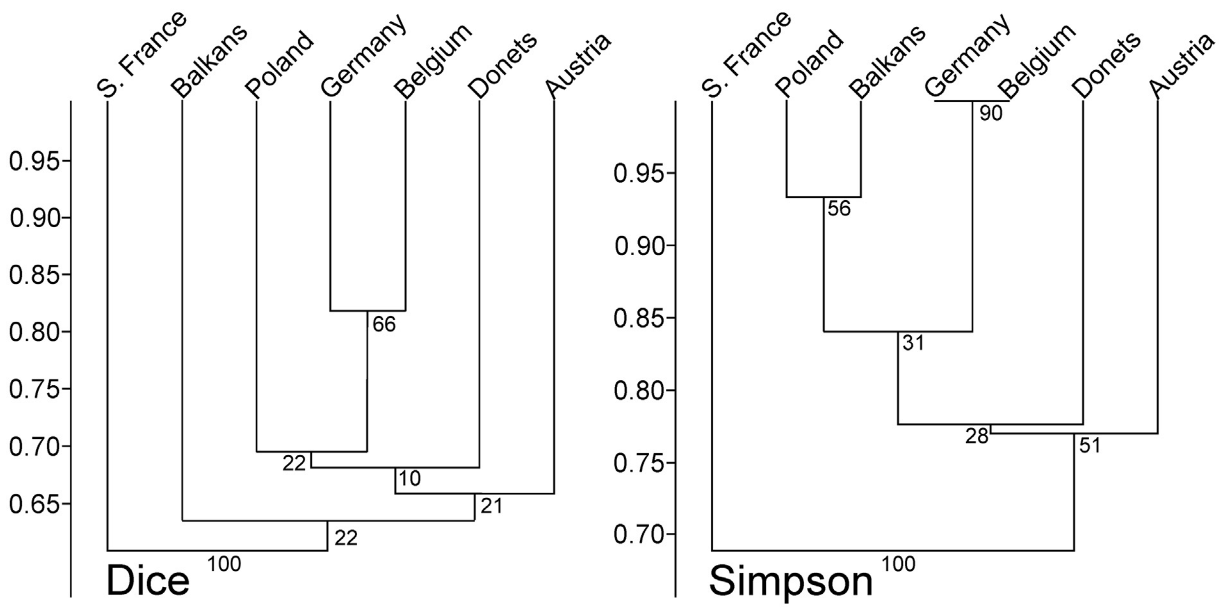

Fig. 5. Paired Group (UPGMA) Hierarchical Cluster analyses using the Dice similarity index (left) and the Simpson similarity index (right).

of the Ukrainian Shield between them (Nikishin et al., 1996), which represented an important barrier. On the contrary, the close relationship of Poland with the Balkans could be related to a free sea connection without any continental barrier between them.

The Austrian outcrops seem to be quite distant from all previously mentioned regions, but again that branch of the cluster is not stable (28% bootstrap support; Fig. 5). It could be due to the fact that the platforms from which the corals were removed were located far away southwards in the Palaeotethys, before they were displaced northwards, first during the Variscan Orogeny and much later during the Alpine Orogeny. However, when comparing by pairs, Austrian assemblages have a high similarity index with Poland and Belgium (0.875 using Simpson index), Donets and Germany (0.75), and somewhat lower with Southern France (0.6875) and the Balkans (0.6). It shows that the Palaeotethyan platforms of Central Europe had a high level of connection during the Visean and Serpukhovian.

The last branch of the clustering, with a 51% bootstrap support, shows that the most isolated region was Southern France, separated from the northern areas of Belgium and Germany by the Armorican and Central Massifs in France, and from the eastern platforms by a longer distance. Finally, the palaeogeography of the studied region during the late Visean based on coral data and in previous papers by different authors (Franke, 2000; Webb, 2002; Cocks and Torsvik, 2006) is shown in Fig. 6.

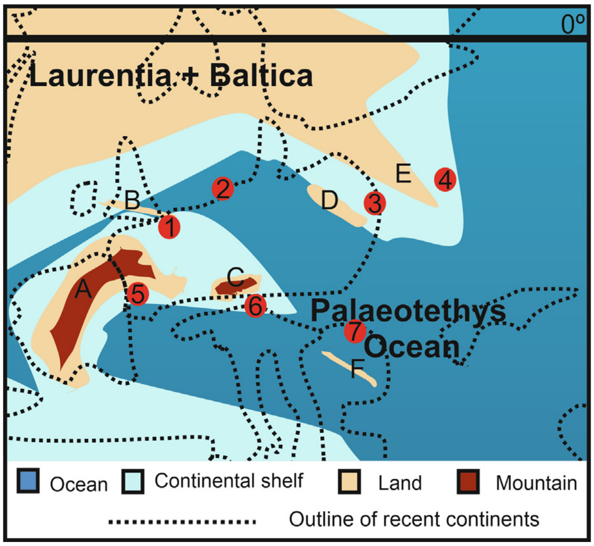

Fig. 6. Palaeogeographic map of the central part of Europe during the late Visean. 1: Belgium; 2: Germany; 3: Poland; 4: Donets; 5: South France; 6: Austria; 7: Balkans. A: Ibero-Armorican Massif; B: London-Brabant Massif; C: Krystalline High; D: Moravo-Silesian massif; E: Ukrainian shield; F: Moesian Platform. Based from Rodríguez-Castro et al. (2023), modified with the data from the present paper.

4. Discussion

4.1. Taxonomic level

The study of the coral assemblage from the Nötsch area and its comparison with other areas from Central Europe (part of the western Palaeotethys) shows several methodological problems already mentioned (low number and uncertainty of many taxa, uncertainty of age in some cases, etc.). Consequently, the comparison was done at the generic level and including Visean and Serpukhovian assemblages. It reduces the value of the comparison, but does not invalidate it. When there are genera in common between two areas in different times, it involves that in earlier or later times there was communication between these areas. Most of the identified corals have long ranges; their main expansion was presented in the late Visean (Rodríguez and Somerville, 2007), but many if not all of them occur also in the Serpukhovian and some of them reach the early Bashkirian. In fact, expanded comparisons could cover gaps in the record at some studied areas. The comparisons made by other authors with foraminifers (Davydov and Cózar, 2017) were formulated at species level because that group allows a more detailed temporal resolution, but Bambach (1990), who worked with different groups of invertebrates, selected the generic level.

Table 3 summarizes the occurrence of the genera in the selected areas. The paired comparison (Table 4) shows high level of similarity. It is because many of the genera are widely distributed along the Palaeotethys Ocean. Such a broad distribution is explained by good marine communications related to a high sea level and equatorial currents (Somerville et al., 2013). Similar wide distribution occurs in other invertebrate groups (Bambach, 1990).

4.2. Selection of areas

The selected areas partially coincide with quite large geographical units. This is not completely subjective as already explained in the chapter of methodology. The choice of smaller areas with very few taxa produces anomalous results. Studies done with different fossil groups usually consider larger areas (Bambach, 1990) such as provinces, which include several of our units. The study made at the level of the Carboniferous system with foraminifers by Davydov and Cózar (2017) shows a similar selection of areas, but they omitted some of those selected here (Belgium, Balkans, Germany, Poland) and changed the name of others (Carnic Alps by Austria, Montagne Noire by South France).

4.3. Comparison of results

The rugose corals biogeographic data confirm the conclusions reached by Davydov and Cózar (2017) with foraminifers and previous palaeogeographic information with other techniques (Franke, 2000; Cocks and Torsvik, 2006; Kalvoda et al., 2008). The closest relationship between Belgium and Germany is well known because there was a continuity along the platforms located in the southern border of Laurussia (Franke, 2000; Cocks and Torsvik, 2006; Figs. 5, 6). The Polish basins were also well connected along the same border, but with a continental area interfering partially: the Moravo-Silesian massif (Pharao, 1999; Franke, 2000; Figs. 5, 6). The Donets basin shows less communication because of the presence of the Ukrainian shield (Kalvoda et al., 2008; Okay et al., 2011). The Balkans would be located southwards, around the Moesian Terrane (Yanev, 2000), with good communication with the Polish basins (Figs. 5, 6). The Austrian platforms and slopes would be separated from the northern areas by the Krystalline high (part of the Moldanubian zone) that was cropping out during the Visean and Serpukhovian (Schönlaub, 1997). The low communication of the Nötsch area with the Balkans is difficult to explain, because their distance should not be large and the latitude could be similar. The Southern France area would be separated westwards by longer distance and an ocean branch, which explain the low similarity shown by the indices.

The palaeogeographic map (Fig. 6) represents the location of the mentioned areas during the late Visean, when the main reliefs produced by the Variscan Orogeny were still beginning to crop out and the late Visean transgression covered most epicontinental platforms. During the Serpukhovian, the elevation of many reliefs and the marine regression reduced the interaction between the different areas.

5. Conclusions

The study of new collections notably increases the knowledge of the coral assemblage from the Nötsch area. The assemblage is composed of 11 rugose coral species, two tabulate species and one heterocoral species. The statistical comparison of the rugose coral assemblages from Austria and other regions from central Europe at the genus level allows a better perception of the distribution of the shallow-water carbonatic platforms in that part of the Western Palaeotethys during the Visean and Serpukhovian. The Austrian areas show a certain degree of isolation from the northern areas (Germany, Belgium, Poland) and from areas located today to the west (South France) or to the east (Balkans).

CRediT authorship contribution statement

Isabel Rodríguez-Castro: Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Herbert Kabon:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Sergio Rodríguez:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation.

Data availability

No data was used for the research described in the article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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5 THE PALAEOBIOGEOGRAPHY OF THE WESTERN PALAEOTETHYS DURING THE LATE VISEAN BASED ON RUGOSE CORALS.

The palaeobiogeography of the western Palaeotethys during the late Visean based on rugose corals

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Abstract Building reliable palaeogeographical maps of the Carboniferous period is a complex effort due to the active tectonics of the Variscan Orogeny. For the western Palaeotethys, which was directly affected by it, numerous maps have been proposed based on tectonic, palaeomagnetic, and sedimentologic data. This paper presents a palaeobiogeographical analysis of the late Visean based on the distribution of rugose corals. The Late Visean in the western Palaeotethys was selected for its high diversity, driven by a significant transgression, and the substantial number of rugose coral studies in the region. Our rugose coral data base of spans from Nova Scotia to the Moscow Basin and from the Sahara to central Europe. We analysed this data using Simpson and Dice indices. The analysis revealed distinct patterns of similarity. The British areas are closely related. NW Spain and North Morocco are most similar to each other, but also share substantial faunal similarities with Belgium and the Sahara. Germany and Poland are grouped together but show different relationships with other areas. Türkiye has a distinct fauna, and the Balkans low diversity and lack of recent studies complicate comparisons. On a more general level, the results indicate a high faunal communication between the six previously proposed sub-provinces. The Atlantic and West Peri-Gondwanan sub-provinces exhibit high similarity, likely due to their connection along the Rheic Ocean. The Central and Eastern European sub-provinces also show significant similarities, while the Mediterranean and Saharan sub-provinces display more complex relationships with the others. Despite limitations from uneven fossil records, these findings provide a nuanced understanding of Visean coral distribution and biogeographic relationships in the western Palaeotethys.

Keywords Biogeography, cluster analysis, sub-provinces, Europe, North Africa

1. Introduction

The understanding of Palaeogeography is crucial for the knowledge of Earth's history. For this reason, there are many papers dedicated to building palaeogeographic reconstructions to different scales, from global (Torsvik et al, 2002; Scotese, 2021) to regional (Schönlaub, 1997; Yanev, 2000; Robardet, 2003; Cocks and Torsvik, 2006; Blakey et al. 2008), and temporal ones (Paproth, 1991, 2006; Cocks, 2000; Golonka, J., 2007; Blakey et al., 2008). Some compendiums have also been published (McKerrow and Scotese, 1990). Some maps have been based on palaeomagnetic data (Tait et al. 1994; Torsvik and Rehnstrom, 2001), on tectonic data (Stampfli et al, 2002; Domeier and Torsvik, 2014), on palaeontological distributions (Hill, 1981; Debrenne et al. 1999; Webb, 2002; Cao et al. 2017), on sedimentological data (Golonka, 2012) or on a combination of several types of data (Harper et al. 1996; Torsvik and Cocks, 2004).

The global Carboniferous palaeogeography based on palaeontological data has been matter of study in some of the previously cited papers and many others. Some of them are very old (Fedorowski, 1981; Hill, 1981; Paproth and Streel, 1985), and although they contain very valuable information, the data base has been improved in the last years. Some others are devoted to relatively small areas such as North Africa (Legrand-Blain et al. 1989; Somerville et al., 2013), the Asian Gondwana margin (Denayer, 2015), the British Isles (Somerville, 2008), Southwestern Spain (Rodríguez-Castro and Rodríguez, 2022), Belgium and surrounding areas (Poty, 1980, 1989) etc. An interesting attempt was made by Aretz (2011a) with some of the areas comprised in the western Palaeotethys, from Belgium to the Saharan basins and including seven different spatial units, but that study was just presented as an abstract without detailed data. The western Palaeotethys Carboniferous palaeogeography as a whole has not been studied in detail, with the exception of the excellent palaeogeographical analysis of the Pensylvanian and Permian by Vai (2003). The present paper is part of a project on the utility of rugose corals in the analysis of the palaeogeography of the Mississippian of the western Palaeotethys. The first period subject of our study is the late Visean, because it corresponds with a major transgression that could favour the displacement of the coral larval stage (the planula) with the currents. It produced the highest level of diversity in the Carboniferous, providing the possibility of building large data bases.

2. Methodology

To get reliable results for the late Visean, we checked multiple bibliographic references, plus the data from our own collections and from the collections in several universities and museums. More than 100 papers containing information about local or global palaeogeography and their corresponding maps have been consulted.

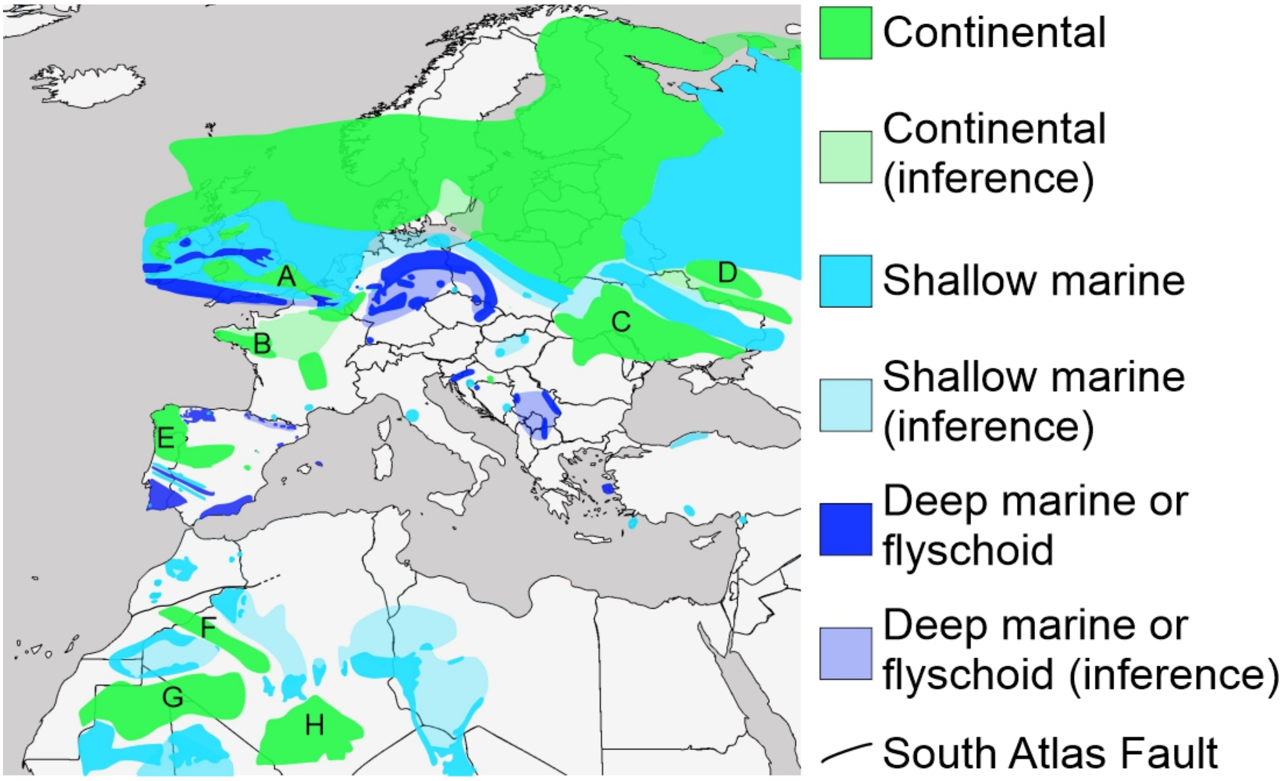

Figure 1: map representing the distribution of Visean basins, platforms and massifs over Europe and North Africa. A Welsh-Anglo-Brabant massif. B Armorican Massif. C Ukranian Shield. D Voronezh High. E Iberian Massif. F Ougarta. G Reguibat Shield. H Hoggart.

A map showing the continental massifs, shallow water carbonate and terrigenous platforms and deep-water facies has been built (Fig. 1). It was built in GIMP and stylized in CorelDraw. It uses a blank European map as a base and incorporates information from more than 30 palaeogeographical maps and articles (Table 1). These maps were superimposed in different layers, adjusting them to reference points (coasts, borders, cities, and rivers), to easily compare different maps of the same places. We also combined information given by papers dealing with plate tectonics (Domeier and Torsvik, 2014, Pharao, 1999) and with previous studies done with other fossil groups (Kalvoda

2003; Davidov and Cózar, 2019). When our references presented conflicting information, we made decisions on which data to represent in the map by considering several criteria. First, we assessed whether multiple papers agreed on specific details, giving more weight to information corroborated by several sources. Second, we evaluated how well the units represented in the maps matched the surrounding areas, ensuring geographical consistency and coherence. Third, we prioritized newer papers, as they typically contain more recent and potentially more accurate data. Finally, we considered the scope of each study: precise maps of smaller areas studied in detail were preferred over general maps of larger areas, which tend to be less precise. This multi-faceted approach allowed us to create a more accurate and reliable map.

Table 1: summary of the main references used for each area for the map in Fig. 1.

Map area	**Main references**
N. Africa	Legrand-Blain (1989); Cózar et al. (2014).
Iberian Peninsula	Martínez Díaz (1983); Rosell & Arribas (1989); Rodrigues et al. (2015).
France	Peret & Semenoff-Tian-Chansky (1971); Vuillemin (1990); Cózar et al. (2019).
UK & Belgium	Poty (1980); Aretz & Chevalier (2007); Somerville (2008); Denayer et al. (2011); Pharaoh et al. (2021).
Germany	Korn (1996); Herbig (1998); Weyer (2000); Herbig (2014).
Poland	Korejwo (1969); Zakowa (1970); Zelichowski (1987); Szulcewski (1995).
Donetz	Dvorjanin et al. (1996); Stovba et al. (1996); Ohar (2012).
Russia	Proust et al. (1998); Kabanov et al. (2016a; 2016b).
Türkiye	Gorur (1997); Groves (2003); Garzanti et al. (2005); Denayer (2014a; 2015); Lowen et al. (2018).
Balkans	Balogh & Barabás (1972); Ramovs (1989).
Italy	Capezzuoli et al. (2021).
General	Paproth (1991).

The information in Fig. 1 shows different terrains, the shallow seas around them, and the deep seas separating them. Consequently, it allows the identification of sedimentary areas that can be considered geographic units, and the barriers between them. For that reason, flyschoid facies have been grouped with deep sea facies, since both of them are marine areas that are not favourable for corals and can act as a partial barrier.

Individual localities or outcrops can be affected by selective preservation, have small sample sizes, or represent a specific environment. To avoid the bias these issues could introduce in the analysis, we compared larger units. We chose fourteen: Newfoundland, North Britain, South England, Belgium, South France, Germany, Poland, the Balkans, the Donets Basin, the Moscow Basin, Türkiye, Southwestern Spain, North Morocco, and the Sahara. Most of these units coincide with individual Visean basins or group several basins that either lack significant barriers between them or share similar faunas, making them consistent with the different terranes known from the late Visean. However, this alignment is not always entirely possible, with Germany, Türkiye, and the Balkans grouping areas that were part of different terranes. The reasons for this are explored further in the discussion.

Once the palaeogeographical units were selected, a presence/absence coral data base was built with our bibliographic data base on Carboniferous corals, composed of 2050 articles, symposiums abstracts and book chapters, of which more than 700 contain data on Visean corals. In addition, several important coral collections have been visited along many years and examined carefully: the British Natural History Museum at London (IRC), the British Geological Survey (IRC), the Institute of Geology, Adam Mickiewicz University, Poznan, Poland (IRC), the Institute for Earth Sciences at the Karl-Franzens-Universität at Graz (SRG), the Vserossiskiy Nauchno-issledovatelskiy Geological Institut (VSEGEI) at Saint Petersburg (SRG), the Museum National d'Histoire Naturelle at Paris (SRG), the Geol.-Palaont. Institut at Tübingen University (SRG), the Museum für Naturkunde at Berlin (SRG), the Leiden University (SRG), the Museum of Natural History at Münster (SRG) and the Division of the Geologic Patrimony at Rabat (SRG). An important percentage of the studied corals are our own collections from Spain and Morocco, stored in the Palaeontological Department of the Complutense University at Madrid.

The previous identifications of the corals checked in the collections have been examined trying to maintain homogeneous criteria. In most cases, pictures of the specimens and of the thin sections studied in the abroad museums have been taken in order to have a large catalogue of Carboniferous corals. The coral assemblages described in the bibliography have been also carefully examined. Unfortunately, in many cases, especially in old papers, the low quality of the figures impedes a precise determination. Two data bases have been built: one with distributions of species, counting about 300 species (supplementary information); and another one with genera distributions, counting 80 genera (Table 2;). The taxonomical concepts of different authors are very different: some of them are “splitters” and others are “lumpers”. For this reason, in some cases it was necessary to make decisions on the taxonomic assignations. Whenever there was not enough data to decide, the identifications by the original authors have been used. Many of the references to species and genera are citations without details. Consequently, a high number of identifications were only done at the generic level because they lack appropriate descriptions, or the illustrations of the corals were not good enough to identify the species. About one third of the species in the data base were left in open nomenclature.

Some attempts to compare the species assemblages were made in areas with homogeneous identifications and well-known assemblages (Rodríguez-Castro and Rodríguez, 2022). However, for the global comparison of the western Palaeotethys, the generic data base has been used, in order to avoid many of the problems caused by the different taxonomic criteria, preservation, and reliability of the data (Bambach, 1990).

All palaeogeographical analyses have been performed using PAST 4 (Hammer et al., 2001). The study uses a paired group (UPGMA) Hierarchical Clustering, with both Simpson and Dice indices. Simpson is less affected by differences in sample size or insufficient sampling (Hammer and Harper, 2006), and it reflects spatial turnover over nestedness (Baselga, 2010). However, 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 other. To address this limitation, we used both Simpson and Dice indices, providing a more nuanced comparison that considers both the presence and absence of taxa.

To test the stability of the resulting clusters, 1000 bootstrap resamples have been performed on them. The branches with a bootstrap value lower than 50% are not stable and should not be considered conclusive or well supported.

Table 2: Presence/Absence table of rugose coral genera in different areas of Europe and North Africa during the Visean.

Subprovinces	**Newfoundland**	**Ireland**	**N. Britain**	**S. England**	**Belgium**	**South France**	**Germany**	**Poland**	**Balkans**	**Donets Basin**	**Moscow Basin**	**Turkey**	**SW. Spain**	**N. Morocco**	**Sahara**	**Total**
Actinocyathus		x	x	x	x	x	x	x		x	x					**9**
Allotropiophyllum.		x	x	x				x		x						**5**
Amplexizaphrentis		x	x	x			x	x		x	x		x	x	x	**10**
Amplexocarinia		x	x	x	x		x	x			x	x	x	x		**10**
Amplexus		x	x	x	x	x	x			x	x		x	x		**10**
Amygdalophyllum				x	x			x	x			x	x		x	**7**
Arachnolasma		x		x	x	x		x		x	x		x	x	x	**10**
Auloclisia				x			x		x				x	x	x	**6**
Aulokoninckophyllum		x	x	x	x	x				x	x		x	x	x	**10**
Aulophyllum		x	x	x	x		x	x	x	x	x	x	x	x	x	**13**
Axoclisia					x		x			x			x	x	x	**6**
Axophyllum	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	**15**
Bifossularia					x			x		x						**3**
Biphyllum								x								**1**
Bothrophyllum					x			x	x	x				x		**5**
Bradyphyllum					x	x		x					x	x		**5**
Calophyllum							x	x								**2**
Campophyllum								x								**1**
Caninia		x	x	x	x		x	x	x	x	x	x	x	x	x	**13**
Caninophyllum			x	x	x				x	x	x	x	x	x	x	**10**
Carruthersella				x			x	x							x	**4**
Ceriodotia												x				**1**
Claviphyllum								x		x				x		**3**
Clisiophyllum		x	x	x	x	x	x	x	x	x	x	x	x	x	x	**14**
Corwenia		x	x	x						x	x			x		**6**
Cravenia				x												**1**
Cryptophyllum								x								**1**
Cyathaxonia	x	x	x	x	x		x	x		x	x		x	x		**11**
Dibunophyllum	x	x	x	x	x	x	x	x	x	x	x		x	x	x	**14**
Diphyphyllum		x	x	x	x	x	x	x		x	x		x	x	x	**12**
Eolithostroniella										x						**1**
Espielia												x	x		x	**3**
Gangamophyllum					x			x	x	x	x	x	x	x	x	**9**
Guadiatia					x											**1**
Haplolasma		x	x	x	x	x		x		x	x	x	x	x	x	**12**
Kizilia					x	x		x			x			x	x	**6**
Koninckinaotum								x			x					**2**
Koninckophyllum	x	x	x	x	x	x	x	x	x	x			x	x	x	**13**
"Koninckophyllum" (colonial)	x	x														**2**
Kwangsiphyllum												x				**1**
Lithostrotion		x	x	x	x	x	x	x	x	x	x	x	x	x	x	**14**

Lonsdaleia	x	x	x	x	x	x	x			x	x	x			x	**11**
Lophophyllidium															x	**1**
Lublinophyllum				x				x								**2**
Melanophyllidium						x										**1**
Merlewoodia					x											**1**
Mirka								x								**1**
Morenaphyllum													x			**1**
Neoclisiophyllum					x			x					x	x		**4**
Neokoninckophyllum								x		x						**2**
Nemistium	x	x	x	x		x		x			x	x				**8**
Nervophyllum								x		x	x					**3**
Orionastraea		x	x	x				x		x	x					**6**
Palaeosmilia		x	x	x	x	x	x	x	x	x	x	x	x	x	x	**14**
Palastraea	x	x	x	x	x	x	x	x		x	x	x	x	x		**13**
Pareynia					x	x								x	x	**4**
Pentaphyllum					x	x	x	x								**4**
Pseudocaninia							x									**1**
Pseudozaphrentoides'		x	x	x	x		x			x	x		x	x	x	**10**
Rotiphyllum		x	x	x	x	x	x	x				x	x	x		**10**
Rozkowskia							x	x								**2**
Rylstonia		x	x	x	x			x		x			x		x	**8**
Saharaphrentis															x	**1**
Semenoffia					x	x								x		**3**
Siphonodendron	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	**15**
Siphonophyllia		x	x	x	x	x	x	x	x	x	x		x	x	x	**13**
Slimoniphyllum				x				x								**2**
Sochkineophyllum												x				**1**
Solenodendron		x	x	x	x	x	x			x			x	x	x	**10**
Spirophyllum								x		x			x			**3**
Tachylasma											x					**1**
Thysanophyllum		x	x	x												**3**
Tizraia										x			x	x	x	**4**
Turbinatocaninia								x		x					x	**3**
Ufimia							x	x		x			x	x		**5**
Viseaulina					x											**1**
Zakowia								x		x						**2**
Zaphrentites		x	x	x	x		x	x			x		x	x	x	**10**
Zaphrufimia		x	x	x			x	x					x	x		**7**
Total genera	**9**	**33**	**32**	**39**	**40**	**25**	**31**	**50**	**15**	**40**	**31**	**20**	**37**	**38**	**33**	

3. Results

The map in Fig. 1 highlights the distribution of Carboniferous facies across Europe and North Africa, revealing significant geological diversity and continuity between regions.

The Baltic region is characterized by continental facies, part of Laurentia and Baltica. In Britain, Scotland also presents continental facies, while the rest of the island is divided into two distinct marine basins, comprising both deep and shallow facies, separated by the Welsh-Anglo-Brabant massif. These basins extend into Ireland and connect with those in Belgium and the Netherlands. Germany predominantly features deep or flyschoid facies. Poland is traversed by a shallow marine basin running from the northwest to the southeast. The extensive Moscow Basin covers much of western Russia, while the Donets Basin, separated by the Voronezh High, has its southern boundary defined by the Ukrainian Shield. The Balkans only show sporadic data points on our map due to limited research and a complex structure that merges different terranes. Italy contains only a small area of Carboniferous marine sediment. Marine facies with corals are also present in southern France (Montagne Noire, Ardengost, and les Haute Corbières) and the Spanish Pyrenean mountains. Besides those in the Pyrenees, the Iberian Peninsula showcases three marine areas: the Cantabrian Zone, part of the Baetic System, and Ossa Morena. The latter, located in southwestern Spain and Portugal, is particularly significant due to its highly diverse Visean coral assemblages. North Africa is divided into two main domains by the South Atlas Fault: the northern Moroccan basins, including Adarouch-Khenifra, and the Saharan basins, separated by the Ougarta and Reguibat Shields. In Türkiye, Carboniferous sediments include multiple areas of shallow marine facies, along with deeper facies found in the Karaburun Peninsula and the island of Chios, Greece.

As previously stated, about 700 papers have been used to build the tables, although most of the data comes from a reduced portion of those papers. In some areas, the data base was easy to build because the coral assemblages had been studied in detail, and extensive papers give general information on the regional assemblages (Semenoff-Tian-Chansky, 1985; Weyer, 2000; Denayer et al, 2011; Rodríguez et al, 2016). In other areas the data base has been compiled checking dozens of papers. The main bibliographic references used have been: Poty (2002) in Nova Scotia, Poty (1981) and Denayer et al. (2011) in Belgium, Mitchell (1989) and Hill (1938-41) in Britain, Weyer (2000) in Germany, Fedorowski (1968, 1975, 1981) and Khoa (1977) in Poland, Rodríguez et al. (2016) in SW Spain, Said et al (2013) in the Azrou-Khenifra Basin), Semenoff-Tian-Chansky (1974, 1985) in the Saharan basins, Vassiljuk (1960) and Fedorowski (2022) in the Donets Basin, Dobrolyubova, (1958) in the Moscow Basin, Aretz and Herbig (2003) in South-west France and Denayer (2021) in

Türkiye. All these papers show reliable data that, in most cases, has been directly incorporated in the data base. Other reviewed papers are old and have less reliable illustrations, or use old criteria for the classification of the corals. Consequently, some re-identifications have been done. It is the case of Kolosvary (1951) and Kostic-Podgorska (1957, 1958) in the Balkans. Many extra papers have been used to provide additional data. They are too many to be cited here, but some relevant input of data is provided by Aretz (2002, 2010a, 2011b), Aretz et al. (2013), Cózar et al. (2005), Flügel (1972), Herbig, (1986), Kozyreva (1974, 1978), Nudds (1979), Perret and Semenoff-Tian-Chansky, (1971), Riley (1995), Rodríguez et al (2013), Semenoff-Tian-Chansky and Ovracht (1965), Somerville (1997), Zukalova (1961, 1965), etc.

Some areas have been excluded from the analyses for different reasons. In several outcrops in Austria there are records of rugose coral assemblages (Hubmann, 2002). However, most corals there occur in reworked facies, and the most recent dating of those facies (Vachard et al., 2017) indicates mainly a Serpukhovian age, excluding them from this study. The sedimentation during the Visean in the Cantabrian mountains occurred mostly in deep waters. The assemblages recorded there have been described by Rodríguez, 1984; Boll, 1985; and Fedorowski and Kullmann, 2013. They are quite poor and contain mainly undissepimented corals. In addition, most assemblages are dated as Serpukhovian and not as Visean.

The results of the compilation of coral data are two tables, one with the species (supplementary information) and one with the genera (Table 2). The latter has been used to compare the different areas.

The analysis has been handled at two different levels. First, we compared the rugose coral assemblages from the fourteen regions established in methods, all of which were part of the Palaeothetys during the late Visean. Such a comparison should test how well the sub-provinces of the western Palaeotethys defined by Somerville et al. (2013) and Rodríguez-Castro et al. (2023) are consistent with the distribution of rugose coral genera. Second, we compared the coral assemblages from the sub-provinces to check the degree of communication between them.

The first comparison has been run including all the regions (Figs. 2A and 3A) and excluding Newfoundland, the Balkans, and Türkiye (Figs. 2B and 3B). They are the least diverse areas, with a low number of genera (9, 15, and 20 respectively), so Dice index (Fig. 2) systematically finds them as the most different from all the others. The combination of these issues and the fact that the Balkans and Türkiye group outcrops from different terranes justified their exclusion.

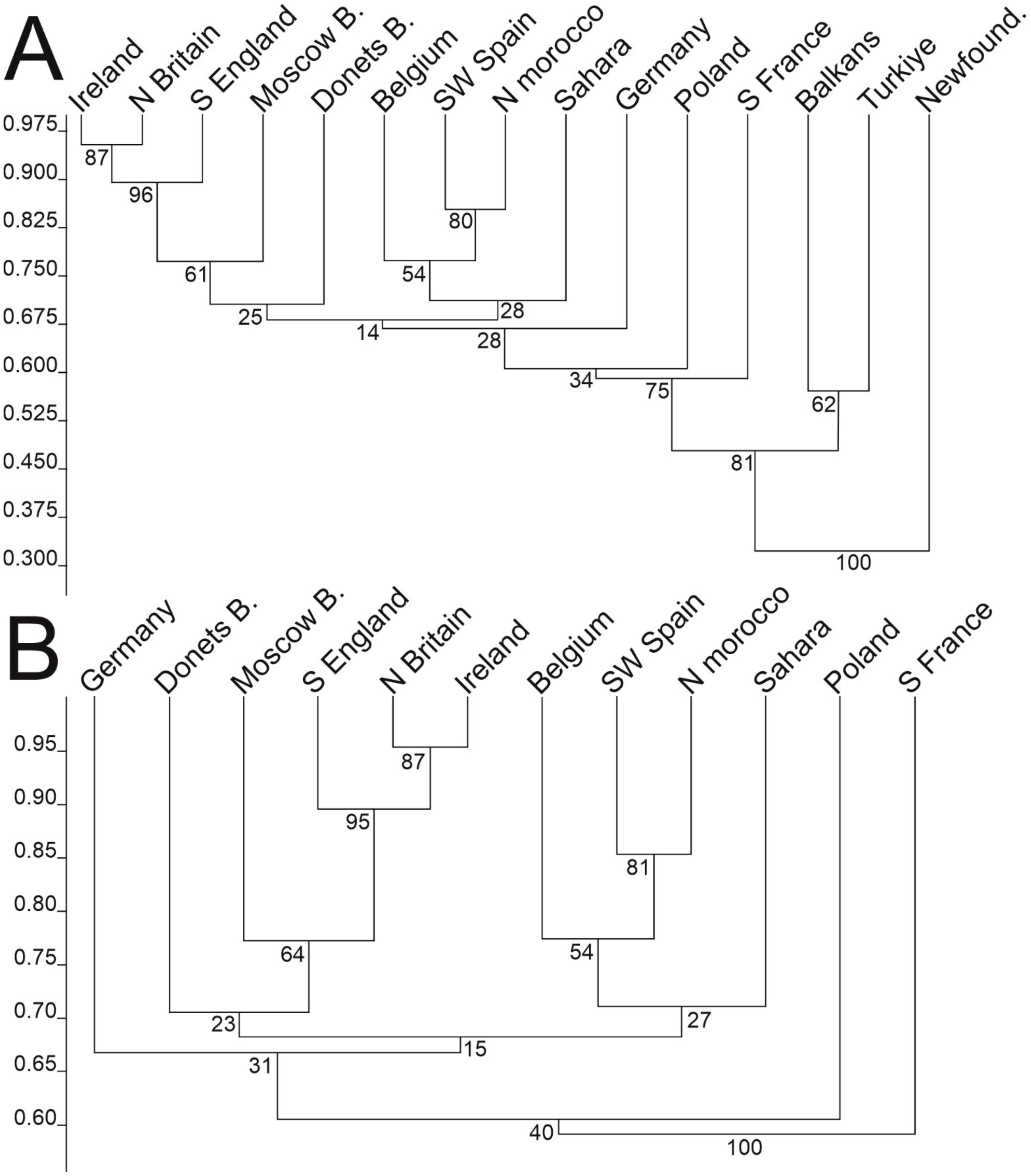

Figure 2: Paired Group (UPGMA) Hierarchical Cluster analyses, comparing the different areas with Dice index. A. All areas. B. Excluding Newfoundland, the Balkans and Türkiye.

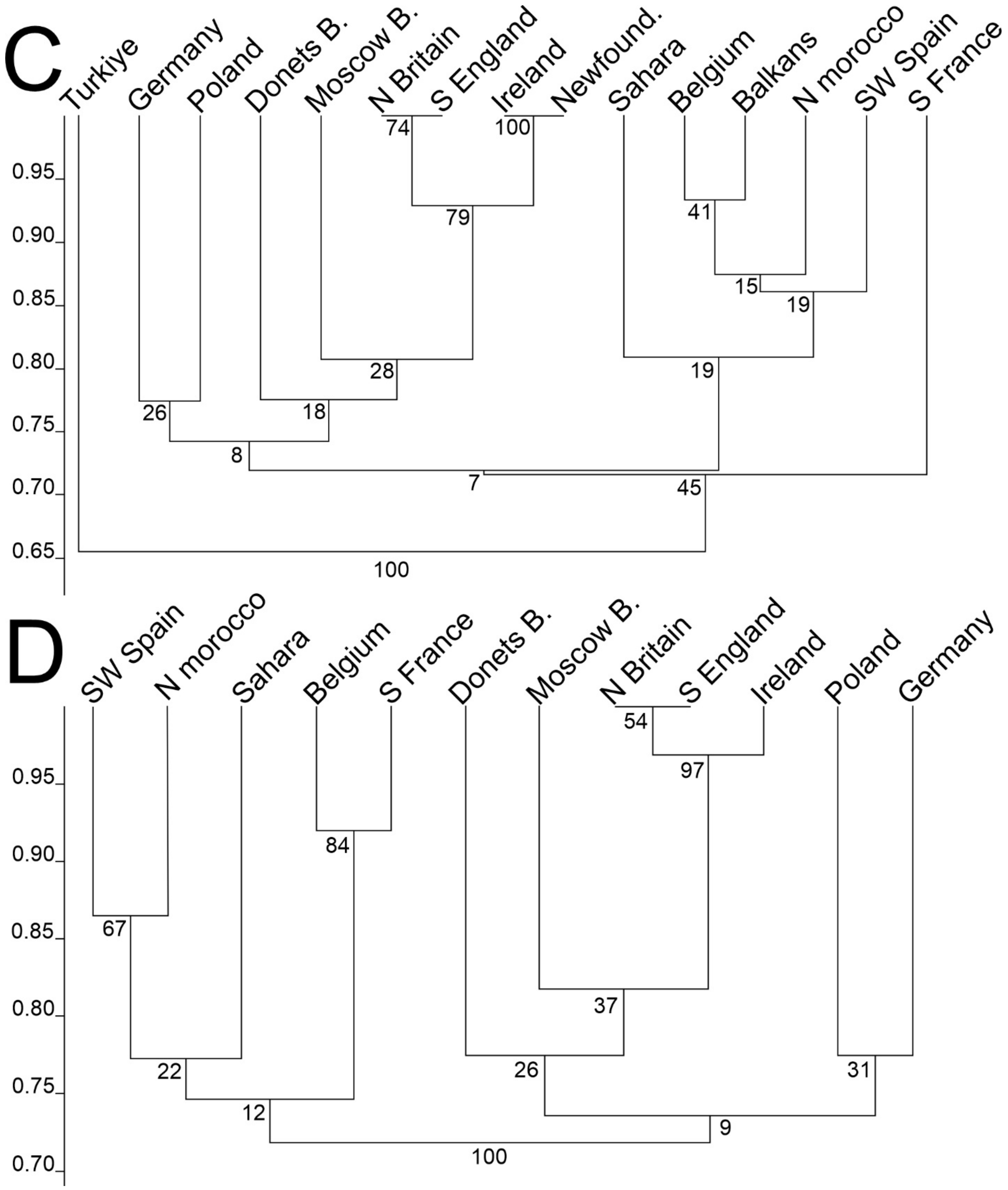

Figure 3: Paired Group (UPGMA) Hierarchical Cluster analyses, comparing the different areas with Simpson index. A. All areas. B. Excluding Newfoundland, the Balkans and Türkiye.

All the cluster analyses show close relationships between Ireland, South England, and North Britain. These similarities are well supported, with bootstrap values higher than 70%. In addition, Simpson index also shows a strong similarity with Newfoundland, since it shares its nine genera with Ireland, and eight of them (excluding a colonial "*Koninckophyllum*") with South and North

England. All clusters also show similarities between these regions and Moscow and Donets Basins, but the support values are lower than 40% for these relationships. Likewise, most clusters show close similarities between North Morocco and SW Spain, with high bootstrap support values. These regions seem to share a similar fauna with Belgium and with Sahara, but the bootstraps show less support for these relationships. Analyses with Sympson index (Fig. 3) indicate a close relationship between Poland and Germany, but the bootstrap support values are always low. Dice identifies less similarities between Germany and Poland than between Germany and most of the other areas, excluding South France, the Balkans, Türkiye, and Newfoundland.

When Türkiye is included in the analysis, Dice index identifies similarities with the Balkans, supported by a bootstrap value of 62%. However, these similarities appear to be primarily due to the absence of most genera in both areas. They share ten genera only (*Amygdalophyllum, Aulophyllum*, *Axophyllum*, *Caninia*, *Caninophyllum*, *Clisiophyllum*, *Gangamophyllum*, *Lithostrotion*, *Palaeosmilia*, and *Siphonodendron*), most of which are cosmopolitan and present in nearly all areas. The three that are not cosmopolitan (*Amygdalophyllum*, *Caninophyllum*, and *Gangamophyllum*) are still widely distributed and found in many other areas, such as Belgium, SW Spain, or the Sahara. Simpson index, however, does not group Türkiye with any other area, finding its fauna significantly different. Türkiye has three genera that are not present in any other studied area during the Visean (*Ceriodotia*, *Kwangsiphyllum*, and *Sochkineophyllum*). Conversely, it lacks representatives of *Dibunophyllum* and *Diphyphyllum*, which are present in all or nearly all other areas.

Regarding the Balkans, Simpson index pairs them with Belgium, as they share fourteen of the fifteen genera found in the Balkans. The only exception is *Auloclisia*, which is absent in Belgium. However, a similar situation occurs with SW Spain, where *Bothrophyllum* is absent during the Visean, and North Morocco, which lacks the genus *Amygdalophyllum*. The low number of genera found in the Balkans, the wide distribution of most of them, and the current state of studies in the region complicate resolving their relationships with other areas, as they share most of their fauna with many regions.

The comparison of the sub-provinces proposed by Somerville et al. (2013) and Rodríguez-Castro et al. (2023) using both indices shows similar results, with higher bootstrap support values obtained from Dice index (Fig. 4). Both indices indicate a well-supported high similarity between the Atlantic and West-Perigondwanan sub-provinces, which can be explained by their connection along the narrow Rheic Ocean. Additionally, both analyses group the Central European and Eastern European sub-provinces together, but with slightly lower support values. Other connections are less clear because the results differ between Simpson and Dice indices. Simpson index connects 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, albeit with a low bootstrap support of 18% in the latter case. In contrast, all branches produced with Dice index have high support values. They join the Central and Eastern European sub-provinces with the West Peri-Gondwanan and Atlantic sub-provinces. This is logical, given the partial continuity of the Atlantic basins and platforms in Germany and Poland, along the south border of Laurussia. These sub-provinces are also connected with the Saharan sub-province, while the Mediterranean sub-province is less connected with the others.

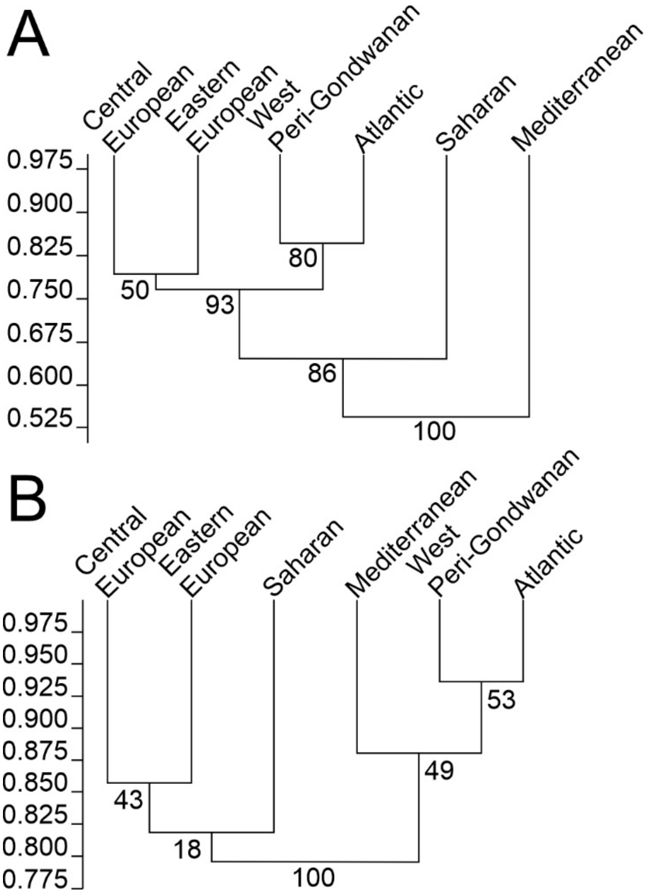

Figure 4: Paired Group (UPGMA) Hierarchical Cluster analyses, comparing the six sub-provinces proposed in Somerville et al. (2013) and Rodríguez-Castro et al. (2023). A. Dice index. B. Simpson index.

The pairwise comparison (Tables 3 and 4) is very significant and reveals similarities that are not always well represented in the clusters. Both indices show that NW Spain and North Morocco, despite being most similar to each other, also share a lot of their fauna with Belgium and the Sahara, and even with the British areas. Germany and Poland, which are joined in Simpson's cluster, have different relationships with other areas: Germany shares more similarities with S England, while Poland's fauna is closer to that of the Moscow Basin.

Table 3: Dice and Simpson similarity indices between all areas.

DICE	**Newfound.**	**Ireland**	**N. Britain**	**S. England**	**Belgium**	**South France**	**Germany**	**Poland**	**Balkans**	**Donets Basin**	**Moscow Basin**	**Turkey**	**SW. Spain**	**N. Morocco**	**Sahara**
Newfound.	1	0,429	0,390	0,333	0,286	0,412	0,350	0,237	0,333	0,286	0,350	0,345	0,261	0,255	0,238
Ireland	0,429	1	0,954	0,889	0,685	0,655	0,719	0,602	0,417	0,712	0,781	0,491	0,714	0,704	0,606
N. Britain	0,390	0,954	1	0,901	0,694	0,632	0,730	0,585	0,468	0,722	0,794	0,538	0,725	0,714	0,615
S. England	0,333	0,889	0,901	1	0,684	0,594	0,714	0,652	0,481	0,684	0,743	0,508	0,737	0,701	0,667
Belgium	0,286	0,685	0,694	0,684	1	0,708	0,648	0,622	0,509	0,675	0,676	0,500	0,753	0,795	0,685
S. France	0,412	0,655	0,632	0,594	0,708	1	0,571	0,480	0,400	0,523	0,607	0,444	0,548	0,635	0,552
Germany	0,350	0,719	0,730	0,714	0,648	0,571	1	0,593	0,478	0,592	0,613	0,431	0,706	0,696	0,594
Poland	0,237	0,602	0,585	0,652	0,622	0,480	0,593	1	0,400	0,667	0,593	0,400	0,621	0,614	0,506
Balkans	0,333	0,417	0,468	0,481	0,509	0,400	0,478	0,400	1	0,473	0,478	0,571	0,538	0,528	0,583
Donets B.	0,286	0,712	0,722	0,684	0,675	0,523	0,592	0,667	0,473	1	0,704	0,400	0,701	0,718	0,658
Moscow B.	0,350	0,781	0,794	0,743	0,676	0,607	0,613	0,593	0,478	0,704	1	0,549	0,647	0,696	0,625
Turkey	0,345	0,491	0,538	0,508	0,500	0,444	0,431	0,400	0,571	0,400	0,549	1	0,526	0,448	0,491
SW. Spain	0,261	0,714	0,725	0,737	0,753	0,548	0,706	0,621	0,538	0,701	0,647	0,526	1	0,853	0,743
N. Morocco	0,255	0,704	0,714	0,701	0,795	0,635	0,696	0,614	0,528	0,718	0,696	0,448	0,853	1	0,704
Sahara	0,238	0,606	0,615	0,667	0,685	0,552	0,594	0,506	0,583	0,658	0,625	0,491	0,743	0,704	1
SIMPSON	**Newfound.**	**Irelan**	**N. Britain**	**S. England**	**Belgium**	**South France**	**Germany**	**Poland**	**Balkans**	**Donets Basin**	**Moscow Basin**	**Turkey**	**SW. Spain**	**N. Morocco**	**Sahara**
Newfound.	1	1	0,889	0,889	0,778	0,778	0,778	0,778	0,444	0,778	0,778	0,556	0,667	0,667	0,556
Ireland	1	1	0,969	0,970	0,758	0,760	0,742	0,758	0,667	0,788	0,806	0,650	0,758	0,758	0,606
N. Britain	0,889	0,969	1	1	0,781	0,720	0,742	0,750	0,733	0,813	0,806	0,700	0,781	0,781	0,625
S. England	0,889	0,970	1	1	0,692	0,760	0,806	0,744	0,867	0,692	0,839	0,750	0,757	0,711	0,727
Belgium	0,778	0,758	0,781	0,692	1	0,920	0,742	0,700	0,933	0,675	0,774	0,750	0,784	0,816	0,758
S. France	0,778	0,760	0,720	0,760	0,920	1	0,640	0,720	0,533	0,680	0,680	0,500	0,680	0,800	0,640
Germany	0,778	0,742	0,742	0,806	0,742	0,640	1	0,774	0,733	0,677	0,613	0,550	0,774	0,774	0,613
Poland	0,778	0,758	0,750	0,744	0,700	0,720	0,774	1	0,867	0,750	0,774	0,700	0,730	0,711	0,636
Balkans	0,444	0,667	0,733	0,867	0,933	0,533	0,733	0,867	1	0,867	0,733	0,667	0,933	0,933	0,933
Donets B.	0,778	0,788	0,813	0,692	0,675	0,680	0,677	0,750	0,867	1	0,806	0,600	0,730	0,737	0,727
Moscow B.	0,778	0,806	0,806	0,839	0,774	0,680	0,613	0,774	0,733	0,806	1	0,700	0,710	0,774	0,645
Turkey	0,556	0,650	0,700	0,750	0,750	0,500	0,550	0,700	0,667	0,600	0,700	1	0,750	0,650	0,650
SW. Spain	0,667	0,758	0,781	0,757	0,784	0,680	0,774	0,730	0,933	0,730	0,710	0,750	1	0,865	0,788
N. Morocco	0,667	0,758	0,781	0,711	0,816	0,800	0,774	0,711	0,933	0,737	0,774	0,650	0,865	1	0,758
Sahara	0,556	0,606	0,625	0,727	0,758	0,640	0,613	0,636	0,933	0,727	0,645	0,650	0,788	0,758	1

Table 4: Dice and Simpson similarity indices between the sub-provinces.

DICE	**Atlantic**	**West Peri-Gondwanan**	**Saharian**	**Mediterranean**	**Central European**	**Eastern European**
Atlantic	1	0,846	0,622	0,561	0,789	0,774
W. Peri-Gond.	0,846	1	0,700	0,583	0,712	0,792
Saharian	0,622	0,700	1	0,552	0,578	0,683
Mediterranean	0,561	0,583	0,552	1	0,512	0,514
Central Eu.	0,789	0,712	0,578	0,512	1	0,792
Eastern Eu.	0,774	0,792	0,683	0,514	0,792	1
SIMPSON	**Atlantic**	**West Peri-Gondwanan**	**Saharian**	**Mediterranean**	**Central European**	**Eastern European**
Atlantic	1	0,936	0,848	0,920	0,789	0,837
W. Peri-Gond.	0,936	1	0,848	0,840	0,787	0,809
Saharian	0,848	0,848	1	0,640	0,788	0,848
Mediterranean	0,920	0,840	0,640	1	0,840	0,760
Central Eu.	0,789	0,787	0,788	0,840	1	0,857
Eastern Eu.	0,837	0,809	0,848	0,760	0,857	1

Examining the similarity indices of the sub-provinces provides additional insights and clarifies the details surrounding low-support groupings. With Simpson index, most information is accurately reflected in the clusters, but the relationship of the Saharan Subprovince with the others is detailed in Table 4: it has the same similarity value with the Atlantic, West Peri-Gondwanan, and Eastern European sub-provinces, and it shares the least fauna with the Mediterranean Subprovince. Similarly, Dice index indicates greater similarity to the West Peri-Gondwanan and Eastern European subprovinces, with the Mediterranean being the least similar. The Mediterranean Subprovince is represented as the least related to the others in Dice index cluster. This might be an artifact of its lower number of genera. Although it has low similarity values with all other sub-provinces, it is more similar to the West Peri-Gondwanan and the Atlantic sub-provinces than to the others, which is consistent with the results obtained using Simpson index.

Moreover, all Simpson index values for the compared areas are above 0.5, and Dice index also shows high levels of similarity. The exceptions are the areas with a low number of identified genera (Newfoundland, the Balkans, and Türkiye) or, to a lesser extent, Poland, which stands out on the opposite end, with 50 different genera, 10 more than the next areas (Donets Basin and Belgium).

The comparison of the sub-provinces shows even stronger similarities between them. This indicates a high level of cosmopolitanism, with most genera being widely distributed. This could be an effect of the late Visean transgression, which facilitated the dispersal of coral larvae (planulae).

Some of the groupings proposed by the clusters do not align with the current geographical distribution of the areas. However, data from other fossil groups, such as foraminifers (Somerville et al., 2013; Davidov and Cózar, 2019), and knowledge of the Variscan orogeny details can explain these apparent inconsistencies. In some cases, the inconsistencies arise from differing levels of knowledge and preservation of the Visean outcrops. For example, Poland has been extensively studied in detail, while the Balkans have only been subject to limited and older studies. Additionally, while the Belgian-Boulonnais platforms and basins were directly related to the British platforms and basins, their rugose coral fauna is more similar to that of SW Spain and North Morocco. This discrepancy could be due to two factors: a low but clear degree of endemism in the British basins and good connectivity along the western coast of the Iberian-Armorican Massif (eastern border of the Rheic Ocean). The Iberian Massif underwent oroclinal bending in a late phase of the Variscan orogeny (Gutiérrez-Alonso et al., 2004, 2012; Murphy et al., 2016) and was later rotated during the Alpine orogeny (de Jong, 1993). Consequently, the SW Spain Carboniferous basins (Santos de Maimona, Guadiato), now oriented southwards, were oriented eastwards during the Visean. This orientation connected them directly with the Rheic Ocean, as well as with the Belgian and Boulonnais basins.

Other results are harder to explain. The Moscow and the Donets basins seem to share more similarities with the British basins than with Poland, Germany, or even with each other. This unexpected finding raises questions about the underlying factors influencing these relationships. It is worth noting that some discrepancies are inevitable due to the complexities and limitations inherent in palaeontological data. Despite this, most groupings in all clusters are logical, especially once the areas with a low number of genera are removed from the analysis. The consistent patterns observed among the majority of the areas highlight the validity of our methodology and comparisons. By focusing on regions with well-preserved and thoroughly studied fossil records, we can draw more reliable conclusions about the distribution of Visean coral faunas. This approach enhances the clarity of our results and underscores the importance of comprehensive sampling and detailed palaeontological research in reconstructing ancient biogeographic patterns.

Fig. 5 shows a reconstruction of the western Palaeotethys Ocean and the margins of Laurusia and Gondwana during the Visean, highlighting the areas and sub-provinces included in the study.

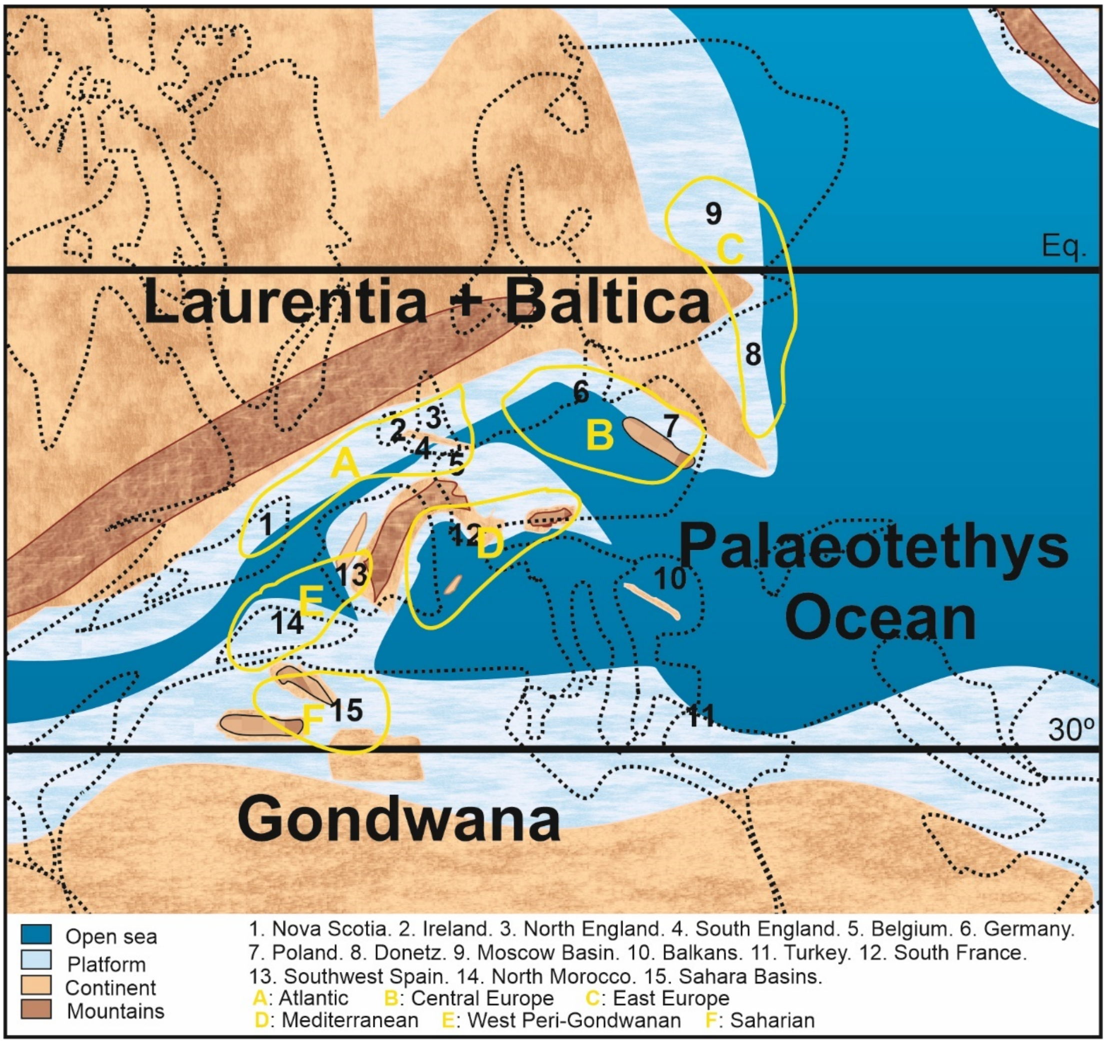

Figure 5: palaeogeographical reconstruction of the Palaeotethys Ocean and the Laurentia + Baltica and Gondwana margins during the late Visean. The six sub-provinces are circled in yellow, with the Balkans and Türkiye separated from them. Modified from Rodríguez et al. (2023).

4. Discussion

There are many obstacles to do a complete and reliable identification of the Visean coral faunas. The knowledge on them is very irregular: in some regions the outcrops of upper Visean rocks are abundant and well exposed (British Isles, Belgium, Morocco); but in other areas, they are scarce

(Germany, Italy, Balkans). As an example, three palaeogeographic domains are recognised for the Carboniferous in Germany, from north to south: the Rhenohercynian, the Saxothuringian and the Moldanubian, (Weyer, 2000). However, coral information in those domains is scarce and in some cases the specimens have been recorded in allochthonous blocks or in reworked facies, although at least the coral identifications are reliable. In other regions, as in the Balkans, there are few outcrops and the papers describing the corals (Kolosvary, 1951; Kostic-Podgorska 1957, 1958) are very old, with figures of low quality in many cases and, consequently, difficult to identify. We decided to consider the whole region as a single area in order to have enough data to compare. The same was done with other areas, such as the Sudetes, Upper Silesian Basin, Lublin Basin, and also its southeastwards prolongation in Ukraine, the Lviv-Volynsk Basin, all of which have been grouped under the name of Poland. In order to avoid unnecessary terminology, we will use generic geographical names as approximations. Thus, Scotland, northern England, NW England, Derbyshire and North Wales can all be included in North Britain, with South Wales, Bristol district and Mendips in Southern Britain.

Finally, Türkiye comprises several terranes that were clearly separated during the Mississippian; there are records of Mississippian corals in at least two of them (Denayer, 2011, 2012, 2014a, 2014b). The Istanbul-Zonguldak terrane was probably an isolated platform whose position in the Visean is not clear (Okay and Tüysuz, 1999), but could be related to the Moesian or Balkan terranes (Yanev, 2000, Okay et al. 2011). The Anatolide - Tauride block is related to the north border of Gondwana (Denayer, 2015).

The recorded assemblages in some areas contain few genera because either the area is geographically small (e.g. Nova Scotia) or the studies there are scarce (e.g. Balkans). In contrast, in other areas many detailed studies and a splitter tendency in the taxonomic studies increased the number of taxa (e.g. Poland), complicating the comparison.

An additional problem is posed by the environmental influence on the coral assemblages. Carboniferous corals are strong palaeoenvironmental indicators and have proven their use in palaeoecological studies (Aretz, 2010b; Kullmann, 1997; Somerville and Rodríguez, 2007). This introduces an additional difficulty when comparing the assemblages, especially for smaller areas, where only similar environments might be preserved in the geological record. However, we compare mostly larger areas and basins, which comprise different environments. This approach reduces the environmental signal, increasing the influence of the palaeogeographical distance on the results (Rodríguez-Castro and Rodríguez, 2022).

Somerville et al, (2013) proposed four sub-provinces for the western Palaeotethys in the late Mississippian. Rodríguez-Castro et al. (2023) extended the sub-provinces for that region to six. The *Atlantic Subprovince* (N. France, Belgium, United Kingdom and Ireland) shows consistent similarities between all their parts. Nova Scotia could possibly be included in that sub-province, but the low number of genera and species identified there introduce complications in the analyses. The *West peri-Gondwanan Subprovince* (SW Spain and Moroccan Meseta) shows high similarities with the *Atlantic Subprovice*, mainly with Belgium and North France, indicating an easy communication between them.

The *Mediterranean Subprovince* (South France, Pyrenean, Cantabrian Mountains, Betic cordillera, Rif, Balearic Islands) comprises numerous outcrops along the eastern and southern borders of the French Massif Central and the Iberian Massif. Most coral assemblages occur in flysch or olistostrome facies and are mainly Serpukovian in age (Semenoff-Tian-Chansky and Ovracht, 1965; Perret and Semenoff-Tian-Chansky, 1971; Rodríguez, 1984; Boll, 1985, Herbig, 1986; Aretz and Herbig, 2003). In this *sub-province,* coral assemblages from the late Visean are found only in South France (Montaigne Noir and Pyrenees) and the Baetic System (Marbella Formation) (Aretz 2002; Herbig and Mamet, 1985). Consequently, these are the only areas of this sub-province considered in our study. It is the least diverse of the sub-provinces included here, with only 25 genera, and shares similarities with the Atlantic and West Peri-Gondwanan sub-provinces.

The *Saharan Subprovince* (Béchar, Regann, Ahnet-Mouydir and Tindouf) is also on the lower end of the diversity spectrum, with 33 genera. It is most similar to the West Peri-Gondwanan

Suprovince, but it also shares close similarity indices with the Atlantic and the Eastern European sub-provinces.

The *Central Europe Subprovince* (Germany, Poland) shows an irregular record due to the effects of the Variscan Orogeny, which produced a structural mélange of domains and occurrences, mainly in allochthonous facies. Finally, the *Eastern European Subprovince* (Moscow Basin, Donetz Basin, Voronezh) also shows diverse assemblages during the upper Visean and Serpukhovian. It displays high similarities with the Central European Subprovince, although comparing the individual areas also indicates similarities to the Atlantic Subprovince.

5. Conclusion

Our analysis of the Visean coral faunas revealed significant insights into the biogeographic relationships among the studied regions. All analysis highlighted the distinct fauna of Türkiye and high similarities between the British areas, between N Morocco and SW Spain, and between the Atlantic and West Peri-Gondwanan sub-provinces. The findings enhance our understanding of Visean coral distributions, supporting a significant faunal connectivity across the Rheic Ocean and adjacent areas, associated with the Visean transgression.

While the study provides valuable insights, it is limited by the uneven quality of fossil records and varying numbers of identified genera across regions. These discrepancies highlight the need for caution in interpreting the results, particularly for regions with less comprehensive data. Future studies should aim to address the gaps in fossil records, especially in underrepresented regions such as the Balkans and Türkiye.

Continuous and detailed palaeontological research is crucial for refining our biogeographic models. By integrating multiple indices and diverse data sources, we can achieve more robust and comprehensive reconstructions of ancient biogeographic patterns, ultimately enhancing our understanding of Earth's historical biodiversity.

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6 RUGOSE CORAL BIOGEOGRAPHY OF THE WESTERN PALAEOTETHYS DURING THE MISSISSIPPIAN.

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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).

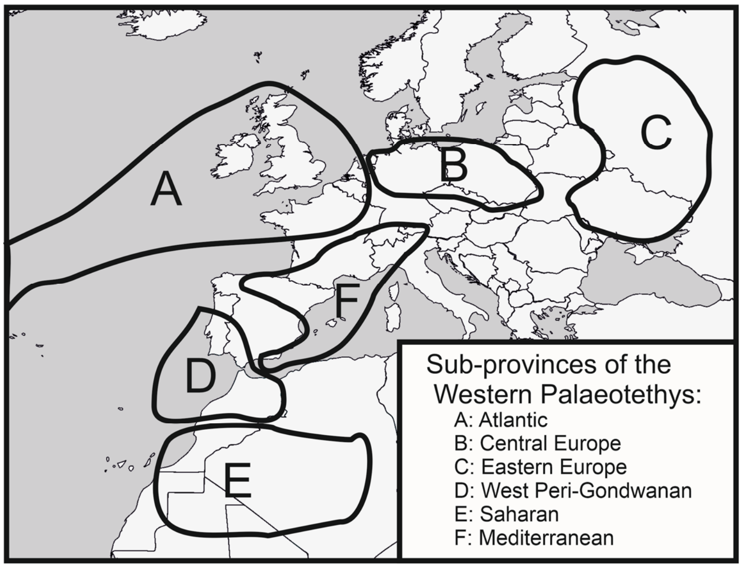

Figure 1. Distribution of the sub-provinces of the Western Palaeotethys in a recent map.

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.

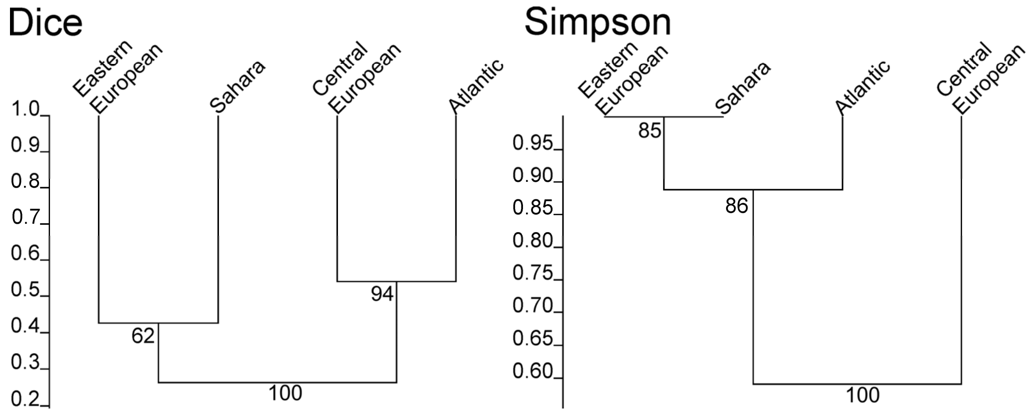

Figure 2. Hierarchical clusters of the sub-provinces during the Tournaisian.

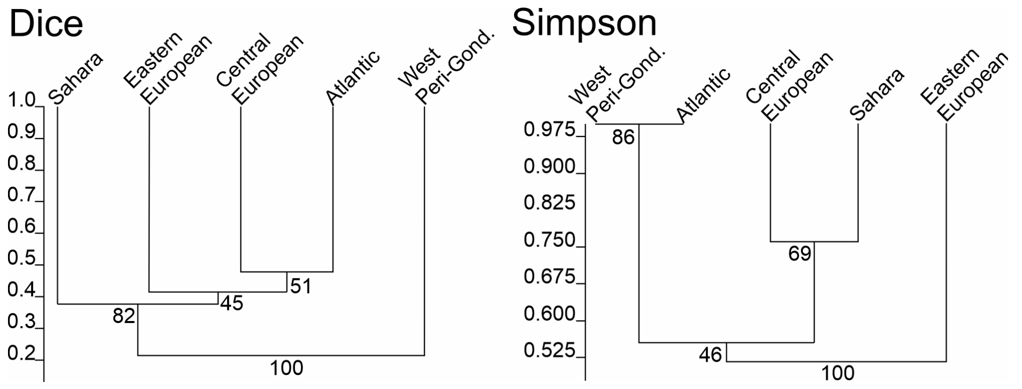

Figure 3. Hierarchical cluster of the sub-provinces during the Early Visean.

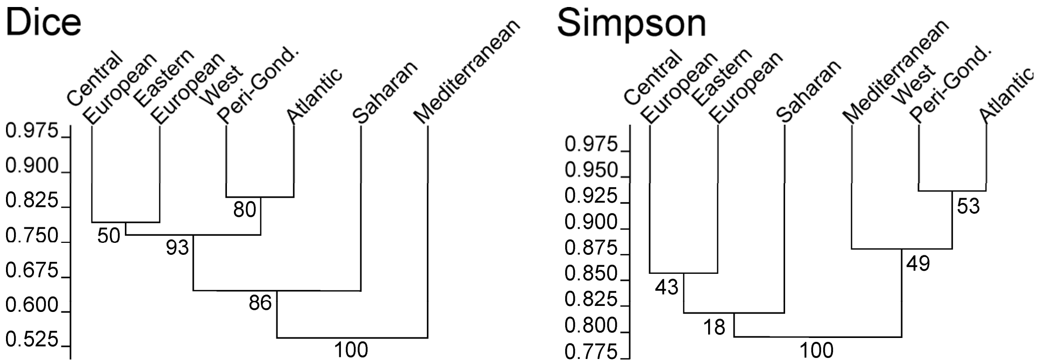

Figure 4. Hierarchical cluster of the sub-provinces during the Late Visean.

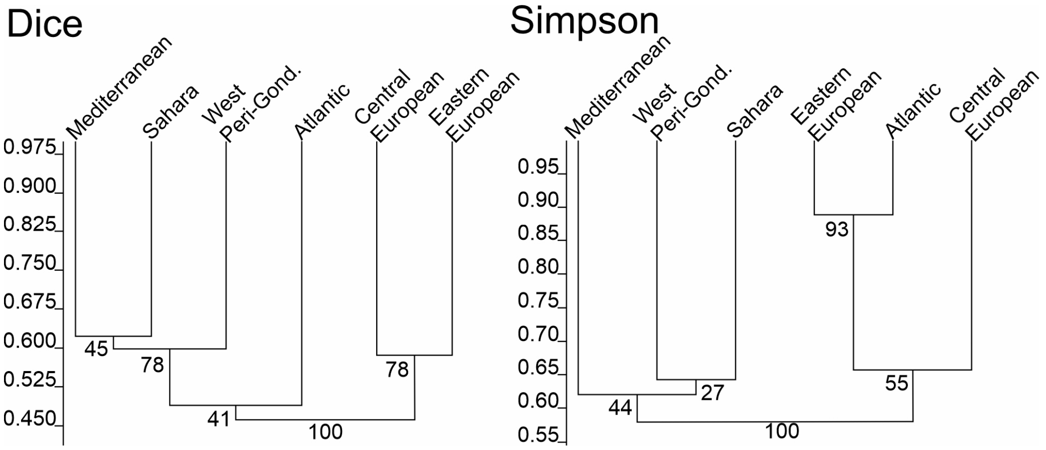

Figure 5. Hierarchical cluster of the sub-provinces during the Serpukhovian.

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).

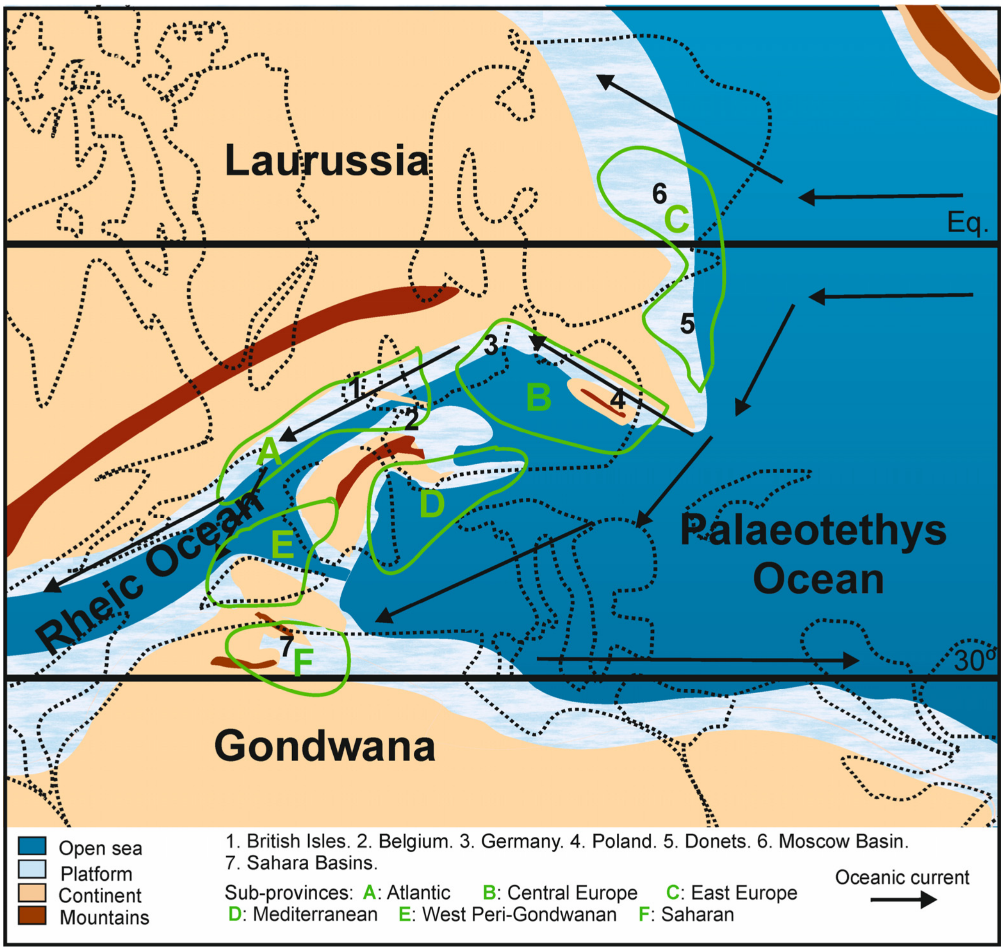

Figure 6. Palaeogeographic map of the Western Palaeotethys during the Tournaisian.

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].

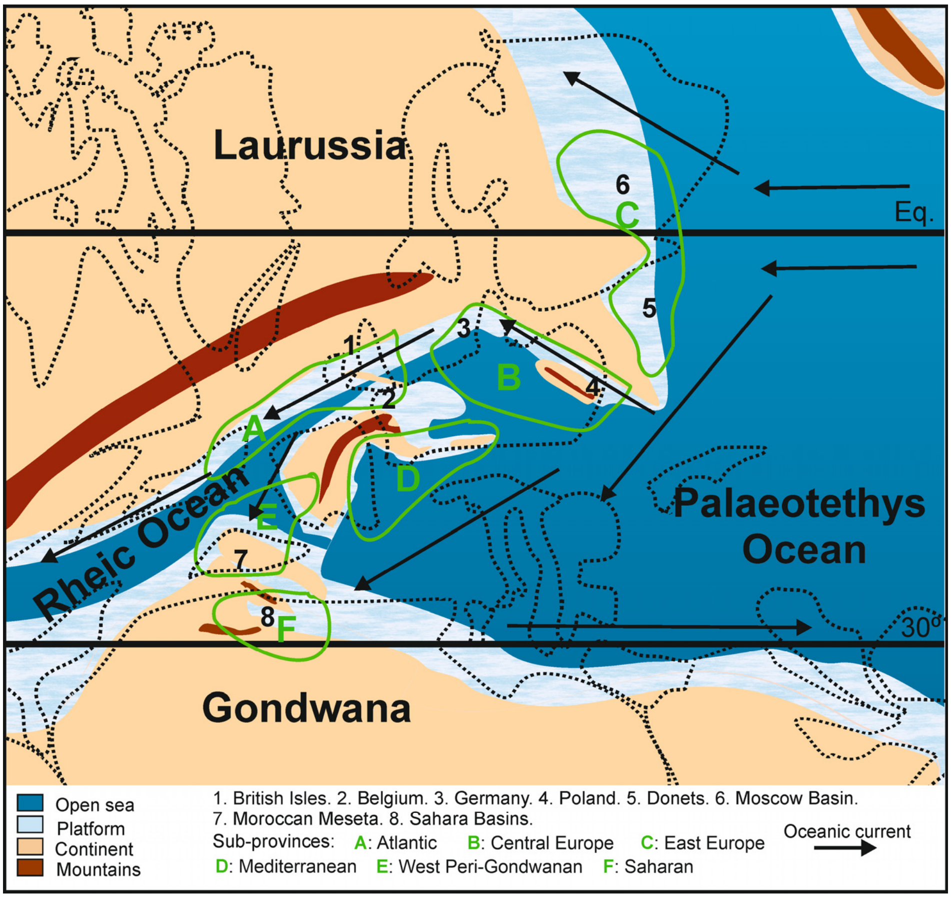

Figure 7. Palaeogeographic map of the Western Palaeotethys during the early Visean.

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).

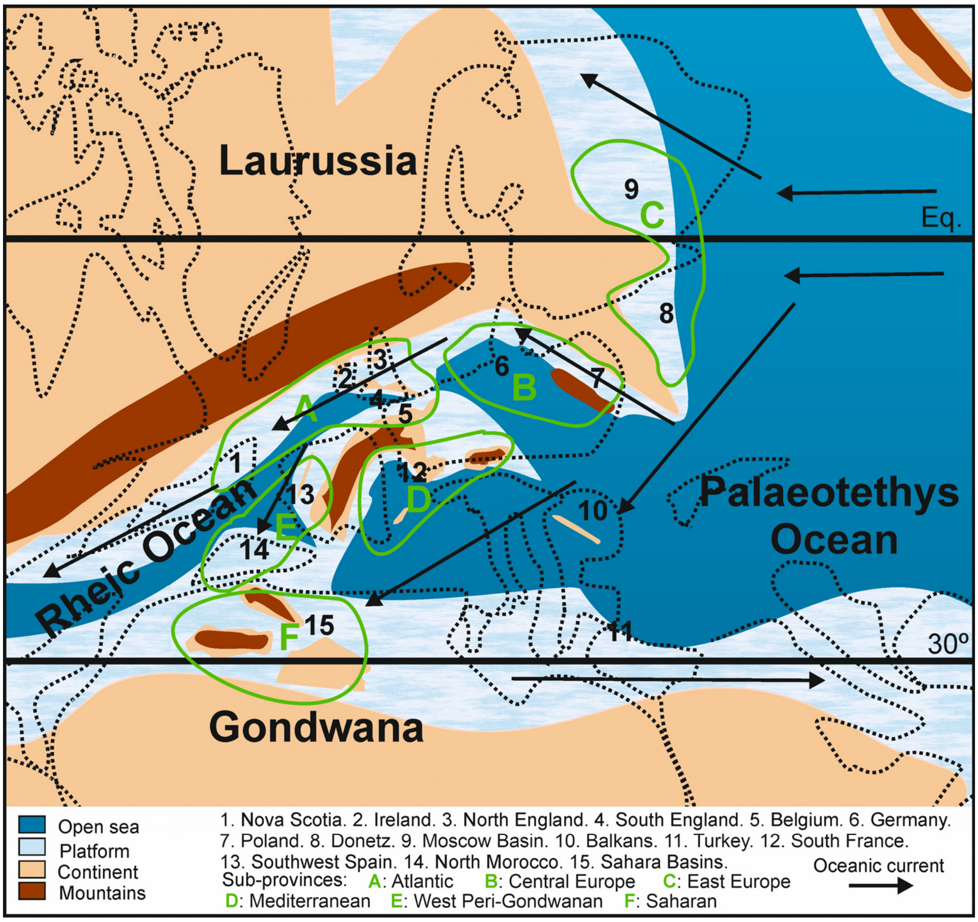

Figure 8. Palaeogeographic map of the Western Palaeotethys during the late Visean.

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].

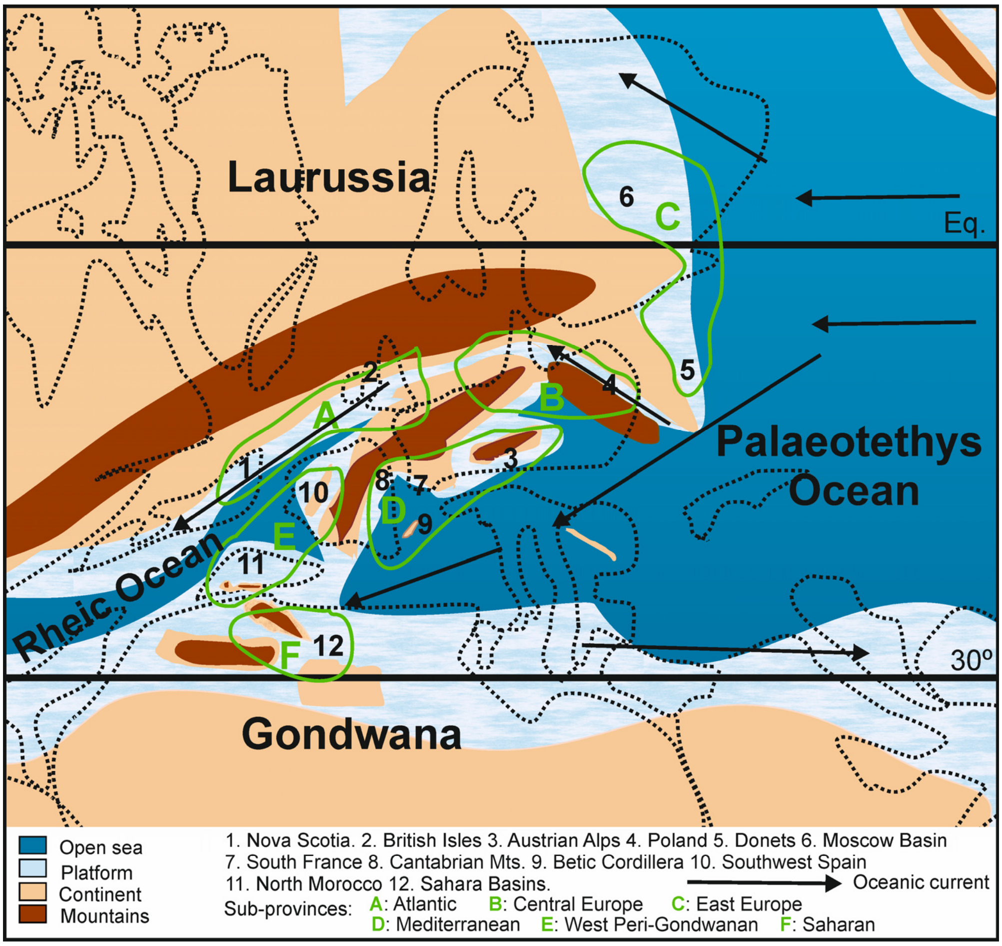

Figure 9. Palaeogeographic map of the Western Palaeotethys during the Serpukhovian.

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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7 SOME FACTS ON THE EVOLUTION OF RUGOSE CORALS DURING THE MISSISSIPPIAN.

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RESEARCH PAPER

Some facts on the evolution of rugose corals during the Mississippian

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Abstract

The Mississippian is an epoch that represents the transition from Devonian greenhouse conditions to Permo-Carboniferous icehouse modes. During that time, the marine faunas experienced a recovery after the late Devonian mass extinctions. This article presents the evolution of the rugose corals during the Mississippian in the western Palaeotethys province, as an example of the general evolution of rugose corals in that epoch. A database based on more than 700 papers and the revision of several collections along Europe has been built with the recorded genera, detailing the areas and times where and when they appear. Although we have a database with the vast majority of the species described or mentioned in the Mississippian of the western Palaeotethys, we have chosen to make the comparison at the genus level. This is based on the very large number of species in open nomenclature (sp., cf., aff.,?, etc.) and the many synonyms that are difficult to verify. With this database, analyses of the appearance/extinction of the genera and the distribution by types of habits have been carried on. These analyses have been compared with environmental data taken from the literature. In addition, evolutionary schemes have been built for some selected families (the Zaphrentidae, the Palaeosmilidae, the Lonsdaleiidae and the Lithostrotionidae) paying special attention to the main trends in the evolution of the rugose corals. In most cases, these evolutionary schemes are based in previous studies, plus the data provided in our research.

Keywords Rugosans · Carboniferous · Western palaeotethys · Climate · Diversity

Resumen

Durante el Misisípico se produce una transición de las condiciones cálidas del Devónico a las glaciaciones del Carbonífero y el Pérmico. Durante esa época, la fauna marina recuperó su diversidad tras las extinciones masivas del Devónico superior. Este artículo presenta la evolución de los corales rugosos durante el Misisípico en la provincia del Paleo-Tetis occidental, como un ejemplo de la evolución general de los corales rugosos durante la época. Se ha construido una base de datos detallando las áreas y los momentos en que aparecen los géneros registrados, para lo que se han recopilado más de 700 artículos y revisado varias colecciones a lo largo de Europa. Aunque se han recopilado también la gran mayoría de las especies descritas o mencionadas en el Misisípico del Paleo-Tetis occidental, la comparación se ha realizado a nivel de género. De este modo, se evitan el gran número de especies en nomenclatura abierta (sp., cf., aff., ?, etc.) y a los numerosos sinónimos difíciles de verificar. Con esta base de datos, se han realizado análisis sobre la aparición/extinción de los géneros y sus tipos de hábitos. Estos análisis se han comparado con los datos ambientales tomados de la literatura. Además, se han construido esquemas evolutivos para algunas familias seleccionadas (Zaphrentidae, Palaeosmilidae, Lonsdaleiidae y Lithostrotionidae), prestando especial atención a las principales tendencias en la evolución de los corales rugosos.

Palabras clave Rugosos · Carbonífero · Paleo-Tetis occidental · Clima · Diversidad

1 Introduction

The Mississippian was an epoch of active earth system changes, when the Variscan orogeny was highly active and when many variations in the climate produced the transition

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from Devonian greenhouse conditions to Permo-Carboniferous icehouse modes (Buggisch et al., 2008). Numerous episodes of glaciation, sea-level changes, variations in the seawater temperature and CO^2 concentration have been recorded (Fielding et al., 2008; Isbell et al., 2012). In addition, intense tectonic activity affected the distribution of seas and land masses (Franke, 2000). During that time, the marine faunas experienced a recovery after the late Devonian mass extinctions (Kellwasser and Hangenberg) (Becker et al., 2016). The rugose corals are not an exception and evolved to get a high diversity during the late Visean.

A strong faunal provincialism resulted from tectonic and climatic changes during that time. Three large super-provinces can be distinguished in the rugose coral faunas during the Mississippian: the North American super-province, the Palaeotethyan superprovince and the Australian superprovince (Fedorowski, 2023). The Palaeotethyan superprovince is divided in three provinces: the western Palaeotethys, comprising Europe, including Donets and Moscow Basins, North Africa and Nova Scotia; the Central Palaeotethys, comprising the Ural Mountains and Middle Asia, including Siberia, Omolon and Kazakhstan; and the eastern Palaeotethys, comprising China, south-east Asia and Japan. The western Palaeotethys has been divided in six sub-provinces (Fig. 1), the Atlantic Sub-province (AT), the West peri-Gondwanan Sub-province (WG), the Mediterranean Sub-province (M), the Saharan sub-province (S), the Central European sub-province (CE) and the Eastern European sub-province (EE) (Somerville et al., 2013; Rodríguez-Castro et al., 2023). The communication between the super-provinces in the Tournaisian and the early Visean was partially restricted (Fedorowski, 2023) because of low sea levels and the cold climate (Montañez & Poulsen, 2013). Global warming in the late Visean allowed easier migrations between different provinces and super-provinces and the differences between the rugose coral assemblages diminished (Fedorowski, 2023).

The purpose of this paper is analysing the evolution of the rugose corals during the Mississippian in the western Palaeotethys province, as an example of the general evolution of rugose corals in that epoch. Of course, the selected epoch and sub-province constitute an open system and influences from earlier times (for instance the Strunian, see Poty, 1999) and from other provinces (for instance the eastern Palaeotethys, see Yao et al., 2020) may produce alterations in the results. However, the western Palaeotethys is one of the richest and the most intensively studied area in the Mississippian, which can palliate these methodological problems. In addition, well preserved rugose corals show in their ontogenetic development a recapitulation of their phylogenetic origin and, consequently, they are quite suitable for analysis of their evolutionary origins.

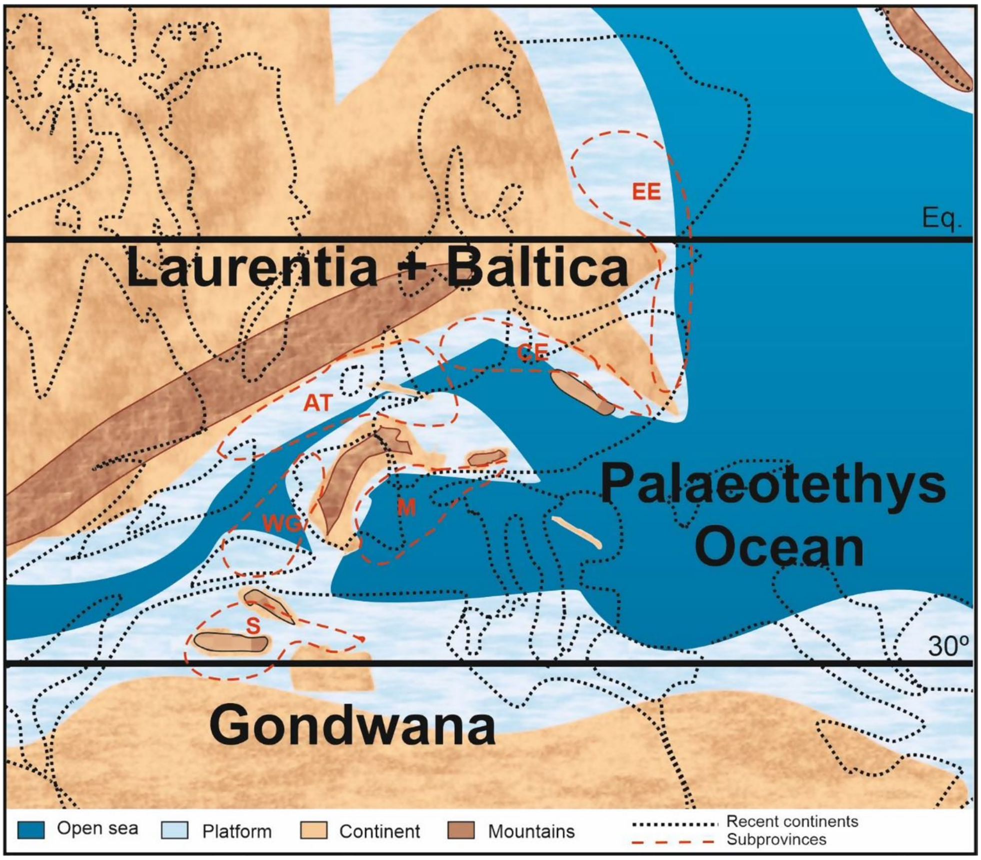


Fig. 1 Distribution of the sub-provinces in the western Palaeotethys. AT, Atlantic sub-province. WG, Western Peri-Gondwanan sub-province. S, Saharan sub-province. M, Mediterranean sub-province. CE, Central European sub-province. EE, East European sub-province. Based on Webb, 2002, Somerville et al., 2020 and Rodríguez-Castro et al., 2023

There is an extensive literature on the evolution of rugose corals, generally focused on specific groups; sometimes with precision at the species level and other times at the genus level. Some of the most relevant examples in the Mississippian are those of the evolution of the zaphrentid corals (Carruthers, 1910), those of the family Lithostrotionidae (Nelson, 1959; Poty, 1984), evolutionary aspects in the family Lonsdaleiidae (Poty & Hecker, 2003; Hecker, 2010; Rodríguez & Somerville, 2014; Rodríguez-Castro et al., 2023), the evolution and phylogenetic relationships of the aulate corals (Somerville et al., 2016) and the evolution of the subfamily Dorlodotinae (Nudds, 1993; Denayer & Poty, 2011). Outside the Mississippian or the western Palaeotethys, it is worthy to mention the examples of the analysis of the evolution of the Durhaminidae (Kossovaya, 1993), the Petalaxidae (Kossovaya, 1998), the cladistic analysis of the Antiphyllidae (Wang, 1994), the evolutionary analysis of the Amplexidae in China (Chen et al., 1997), and the analysis of the variation and evolution of the *Cyathaxonia* fauna in the eastern Palaeotethys (Wang et al., 2010).

From a more theoretical point of view, there are also many studies that have addressed the subject of the evolution of rugose corals. Thus, Sando (1989) relates environmental variations to the emergence of new genera. Fedorowski (1989) discusses some problems in the specific identification of rugose corals because of parallel, iterative, and convergent evolution phenomena. Webb (1993, 1994) explores the establishment of phylogenies in Palaeozoic corals and the use of cladistics in rugose corals and its methodological problems such as the existence of frequent homeomorphism, intraspecific variations, etc. Kossovaya (1995) discusses the morphoecotypic differentiation of the rugose corals in the late Palaeozoic. Scrutton (1997) describes the evolutionary tendency of colonial corals towards greater integration of individuals. Poty (2010), in his analysis of the limits to the diversification of rugose corals, evaluates the paedomorphic processes that are common in rugose corals. Rodríguez and Somerville (2010) discuss the evolution from solitary to fasciculate corals and the most suitable environments for that evolution.

2 Methodology

In order to carry out a detailed analysis of the evolution of the rugose corals in the Mississippian of the western Palaeotethys, we have first completed an exhaustive literature review of more than 700 articles and books dealing with rugose corals of that time and geographic area. In addition, several collections from various museums in Europe have been reviewed (the list is detailed in Rodríguez-Castro & Rodríguez, 2024) and our own collections. Although we have a database with the vast majority of the species described or mentioned in the Mississippian of the western Palaeotethys, we have chosen to make the comparison at the genus level. This is based on the very large number of species in open nomenclature (sp., cf., aff., ?, etc.) and the existence in many cases of synonyms that are very difficult to verify. Bambach (1990) has already pointed out that a compilation of a complete record of species occurrences is just not practical and that generic comparisons are more operative.

The database, built with the recorded genera, details the areas and times where and when they appear (Table 1). The areas used as a reference were the four sub-provinces defined by Somerville et al. (2013) plus the two additional ones proposed by Rodríguez-Castro et al. (2023) (Fig. 1, A, Atlantic; G, west Perigondwanan; M, Mediterranian; C, central European; E, eastern European and S, Saharan). The temporal divisions applied have been the rugose coral zones proposed by Poty (1985) and detailed by Poty et al. (2006). A number of record problems are observed in this database. There are genera that appear in a certain biozone, disappear during one or more biozones and then reappear later. These intervals of absences can be due to two principal causes:

i) The scarcity and incompleteness of the record or the lack of studies in some areas, in which case these genera should be considered as existing but not recorded. In Table 1, they are marked with hyphens.
ii) That they are cases of homeomorphism, in which case we can consider them as genera that should be named differently.

The casuistry is very varied, and in many cases it has not been possible to contrast the second possibility because of the lack of quality or total absence of adequate illustrations and/or descriptions. In many instances the records are only mentions without figures or descriptions, so the first possibility has been accepted as general.

With this database, graphs of the appearance/extinction of the genera (Figs. 2 and 3) and the distribution by types of habits have been created (Figs. 4 and 5). In both cases, two graphs have been built, taking into account in one case the verified records and in the other one the assumed records. These graphs have been compared with environmental data taken from Yao et al. (2020) to try to correlate the phases of major occurrences and extinctions to these environmental factors (Fig. 6).

The detailed evolution of many families is difficult to evaluate because of the already mentioned problems of homoemorfism, but some families are well established and it is possible to build suitable evolutionary charts. So, evolutionary schemes have been built for the Zaphrentidae, the

Table 1 Distribution of the rugose coral genera during the Mississippian in the western palaeotethys. The letters represent: (1) the occurrence in the sub-provinces of the western Palaeotethys (Rodríguez-Castro et al., 2023). A: Atlantic; C: Central European; E: Eastern European; G: western Peri-gondwanan; M: Mediterranean; S: Saharan. (2) the type of habit. SD: solitary dissepimented; SU: solitary undissepimented; F: Fasciculate; M: massive. The average duration of the zones is approximately 3 million years

GENERA	Habit	RC1	RC2	RC3	RC4α	RC4β	RC5	RC6	RC7	RC8	Pen.	Arn.
Actinocyathus d'Orbigny, 1852	M								CE	AEM	ASE	SE
Adamanophyllum Vassilyuk, 1959	SD											E
Allotropiophyllum Grabau, 1928	SU			A	-	-	A	A	A	E		
Amplexizaphrentis Matley & Vaughan, 1906	SU			C	-	-	A	A	ASE	AGSE	A	A
Amplexocarinia Soshkina In Soshkina et al., 1928	SU			C	A	-	-	-	A G S	G S	G	
Amplexus Sowerby, 1814	SU		A E	A	AS	ACE	AC	AC	AGC	A GC	G	
Amygdalophylloides Dobr. & Kabak., 1948	SD									G		
Amygdalophyllum Dun & Benson, 1920	SD				AC	ACE	A	AS	AS	GS	GS	
Antiphyllites Fedorowski, 2012a	SU										C	
Antiphyllum Schindewolf, 1952	SU									CE	C	
Arachnolasma Grabau, 1922	SD						C	A C	AGSC	GSCE	GSE	GSE
Aulina Smith, 1917	M								S	E	SE	E
Auloclisia Lewis, 1927	SD					S	A C	-	GC	G	E G	
Aulokoninckophyllum Sando, 1976	SDF			A E	A	A	A E	A S E	AGS E	GSM E	GS E	G
Aulophyllum Milne-Edwards & Haime, 1850	SD								AGSCE	AGSCE	AGS C	AG
Axoclisia Semenoff-Tian-Chansky, 1974	SD					A	E	SE	AG	G	G	S
Axophyllum Milne-Edwards & Haime, 1850	SD				A	A E	AC	ASC E	AGSC E	AGSM	GSM	GSEM
Barytichisma Moore & Jeffords, 1945	SU										C	
Bathybalva Weyer, 1981	SU	C										
Biphyllum Fedorowski, 1971	SD									C		
Bothrophyllum Trautschold, 1879	SD								A	S	SC	S
Bifossularia Dobrol. In Dobrolyubova et al. 1966	SD	C	C	AC	A C	A SC	A	A	ACEG			
Bradyphyllum Grabau, 1928	SU					C	-	-	A	GC		
Calmiussiphyllum Vassilyuk, 1959	SD			AE								
Calophyllum Dana, 1846	SU					C	-	-	C			
Campophyllum Milne-Edwards & Haime, 1850	SD	ACE	-	-	-	-	-	-	C			
Caninia Michelin in Gervais, 1840	SD	ACE	AC	AC	AC	AC	A C	A	AGSCE	AGSC	AC	E
Caninophyllum Lewis, 1929	SD		E	ACE	A	A E	A E	A	AG	C	SE	
Caninostrotion Easton, 1943	SD											M
Carruthersella Garwood, 1913	SD				C	A C	AC	C	-	S	S	
Ceriodotia Denayer, 2011	F					E	E					
Claviphyllum Hudson, 1942	SU	C	C	C	C	-	-	-	G	GC	E	
Clinophyllum Grove, 1935	SU						C					
Clisiophyllum Dana, 1846	SD	C	-	-	A C	A C	ACE	AC	AGSC	AGSCEM	AGS	G
Commutia Fedorowski, 1973	SU	C										
Conilophyllum Poty & Boland, 1994	SD	ACE										
Corphalia Poty, 1975	SD				E		A					
Corwenia Smith & Ryder, 1926	F								GE	AGE	GE	GE
Cravenia Hudson, 1928	SU			A	A	AGS	A	-	A			

Table 1 (continued)

GENERA	Habit	RC1	RC2	RC3	RC4α	RC4β	RC5	RC6	RC7	RC8	Pen.	Arn.
Cryptophyllum Carruthers, 1919	SU						A	-	-	GE		
Cyathaxonia Michelin, 1847	SU	AC	ACE	ACE	ACE	ACE	ACE	ACE	AGCE	AGCEM	AGE	GE
Cyathoclisia Dingwall, 1926	SD		E	AE	ACE	ASC						
Delepinella Vuillemin, 1985	SD			A	A	A						
Diaschophyllum Semenoff-Tian-Chansky, 1974	SD										S	
Dibunophyllum Thomson & Nicholson, 1876	SD						A S	A SC	AGSCE	AGSCEM	AGSEM	GSE
Diphyphyllum Lonsdale, 1845	F							A	AGCE	AGSCM	AGSM	GSEM
Dorlodotia Salee, 1920	F				E	AE	AC	E	-	E	M	
Drewerelasma Weyer, 1973	SU	C	-	-	C	C						
Effigies Fedorowski, 2012a	SU										C	
Enniskillenia Kabakovich in Soshkina et al., 1962	SU									E		
Eostrotion Vaughan, 1915	SD	C	AC	AC	C	-	-	-	-	--	E	
Espielia Rodríguez & Hernando, 2005	F								S	G		
Fasciculophyllum Thomson, 1883	SU		A	A	A	A	A	-	-	-	C	
Gangamophyllum Gorsky, 1938	SD								AGE	GSEM	GSEM	GSEM
Guadiatia Gómez-Herguedas & Rodríguez, 2005	F									A	G	
Haplolasma Semenoff-Tian-Chansky, 1974	SD					AE	A E	AS E	AGS	AGS	AGS	G
Hapsiphyllum Simpson, 1900	SU			A	-	C	-	-	-	C	E	
Hebukophyllum Liao & Cai, 1987	SD	C										
Heterostrotion Poty & Xu, 1997	F			A								
Hettonia Hudson & Anderson, 1928	SD					C						
Howthia Somerville & Rodríguez, 2010	F				A							
Kabakovitchiella Weyer, 1972	SU	C										
Kazachiphyllum Bykova, 1966	SD										E	
Keyserlingophyllum Stukenberg, 1895	SD		C	A E C	C E	C						
Kizilia Degtjarev, 1965	SD	A	-	-	-	-	-	A	AG	GSM	GS	
Koninckonaotum Fedorowski, 1971	SD									C		
Koninckophyllum Thomson & Nicholson, 1876	SD				A	AS	AC	AS C	AGSC	AGSCEM	AGSCE	GSE
Koninckophyllum (colonial)	F								A	A		
Laccophyllum Simpson, 1900	SU	C	-	-	-	C						
Leonardophyllum Moore & Jeffords, 1941	SU											M
Lithostrotion Fleming, 1828	M						AS	ASC	AGSCE	AGSCEM	AGSEM	GSEM
Lonsdaleia McCoy, 1849	F								E	ASEM	ASE	EM
Lophophyllidium Grabau, 1928	SU					A	-	S	-	C	C	
Lophophyllum Milne-Edwards & Haime, 1850	SD	C	A C	A	C	-	-	-	C			
Lublinophyllum Khoa, 1977	F								C	A C	C	
Lytvophyllum Dobrolyubova In Soshkina et al., 1941	SD											E
Melanophyllidium Kropacheva, 1966	F									M	M	
Merlewoodia Pickett, 1966	SD				A E	AS	-	-	A	A		
Mirka Fedorowski, 1974	SD									C	C	

Table 1 (continued)

GENERA	Habit	RC1	RC2	RC3	RC4α	RC4β	RC5	RC6	RC7	RC8	Pen.	Arn.
Morenaphyllum Rodríguez & Somerville, 2014	SD									G	G	
Nemistium Smith, 1928	F								E	AM	SM	
Neoclisiophyllum Wu in Yü et al., 1963	SD					A						
Neokoninckophyllum Fomichev, 1939	SD									C	CE	
Nervophyllum Vassilyuk, 1959	SD								C	C	C	E
Nina Fedorowski, 2017	SD									E	E	E
Nominoephyllum Vuillemin, 1990	SU					A						
Orionastraea Smith, 1917	M								E	ACE		
Ostravaia Fedorowski, 2010	SU										C	
Palaeosmilia Milne-Edwards & Haime, 1848	SD				A	ASC	ASC	ASCE	AGSCE	AGSCEM	AGSCEM	GSEM
Palastraea McCoy, 1851	M								GE	AGCEM	AGS	GS
Pareynia Semenoff-Tian-Chansky, 1974	SD							S	AS	SM	GS	
Pentaphyllum de Koninck, 1872	SU	C	-	A	C	ASC	C	-	AC	C		
Proheterelasma Cotton, 1973	SU			A E	A E	A	A	A				
Protolonsdaleia Lissitzin, 1925						E	E					
Pseudoaulina Minato & Rowett, 1967	M										S	AS
Pseudoclaviphyllum Vassilyuk, 1964	SU									E		
Pseudouralinia Yü, 1931	SD					C						
Pseudozaphrentoides’ Stukenberg, 1904	SD								AGSC	AGSCEM	AGSCEM	
Richrathina Weyer, 1987	SU					C						
Rhopalolasma Hudson, 1936	SU				A C							
Rotiphyllum Hudson, 1942	SU	C	C	A C	AC	AC	AC	AC	AGC	GCM	GC	
Rozkowskia Fedorowski, 1970	SD							C	-	C		
Rylstonia Hudson & Platt, 1927	SD	C	-	A	A SC	ASC	AC	A	AG	A GSE	E	
Sabolia Vuillemin, 1990	SD						A	A				
Saharaphrentis Aretz, 2011	SU									S		
Saleelasma Weyer, 1970	SU	A	A	A	C							
Schoenophyllum Simpson, 1900	F									E	E	
Semenoffia Poty, 1981	SD			A	-	-	-	-	AG	-	G	
Serraphyllum Poty, in Poty & Hecker, 2003	FM										M	
Silesamplus Fedorowski, 2009	SU										C	
Siphonodendron McCoy, 1849	F					SC	ACE	ASCE	AGSCE	AGSCEM	AGSEM	GSE
Siphonophyllia Scouler in McCoy, 1844	SD	ACE	ACE	AE	AE	AGSCE	ASC	ASC	AGS	AGSM	GCS	
Slimoniphyllum Kato & Mitchell, 1961	SD									A C	A	
Sochkineophyllum Grabau, 1928	SU	C	-	-	-	-	-	-	G	G		
Solemnophyllum Vuillemin, 1990	SD					A	A					
Solenodendron Sando, 1976	F			A	A S	A	AC	-	AGCE	AGM	GS	G
Spirophyllum Fedorowski, 1970	SD					AC	A	-	C	CE	GC	
Stelechophyllum Tolmachev, 1933	M									E	E	
Sychnoelasma Lang et al., 1940	SU	C	ACE	ACE	ACE	AGSCE	AC	C				

Table 1 (continued)

GENERA	Habit	RC1	RC2	RC3	RC4α	RC4β	RC5	RC6	RC7	RC8	Pen.	Arn.
Syringaxon Lindström, 1882	SU	C	-	-	-	A	-	-	-	M		
Tachylasma Grabau, 1922	SU									C	E	
Thysanophyllum Nicholson & Thomson, 1876	F									AM	A	
Thuriantha Weyer, 1981	SU	C										
Tizraia Said & Rodríguez, 2007	F								G	GS	GS	
Turbinatocaninia Dobrolyubova, 1970	SD								C	E	ACE	E
Ufimia Stukenberg, 1895	SU	C	-	-	C	C	C	-	GC	GC	GC M	
Uralinia Stukenberg, 1895	SD	A	AE	AE	CE	C						
Variaxon Fedorowski, 2010	SU										C	
Vassiljukia Denayer & Ogar, 2016	M						E					
Viseaulina Poty, 1981	SD								A			
Vojnimitor Fedorowski & Kullmann, 2013	SU										M	
Vojnovskytes Fedorowski, 2009	SU									M	M	
Zakowia Fedorowski, 1971	SD									C	C	
Zaphrentites Hudson, 1941	SU	AC	ACE	ACE	ACE	ASC	C	-	GC	AGSC	AGSCE	G
Zaphrentoides Stukenberg, 1895	SU					C	-	-	GS			
Zaphriphyllum Sutherland, 1954	SD				S	S						
Zaphrufimia Fedorowski, 2012b	SU									AGSC	GC	E
Total genera		28	17	30	36	50	39	32	61	81	77	34
New genera		17	5	13	12	19	8	5	35	27	11	4
Extinct genera		4	16	0	6	5	19	12	6	7	15	47
Total assumed		28	27	39	46	60	55	54	71	82	76	34
New genera assumed		17	5	12	9	17	7	2	20	17	11	4
Extinct genera assumed			6	0	2	3	12	3	3	6	17	46
		RC1	RC2	RC3	RC4α	RC4β	RC5	RC6	RC7	RC8	Pen.	Arn.

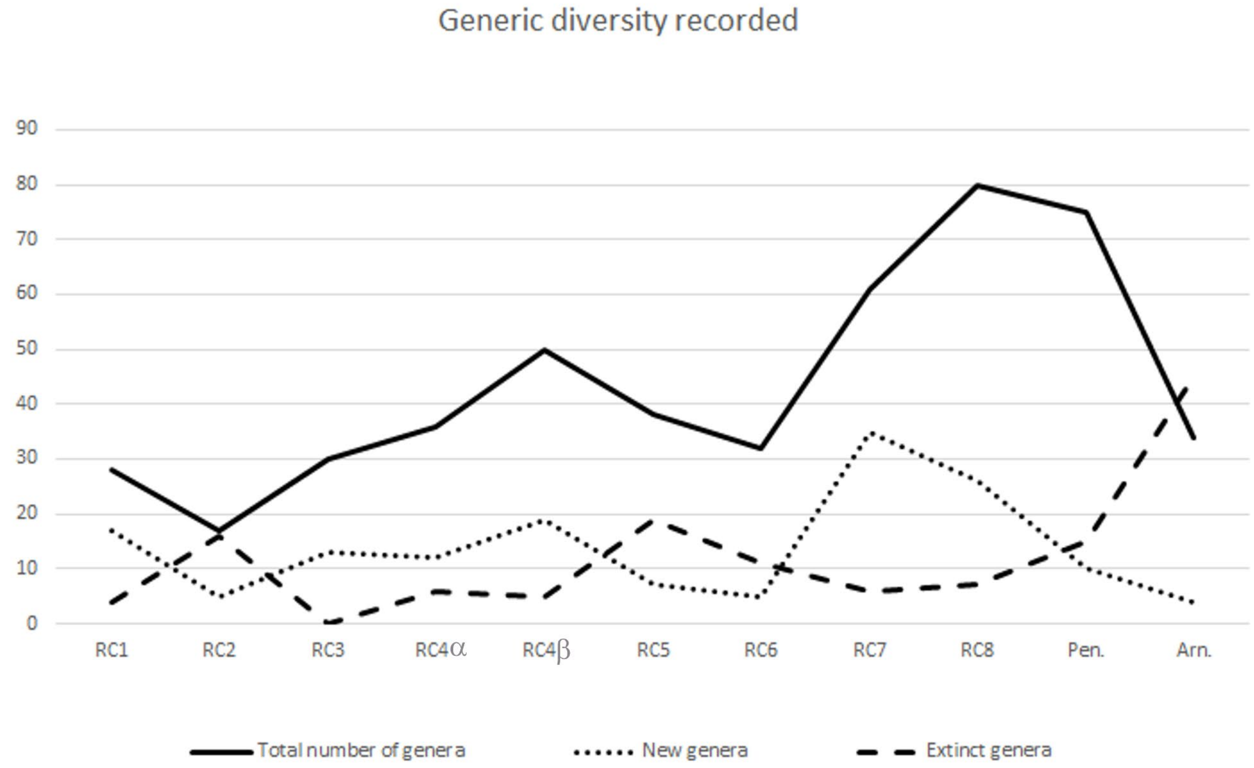
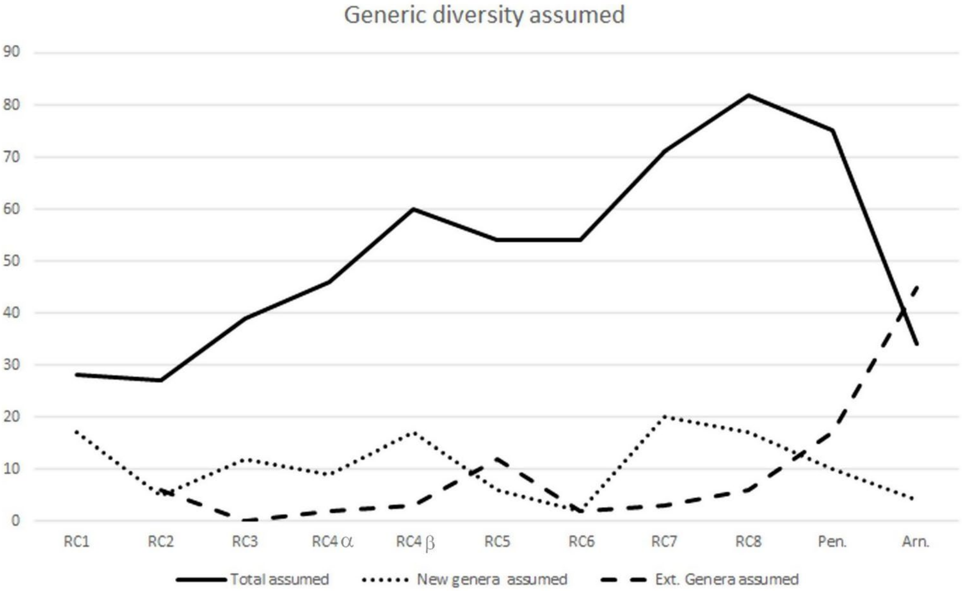


Fig. 2 Variation of the generic diversity registered along the Mississippian. Data based on Table 1

Fig. 3 Variation of the generic diversity assumed along the Mississippian. Data based on Table 1. Comparing to the Fig. 2, note the lower rate of appearances and extinctions when the possible gaps in the record are covered



Palaeosmilidae, the Lonsdaleiidae and the Lithostrotionidae. Some of these evolutive schemes are based in previous studies already mentioned, plus the data provided in our research. Other families contain too many genera (Aulophyllidae), few genera (Uralinidae, Bothrophyllidae, Kizilidae), their representatives in the Mississippian from the western Palaeotethys are scarce (Petalaxidae, Laccophyllidae, Geyerophyllidae) or they show so many phenomena of homeomorphism that any phylogenetic scheme would be uncertain (Plerophyllidae, Antiphyllidae).

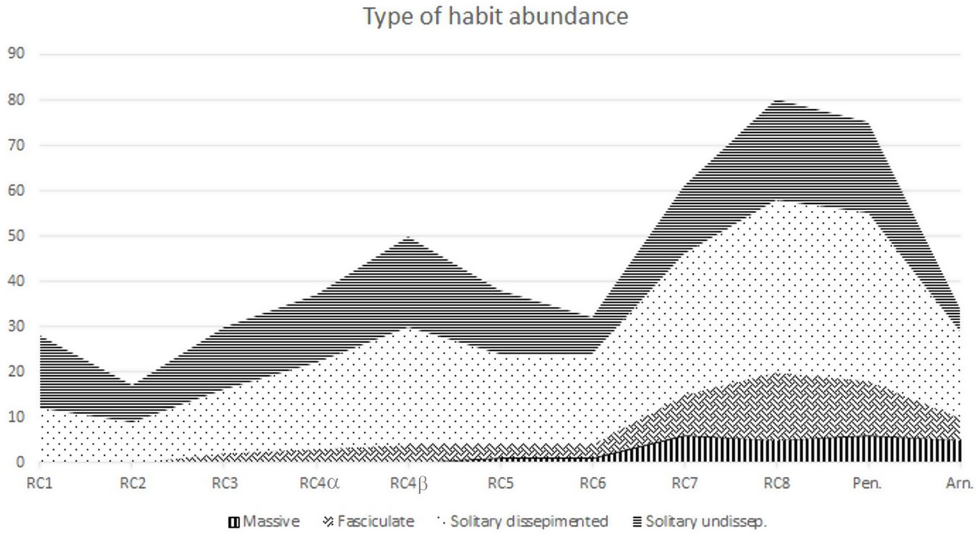


Fig. 4 Variation of the main habit types registered along the Mississippian. Data based on Table 1

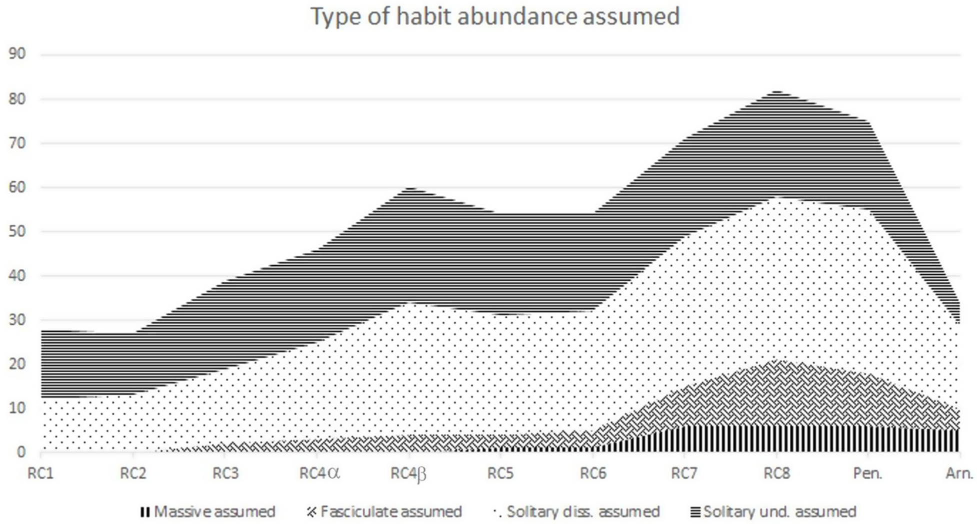


Fig. 5 Variation of the main habit types assumed along the Mississippian. Data based on Table 1. Comparing to the Fig. 4, note the higher generic diversity of solitary corals when the possible gaps in the record are covered

3 Results

Table 1 shows the distribution of the rugose coral genera along the Mississippian indicating the records in the different coral zones (Poty, 1985) and in the different sub-provinces (Rodríguez-Castro et al., 2023). The gaps in the occurrences of some genera between different biozones show the incompleteness of the record and are marked with stripes. The habits of the corals have also been indicated. That table readily shows the increase in records from the Tournaisian to the late Visean, and the decrease in the diversity and appearances of rugosans in the Serpukhovian. The predominance of the letters A, G and C indicates the sub-provinces where studies of rugose corals have been most intensive (Atlantic, west Peri-Gondwanan and central European). The absence of the letters S, G and M (Saharan, west-Peri-Gondwanan and Mediterranean) in the Tournaisian indicates lack or scarcity of marine carbonate rocks in those sub-provinces for that age.

With this database we built the graphs showing the lines of appearances/extinctions (Figs. 2 and 3) and the graphs of abundance of habits along the Mississippian (Figs. 4 and 5). The interpretation of these graphs will be explained in the discussion chapter.

There are several trends in the evolution of the rugose corals that have been used to create new genera. Some of the most important are:

- Development of dissepiments. The oldest rugose corals and those that live in less favourable environments (deep waters, influence of terrigenous sediments) lack dissepiments. But when those corals live in shallow and/or in clean waters, they tend to increase their size and develop dissepiments. One of the best examples is found in the family Zaphrentidae with the appearance of the

Fig. 6 Comparison of the appearance and extinction rates with the climate changes during the Mississippian. For interpretation of lines and plots see Figs. 2, 3, 4 and 5. Climate curves taken from Ogg et al., 2016 and Yao et al., 2020. The band with the blue colour represents the late Visean transgression

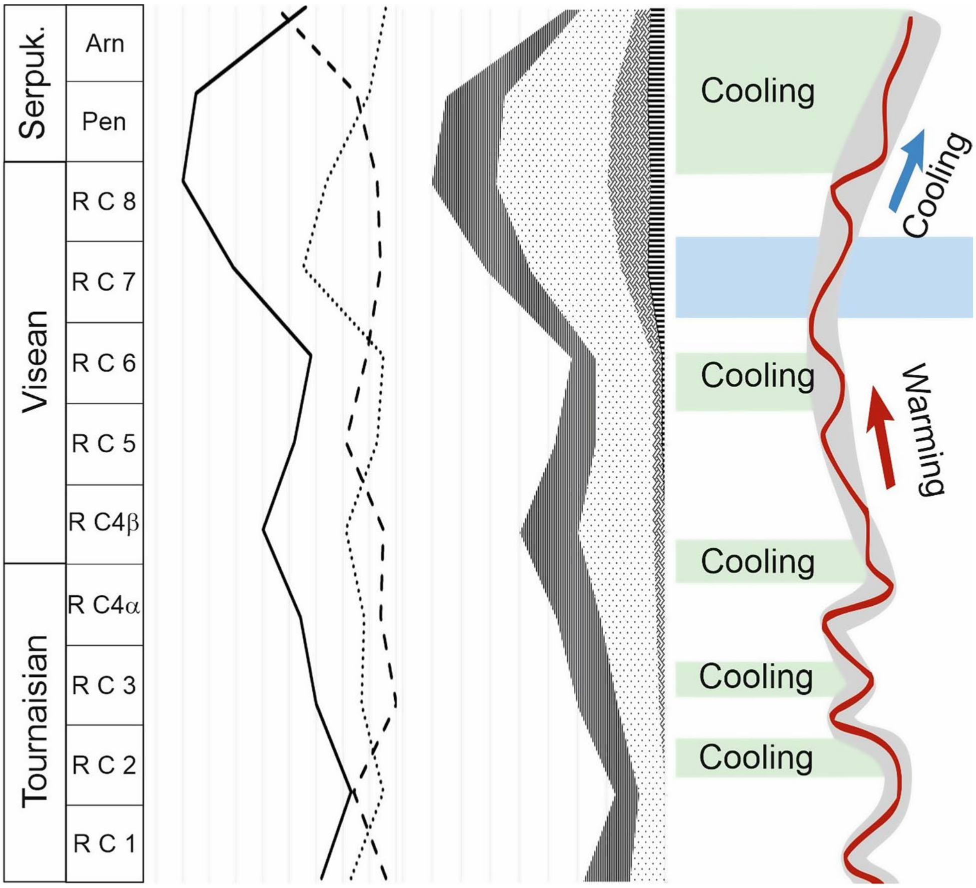
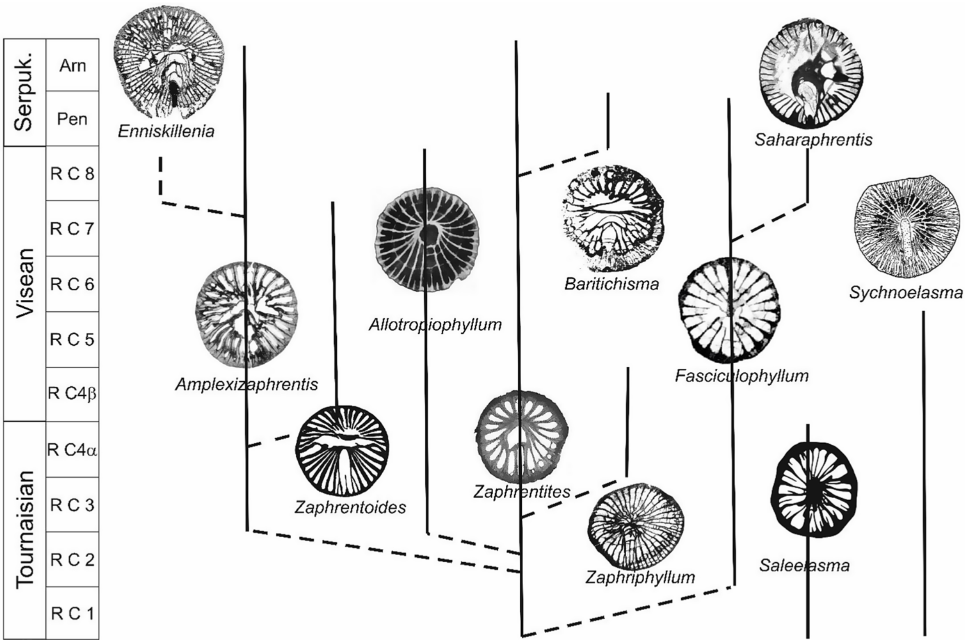


Fig. 7 Possible evolution of the Zaphrentidae during the Mississippian. Data based on Weyer (1970), Hill (1981) and own information. Drawings of the genera are not to scale



genus *Zaphriphyllum* Sutherland, 1954 (Fig. 7). In fact, many dissepimented corals show a zaphrentid structure in their early ontogenetic stadiums, implying that they evolved from zaphrentid corals. The presence and the type of dissepiments are used in taxonomy to differentiate genera or families.

- Development of amplexoid structures. That is shortening of the septa, which are long only on the upper surfaces of the tabulae. The Zaphrentidae also show this trend, developing adult stages with the septa withdrawn from the axis in some advanced forms of the group. The genus *Caninia* Michelin in Gervais, 1840 and the family Cyathopsidae descend from the zaphrentidae by the development of amplexoid stages and dissepiments (Carruthers, 1908; Semenoff-Tian-Chansky, 1974). Diverse genera showing amplexoid structures have been grouped in the families Amplexidae and Laccophyllidae, and the amplexoid structures are frequently combined with aulos. However, the absence in some cases of studies on the ontogeny of these corals makes difficult the analysis of the phylogenetic relationships between these genera.

- Development of aulos. This term was proposed by Smith and Yü (1943) for a cylindrical tube composed of the union of the axial ends of the major septa and the axial tabulae. Its presence was considered as a generic criterion, and many of the genera having aulos were included in the genus *Aulina* Smith, 1917. However, Sando (1976) demonstrated the different evolutionary origin of most species included in that genus. So, this structure occurs in different phylogenetic lineages, such as the Lithostrotionidae, the Palaeosmilidae, the Aulophyllidae, etc. (Fig. 8, Somerville et al., 2016).
- Development of carinae. The carinae are lateral structures to the septa that could be used as their reinforcement. There are several types of carinae (see Fedorowski, 1986). In the Mississipian, an interesting case is that of *Saleelasma* Weyer, 1970, who interpreted it as descendent of *Fasciculophyllum* Thomson, 1883 and basically identical to it, but showing carinae (Fig. 7).
- Development of lonsdaleoid dissepiments. They are large vesicular dissepiments that interrupt the trace of the septa in the peripheral part of the corallites. They occur in many groups of corals and they have been used to differentiate species, genera or families. They are a distinctive feature of the family Lonsdaleiidae (Fig. 9).
- Protosepta that grew longer and sometimes thicker than the metasepta. It is very variable because the longer septa may differ. They may be the counter septum, the counter-lateral septa, the alar septa and, less frequently, the cardinal septum. The presence of longer septa has been the basis for the identification of families, like the Polycoeliidae or the Plerophyllidae, and genera like *Enniskillenia* Kabakovich In Soshkina et al., 1962 (Fig. 7).
- Development of colonialism. The development of new genera of fasciculate corals may have two different

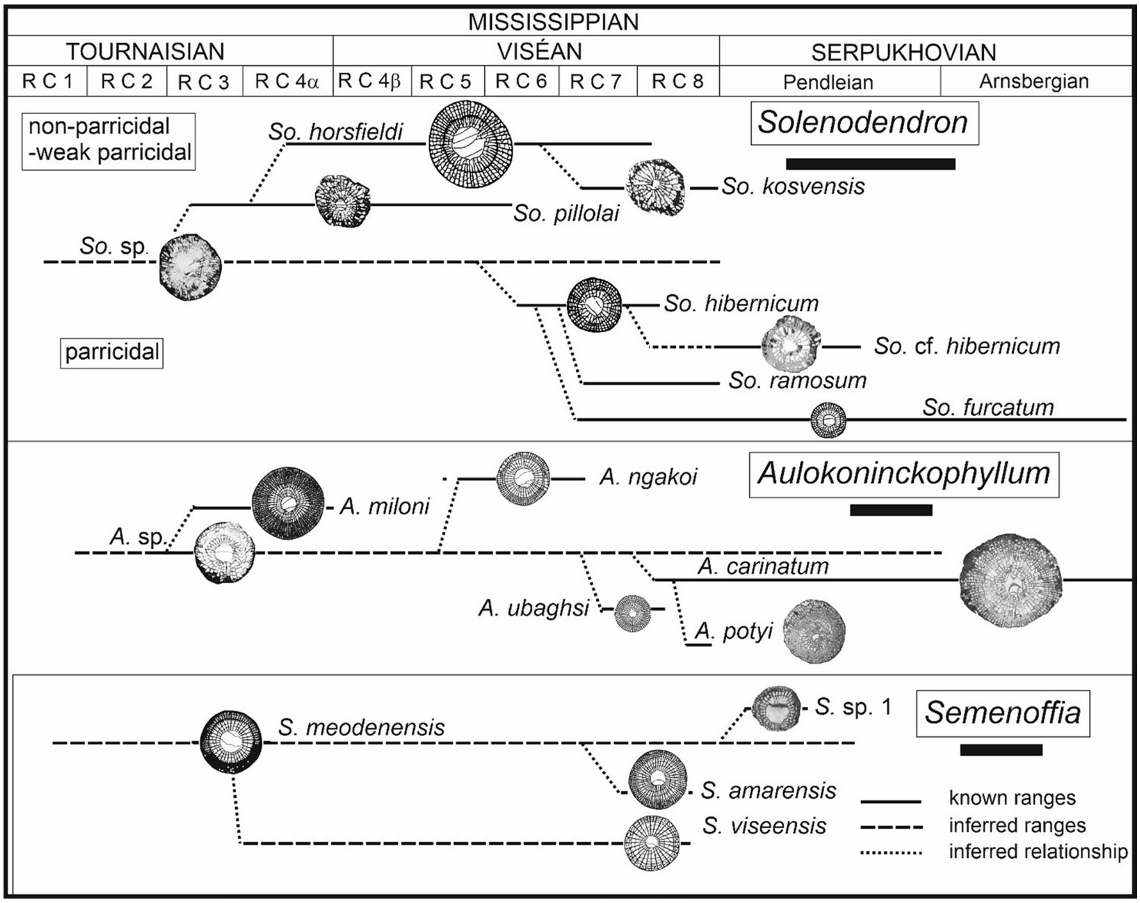


Fig. 8 Development of aulos in different evolutionary lines. (modified from Somerville et al., 2016)

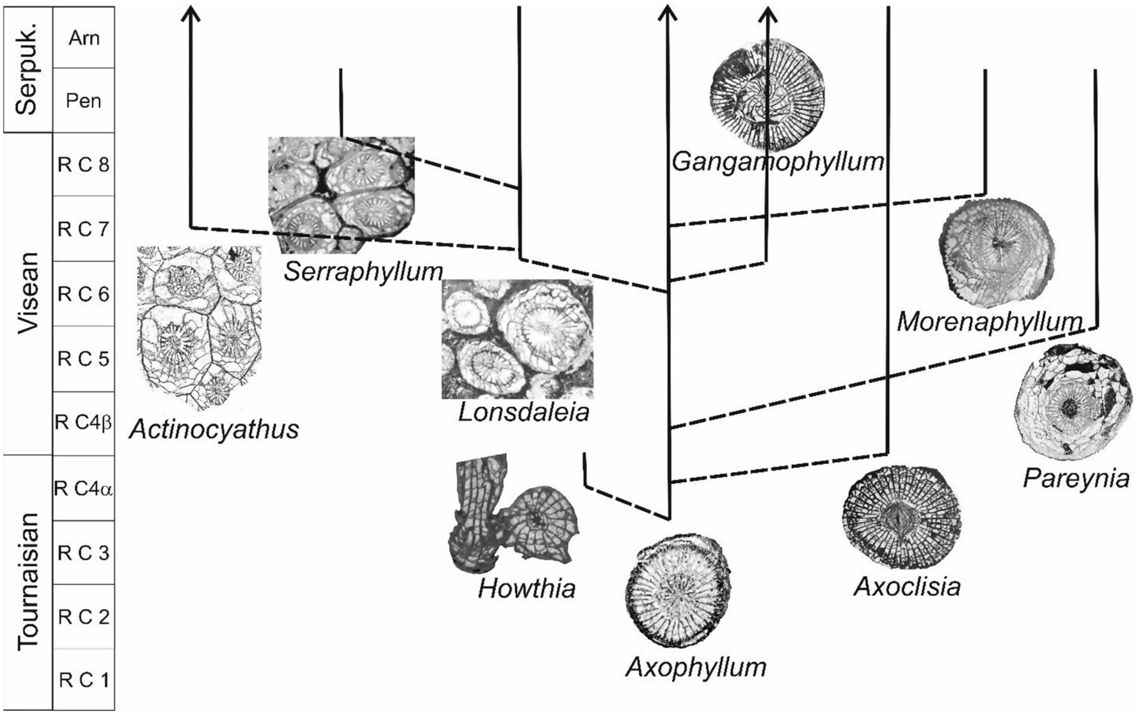


Fig. 9 Evolution in the family Lonsdaleiidae. Data based on Semenoff-Tian-Chansky (1974), Poty and Hecker (2003), Rodríguez and Somerville (2014). Drawings of the genera are not to scale

origins: the modification of structures from other fasciculate corals, or the development of colonialism from solitary corals (Rodríguez & Somerville, 2010). It is usually combined with the increase in the integration of the corallites of the colonies, reaching cerioid, thamnasterioid and aphroid habits (Scrutton, 1997). The different habits have been regarded usually as criterion for distinguishing genera and families (Figs. 9, 10 and 11).

- The increase/decrease in size of alar diameter, tabularium diameter, or in number of septa is common in the evolution of Mississippian corals. It is usually a specific criterion. Poty (1984) and Hecker (2010) provided excellent examples in the Lithostrotionidae and the Lonsdaleiidae, respectively.
- The increase in the complexity of different structures of corals (septa, dissepiments, tabulae, etc.) is a clear tendency in the Mississspian rugose corals (Nelson, 1959; Poty, 2010). Drawings showing the evolution of some of the most representative families in the Mississippian have been built for illustration of the main tendencies in rugose corals (Figs. 7, 8, 9, 10 and 11).

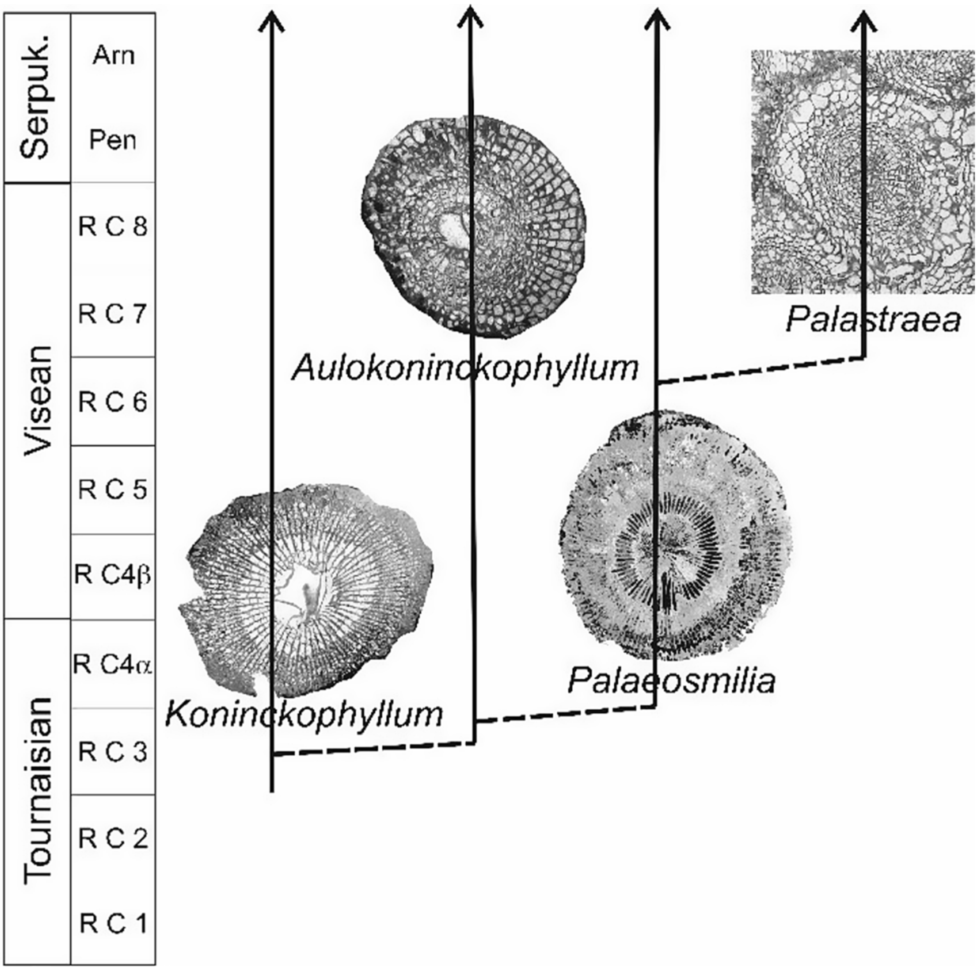
4 Discussion

The Mississipaian epoch runs between two great extinctions that, however, have not received as much attention from specialists as they deserve. The Mississippian begins with the Hangenberg event, which wiped out a high proportion of skeletal invertebrates. It involved subaerial, shallow and deep marine ecosystems, affecting many fossil groups, including corals. It was not a single catastrophic event, but a series of extinctions (Yao et al., 2020). That marine extinction has been called the "Natural Devonian-Carboniferous Boundary" (Aretz et al., 2020).

The Mississipian finished with another extinction at the end of the Serpukhovian, which has been proposed as one of the largest extinctions, surpassing even that of the Ordovician (McGhee et al., 2012). It has been placed fifth among the major Phanerozoic biodiversity crises. Global cooling and environmental deterioration driven by the late Paleozoic ice age have been cited as potential grounds for the Serpukhovian extinction (Hu et al., 2022). However, several macrofaunas and microfossils have longer stratigraphic ranges than the ones they have in most basins in the eastern and western Palaeotethys realms. Several rugose coral genera and species that previously were considered to have disappeared in the Serpukhovian have been recorded in the early Bashkirian in the Tindouf Basin (Cózar et al., 2014), the Canadian Artic (Fedorowski & Bamber, 2012) and Novaya Zemlja (Kossovaya, 1996).

Returning to the late Devonian extinction, after the Hangenberg event the rich rugose coral diversity of the Strunian is replaced by a poor fauna in the western Palaeotethys (less than 30 genera, Figs. 2, 3, 4 and 5). Most genera were undissepimented corals, which stand adverse environmental

Fig. 10 Evolution in the family Palaeosmilidae. Data based on Poty (2010) and Rodríguez and Somerville (2010). Drawings of the genera are not to scale



conditions better than the dissepimented corals (Figs. 4 and 5). During the early Tournaisian (zones RC1 and RC2 of Poty, 1985), the severe conditions that caused the extinction probably remained, because the generic diversity diminished even more. The seas at that time were dominated by microbes (Riding, 2006), which built some Waulsortian mud mounds (Lees & Miller, 1985).

The generic diversity increased first during the zone RC3, when favourable environments for the development of corals enlarged in extension (Figs. 2 and 3). It is also the period when the first colonial corals appear in the western Palaeotethys (Figs. 4 and 5), but they didn't build reefs at that time. The re-establishment of the coral diversity could be related with the development of more open marine environments that contrasted with the previous siliciclastic-dominated nearshore conditions (Poty, 1999). The generic diversity continues increasing during the late Tournaisian and reaches a maximum during the early Visean (RC4β zone), especially in the Atlantic, central and eastern European sub-provinces (Mitchell, 1989; Poty, 1981; Weyer, 2000; Ohar, 2016, 2020; Ohar & Denayer, 2021). In the zone RC5 the first massive corals appear (Figs. 4 and 5), which means an active diversification, but along the zones RC5 and RC6 the global generic diversification diminishes.

The tendency changes during the late Visean transgression of zone RC7 and reaches the maximum generic diversity in the zone RC8, coinciding also with a maximum of colonial rugose genera. It is also related with a metazoan reef proliferation (the first one after the Hangenberg extinction), which produced a global reef expansion during the CR7 and CR8 zones (Yao et al., 2020). However, in the RC8 zone the appearance of new genera begins to diminish (Figs. 2 and 3). During the Serpukhovian, the generic diversity decreases conspicuously. First slightly (during the Pendleian), later dramatically (during the Arnsbergian). The most marked reduction affects the solitary undissepimented corals, and the less affected are the massive corals that reached their maximum during the RC8 (Figs. 4 and 5), when they became important components of reefs (Yao et al., 2020).

Most of the evolutionary tendencies are present in some of the most representative families:

The Zaphrentidae represent the corals with more simple structure in the Mississippian. The basic structure is shown

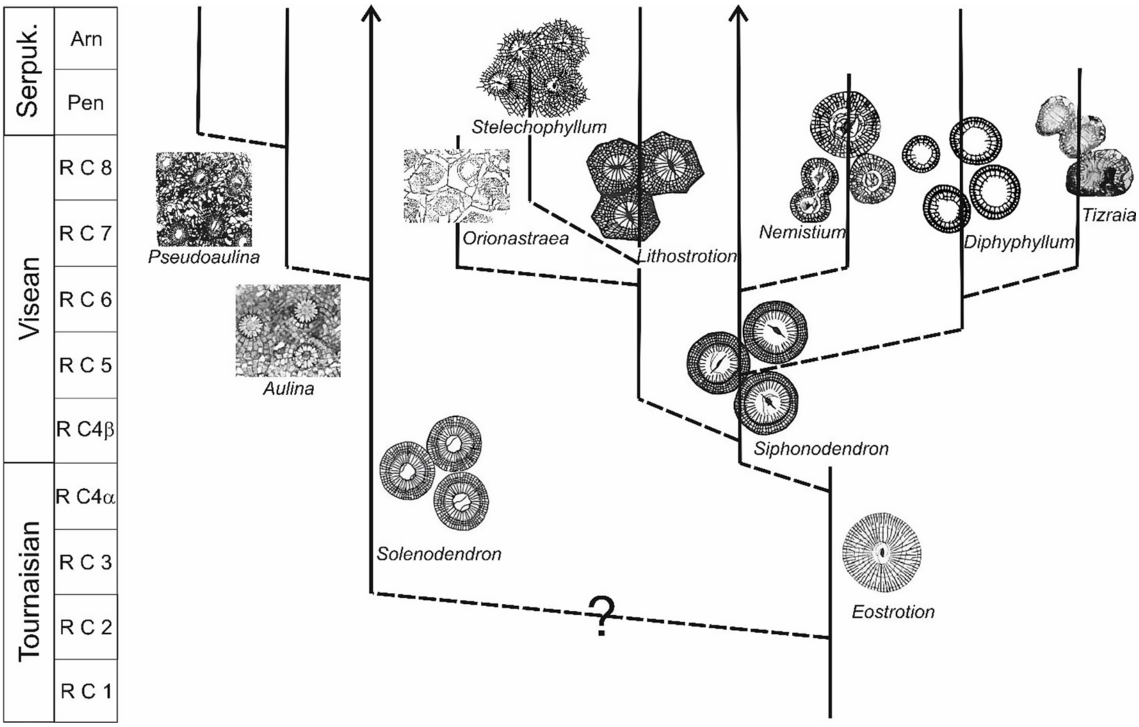


Fig. 11 Evolution in the family Lithostrotionidae. Data based on Nudds (1975, 2013), Poty (1984, 2010) and own information. Drawings of the genera are not to scale

by *Zaphrentites* with a well-defined cardinal fossula, pinnate organisation of the septa in the cardinal quadrants and radial in the counter quadrants (Hill, 1981). Some variations arrive by the development of dissepiments (*Zaphriphyllum*), development of a longer counter septum (*Barytichisma*, *Fasciculophyllum*, *Saharaphrentis*), development of free axial zones (amplexoid tendency, *Allotropiophyllum*, *Zaphrentoides*, *Amplexizaphrentis*), development of longer counter-laterals (*Amplexizaphrentis*, *Enniskillenia*, see Bamber et al., 2017) and development of carinae (*Saleelasma*). *Sychnoelasma* seems to represent a parallel line without a direct connection with the true zaphrentids. The most controversial point is that *Saleelasma* is believed to descend from *Fasciculophyllum* (Weyer, 1970), but *Saleelasma* is recorded earlier than *Fasciculophyllum* (Fig. 7). The genus *Zaphrufimia* Fedorowski, 2012b represents the transition to the family plerophyllidae by the selective development of longer and rhopaloid protosepta.

In the Lonsdaleiidae, an evolutionary line produces an increase of the integration from the oldest and most basic solitary form (*Axophyllum* Milne-Edwards & Haime, 1850), creating first fasciculate forms (*Howthia* Somerville and Rodríguez, 2010 and *Lonsdaleia* McCoy, 1849), then submassive (*Serraphyllum*) and massive (*Actinocyathus* d'Orbigny, 1849) forms (Poty & Hecker, 2003). Meanwhile, in the solitary genera variations in the axial structure evolved in *Gangamophyllum* Gorsky, 1938 and *Axoclisia* Semenoff-Tian-Chansky, 1974; the increase in the development of lonsdaleoid dissepiments evolved in *Pareynia* Semenoff-Tian-Chansky, 1974 and the combination of reduction of the axial structure plus increase in the lonsdaleoid dissepimentarium evolved in *Morenaphyllum* Rodríguez & Somerville, 2014 (Fig. 9). The evolution of this family didn't finish in the Mississippian. It produced a new form in the Bashkirian, *Semenophyllum* Rodríguez, 1984, which is not included in our Mississippian graph.

The family Palaeosmilidae is characterised by the existence of a typical microstructure that distinguishes their components from the representatives of the family Aulophyllidae (Rodríguez et al., 2001). The septa in the dissepimentarium are composed of thick trabeculae that gives them a carinated aspect. In the tabularium they show a water-jet microstructure similar to that of many aulophyllids. This trabecular microstructure appeared first in some representatives of the genus *Koninckophyllum* Thomson & Nicholson, 1876, but not in all of them (Semenoff-Tian-Chansky, 1974). These corals evolved to the genus *Aulokoninckophyllum* Sando, 1976 and later to *Palaeosmilia* Milne-Edwards & Haime, 1848 (Poty, 2010; Rodríguez & Somerville, 2010). The genus *Palastraea* McCoy, 1851 appeared in the late Visean. There are some transitional forms (quasicolonial or incipient colonial after Fedorowski, 1978), but contrarily to what happens with most colonial derived from solitary corals, *Palastraea* is a massive coral but there is no fasciculate *Palaeosmilia* (Poty, 2010).

The evolution of the family Lithostrotionidae has been explained by Nudds (1979, 1980) Sando (1983) and Poty (1984, 1993). The main question in the evolution of the Lithostrotionidae is the origin of the first colonial genus, *Siphonodendron* McCoy, 1849. Poty (1984) indicates its possible descendence from the genus *Dematophyllum* Wu and Jiang in Wu et al., 1981. But more recently Poty (2010) indicated that it possibly descended from *Eostrotion* Vaughan, 1915 by developing a colonial habit. This proposal is adopted here. There are several evolutionary lines in the family. The best explained are the development of massive habit (*Lithostrotion* Fleming, 1828), the increase of the integration with the development of astreoid habit (*Stelechophyllum* Tolmachev, 1933) and the development of lonsdaleoid dissepiments (*Orionastraea* Smith, 1917). In other evolutionary line, *Siphonodendron* would derivate in a more complex axial structure (*Nemistium* Smith, 1928) or in a reduction of it associated to a parricidal increase (*Diphyphyllum* Lonsdale, 1845) and development of lonsdaleoid dissepiments (*Tizraia* Said & Rodríguez, 2007).

The evolutive line of aulate genera consists also in the increase of integration (*Solenodendron-Aulina-Pseudoaulina*). This line is usually included in the Lithostrotionidae, but it could have phylogenetic relationships with *Aulokoninckophyllum* (Sando, 1976).

The evolutive graphs of the selected families (Figs. 7, 8, 9, 10 and 11) and the comparison of the curves of appearances matched with the climate changes (Fig. 6) show some clear tendencies:

The appearances of the undissepimented rugosans (Figs. 4 and 7) occur along all the zones, showing somewhat independence of the climate changes (Fig. 6). There is a lower rate only during the early-middle Visean, perhaps related to the cooling during the zone RC6 (Fig. 6).

The arrival of solitary dissepimented corals shows a high dependence of the climate, because its rate of appearances increases progressively along the Tournaisian and early Visean, but reveals a notable augment during the warming time at the late Visean and a quick decrease during the Serpukhovian cooling.

The colonial corals have a slow recovery after the Hangenberg extinction and only got a notable increase during the late Visean (zones RC7 and 8), coinciding with a general warming and marine transgression (Ramsbottom, 1973; Ross & Ross, 1985; Herbig, 1998, 2016), which augmented the surface of the shallow carbonate platforms, increasing the ecologic niches favourable for colonial corals and facilitating the migrations of the corals (Bamber et al., 2017).

The appearance of new genera is concentrated during the Tournaisian in the Atlantic, central European and eastern European sub-provinces. The reasons may be several. These sub-provinces are directly affected by the equatorial current that could provide an effective transportation of the corals' planulae (larval stage) from the eastern areas of the Palaeotethys. In addition, they are located close to the Equator, with warm seas that are minimally affected by the climate changes. Moreover, although the intermittent nature of crustal growth is a matter for discussion, there are distinct regional deformation events (Schulmann et al., 2014). During the Tournaisian, the tectonic activity in the western Palaeotethys is not extremely intense (Franke, 2014; Fernández et al., 2016) and shallow marine environments with abundant limestone facies occur. It allows the settlement of the planulae in favourable environments favouring the recovery of the rugose coral faunas. In contrast, the west Peri-Gondwanan and the Saharan sub-provinces comprise mainly epicontinental areas that were not invaded by the seas during the Tournaisian, and the Mediterranean sub-province comprises very unstable environments related to orogenic areas (Fernández et al., 2016).

The late Visean transgression allows a maximum development of the rugose corals in all sub-provinces, and consequently the main development of coral reefs. However, the intensification of the tectonic activity during the Serpukhovian, with the consequent deposition of terrigenous material in the areas near Laurentia and Baltica (Franke & Engel, 1986), produced the extinction of many of the genera in the Atlantic and central European sub-provinces. The Saharan and the west Peri-Gondwanan sub-provinces, less affected by these tectonic movements, preserved during the Serpukhovian some of these genera, which were disappearing in the northern areas. In addition, the partial isolation of the different basins in these sub-provinces also produced the appearance of new genera and species. The East European sub-province maintained also the presence of epicontinental seas (Moscow and Donets basins), and conserved a quite high diversity during the Serpukhovian.

Finally, the Saharan basins provided a refuge during the Bashkirian to the remaining survivor genera.

5 Conclusion

The data base of the occurrence of rugose coral genera during the Mississippian in the western Palaeotethys gives a general view of their evolution throughout that epoch.

The recovering after the Hangenberg extinction at the late Devonian was slow during the Tournaisian and early Visean. However, the favourable climate and tectonic backgrounds during the late Visean produced an important diversification during the zones RC7 and RC8 (Poty, 1985).

The changing climate and tectonic conditions produced an important rate of extinctions during the Serpukhovian.

The evolution of some of the main families of rugose corals of the Mississippian (Zaphrentidae, Palaeosmilidae, Lithostrotionidae and Lonsdaleiidae), which comprise solitary and colonial corals, shows some tendencies that are in some cases homeomorphic. These are the development of dissepiments, of aulos, of amplexoid structures, of carinae, etc. The trend to an augment in the complexity helped the appearance of colonial forms and the increase of the integration of the corallites in the colonies, evolving from fasciculate to aphroid forms with intermediate cerioid and astraeoid forms.

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Declarations

Competing interests The authors have no competing interests to declare.

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8 INTEGRATING DISCUSSION

8.1 UPDATES TO THE ARTICLES

The nature of this thesis by publications, where chapters two to seven consist of published or submitted articles, entails that those articles stay unchanged since their publication date. Thus, these chapters cannot be updated or revised. However, ongoing work with the same dataset, the discovery of previously inaccessible literature, and the examination of new collections are bound to bring to our attention new information and provide additional insights, which sometimes affects our conclusions and results. Therefore, we discuss here updates to the publications:

One of the most significant updates concerns most of the articles. Our rugose corals database has grown and evolved significantly during the thesis. Currently it is based on more than 700 sources (articles, abstracts, books and book chapters), and it has been improved through the examination of multiple collections (the list is detailed in Chapter 6). Numerous additions and amendments have been made to the database entries throughout this PhD, resulting in minor variations in the data presented across the different articles during the years. While changes between the last three articles (Chapters 5, 6 and 7) are minimal, they are still present. The latest version of the database is included in Annex 1, as a compilation of presence/absence tables for rugose coral genera and species throughout the stages of the Mississippian. However, this is not a final version. Many areas in the Western Palaeotethys need more sampling and research, and our goal is to further expand the database to other palaeobiogeographical provinces and time periods, particularly the Pennsylvanian, to eventually encompass the entire Carboniferous period.

Another key update concerns the genus *Lonsdaleia* discussed in chapter three. This chapter addresses the earliest records of the genus *Lonsdaleia*. The species *Lonsdaleia praenuntia* Smith (1915) was collected by Garwood (1912) in the lower Visean of Arnside (NW England). In Garwood (1912), those specimens are referenced as "*Thysanophyllum* or *Lonsdalia*" (instead of the accepted spelling *Lonsdaleia*), collected at Meathop, in the "*Seminula gregaria* subzone". However, as noted in chapter three, the identification of these specimens as *Lonsdaleia* is debated. A primary reason was the absence of budding structures that would demonstrate its coloniality, despite Smith (1915) describing the species as "an early fasciculate". After the article's publication, we obtained photographs of the slides cited in Smith (1915) from the British Geological

Survey (Keyworth), where they are deposited, and re-examined them for this thesis (Figure 1). All specimens observed are individual corallites, with no trace of budding. Additionally, despite further examining the collection, we did not find any hand specimens matching the slides that would prove the colonial nature of *Lonsdaleia praenuntia*. More recent sampling in the same locality also yielded only solitary *Axophyllum* specimens, and not a single *Lonsdaleia* (Poty, personal communication).

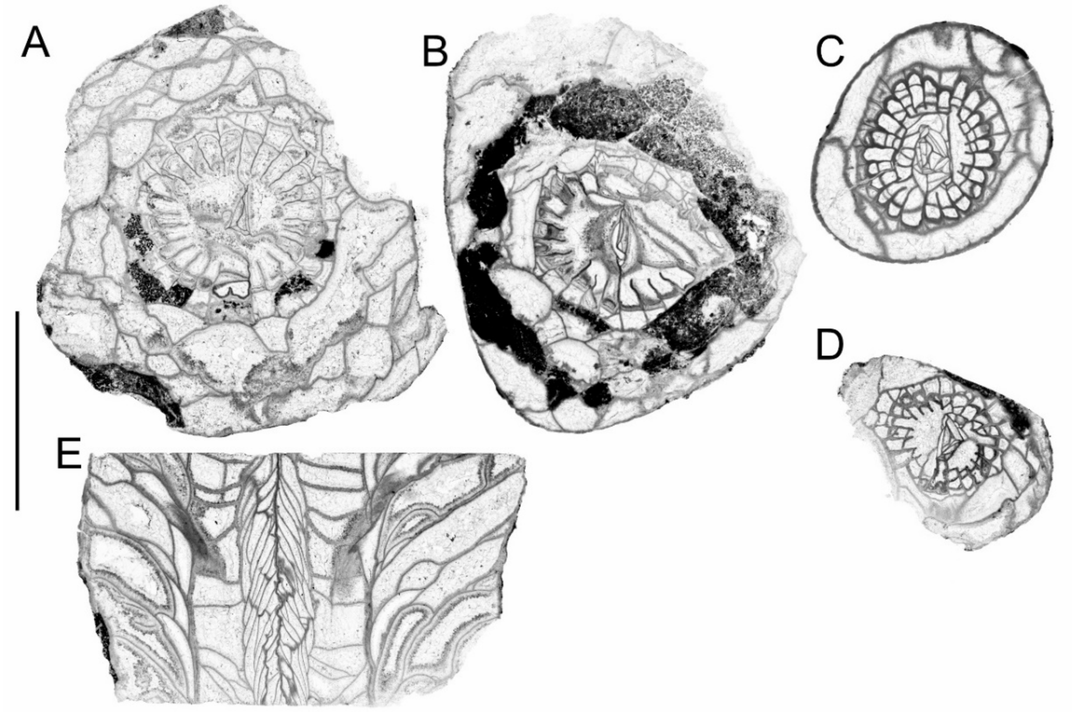

Figure 1: Transverse (A, B, C, D) and longitudinal (E) sections of the specimens previously identified as Lonsdaleia praenuntia. None of the individual corallites shows evidence of budding, or traces of neighbouring corallites. Scale bar: 10mm. Specimens from the BGS collection in Keyworth. A: PF4435; B: PF4436; C: PF4437; D: PF4439; E: PF4438. Pictures taken by Simon Harris (BGS).

The presence of *Lonsdaleia* in Arnside during the lower Visean was the basis for the first hypothesis on the origin and dispersal of the genus, as discussed in chapter three. This hypothesis suggested that *Lonsdaleia praenuntia* was the genus's ancestor, originating in Arnside during the early Visean and remaining largely restricted until the late Visean, when it began to diversify and spread due to the late Visean marine transgression. However, with no actual evidence of the specimens cited in Garwood (1912) and Smith (1915) being colonial, we must discard that hypothesis. This leaves two possibilities for the origin of the genus. The first *Lonsdaleia* could be the specimen recorded in the Tianshan Mountains in the early Visean (Wang et al., 1994). We have not been able to find pictures or a description of the specimen, so that record is not verified. The second hypothesis is that the genus is polyphyletic, with several species appearing in different locations throughout the Palaeotethys during the late Visean.

8.2 UTILITY OF RUGOSE CORALS FOR PALAEOGEOGRAPHICAL STUDIES

The use of corals for palaeogeographical studies is well-established (Hill, 1973; Sando, 1975; Poty, 1980; Rodríguez et al., 1986; Denayer, 2015; Bamber et al., 2017; Fedorowski, 2023). However, most analyses have been largely qualitative. To examine in greater depth the palaeogeographical signal in rugose corals, we combined quantitative analyses with qualitative data, comparing different geographical and temporal scales using various similarity indices.

There is extensive literature covering the use of similarity indices for palaeogeographical studies (Hubálek, 1982; Rodríguez, 1986; E. D. McCoy & Heck, 1987; Shi, 1993; Hammer & Harper, 2005; Schmachtenberg, 2008). Among the most commonly applied indices in this field are Jaccard (Jaccard, 1901), Simpson (Simpson, 1943, 1947), Dice (Dice, 1945) and Raup-Crick (Raup & Crick, 1979), due to their suitability for presence-absence data. Authors' recommendations vary; for instance, Rodríguez (1986), in a comparison of over forty indices, found Dice, Jaccard and Simpson to be especially useful for rugose corals studies, though Raup-Crick was not assessed. McCoy & Heck (1987) recommend probabilistic indices, such as Raup-Crick. Other studies (e. g. Shi, 1993; Schmachtenberg, 2008) have found that the Jaccard index correlates more precisely with palaeogeographical differences and distances than other indices. Baselga (2010, 2012) explores how Simpson and Dice indices reflect different phenomena and processes: species loss or nestedness, and species replacement or turnover, which is better reflected by Simpson.

The Raup-Crick index gave satisfactory results when analysing the coral faunas in El Guadiato Area (Chapter 2, Figs. 3 and 4). However, as McCoy & Heck (1987) observed, probabilistic indices are harder to apply. They are less replicable, with each analysis iteration potentially yielding different results. Additionally, the more complex calculations complicate the identification of specific factors influencing the results. For these reasons, we ultimately excluded Raup-Crick from most of our analyses.

The Dice and Jaccard indices, on the other hand, proved redundant across all our studies, so we opted to include only one of them in each article. Following the recommendations of Shi (1993) and Schmachtenberg (2008), we initially used the Jaccard index in our first analysis (Chapter 2, Figs. 3 and 4). When comparing the Austrian coral faunas with those from other European regions (Chapter 4), we found the clusters generated with the Dice index were slightly more robust, showing higher bootstraps values. Thus, we included Dice instead of Jaccard in subsequent analyses (Chapters 4, 5 and 6), though both indices consistently yielded coherent results.

It is important to note that both the Jaccard and Dice indices are sensitive to sample size (Hammer et al., 2001). Areas with fewer taxa tended to show greater differentiation from others across all analyses, which over-emphasised the differences in understudied regions or areas with fewer Mississippian outcrops. This effect was reduced in our analysis by using the Simpson index, which is independent of sample size (Hammer & Harper, 2005) and focuses on shared taxa while disregarding absences. The Simpson index emphasises species replacement between areas (Baselga, 2010, 2012), and thus it is less impacted by insufficient sampling or lack of data. However, it has its own limitations, as it may overestimate the similarity between areas with mostly widespread taxa. The combined use of both indices proved largely effective, allowing us to identify in our results the effects of the uneven knowledge of the rugose coral faunas across regions.

While our choice of similarity indices has played a key role in refining our palaeogeographical interpretations, the scale of the analyses also influenced their outcomes. Our first study (Chapter 2) focuses on El Guadiato Area, a small region with well-known assemblages. The detail with which these faunas have been studied, and the limited geographical scale, allowed us to work at a high taxonomic resolution, comparing coral species. However, several complicating factors required consideration.

First, there was a small age variation within the assemblages (Chapter 2, Fig. 2). Although all outcrops in El Guadiato Area are late Visean in age, using the biozones established by Poty (1985) and Poty et al. (2006) reveals slight differences in their ages: some assemblages belong to Zone RC7, others to Zone RC8, and some span both. Narrowing the analysis to a single biozone left too few species to produce stable clusters or meaningful comparisons. A similar challenge was found when comparing the Austrian faunas to those of other regions in Central and Eastern Europe (Chapter 4), as the selected areas contain late Visean and Serpukhovian coral faunas, and in some cases the dating is uncertain. Nonetheless, the presence of taxa in two areas of close age also suggests a certain degree of palaeobiogeographical connection (Bambach, 1990). While it is crucial to carefully examine the data to avoid misinterpretations due to age variations, the analyses are still meaningful and offer valuable insights despite the broader temporal range.

The second complicating factor was the variability in the palaeoenvironments represented by the outcrops compared in this study. Most consist of shallow-water carbonate ramp facies, but some indicate deposition in deeper environments, and a few are olistoliths, containing allochthonous assemblages from different settings. Given the sensitivity of rugose corals to ecological conditions, we analysed two datasets to minimise environmental signals in our results. The first dataset included all the rugose coral species from each of the studied units; analyses based on this dataset tended to associate the units with more outcrops from deeper environments. In the second dataset, we excluded deeper facies outcrops and removed undissepimented corals from the remaining outcrops, as these taxa are typical of deeper and/or turbid waters (Hill, 1981; Kullmann, 1997). Focusing on faunas representative of shallow-water environments yielded results more consistent with the tectonic framework of the region. A complementary analysis of assemblages from deeper waters was not possible, as excluding the shallow-water environments would have left few species and outcrops for a meaningful comparison.

The analysis of the Austrian faunas (Chapter 4) also excluded undissepimented corals from the comparison with Central and Eastern Europe, as the assemblages from Nötsch did not include these taxa, with the unique exception of the genus *Lophophyllidium*, which is often found with shallow-water faunas (Moore & Jeffords, 1945).

While reducing the environmental signal in our analyses improved the clarity of the results in El Guadiato Area, some factors beyond palaeogeography still appeared to influence them, likely reflecting subtle environmental variation that persisted despite efforts to control more evident ones. However, comparisons with faunas of the same age from Los Santos de Maimona (southwestern Spain) and Kingscourt (Ireland) showed patterns more closely linked to palaeogeographical distance. Both regions are comparable in size and age to the entire El Guadiato Area (rather than individual outcrops within it), so these results were promising for larger-scale analyses, which encompass regions where environmental differences average out, minimizing their impact on faunal assemblages. This trend was further confirmed in broader analyses (Chapters 5 and 6): excluding undissepimented faunas from the larger datasets did not improve the results but reduced cluster stability, and these clusters were therefore omitted from the final analyses.

Even though the broader analyses (Chapters 3 to 7) benefit at times from the averaging out of different environments, they face a new challenge: the uneven knowledge of rugose coral faunas throughout the Western Palaeotethys. The three main aspects of these irregularities are: the existence of understudied regions that require further sampling (e. g., the Balkans); the varying taxonomic approaches among experts (splitters versus lumpers), and the high number of species left in open nomenclature (sp., cf., aff., ?, etc.).

The first issue, the existence of understudied areas, can only be fully addressed through more sampling and research, an extensive process that requires years, if not decades, of ongoing work. Nevertheless, palaeoecological and palaeogeographical research must proceed even as the databases are continually improved and refined. While this lack of coverage will inevitably impact the results of any analysis, careful attention to the data and deliberate consideration during interpretation reduces the risk of drawing wrong conclusions. Furthermore, as previously discussed, the use of multiple similarity indices and mathematical approaches strengthens the reliability of the results, by making it easier to single out the effects of the sample size.

The variation in taxonomic interpretations presents a similar, ongoing challenge. The taxonomic approach varies by region. For example, the studies of Dorothy Hill (e. g., Hill, 1938, 1973, 1981), in the United Kingdom, favour lumper criteria. On the other hand, the work of Fedorowski (e. g., Fedorowski, 1973, 1984, 2017), in Poland, tends towards a more detailed differentiation, defining new taxa with a splitter approach. These differences cannot be easily corrected within a reasonable timeframe and inevitably influences the data that inform our analyses. However, as with sampling gaps, an awareness of this variability allows us to adopt similar strategies to maintain the reliability of the results despite the unavoidable inconsistencies.

The abundance of species in open nomenclature throughout the Western Palaeotethys, however, is an issue that can be managed by conducting analyses at the genus level. While working with species is a more detailed approach, genera are more practical for large-scale studies. Given the limitations of the fossil record and the impracticality of compiling a complete record of species distributions, using genera is more effective for palaeobiogeographical analysis over large regions (Bambach, 1990). This approach is also common in qualitative studies, where some rugose coral genera have been used as markers that define biogeographical provinces. A representative example is the genus *Kueichouphyllum*, which is present in the Eastern and Southern Palaeotethys, but not in the Western Palaeotethys (Hill, 1973), and it has been regarded as the marker of the southern palaeoprovince in the Pennsylvanian of East Asia (Liao, 1990).

In the third chapter of this thesis we take a different approach, still qualitative and based on genera. Rather than focusing on the endemism of a genus to define palaeogeographical provinces, we examine the dispersion and distribution of two related genera, *Lonsdaleia* and *Actinocyathus*, both widely distributed and represented by multiple species. The progression of their appearances in across the Palaeotethys, and their persistence in basins such as the Sverdrup and the Tindouf Basins, reveals migration paths, marine currents, inter-regional connectivity and the existence of ecological refugia after their extinction in most of the Western Palaeotethys.

Overall, rugose corals have demonstrated their utility in palaeogeography throughout our studies. The distribution of their species and genera highlights distances, connections, and barriers between basins. While certain limitations exist, they can be effectively managed through careful examination of the data and critical evaluation of interpretations. The constant improvement of the datasets promises even stronger analyses and conclusions in future research.

8.3 THE WESTERN PALAEOTETHYS DURING THE MISSISSIPPIAN

The palaeogeography of the Western Palaeotethys during the Mississippian was shaped by the gradual convergence of Gondwana and Laurussia, in the context of the Variscan orogeny. Our palaeogeographical maps for each stage (Chapter 6, figures 6-9) illustrate how this process progressively narrowed the Rheic Ocean, with the Iberian and Armorican massifs emerging as significant barriers between it and the Palaeotethys sensu stricto. By the Serpukhovian, the effects of the orogeny on the size of the Rheic Ocean became evident. This process continued into the Pennsylvanian, ultimately closing the Rheic Ocean during the Bashkirian (Davydov & Cózar, 2019) or possibly even the Moscovian (Vai, 2003; García-Bellido & Rodríguez, 2005).

The equatorial and subtropical positioning of the Palaeotethys during the Mississippian (Torsvik et al., 2024) provided favourable climate conditions for coral and reef proliferation. A warming trend in the early Visean culminated in peak temperatures during the late Visean (Ogg et al., 2016; Yao et al., 2020), coinciding with significant transgressive events (Ramsbottom, 1973; Somerville, 2008). However, despite the increase in temperatures during the first half of the Mississippian, the climate curves of the period (Chapter 7, figure 6) reveal a shift toward cooling during the Serpukhovian. This cooling phase aligns with intensified tectonic activity in the Palaeotethys, leading to greater isolation of marine basins, increased terrigenous clastic input, and the uplifting of tectonic barriers that further fragmented marine environments (Franke & Engel, 1986; Cózar et al., 2014). The climate conditions, tectonic changes and sea level variations are closely related to the evolution of the rugose coral faunas, with increases in temperature and sea level aligning with increases in diversity, and the adverse conditions of the Serpukhovian causing a noticeable extinction (Chapter 7, figure 6).

Four biogeographical sub-provinces have been previously established for the Western Palaeotethys during the Mississippian (Somerville et al., 2013). Building on this framework, we propose two additional sub-provinces (Figure 2), based on the distribution of the genera *Lonsdaleia* and *Actinocyathus* during the Visean. These are the Central European sub-province, characterised by an irregular and sparse record of these genera, and the Eastern European sub-province, which shows an abundance of *Lonsdaleia* and *Actinocyathus* during the Visean and Serpukhovian stages. The addition of these sub-provinces enriches our understanding of the Mississippian palaeogeography, acknowledging regions that were not included in previous proposals.

However, two key areas remain outside of the current sub-provinces division: the Balkans and Türkiye. Studies in the Balkans are scarce and dated (e. g., Kolosvary, 1951; Kostic-Podgorska, 1957, 1958), with only fifteen genera recorded from the region during the late Visean, the Mississippian stage with the highest diversity of rugose corals. The tectonic complexity of the Balkans, comprising several terranes aggregated by the Variscan orogeny, and the low sample size prevent us from reliably establishing its connections to other regions. Similarly, Türkiye consists of several terranes that were separated during the Mississippian. The Istanbul-Zonguldak terrane and the The Anatolide-Tauride block both contain records of Mississippian rugose corals, and there have been significant advances in the study of these faunas over the past decade (Denayer, 2011, 2012, 2014, 2015, 2016, 2021; Denayer & Hoşgör, 2014). Our analyses consistently show that the rugose coral assemblages from Türkiye are significantly different to those of the other regions in the Western Palaeotethys, likely reflecting the influence of The Anatolide-Tauride block, which is related to the northern margin of Gondwana (Denayer, 2015).

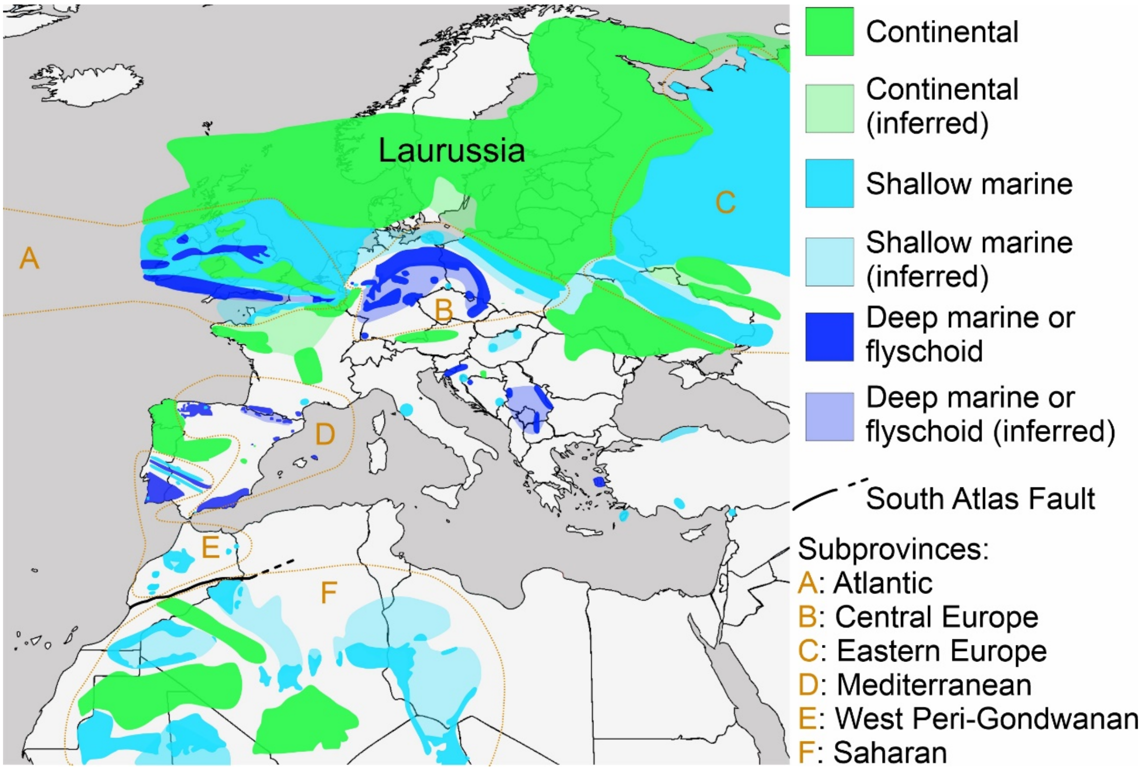

Figure 2: facies map of the current regions comprising the Western Palaeotethys (excluding Nova Scotia, in North America). The approximate boundaries of the six sub-provinces are outlined. The details behind the construction of the facies map are provided in chapter five.

The sub-provinces of the Western Palaeotethys experienced varied evolutionary and palageographical histories throughout the Mississippian. The changes in generic diversity of each sub-province through the different stages are shown in Table 1. In the Tournaisian, the Atlantic sub-province had the highest diversity of rugose corals among all sub-provinces during that period. Our analyses indicate good connectivity across marine platforms along Laurussia's southern margin (the Atlantic and Central European sub-provinces) until the late Visean. During the Visean, the Atlantic sub-province was also well connected with the West Peri-Gondwanan sub-province, along the eastern coast of the Rheic ocean. This connectivity and the extensive shallow marine platforms caused by the Visean transgression were favourable for corals, keeping the sub-province among the most diverse until the late Visean, when coral diversity peaks throughout all the Western Palaeotethys (Herbig, 1998; Fedorowski, 2023). However, in the Serpukhovian, coral diversity in the Atlantic sub-province declines sharply as it becomes increasingly isolated due to the uplift of the Welsh-Anglo-Brabant and Armorican massifs, which substantially reduces the size of the marine areas in the region.

The Central European sub-province shows a marked increase in diversity between the Tournaisian and the late Visean, becoming one of the most diverse sub-provinces. Its faunal affinities evolve during the Mississippian: during the Tournaisian, it is more similar to the Atlantic sub-province, but its similarities with Eastern European faunas increase in the Visean. A detailed analysis of the late Visean highlights nuances in these affinities: Poland's coral faunas share more similarities with those of the Donets and Moscow basins, while German faunas show affinities with the Atlantic and West Peri-Gondwanan regions (Chapter 5, table 3). Following a peak in diversity in the late Visean, the Central European assemblages are impacted by the Serpukhovian extinction, as marine habitats are reduced by the uplift of the Ukrainian shield and the Variscan massifs in southern Germany and northern Italy (Schönlaub, 1997b). However, the decline in diversity is less severe than in the Atlantic sub-province.

The Eastern European sub-province has complex relationships with other sub-provinces, which are not always reliably solved by our analyses. In the Tournaisian, it shares more similarities with the Saharan sub-province, but this shifts in the early Visean, when its rugose corals show more affinity with those of the Central European and Atlantic sub-provinces. These similarities with Central European faunas persist into the late Visean and the Serpukhovian. The Serpukhovian extinction has a limited impact on the diversity of Eastern European rugose coral faunas, as the sub-province's location in the eastern coast of Laurussia partially shields it from the effects of the Variscan orogeny.

During the Tournaisian, the West Peri-Gondwanan sub-province consisted mostly of uplifted continental terranes (Gabaldón et al., 1985; Cózar et al., 2020), with no records of rugose corals. By the early Visean, the Khenifra area was submerged under an epicontinental sea, allowing a low-diversity assemblage of rugose corals to establish there, marking the first Mississippian record of corals in the sub-province (Rodríguez et al., 2020b). Only four genera have been recorded from this stage, all of which are present in the Atlantic sub-province, suggesting a degree of connectivity between these regions. In the late Visean, coral diversity in the epicontinental seas and marine basins of the sub-province increases, with continued similarities to the Atlantic sub-province, particularly to the Belgian assemblages. The position of the Iberian Peninsula prior to the oroclinal bending of the Iberian Massif (Gutiérrez-Alonso et al., 2004, 2012; Murphy et al., 2016) placed the marine basins of southwestern Spain closer to the Atlantic sub-province, facilitating high connectivity through the Rheic Ocean through favourable currents. Although the similarities between the Atlantic and West Peri-Gondwanan sub-provinces are noticeable, and their designation as separate sub-provinces could be questioned, there are relevant differences. For instance, *Lonsdaleia* and *Actinocyathus* are abundant in the Atlantic but completely absent from the West Peri-Gondwanan, supporting their separation as distinct sub-provinces. By the Serpukhovian, coral diversity in the West Peri-Gondwanan sub-province declines, although less severely than in the Atlantic sub-province, highlighting further differences in the trajectories of the two regions.

The Mediterranean sub-province also lacks rugose coral records in the Tournaisian and even into the early Visean, as the regions comprising the sub-province remained part of deep marine environments (Rodríguez et al., 1986; Herbig et al., 2014). By the late Visean, however, suitable habitats for corals emerged, with the sub-province registering 33 genera of rugose corals. Despite high connectivity during the late Visean, the fauna in the Mediterranean sub-province does not show strong affinities with other sub-provinces, because the Iberian and Armorican massifs acted as geographical barriers. Nonetheless, there are slightly higher similarities with the West Peri-Gondwanan and the Atlantic sub-provinces than with the others. In the Serpukhovian, while most sub-provinces experience a decrease in faunal similarities, the Mediterranean sub-province shows a slight increase in similarity with the Saharan sub-province (Chapter 6, table 6), as Gondwana's advance brings them closer together. Although the Mediterranean diversity does not decline drastically in the Serpukhovian, a closer look to the Pendleian and Arnsbergian substages (Annex 1, table 13) reveals the extinction effects of, especially in the latter.

Table 1: number of genera recorded in the sub-provinces of the Western Palaeotethys during each stage of the Mississippian. Data from Annex 1.

	Tournaisian	Early Visean	Late Visean	Serpukhovian
Atlantic	50	30	54	18
Central European	34	32	57	34
Eastern European	16	17	48	42
West Peri-Gondwanan	-	4	49	28
Mediterranean	-	-	28	26
Saharan	5	12	32	30
Total	63	56	84	79

The Saharan sub-province is among the least diverse during the Tournaisian and Visean. This low diversity complicates comparisons with other sub-provinces, and its relationships are not reliably solved in most analyses. However, it shows stronger ties with the Eastern European sub-province during the Tournaisian and with the Central European sub-province in the early Visean. This suggests a connection through the western coast of the Palaeotethys sensu stricto, likely facilitated by the equatorial current turning southwards along Laurussia's margin. Throughout the Visean, the Saharan sub-province remains relatively distinct from others, although not to the same degree as the Mediterranean sub-province. In the Serpukhovian, the Saharan basins act as refugia for rugose coral faunas (Cózar et al., 2014; Fedorowski, 2023), and the overall diversity in the sub-province does not decrease in this stage. However, as in the Mediterranean sub-province, the Arnsbergian shows a clear reduction in diversity (Annex 1, table 13).

Beyond the distinct characteristics of each sub-province, broader patterns in endemism and evolutionary trends of rugose corals reveal further insights into their adaptative responses. Across the stages of the Mississippian, endemism levels and disparity shifted with the creation of barriers and changes in environmental factors, reflecting both the tectonic and climatic evolution of the Western Palaeotethys and general evolutionary processes. After the extinctions that characterize the Hangenberg event at the end of the Devonian (Yao et al., 2020), rugose coral faunas began the Mississippian with low diversity and significant endemism. In the Tournaisian and early Visean, over half of the genera recorded in the Western Palaeotethys are geographically restricted to only one sub-province, rather than occurring across several of them. Additionally, at the start of the Tournaisian, all recorded rugose coral taxa in the Western Palaeotethys are solitary corals (Chapter 7, figures 4-5). Most of them are undissepimented corals, which are better adapted to adverse environmental conditions (Hill, 1981; Kullmann, 1997). Colonial fasciculate corals begin to evolve from the solitary forms during the Tournaisian, with massive colonies evolving later in the early Visean (Chapter 7, figures 4-5).

Diversity increases progressively, peaking in the late Visean, when rugose coral faunas reach their highest diversity in the Mississippian, and colonial corals represent a significant proportion of genera. This aligns with a reduced endemism: only about one-fourth of the genera are restricted to a single sub-province, while the rest are more widely distributed. However, this trend reverses in the Serpukhovian, which is marked by significant extinctions driven by climate change and tectonic activity. Although the total number of genera in the Serpukhovian remains high (Annex 1, table 10), endemism rises due to the creation of barriers by the Variscan orogeny and the isolation between the sub-provinces and, with almost half the genera restricted to one of them. Most sub-provinces experience substantial reductions in diversity. Nonetheless, colonial corals are still a significant component of that diversity, particularly massive forms (Chapter 7, figures 4-5).

The development of colonialism and the increase in colony integration are known evolutionary trends in rugose corals during the Palaeozoic (Scrutton, 1997; Rodríguez & Somerville, 2010). Another notable trend, affecting both solitary and colonial forms, is the tendency toward greater complexity in rugose coral features, such as septa, dissepiments, or tabulae (Nelson, 1959; Poty, 2010). Our study of the Mississippian rugose coral families Lithostrotionidae, Lonsdaleiidae, Palaeosmiliidae and Zaphrentidae (Chapter 7, figures 7, 9-11) highlights these patterns, aligning with known evolutionary trends in rugose corals and confirming the Western Palaeotethys as a key region for studying rugose coral evolution.

Our palaeogeographical findings also correlate with established literature, offering additional insights into the changes experienced by the Western Palaeotethys during the Mississippian. Aretz (2011) conducted a cluster analysis of late Visean rugose coral faunas at the species level using the Raup-Crick similarity index. This study focuses on the western regions of the Western Palaeotethys, including Nova Scotia and Belgium (Atlantic sub-province), North Morocco and Southwestern Spain (West Peri-Gondwanan sub-province), the Baetic System and South France (Mediterranean sub-province) and the Sahara Platform (Saharan sub-province). The Baetic System was excluded from our late Visean analysis (Chapter 5) due to uncertainties surrounding the age of its assemblages, despite some studies assigning them a late Visean age (Herbig & Mamet, 1985). While Aretz (2011) includes the Baetic System in his analysis and excludes the British Isles fauna, our results (Chapter 5) are consistent with his findings, and his cluster clearly correlates with the sub-provinces of the Western Palaeotethys. The distinct separation between the Mediterranean regions and the others in Aretz's analysis drives him to suggest a significant barrier, which aligns with the presence of the Iberian and Armorican massifs.

Some palaeogeographical reconstructions present more differences with our results. In Cocks & Torsvik's (2006) Tournaisian map (340 Ma), the northern margin of Gondwana is placed halfway between the 30º and the 60º latitude parallels, creating a large distance between the Saharan basins and all other areas included in our study. Our findings do not support this placement, as the Saharan sub-province is not markedly distinct from the regions of the Western Palaeotethys. Another Tournaisian map (330 Ma) from some of the same authors (Torsvik et al., 2024), incorporating climate data, aligns more with our reconstructions (Chapter 6, figure 6), placing Gondwana's northern coast at the 30º parallel. However, it still positions North Africa closer to Florida and its neighbouring states than to the Iberian plate. Additionally, it depicts a fully uplifted Armorican Massif, isolating the British Isles from the Central European sub-province, and even includes Belgium as part of the continent, despite coral faunas being recorded in the region (Poty, 1999; Poty et al., 2006; Denayer et al., 2011).

Scotese's (2021) middle Visean map has a similar issue. Although it changes Belgium's facies to shallow marine, connecting the Atlantic and Central European sub-provinces, it shows southwestern Spain and north Morocco as an elevated cordillera that separates the British Isles from the Saharan basins. It also represents Nova Scotia as continental. These inaccuracies in widely used palaeogeographical maps underscore the importance of detailed palaeontological research in informing palaeogeographical reconstructions and highlight the relevance of our results.

The evolution of Gondwana's approach to Laurussia is reflected in the Moscovian map in Vai (2003), where the Rheic ocean is reduced to a narrow band of shallow coastal environments dominated by terrigenous clastics. This map mostly agrees with our interpretations, presenting a palaeogeographical evolution of the trends observed in the Mississippian. However, the later stages of the Variscan orogeny resulted in the oroclinal bending of the Iberian Massif (Gutiérrez-Alonso et al., 2012; Murphy et al., 2016), a feature preserved in Vai's maps despite occurring in later stages. In contrast, our reconstructions (Chapter 5, figure 5; Chapter 6, figures 6-9) depict a 'straightened' Iberian Massif, aligning with palaeontological evidence and tectonic studies that support this interpretation. While less common in maps of the Western Palaeotethys, this approach provides an alternative view that may better represent the region's Mississippian palaeogeography. Together, our findings contribute to a refined understanding of Mississippian palaeogeography and underscore the impact of precise coral-based analyses in reconstructing the Western Palaeotethys.

8.4 AVENUES FOR FUTURE RESEARCH

While this research has provided new insights into the palaeogeography of the Western Palaeotethys and the evolution of Mississippian rugose corals, certain limitations in the available data remain, as discussed in chapter 8.2. Our database is continually evolving and incorporating new records, but addressing the main gaps in the knowledge of rugose coral faunas will require extensive sampling efforts in understudied areas, especially the Balkans. Reviewing of Kostic-Podgorska's collection (Kostic-

Podgorska, 1957, 1958) would also be valuable for updating the knowledge of the region, though it is difficult to track, and it may even be lost, after Yugoslav Wars.

Further analysis is also needed for the faunas in Türkiye, with particular focus on the distinct terranes. For instance, while the Anatolide - Tauride block is linked to the northern border of Gondwana (Denayer, 2015), the Visean position of the Istanbul-Zonguldak terrane's position is uncertain (A. I. Okay & Tüysüz, 1999). This terrane could relate to the Moesian or Balkan terranes (Yanev, 2000; N. Okay et al., 2011). Detailed comparisons of faunas from the Istanbul-Zonguldak terrane and the Balkans, once the records are more complete, could provide valuable insights into these connections.

Future plans include extending the database to encompass the Pennsylvanian, enabling a comprehensive study of the entire Carboniferous period. Such an extension would face new limitations and constraints, since the progression of the Varican Orogeny and the closure of the Rheic Ocean significantly reduced the extent of marine basins in many regions (Vai, 2003). However, there are limestone beds with rugose coral records in the Saharan Basins in North Africa (Semenoff-Tian-Chansky, 1985), the Cantabrian Mountains in Spain (De Groot, 1963; Rodríguez, 1984; Boll, 1985), the Carnic Alps in Italy and Austria (Samankassou, 2003), the Donets Basin in Ukraine (Fomichev, 1953; Fedorowski, 2022), the Moscow Basin (Kossovaya, 1996, 1997; Briand et al., 1998) and Turkey (Vachard & Moix, 2011), which offer promising research opportunities. The study of these regions during the Pennsylvanian would allow for a more continuous analysis of rugose coral evolution across major geological events. Additionally, our current framework can serve as a foundation for more detailed studies. For stages with higher coral diversity, narrowing down the temporal scale at the biozone level could be beneficial. This level of detail would enhance the resolution of palaeogeographical interpretations and improve our understanding of evolutionary responses to environmental changes in the Mississippian.

Our palaeogeographical reconstructions could also benefit from implementing GPlates software (Müller et al., 2018), which enables model building and temporal visualization of data. Cao et al. (2017) described a methodology within this platform to improve the accuracy of coastal reconstructions incorporating palaeontological data, a technique that could further refine our Mississippian maps. Notably, a recent palaeogeographical reconstruction (Cao et al., 2024) has demonstrated the potential of this software, producing maps that trace 1.8 billion years of Earth's history. Applying similar methods to our dataset could provide a dynamic and visually enriched perspective of the Western Palaeotethys through the Mississippian.

Expanding the evolutionary analysis of Mississippian rugose corals (Chapter 7) to include additional families would benefit future studies. While the Lithostrotionidae, Lonsdaleiidae, Palaeosmiliidae and Zaphrentidae illustrate key evolutionary trends and processes, incorporating families such as the Aulophyllidae, Plerophyllidae, and Antiphyllidae could provide a broader view of rugose coral evolution during the Mississippian. Additionally, the tendency towards greater complexity observed qualitatively could be further studied with morphological disparity analysis. Examining the disparity of rugose corals through time could offer new insights into the evolutionary processes of the clade (Müller et al., 2018).

9 CONCLUSIONS

Our results and conclusions combine methodological and analytic contributions, as our objectives included the testing the utility of rugose corals for quantitative palaeogeographical studies, as well as conducting palaeogeographical, palaeobiogeographical, and evolutionary studies of the Mississippian rugose corals in the Western Palaeotethys.

One key outcome of this work is the compilation of a database including most rugose coral species and genera recorded in the Western Palaeotethys during the Mississippian period. It presents presence/absence data for the Tournaisian, the early Visean, the late Visean and the Serpukhovian, using both sub-provinces and more detailed palaeogeographical units. Partial versions of this database are featured in chapters five and six, with chapter seven including a more temporally precise synthesis, using the coral biozones proposed by Poty (1984) instead of stages. The updated version is included in Annex 1.

Our study also produced four palaeogeographical maps of the Western Palaeotethys, covering the Tournaisian, early Visean, late Visean and Serpukhovian stages (Chapter 6, figures 6-9). These maps document the approach of Gondwana toward Laurussia and the resulting formation, destruction and isolation of marine basins. They are based on previous palaeogeographical frameworks for the region (Webb, 2002; Somerville et al., 2020), and incorporate changes based on rugose coral distribution data. To support and inform these reconstructions, we developed a facies map of the late Visean Western Palaeotethys (Chapter 5, figure 1), comparing over thirty maps and articles (Chapter 5, table 1) to. This approach illustrates how coral fossil evidence can inform our understanding of Mississippian palaeogeography.

Quantitative analysis of rugose coral assemblages and their distribution can improve our palaeogeographical knowledge. Rugose corals have proven their utility in studies of various scales, from local (Chapter 2) to regional (Chapter 4) and provincial (Chapters 5 and 6). Large-scale analyses tend to average out the environmental influence, but for studies of local assemblages it is important to carefully considerate its effect on the results and select suitable data to reduce its impact.

Qualitative analysis of the distribution of particular genera and/or families also provides important palaeogeographical information (Chapter 3). The dispersal of specific taxa can offer insights into region connectivity, current dynamics and palaeobiogeographical barriers.

The compilation of extensive and detailed databases is also useful for evolutionary trends analysis (Chapter 7). It allowed us to observe the recovery of the rugose coral faunas after mass extinctions and the changes in their generic diversity in the Western Palaeotethys, highlighting the development of new colonial habits and more complex structural features among Mississippian rugose corals.

The studies and material featured in this thesis offer a detailed view of the Mississippian palaeogeography in the Western Palaeotethys and the distributions of rugose corals. They compile previously scattered data (Annex 1), describe new assemblages (Chapter 4), provide detailed analysis of local areas (Chapter 2), particular taxa (Chapter 3) and specific stages (Chapters 4 and 5), as well as presenting more general studies with provincial scope and conclusions (Chapters 6 and 7). Overall, this thesis builds upon previous knowledge to improve our understanding of the region and its rugose coral fauna.

However, our results are not without limitations. Homogenising data for Mississippian rugose corals presents challenges, mainly due to variations in specimen preservation, differences in material quality and availability across regions, imbalances in study detail and abundance, and diverse taxonomic approaches among experts. Any study relying on these databases requires careful consideration of the data and its inherent biases. Continued sampling and research efforts in the future will help mitigate some of these issues, refining the database and ultimately improving our knowledge and understanding of Mississippian rugose coral faunas.

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ANNEX 1

1.1 TOURNAISIAN:

Table 1: Presence/absence data of rugose coral genera across sub-provinces in the Western Palaeotethys during the Tournaisian.

Tournaisian Genera	Atlantic	Central European	Eastern European	Saharan
Allotropiophyllum	x			
Amplexizaphrentis		x		
Amplexocarinia	x	x		
Amplexus	x		x	x
Amygdalophyllum	x	x		
Aulina	x			
Aulokoninckophyllum	x			
Axophyllum	x			
Batybalva		x		
Bifossularia	x	x		
Calmiussiphyllum	x		x	
Campophyllum		x	x	
Caninophyllum	x	x		
Caninia	x	x	x	x
Carruthersella	x			
Claviphyllum		x		
Clisiophyllum	x	x		
Commutia		x		
Conilophyllum	x	x		
Corwenia	x			
Cravenia	x			
Cryptophyllum	x			
Cyathaxonia	x	x		
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	x		
Kueichouphyllum			x	
Laccophyllum		x		
Lophophyllidium		x		
Lophophyllum	x	x		
Lublinophyllum			x	
Melanophyllum	x			
Merlewoodia	x			
Nominoephyllum	x			
Palaeosmilia	x	x		
Pentaphyllum	x	x		
Proheterolasma	x		x	
Rhopalolasma	x			
Rotiphyllum	x	x	x	
Rylstonia	x		x	x
Saleelasma	x	x		
Semenoffia	x			
Siphonophyllia	x	x	x	x
Sochkineophyllum		x		
Solenodendron	x			
Sychnoelasma	x	x	x	x
Syringaxon	x			
Thuriantha		x		
Ufimia	x	x		
Uralinia	x		x	
Zaphrentites	x	x	x	
Zaphriphyllum	x			

Table 2: Presence/absence data of rugose coral genera across different regions in the Western Palaeotethys during the Tournaisian.

Tournaisian Genera	British Isles	Belgium N France	Germany	Poland	Donets	Moscow Basin	Türkiye	Sahara
Allotropiophyllum	x							
Amplexizaphrentis				x				
Amplexocarinia	x			x				
Amplexus	x	x			x			x
Amygdalophyllum	x	x		x				
Aulokoninckophyllum		x						
Axophyllum	x							
Batybalva			x					
Bifossularia		x		x				
Calmiussiphyllum		x			x		x	
Campophyllum	x		x		x			
Caninophyllum	x	x	x		x		x	
Caninia	x	x	x	x		x	x	x
Claviphyllum				x				
Clisiophyllum		x	x					
Commutia			x	x				
Conilophyllum	x	x	x	x				
Corwenia	x							
Cravenia	x	x						
Cryptophyllum	x							
Cyathaxonia	x	x	x	x		x		
Cyathyoclisia	x	x	x	x	x	x		
Delepinella		x						
Dorlodotia		x			x			
Drewerelasma	x		x	x				
Eostrotion		x		x				
Fasciculophyllum	x							
Hapsiphyllum		x		x				
Hebukophyllum			x	x				
Heterostrotion		x						
Howthia	x							
aff. *Kabakovitchiella*				x				
Keyserlingophyllum		x	x	x	x		x	
Kizilia		x						
Koninckophyllum	x			x				
Kueichouphyllum							x	
Laccophyllum			x					
Lophophyllum	x	x		x				
Lublinophyllum					x			
Merlewoodia		x						
Nominoephyllum		x						

Palaeosmilia		x		x				
Pentaphyllum	x	x	x					
Proheterolasma	x	x			x		x	
Rhopalolasma	x		x					
Rotiphyllum	x	x	x	x	x			
Rylstonia	x	x						x
Saleelasma	x	x	x					
Semenoffia		x						
Siphonophyllia	x	x	x	x		x	x	x
Sochkineophyllum			x					
Solenodendron	x	x						x
Sychnoelasma	x	x		x	x	x		x
Syringaxon		x						
Thuriantha			x					
Ufimia	x		x	x				
Uralinia		x				x	x	
Zaphrentites	x	x	x	x		x		
Zaphriphyllum		x						

Table 3: Presence/absence data of rugose coral species across different regions in the Western Palaeotethys during the Tournaisian.

Tournaisian species	British Isles	Belgium N France	Germany	Poland	Donets	Moscow Basin	Türkiye	Sahara
Allotropiophyllum burlingtonense	x							
Amplexizaphrentis parallela				x				
Amplexizaphrentis sp.				x				
Amplexocarinia cravenensis	x							
Amplexocarinia sp.				x				
Amplexus coralloides	x	x			x			x
Amygdalophyllum praecursor	x	x						
Amygdalophyllum sp.		x						
Amygdalophyllum sudeticum		x		x				
Amygdalophyllum vesiculosum	x	x						
Aulokoninckophyllum sp.		x						
Aulokoninckophyllum ngakoi		x						
Aulokoninckophyllum miloni		x						
Axophyllum. simplex	x							
Bathybalva crassa			x					
Bifossularia tictensis		x						
Bifossularia usowi		x						
Bifossularia sp.				x				
Calmiussiphyllum calmiusi					x			
Calmiussiphyllum dobrolyubovae							x	
Calmiussiphyllum sp.		x			x			
Campophyllum caninoides					x			
Campophyllum flexuosum			x					
Campophyllum sp.	x							
Caninophyllum archiaci		x						
Caninophyllum patulum	x	x					x	
Caninophyllum sp.	x	x	x		x			
Caninia dorlodoti				x				
Caninia comucopiae	x	x	x	x		x	x	x
Caninia lanceolata				x				
Caninia patula				x				
Caninia tregaensis		x						
Caninia sp.		x		x				
Claviphyllum eruca				x				
Clisiophyllum omaliusi			x					
Clisiophyllum parkinsoni		x						
Commutia longiseptata			x	x				
Conilophyllum priscum	x		x	x	x			
Conilophyllum streeli		x						
Conilophyllum tregaense			x					
Corphalia simplex					x			

Corwenia vaga	x							
Cravenia rhytoides	x	x						
Cravenia tela	x							
Cravenia sp.	x	x						
Cryptophyllum hibernicum	x							
Cyathaxonia cornu	x	x	x	x		x		
Cyathaxonia fameniana				x				
Cyathoclisia modavense	x	x	x	x	x	x		
Cyathoclisia monicae		x						
Cyathoclisia soshkinae		x						
Cyathoclisia uralensis					x			
Cyathoclisia sp.	x							
Delepinella anastomosa		x						
Dorlodotia pseudovermiculare		x			x			
Dorlodotia sp.		x						
Drewerelasma schindewolfi			x					
Drewerelasma sp.	x			x				
Eostrotion tortuosum		x		x				
Eostrotion sp.		x						
Fasciculophyllum ambiguum	x							
Fasciculophyllum densum	x	x						
Hapsiphyllum sp.		x		x				
Hebukophyllum priscum			x	x				
Heterostrotion sp.		x						
Howthia suttonensis	x							
aff. *Kabakovitchiella* sp.				x				
Keyserlingophyllum obliquum		x	x	x	x		x	
Kizilia kremersi		x						
Koninckophyllum praecursor	x							
Koninckophyllum tortuosum	x							
Kueichouphyllum alborzense							x	
Laccophyllum sp.			x					
Lophophyllum konincki		x						
Lophophyllum sp.	x			x				
Lublinophyllum sp.					x			
Merlewoodia avesnensis		x						
Nominoephyllum lardeuxi		x						
Palaeosmilia sp.		x						
Pentaphyllum hibernicum	x		x					
Pentaphyllum sp.		x						
Proheterelasma omaliusi	x	x			x		x	
Rhopalolasma tachyblastum	x		x					
Rotiphyllum ambiguum			x					
Rotiphyllum densum	x	x	x					

Rotiphyllum sp.	x	x		x				
Rotiphyllum omaliusi					x			
Rylstonia benecompacta	x	x						
Rylstonia laxocolumnata		x						x
Rylstonia smythi	x			x				
Saleelasma delepinei	x	x	x					
Semenoffia meodenensis		x						
Siphonophyllia caninoides		x						
Siphonophyllia cylindrica	x	x		x				
Siphonophyllia garwoodi		x						
Siphonophyllia gigantea	x	x						
Siphonophyllia hastariensis		x	x	x				
Siphonophyllia hettonensis		x						x
Siphonophyllia rivagensis		x						
Siphonophyllia sp.		x				x	x	
Sochkineophyllum sp.			x					
Solenodendron horsfieldi	x							
Solenodendron pillolai		x						
Solenodendron sp.		x						x
Sychnoelasma clevedonensis	x							
Sychnoelasma hawbankensis	x	x						
Sychnoelasma konincki	x	x		x	x	x		
Sychnoelasma sp.								x
Syringaxon beruinensis		x						
Thuriantha muelleri			x					
Ufimia tachyblastum	x		x					
Ufimia sp.			x	x				
Uralinia lobata		x						
Uralinia multiplex		x					x	
Uralinia sp.						x	x	
Zaphrentites crassus	x							
Zaphrentites delanouei	x	x					x	
Zaphrentites parallela				x		x		
Zaphrentites vaughani	x							
Zaphrentites sp.	x	x	x	x		x		

1.2 EARLY VISEAN

Table 4: Presence/absence data of rugose coral genera across different sub-provinces in the Western Palaeotethys during the early Visean.

Early Visean Genera Subprovinces	Atlantic	Central European	Eastern European	West Peri-Gondwanan	Saharan
Allotropiophyllum	x				
Amplexizaphrentis	x				
Amplexocarinia					x
Amplexus	x	x	x		
Amygdalophyllum	x		x		
Aulina					x
Auloclisia	x	x			
Aulokoninckophyllum	x				
Axoclisia	x				
Axophyllum	x	x			
Bifossularia	x	x			x
Bradyphyllum		x			
Calmiussiphyllum			x		
Calophyllum		x			
Campophyllum			x		
Caninia	x	x	x		x
Caninophyllum	x		x		
Carruthersella	x	x			
Clinophyllum		x			
Clisiophyllum	x	x	x		
Corphalia	x				
Cravenia	x			x	
Cyathaxonia	x	x		x	
Cyathoclisia	x	x	x		
Dibunophyllum		x			
Diphyphyllum	x		x		
Dorlodotia	x	x	x		
Drewerelasma		x	x		
Eolithiostrotionella			x		
Fasciculophyllum	x				
Haplolasma	x		x		
Hettonia		x			
Koninckophyllum	x		x		
Kueichouphyllum					
Laccophyllum		x			
Lithostrotion	x	x			
Merlewoodia	x				
Palaeosmilia	x	x			x

Pentaphyllum		x			
Proheterelasma	x				
Richrathina		x			
Rotiphyllum		x	x		
Rylstonia		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		
Zaphrentites	x	x	x		x
Zaphrentoides		x			x
Zaphriphyllum					x

Table 5: Presence/absence data of rugose coral genera across different regions in the Western Palaeotethys during the early Visean.

Early Visean Genera	British Isles	Belgium N France	Germany	Poland	Donets	Moscow Basin	Turkiye	Morocco	Sahara
Allotropiophyllum	x								
Amplexizaphrentis	x								
Amplexocarinia									x
Amplexus	x	x	x		x				
Amygdalophyllum	x	x			x		x		
Arachnolasma	x			x					
Aulina									x
Auloclisia	x		x						x
Aulokoninckophyllum		x							
Axoclisia		x							
Axophyllum	x	x	x						
Bifossularia		x		x			x		x
Bradyphyllum				x					
Calmiussiphyllum					x				
Calophyllum			x						
Campophyllum					x				
Caninia	x	x	x		x	x			x
Caninophyllum	x	x			x				
Carruthersella	x		x						
Clinophyllum			x						
Clisiophyllum	x	x	x		x				
Corphalia		x							
Cravenia	x	x						x	
Cyathaxonia	x	x	x					x	
Cyathoclisia	x	x	x		x	x			
Dibunophyllum			x						
Diphyphyllum	x				x				
Dorlodotia	x	x	x		x				
Drewerelasma			x						
Eokoninckocarinia							x		
Eolithiostrotionella					x				
Fasciculophyllum	x								
Haplolasma	x	x			x				
Hettonia			x						
Koninckophyllum	x	x			x				
Kueichouphyllum							x		
Laccophyllum			x						
Lithostrotion	x	x	x						
Merlewoodia		x							
Palaeosmilia	x	x	x				x		x
Pentaphyllum			x						

Proheterelasma		x							
Protolonsdaleia					x				
Richrathina			x						
Rotiphyllum			x		x				
Rylstonia			x						x
Siphonodendron	x	x	x	x	x	x			x
Siphonophyllia	x	x	x			x		x	x
Solenodendron	x	x	x						x
Spirophyllum				x					
Sychnoelasma	x	x	x		x	x		x	x
Syringaxon				x					
Ufimia			x						
Uralinia			x			x			
Vassiljukia					x				
Verneuilites					x				
Zaphrentites	x	x	x			x			x
Zaphrentoides			x						x
Zaphriphyllum									x

Table 6: Presence/absence data of rugose coral species across different regions in the Western Palaeotethys during the early Visean.

Early Visean Species	British Isles	Belgium N France	Germany	Poland	Donets	Moscow Basin	Turkiye	Morocco	Sahara
Allotropiophyllum burlingtonense	x								
Amplexizaphrentis ashfellensis	x								
Amplexizaphrentis enniskilleni	x								
Amplexocarinia sp.									x
Amplexus coralloides	x	x			x				
Amplexus sp.	x		x						
Amygdalophyllum meathopense					x				
Amygdalophyllum praecursor	x	x							
Amygdalophyllum tanaicum					x				
Amygdalophyllum sp.		x					x		
Aulina horsfieldi	x								
Auloclisia sp.			x						
Aulokoninckophyllum ngakoi		x							
Axoclisia cuspiforma		x							
Axophyllum excentricum			x						
Axophyllum mendipense	x	x							
Axophyllum nanum		x							
Axophyllum simplex	x	x			x				
Axophyllum vaughani	x	x							
Axophyllum sp.		x							
Bifossularia tictensis		x							
Bifossularia sp.		x		x			x		x
Bradyphyllum bojkowskii				x					
Calmiussiphyllum sp.					x				
Calophyllum carbonicum			x						
Calophyllum compacta			x						
Calophyllum quadriseptatum			x						
Campophyllum caninoides					x				
Caninia aberrans					x				
Caninia cornucopiae	x	x				x			x
Caninia subibicina					x				
Caninia sp.	x		x						
Caninophyllum archiaci	x	x							
Caninophyllum bristoliense	x								
Caninophyllum patulum	x	x							
Caninophyllum robustum					x				
Carruthersella compacta	x								
Carruthersella sp.			x						
Ceriodotia bartinensis					x				
Ceriodotia petalaxoides					x				
Clinophyllum sp.			x						

Clisiophyllum garwoodi		x							
Clisiophyllum ingletonense	x								
Clisiophyllum multiseptatum	x				x				
Clisiophyllum parkinsoni		x							
Clisiophyllum rigidum	x								
Clisiophyllum sp.	x	x	x						
Corphalia mosae		x							
Corphalia sp.		x							
Cravenia lamellata	x							x	
Cravenia rhytoides	x	x						x	
Cravenia tela	x							x	
Cyathaxonia cornu	x	x	x						
Cyathaxonia rushiana	x		x						
Cyathaxonia sp.			x					x	
Cyathoclisia modavense	x	x	x		x	x			
Cyathoclisia sukhensis					x				
Cyathoclisia sp.		x							
Dibunophyllum sp.			x						
Diphyphyllum lateseptatum					x				
Diphyphyllum smithi	x								
Dorlodotia briarti	x	x	x		x				
Dorlodotia pseudovermiculare	x				x				
Dorlodotia sp.		x							
Drewerelasma sp.			x						
Eokoninckocarinia gemmina							x		
Eolithostrotionella zizhinae					x				
Fasciculophyllum densum	x								
Fasciculophyllum omaliusi	x								
Fasciculophyllum sp.	x								
Haplolasma conili		x							
Haplolasma subibicinum	x				x				
Haplolasma sp.		x							
Hettonia sp.			x						
Koninckophyllum ashfellense	x								
Koninckophyllum carlyanense	x								
Koninckophyllum clitheroense	x								
Koninckophyllum cyathophylloides	x								
Koninckophyllum fragile	x								
Koninckophyllum meathopense	x								
Koninckophyllum praecursor	x								
Koninckophyllum vesiculosum	x								
Koninckophyllum sp.		x			x				
Kueichouphyllum alborzense							x		
Kueichouphyllum yabei							x		

Kueichouphyllum sp.							x		
Laccophyllum sp.			x						
Lithostrotion araneum	x	x	x						
Lithostrotion decipiens	x								
Lithostrotion pelhatae		x							
Lithostrotion vorticale	x								
Merlewoodia avesnensis		x							
Merlewoodia sp.		x							
Palaeosmilia murchisoni	x	x	x				x		x
Palaeosmilia sp.	x		x						
Pentaphyllum sp.			x						
Proheterolasma sp.		x							
Protolonsdaleia mariupolensis					x				
Richrathina pauli			x						
Rotiphyllum nodosum			x						
Rotiphyllum omaliusi			x		x				
Rylstonia sp.			x						x
Siphonodendron columnariformis					x				
Siphonodendron irregulare		x			x				
Siphonodendron martini	x	x							x
Siphonodendron multiradiale	x								
Siphonodendron ondulosum		x			x				
Siphonodendron pauciradiale									x
Siphonodendron sarthensis		x							
Siphonodendron scaleberense	x								
Siphonodendron sociale	x	x	x						
Siphonodendron tanaicum					x				
Siphonodendron sp.	x		x		x	x			
Siphonophyllia benburbensis			x						
Siphonophyllia caninoides	x								
Siphonophyllia casweliense	x								
Siphonophyllia ciliata	x								
Siphonophyllia cylindrica	x	x	x			x			
Siphonophyllia garwoodi	x		x						
Siphonophyllia hettonensis	x								x
Siphonophyllia khenifrense								x	
Siphonophyllia siblyi		x							
Solenodendron hibernicum			x						
Solenodendron horsfieldi	x								x
Solenodendron pillolai		x							
Spirophyllum sp.				x					
Sychnoelasma hawbankense	x	x			x				
Sychnoelasma konincki	x	x							
Sychnoelasma urbanowitschi	x	x	x		x	x		x	

Sychnoelasma sp.	x								x
Syringaxon sp.				x					
Ufimia hudsoni			x						
Ufimia inaequalis			x						
Ufimia longiseptata			x						
Ufimia tricyclica			x						
Uralinia sp.			x			x			
Vassiljukia columnariformis					x				
Verneuilites konicki					x				
Zaphrentites crassus	x	x							
Zaphrentites delanouei									x
Zaphrentites sp.	x		x			x			
Zaphrentoides sp.			x						x
Zaphriphyllum sp.									x

1.3 LATE VISEAN

Table 7: Presence/absence data of rugose coral genera across different sub-provinces in the Western Palaeotethys during the late Visean.

Late Visean Genera	Atlantic	West Peri-Gondwan	Saharan	Mediterranean	Central European	Eastern European
Actinocyathus	x			x	x	x
Allotropiophyllum.	x				x	x
Amplexizaphrentis	x	x	x		x	x
Amplexocarinia	x	x	x		x	x
Amplexus	x	x		x	x	x
Amygdalophylloides		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	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	
Claviphyllum		x			x	x
Clisiophyllum	x	x	x	x	x	x
Corwenia	x	x				x
Cravenia	x	x				
Cryptophyllum					x	
Cyathaxonia	x	x			x	x
Dibunophyllum	x	x	x	x	x	x
Diphyphyllum	x	x	x	x	x	x
Enniskillenia	x					x
Eolithostroniella						x
Espielia		x	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					
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	x
Pareynia	x	x	x	x		
Pentaphyllum	x			x	x	
Permia						x
Pseudocaninia					x	
Pseudozaphrentoides’	x	x	x		x	x
Rotiphyllum	x	x		x	x	
Rozkowskia					x	
Rylstonia	x	x	x		x	x
Saharaphrentis			x			
Semenoffia	x	x		x		
Siphonodendron	x	x	x	x	x	x
Siphonophyllia	x	x	x	x	x	x
Slimoniphyllum	x				x	
Sochkineophyllum		x				
Solenodendron	x	x		x	x	x
Spirophyllum	x	x			x	x
Syringaxon				x		
Tachylasma					x	
Thysanophyllum	x			x		
Tizraia		x	x			x
Turbinatocaninia			x		x	x
Ufimia		x			x	x
Viseaulina	x					
Vojnovskytes				x		
Zakowia					x	
Zaphrentoides		x				
Zaphrentites	x	x	x		x	x
Zaphrufimia	x	x			x	

Table 8: Presence/absence data of rugose coral genera across different regions in the Western Palaeotethys during the late Visean.

Late Visean Genera	Nova Scotia	Ireland	N. Britain	S. Britain	Belgium - N. France	South France - Cantabrian	Germany	Poland	Balkans	Donets Basin	Moscow Basin	Turkiye	SW Spain	N. Morocco	Sahara
Actinocyathus		x	x	x	x	x	x	x		x	x				
Allotropiophyllum.		x	x	x				x		x					
Amplexizaphrentis		x	x	x			x	x		x	x		x	x	x
Amplexocarinia		x	x	x	x		x	x			x	x	x	x	x
Amplexus		x	x	x	x	x	x			x	x		x	x	
Amygdalophylloides													x		
Amygdalophyllum				x	x			x	x			x	x		x
Antiphyllum										x					
Arachnolasma		x		x	x	x		x		x	x		x	x	x
Auloclisia				x			x		x				x	x	x
Aulokoninckophyllum		x	x	x	x	x	x	x	x	x	x	x	x	x	x
Aulophyllum		x	x	x	x		x	x	x	x	x	x	x	x	x
Axoclisia					x		x			x			x	x	x
Axophyllum	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Bifossularia					x			x		x				x	
Biphyllum								x							
Bothrophyllum					x			x	x	x				x	
Bradyphyllum					x	x		x					x	x	
Calophyllum							x	x							
Campophyllum								x							
Caninia		x	x	x	x		x	x	x	x	x	x	x	x	x
Caninophyllum			x	x	x				x	x	x	x	x	x	x
Carruthersella				x			x	x							x
Ceriodotia												x			
Claviphyllum								x		x				x	
Clisiophyllum		x	x	x	x	x	x	x	x	x	x	x	x	x	x
Corwenia		x	x	x						x	x	x		x	
Cravenia				x										x	
Cryptophyllum								x							
Cyathaxonia	x	x	x	x	x		x	x		x	x		x	x	
Dibunophyllum	x	x	x	x	x	x	x	x	x	x	x		x	x	x
Diphyphyllum		x	x	x	x	x	x	x		x	x		x	x	x
Enniskillenia				x						x	x				
Eolithostroniella										x					
Espielia						x						x	x		x
Gangamophyllum					x	x		x	x	x	x	x	x	x	x
Guadiatia					x										
Haplolasma		x	x	x	x	x		x		x	x	x	x	x	x
Kizilia					x	x		x			x			x	x
Koninckinaotum								x			x				

Koninckophyllum	x	x	x	x	x	x	x	x	x	x			x	x	x
"Koninckophyllum" (colonial)	x	x													
Kwangsiphyllum												x			
Lithostrotion		x	x	x	x	x	x	x	x	x	x	x	x	x	x
Lonsdaleia	x	x	x	x	x	x	x			x	x	x			x
Lophophyllidium															x
Lophophyllum								x							
Lublinophyllum				x				x							
Melanophyllidium						x									
Merlewoodia					x										
Mirka								x							
Morenaphyllum													x		
Neoclisiophyllum					x			x					x	x	
Neokoninckophyllum								x		x					
Nemistium	x	x	x	x		x		x		x	x	x			
Nervophyllum								x		x	x				
Orionastraea		x	x	x				x		x	x				
Palaeosmilia		x	x	x	x	x	x	x	x	x	x	x	x	x	x
Palastraea	x	x	x	x	x	x	x	x		x	x	x	x	x	x
Pareynia					x	x								x	x
Pentaphyllum					x	x	x	x							
Permia										x					
Pseudocaninia							x								
Pseudoclaviphyllum										x					
Pseudozaphrentoides’		x	x	x	x	x	x			x	x		x	x	x
Rotiphyllum		x	x	x	x	x	x	x				x	x	x	
Rozkowskia							x	x							
Rylstonia		x	x	x	x			x		x			x		x
Saharaphrentis															x
Semenoffia					x	x								x	
Siphonodendron	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Siphonophyllia		x	x	x	x	x	x	x	x	x	x		x	x	x
Slimoniphyllum				x				x							
Sochkineophyllum												x			
Solenodendron		x	x	x	x	x	x			x			x	x	
Spirophyllum					x			x		x			x		
Tachylasma											x				
Thysanophyllum		x	x	x											
Tizraia										x			x	x	x
Turbinatocaninia								x		x					x
Ufimia							x	x		x			x	x	
Viseaulina					x										
Vojnovskytes						x									
Zakowia								x							
Zaphrentites		x	x	x	x		x	x		x	x		x	x	x
Zaphrufimia		x	x	x			x	x					x	x	

Table 9: Presence/absence data of rugose coral specoes across different regions in the Western Palaeotethys during the late Visean.

Late Visean Species	Nova Scotia	Ireland	N. Britain	S. Britain	Belgium - N France	South France-Cantabrian Mnts.	Germany	Poland	Balkans	Donets basin	Moscow Basin	Turkiye	SW Spain	N. Morocco	Sahara
Actinocyathus bronni											x				
Actinocyathus floriformis		x		x	x	x		x		x	x				
Actinocyathus crassiconus										x	x				
Actinocyathus latevesiculosus											x				
Actinocyathus longiseptatus										x					
Actinocyathus sp.			x			x	x								
Allotropiophyllum sp.		x	x	x				x		x					
Amplexizaphrentis derbiensis				x											
Amplexizaphrentis enniskilleni				x							x				
Amplexizaphrentis sp.		x	x				x	x		x	x		x	x	x
Amplexocarinia sp.				x	x		x	x			x		x	x	x
Amplexocarinia gregaria							x							x	
Amplexocarinia cravenensis				x								x			
Amplexus coralloides				x	x	x							x	x	
Amplexus sp.		x	x	x			x			x	x		x	x	
Amygdalophylloides anticuum													x		
Amygdalophyllum asselense															x
Amygdalophyllum axophylloides								x							
Amygdalophyllum etheridgei				x	x										x
Amygdalophyllum turbophylloides															x
Amygdalophyllum sp.					x				x			x	x	x	x
Antiphyllum eruca										x					
Arachnolasma biseptatum								x							
Arachnolasma castelsecensis						x									
Arachnolasma djihaniense															x
Arachnolasma irregulare										x					
Arachnolasma lapparenti															x
Arachnolasma sinense					x			x					x	x	x
Arachnolasma cylindrica								x		x	x			x	x
Arachnolasma microcolumella								x							
Arachnolasma subpercrassum								x							
Arachnolasma sp.		x		x	x										x
Auloclisia sp.				x			x		x				x	x	x
Aulokoninckophyllum amarensis															
Aulokoninckophyllum carinatum					x	x				x	x		x	x	x
Aulokoninckophyllum ubagshi					x										
Aulokoninckophyllum sp.		x	x	x										x	
Aulophyllum fungites		x	x	x	x		x	x	x	x	x	x	x	x	x
Axoclisia cuspiforma					x					x			x	x	x
Axoclisia sp.							x								

Axophyllum densum		x			x	x					x		x	x	x
Axophyllum dibunoides															x
Axophyllum dibunophylloides														x	
Axophyllum expansum					x	x					x			x	
Axophyllum kirsopianum				x	x					x	x		x	x	
Axophyllum lonsdaleiforme				x	x	x				x	x				
Axophyllum nanum					x	x							x	x	
Axophyllum parkinsoni				x											x
Axophyllum pseudokirsopianum					x	x						x	x	x	x
Axophyllum tazoultense															x
Axophyllum vaughani			x		x			x							
Axophyllum sp.	x					x	x	x	x						
Bifossularia sp.					x			x		x				x	
Biphyllum vallum								x							
Bothrophyllum archiaci								x							
Bothrophyllum berestovensis										x					
Bothrophyllum juddi								x							
Bothrophyllum lateseptatum					x										
Bothrophyllum pater								x							
Bothrophyllum sp.					x			x	x					x	
Bradyphyllum sp.					x	x		x					x	x	
Bradyphyllum rotiphylloides					x								x	x	
Calophyllum sp.							x	x							
Campophyllum compressum								x							
Caninia cornucopiae		x		x	x			x			x	x			
Caninia matea															x
Caninia sp.			x	x	x		x	x	x	x	x	x	x	x	
Caninophyllum archiaci			x	x	x						x	x		x	x
Caninophyllum becharense													x	x	x
Caninophyllum bristoliense				x											
Caninophyllum halkynense					x										
Caninophyllum sp.									x	x					
Carruthersella garwoodi								x							x
Carruthersella longiseptata								x							
Carruthersella menchikovi															x
Carruthersella sp.				x			x								
Ceriodotia bartinensis												x			
Ceriodotia petalaxoides												x			
Claviphyllum sp.								x		x				x	
Clisiophyllum benziregense													x		x
Clisiophyllum crasiseptatum					x									x	x
Clisiophyllum delicatum								x							
Clisiophyllum garwoodi				x	x	x		x			x	x	x	x	
Clisiophyllum keyserlingi		x	x	x	x	x		x		x	x			x	x
Clisiophyllum macrocolumellatum														x	
Clisiophyllum monoseptatum								x							
Clisiophyllum neaversoni								x							
Clisiophyllum reticulatum										x					
Clisiophyllum subturbinatum											x				
Clisiophyllum vacuum								x							

Clisiophyllum sp.			x		x		x		x	x	x	x			
Corwenia densivesiculosa											x				
Corwenia eichwaldi											x				
Corwenia rugosa		x	x	x						x	x				
Corwenia vaga				x						x	x				
Corwenia verneuili											x				
Corwenia sp.			x									x		x	
Cravenia				x											
Cryptophyllum hibernicum								x							
Cyathaxonia cornu	x	x	x	x	x		x	x		x	x		x	x	
Cyathaxonia rushiana				x	x								x		
Cyathaxonia sp.							x								
Dibunophyllum arachnoforme															x
Dibunophyllum akachaense															x
Dibunophyllum bipartitum	x	x	x	x	x	x	x	x	x	x	x		x	x	x
Dibunophyllum bourtonense		x		x											
Dibunophyllum burhennei							x								
Dibunophyllum dobroljubovae										x					
Dibunophyllum fomitschevi										x					
Dibunophyllum lambii	x														
Dibunophyllum linnense				x				x							
Dibunophyllum lissitzini								x		x					
Dibunophyllum longiseptatum										x					
Dibunophyllum pachyseptatum											x				
Dibunophyllum percrassum								x		x	x				
Dibunophyllum pruvosti															x
Dibunophyllum pseudoturbinatum								x		x	x				
Dibunophyllum turbinatum										x	x				
Dibunophyllum sp.						x	x	x		x					x
Diphyphyllum concinnum							x								
Diphyphyllum fasciculatum				x	x					x	x			x	
Diphyphyllum furcatum		x	x	x	x	x				x	x		x	x	
Diphyphyllum gracile											x				x
Diphyphyllum irregulare								x							
Diphyphyllum lateseptatum		x		x	x		x	x		x	x			x	
Diphyphyllum maximum					x						x				
Diphyphyllum multicystatum											x				
Diphyphyllum rarevesiculosum								x							
Diphyphyllum vermiculare											x				
Dorlodotia briarti												x			
Dorlodotia delepinei												x			
Dorlodotia euxinensis												x			
Enniskillenia curvilinea				x						x	x				
Eolithostroniella zhizhinae										x					
Espielia columellata													x		x
Espielia sp.						x						x	x		x
Gangamophyllum boreale						x		x	x	x	x	x	x	x	x
Gangamophyllum densitabulatum					x										
Gangamophyllum gorskyi										x					
Gangamophyllum grandis										x					

Gangamophyllum kumpani										x					
Gangamophyllum latum						x									
Guadiatia sp.					x										
Haplolasma arciferum															x
Haplolasma conili				x	x										
Haplolasma lamelliferum													x	x	x
Haplolasma densum		x	x	x	x	x		x			x			x	
Haplolasma paraarciferum															x
Haplolasma parvicarinatum															x
Haplolasma sp.			x			x		x		x		x		x	
Kizilia concavitabulata					x	x					x			x	x
Kizilia crassiseptata						x									
Kizilia gregaria					x										
Kizilia sp.					x			x			x			x	x
Koninckinaotum pseudocoloniale								x							
Koninckinaotum volgensis											x				
Koninckophyllum cinctum								x							
Koninckophyllum complexum															
Koninckophyllum delepinei															x
Koninckophyllum destitum															x
Koninckophyllum distans															x
Koninckophyllum interruptum		x		x	x	x		x		x			x	x	x
Koninckophyllum magnificum	x	x		x	x	x		x					x	x	x
Koninckophyllum meathopense				x				x							
Koninckophyllum variabile					x										x
Koninckophyllum vaughani				x				x							
Koninckophyllum proprium				x				x							
Koninckophyllum protocolonicum				x				x							
Koninckophyllum sp.			x			x	x							x	x
Koninckophyllum sp. colonial	x	x													
Kwangsiphyllum sp.												x			
Lithostrotion acolumellata											x				
Lithostrotion araneum		x		x	x		x			x		x	x	x	x
Lithostrotion columellata											x				
Lithostrotion decipiens		x		x	x	x		x	x	x	x		x	x	x
Lithostrotion maccoyanum		x	x	x	x			x		x	x	x	x	x	
Lithostrotion? tareense						x									
Lithostrotion termieri														x	
Lithostrotion vorticale		x	x	x	x					x	x		x	x	x
Lithostrotion aff. *vorticale*													x		
Lithostrotion sp.							x							x	
Lonsdaleia bashkirica						x									
Lonsdaleia corbariensis						x									
Lonsdaleia crassiconus	x														
Lonsdaleia duplicata	x	x	x	x	x	x				x	x	x			x
Lonsdaleia redondensis						x									
Lonsdaleia tschussoviana										x					
Lonsdaleia sp.					x	x	x			x					
Lophophyllidium sp.															x
Lophophyllum confertum								x							

Lophophyllum sp.								x							
Lublinophyllum fedorowskii								x							
Lublinophyllum sp.				x											
Melanophyllidium sp.						x									
Merlewoodia sp.					x										
Mirka prima								x							
Morenaphyllum antolinense															
Morenaphyllum boyerense															
Morenaphyllum sp.															
Neoclisiophyllum ingletonense					x			x					x	x	
Neokoninckophyllum soshkinae								x		x					
Neokoninckophyllum tanaicum								x		x					
Nemistium edmonsi				x											
Nemistium grandis										x					
Nemistium sp.	x	x	x	x		x		x			x	x			
Nervophyllum beshevensis										x					
Nervophyllum intermedium								x			x				
Nervophyllum primitivum								x							
Orionastraea ensifer			x	x				x			x				
Orionastraea garwoodi				x							x				
Orionastraea kurakovensis								x			x				
Orionastraea magna								x							
Orionastraea phillipsi			x							x					
Orionastraea placenta		x	x	x						x					
Orionastraea prerete				x						x	x				
Orionastraea rareseptata											x				
Orionastraea rete		x	x												
Palaeosmilia multiseptata												x			x
Palaeosmilia murchisoni		x	x	x	x	x	x	x	x	x	x	x	x	x	x
Palaeosmilia ressoti															x
Palaeosmilia stutchburyi		x	x	x	x		x								
Palastraea carbonaria			x			x							x		x
Palastraea microcellularia			x												
Palastraea regia	x	x	x	x	x	x	x	x		x	x	x	x	x	x
Palastraea vermiformis			x												
Pareynia gangamophylloides															x
Pareynia splendens					x	x								x	x
Pentaphyllum bulbosum							x								
Pentaphyllum sp.					x	x		x							
Permia stuckenbergi										x					
Pseudocaninia longisepta							x								
Pseudoclaviphyllum tenuiseptata										x					
Pseudodorlodotia subkakimii										x					
Pseudozaphrentoides' alloiteaui															x
Pseudozaphrentoides' juddi		x	x	x	x		x			x	x		x	x	x
Pseudozaphrentoides sp.						x	x								
Rotiphyllum densum				x								x			
Rotiphyllum rushianum					x	x		x					x	x	
Rotiphyllum sp.		x	x		x		x	x					x	x	
Rozkowskia compacta								x							

Rozkowskia parva							x	x							
Rozkowskia sp.								x							
Rylstonia benecompacta		x	x	x	x			x		x			x		x
Saharaphrentis illizidensis															x
Saharaphrentis tirechouminoidense															x
Semenoffia viseensis					x	x								x	
Siphonodendron crassocolumennatum										x					
Siphonodendron curvatum										x					
Siphonodendron' dobrolyubovae								x							
Siphonodendron intermedium	x	x		x	x					x	x			x	x
Siphonodendron irregulare	x	x		x	x	x		x		x	x	x	x	x	x
Siphonodendron junceum		x	x	x	x			x		x	x	x	x	x	
Siphonodendron kleffense					x		x						x	x	
Siphonodendron martini		x	x	x	x			x		x	x	x	x	x	x
Siphonodendron multiradiale				x						x				x	
Siphonodendron ondulosum					x							x			
Siphonodendron pauciradiale	x	x	x	x	x	x		x		x	x	x	x	x	x
Siphonodendron rossicum										x	x				
Siphonodendron scaleberense		x	x	x	x								x	x	
Siphonodendron sociale				x	x		x			x	x		x	x	x
Siphonodendron tanaicum										x					
Siphonodendron sp.			x				x					x			x
Siphonophyllia benburbensis							x								
Siphonophyllia garwoodi							x								
Siphonophyllia samsonensis		x		x	x	x							x	x	x
Siphonophyllia siblyi			x	x	x	x		x	x	x	x		x	x	x
Siphonophyllia sp.														x	
Slimoniphyllum quadrifossulum								x							
Slimoniphyllum slimonianum				x				x							
Sochkineophyllum sp.												x	x		
Solenodendron furcatum		x	x	x	x	x				x			x	x	
Solenodendron hibernicum				x			x							x	
Solenodendron horsfieldi				x						x			x		
Solenodendron ramosa															
Spirophyllum bifurcatum								x							
Spirophyllum clisium								x							
Spirophyllum complexum								x							
Spirophyllum densum								x							
Spirophyllum divisum								x							
Spirophyllum geminum															
Spirophyllum histiophylloides								x					x		
Spirophyllum multilamellatum								x					x		
Spirophyllum nexilis								x		x			x		
Spirophyllum perditum								x							
Spirophyllum regulare								x							
Spirophyllum sanctaecrucense								x							
Syringaxon sp.						x									
Tachylasma sp.											x				
Thysanophyllum		x	x	x											
Tizraia berkhlii														x	x

Tizraia sp.													x	x	
Tschernowiphyllum podboriensis											x				
Turbinatocaninia tyszowcensis								x							
Turbinatocaninia sp.										x					x
Ufimia bradbournense							x								
Ufimia infracarbonica								x							
Ufimia sp.										x			x	x	
Viseaulina singularis					x										
Vojnovskkytes marcinowskii						x									
Zakowia parva								x							
Zakowia sanctaecrucensis								x							
Zakowia sp.								x							
Zaphrentites delanouei				x						x					
Zaphrentites parallela				x						x			x		
Zaphrentites sp.		x	x		x		x	x		x	x		x	x	x
Zaphrentoides sp.													x		
Zaphrufimia sp.		x	x	x			x	x					x	x	

1.4 SERPUKHOVIAN

Table 10: Presence/absence data of rugose coral genera across different sub-provinces in the Western Palaeotethys during the Serpukhovian.

Serpukhovian Genera Sub-provinces	Atlantic	West Peri-Gondwanan	Saharan	Mediterranean	Central European	Eastern European
Actinocyathus			x	x		x
Adamanophyllum						x
Amplexizaphrentis	x					x
Amplexocarinia		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
Caninophyllum			x			x
Caninostrotion				x		
Carruthersella			x			
Claviphyllum		x			x	x
Clisiophyllum	x	x	x	x	x	x
Corwenia		x				x
Cyathaxonia		x			x	x
Cystolonsdaleia						
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	x
Guadiatia		x				
Haplolasma			x	x		
Hapsiphyllum						x
Kizilia		x	x	x		x
Koninckophyllum	x		x	x	x	x
Leonardophyllum				x		
Lithostrotion	x	x	x	x	x	x
Lonsdaleia	x		x	x	x	x
Lophophyllidium					x	
Lublinophyllum					x	

Lytvophyllum						x
Melanophyllidium				x		
Mirka					x	
Morenaphyllum		x				
Nemistium			x	x		
Nervophyllum						x
Nina						x
Ostravaia					x	
Palaeosmilia	x	x	x	x	x	x
Palaeosmilia			x			
Palastraea	x	x	x	x		
Pareynia		x	x			
Plerophyllum				x		
Pseudoaulina			x			
Pseudozaphrentoides’	x	x	x	x	x	
Rotiphyllum		x			x	
Rylstonia						x
Schoenophyllum						x
Serraphyllum				x		
Silesamplus					x	
Siphonodendron	x	x	x	x	x	x
Siphonophyllia		x	x	x	x	
Slimoniphyllum					x	x
Solenodendron		x			x	
Spirophyllum			x		x	
Tachylasma					x	x
Thysanophyllum	x					
Tizraia		x	x			
Turbinatocaninia	x				x	x
Ufimia				x		x
Variaxon						x
Vojnimitor				x		
Vojnovskytes				x		
Zakowia					x	
Zaphrentites	x	x		x	x	x
Zaphriphyllum						x
Zaphrufimia					x	x

Table 11: Presence/absence data of rugose coral genera across different regions in the Western Palaeotethys during the Serpukhovian.

Serpukhovian Genera	Nova Scotia	British Isles	Austria	Poland	Donets Basin	Moscow Basin	South France	Cantabrian Mts.	Baetic Cordillera	SW Spain	N. Morocco	Sahara
Actinocyathus					x	x	x	x	x			x
Adamanophyllum					x							
Amplexizaphrentis	x	x			x	x						
Amplexocarinia										x	x	
Amplexus		x			x					x	x	
Amygdalophyllum										x		x
Antiphyllites				x								
Antiphyllum				x								
Arachnolasma			x		x	x				x	x	x
Aulina		x			x	x	x					x
Auloclisia						x					x	
Aulokoninckophyllum			x		x					x	x	x
Aulophyllum		x			x	x				x	x	x
Axophyllum		x	x		x		x	x	x	x	x	x
Barytichisma					x							
Bothrophyllum				x	x	x						x
Caninia		x	x	x	x							
Caninophyllum					x							x
Caninostrotion								x				
Carruthersella												x
Claviphyllum				x		x					x	
Clisiophyllum		x	x		x	x	x		x	x	x	x
Corwenia		x			x	x					x	
Cyathaxonia			x		x	x					x	
Diaschophyllum												x
Dibunophyllum		x	x		x	x	x	x	x	x	x	x
Diphyphyllum		x	x		x	x	x	x		x	x	x
Effigies				x								
Eostrotion					x							
Fasciculophyllum				x								
Gangamophyllum					x	x	x	x	x			x
Guadiatia										x		
Haplolasma										x	x	x
Hapsiphyllum					x							
Kizilia						x	x			x		x
Koninckophyllum		x	x		x	x	x	x	x			x
Leonardophyllum							x					
Lithostrotion		x		x	x	x	x			x	x	x
Lonsdaleia		x	x		x	x	x	x	x			x
Lophophyllidium			x									
Lublinophyllum			x									

Lytvophyllum						x						
Melanophyllidium							x					
Mirka				x								
Morenaphyllum										x		
Nemistium							x					x
Neokoninckophyllum				x	x							
Nervophyllum					x							
Nina					x							
Ostravaia				x								
Palaeosmilia		x	x		x	x	x	x	x	x	x	x
Palastraea		x					x				x	x
Pareynia										x	x	x
Plerophyllum								x				
Pseudoaulina												x
Pseudozaphrentoides’		x	x				x	x	x	x	x	x
Rotiphyllum				x							x	
Rylstonia						x						
Schoenophyllum						x						
Serraphyllum							x					
Silesamplus				x								
Siphonodendron		x	x	x	x	x	x	x	x		x	x
Siphonophyllia			x							x	x	x
Slimoniphyllum			x		x							
Solenodendron			x									x
Spirophyllum				x							x	
Tachylasma				x	x	x						
Thysanophyllum		x										
Tizraia										x		x
Turbinatocaninia	x			x	x	x						
Ufimia				x	x			x				
Variaxon					x							
Vojnimitor								x				
Vojnovskytes								x				
Zakowia					x							
Zaphrentites		x		x	x					x		x
Zaphrufimia				x	x							

Table 12: Presence/absence data of rugose coral species across different regions in the Western Palaeotethys during the Serpukhovian

Serpukhovian species	Nova Scotia	British Isles	Austria	Poland	Donets Basin	Moscow Basin	South France	Cantabr. Mountains	Betic Cordillera	SW Spain	N. Morocco	Sahara
Actinocyathus borealis						x						
Actinocyathus crassiconus					x	x	x	x	x			x
Actinocyathus floriformis						x						
Actinocyathus gorskyi						x						
Actinocyathus heckeri						x						
Actinocyathus latevesiculosus						x						
Actinocyathus rossicus						x						
Actinocyathus saritschevae						x						
Actinocyathus subtilis						x						
Actinocyathus sp.						x						
Adamanophyllum incertus					x							
Amplexizaphrentis derbiensis		x										
Amplexizaphrentis enniskilleni	x				x	x						
Amplexocarinia sp.										x	x	
Amplexus sp.		x			x					x	x	
Amygdalophyllum cornudensis										x		
Amygdalophyllum sp.												x
Antiphyllites pauperculus				x								
Antiphyllites simplex				x								
Antiphyllites sp.				x								
Antiphyllum inopinatum				x								
Arachnolasma cylindrica			x		x	x					x	x
Arachnolasma djhaniense												x
Arachnolasma irregulare					x							
Arachnolasma lapparenti												x
Arachnolasma sp.										x		
Aulina parasenex					x							
Aulina rotiformis		x			x	x	x					x
Auloclisia sp.						x					x	
Aulokoninckophyllum carinatum					x					x	x	x
Aulokoninckophyllum sp.			x							x		
Aulophyllum fungites		x			x	x				x	x	x
Axophyllum coronatum												x
Axophyllum pseudokirsopianum										x	x	x
Axophyllum septentrionale					x							
Axophyllum sp.		x	x		x		x	x	x	x	x	x
Barytichisma sp.					x							
Bothrophyllum proteum												x
Bothrophyllum sp.				x	x	x						x
Caninia amplexoides					x							
Caninia cornucopiae		x		x	x							
Caninia sp.			x	x								

Caninophyllum becharense					x							x
Caninostrotion perejoni								x				
Carruthersella garwoodi												x
Claviphyllum magnificum				x								
Claviphyllum pauperculum						x						
Claviphyllum sp.											x	
Clisiophyllum benzigerense										x		x
Clisiophyllum crassiseptatum												x
Clisiophyllum garwoodi										x	x	
Clisiophyllum keyserlingi		x	x		x	x	x		x	x	x	x
Clisiophyllum macrocolumellatum											x	
Clisiophyllum sp.										x	x	
Corwenia progressiva					x							
Corwenia rugosa		x			x	x					x	
Cyathaxonia cornu			x		x	x					x	
Diaschophyllum chevalieri												x
Dibunophyllum arachnoformis					x							
Dibunophyllum bipartitum		x	x		x	x	x	x	x	x	x	x
Dibunophyllum derbiensiformis					x							
Dibunophyllum dobrolyubovae					x					x		
Dibunophyllum longiseptatum					x							
Dibunophyllum lonsdaleoides					x							
Dibunophyllum pruvosti												x
Dibunophyllum subpercrassum					x							
Dibunophyllum sp.												x
Diphyphyllum carinatum					x							
Diphyphyllum fasciculatum		x			x	x	x	x		x	x	x
Diphyphyllum furcatum			x									
Diphyphyllum gracile										x		
Diphyphyllum lateseptatum		x										x
Diphyphyllum platiforme					x							
Effigies silesiacus				x								
Eostrotion sp.					x							
Fasciculophyllum tripus				x								
Gangamophyllum boreale					x	x	x	x	x			x
Gangamophyllum kumpani					x							
Guadiatia pseudocoloniale										x		
Haplolasma lamelliferum										x		
Haplolasma paraarciferum										x	x	x
Hapsiphyllum sp.					x							
Kizilia sp.						x	x			x		x
Koninckophyllum complexum												x
Koninckophyllum destitum												x
Koninckophylum interruptum		x			x							x
Koninckophyllum magnificum		x			x	x	x	x	x			x
Koninckophyllum variabile												x
Koninckophyllum sp.			x									x
Leonardophyllum leonense							x					
Lithostrotion decipiens		x		x	x	x	x				x	x

Lithostrotion maccoyanum		x			x					x		x
Lonsdaleia arctica					x							
Lonsdaleia carnica			x									
Lonsdaleia corbariensis							x		x			
Lonsdaleia duplicata		x			x	x	x	x				x
Lonsdaleia permanoseptata					x							
Lophophyllidium sp.			x									
Lublinophyllum			x									
Lytvophyllum						x						
Melanophyllidium							x					
Mirka prima				x								
Morenaphyllum sp.										x		
Nemistium sp.							x					x
Neokoninckophyllum trifossulum				x	x							
Nervophyllum besheviensis					x							
Nina berestovensis					x							
Opiphyllum fomitchevi												x
Ostravaia silesiaca				x								
Palaeosmilia murchisoni		x	x		x	x	x	x	x	x	x	x
Palaeosmilia ressoti												x
Palastraea regia		x					x				x	x
Pareynia splendens										x	x	x
Plerophyllum sp.							x					
Pseudoalulina parasenex												x
Pseudozaphrentoides' juddi		x	x				x	x	x	x	x	x
Rotiphyllum sp.				x							x	
Rylstonia sp.						x						
Schoenophyllum sp.						x						
Serraphyllum serraensis							x					
Serraphyllum vineensis							x					
Silesamplus tripus				x								
Siphonodendron dutroi												x
Siphonodendron pauciradiale		x			x							
Siphonodendron junceum		x		x	x	x	x	x	x		x	x
Siphonodendron martini			x									
Siphonodendron sp.												x
Siphonophyllia benburbensis										x	x	x
Siphonophyllia samsonensis												x
Siphonophyllia sp.			x									
Slimoniphyllum slimonianum		x			x							
Solenodendron furcatum			x									x
Solenodendron horsfieldi			x									
Spirophyllum				x							x	
Tachylasma silesiacum				x	x	x						
Tachylasma tenue					x							
Thysanophyllum sp.		x										
Tizraia										x		x
Turbinatocaninia davidsoni	x				x	x						
Turbinatocaninia tyszowcensis				x								

Ufimia schwarzbachi				x	x			x				
Variaxion radians				x								
Variaxon repressus				x								
Vojnimitor proiectus								x				
Vojninovskytes marcinowskii								x				
Vojnovskytes arcuatus								x				
Zakowia					x							
Zaphrentites illidizensis												
Zaphrentites sp.		x		x	x					x		x
Zaphriphyllum					x							
Zaphrufimia disjuncta				x								
Zaphrufimia praematura				x								
Zaphrufimia serotina				x								
Zaphrufimia subcarruthersi					x							
Zaphrufimia sp.				x								

1.5 CORAL BIOZONES

Table 13: distribution of rugose coral genera across the subprovinces of the Western Palaeotethys during the Mississippian, which includes the coral zones by Poty (1985) (RC1-RC8), the Pendleian (Pendl.) and the Arnsbergian (Arns.). **A**: Atlantic sub-province. **G**: West Peri-Gondwanan sub-province. **S**: Saharan sub-province. **M**: Mediterranean sub-province. **C**: Central European sub-province. **E**: Eastern European sub-province. Habit abbreviations: **SD** – solitary dissepimented; **SU** – solitary undissepimented; **F** – fasciculate; **M** – massive. (Authors in Chapter 7 table 1).

GENERA	Habit	RC1	RC2	RC3	RC4α	RC4β	RC5	RC6	RC7	RC8	Pendl.	Arns.
Actinocyathus	**M**								**CE**	**AEM**	**MSE**	**SE**
Adamanophyllum	**SD**											**E**
Allotropiophyllum	**SU**			**A**	**-**	**-**	**A**	**A**	**AC**	**E**		
Amplexizaphrentis	**SU**			**C**	**-**	**-**	**A**	**A**	**ASCE**	**AGSE**	**AE**	**A**
Amplexocarinia	**SU**			**C**	**A**	**-**	**-**	**S**	**AGCS**	**GS**	**G**	
Amplexus	**SU**		**A E**	**A**	**AS**	**AC**	**ACE**	**ACE**	**AGCE**	**AGCM**	**AEG**	
Amygdalophylloides	**SD**									**G**		
Amygdalophyllum	**SD**				**AC**	**AC**	**AE**	**AE**	**ASEC**	**GS**	**GS**	
Antiphyllites	**SU**										**C**	
Antiphyllum	**SU**										**C**	
Arachnolasma	**SD**						**C**	**A C**	**AGSC**	**GSCEM**	**GSCE**	**GSE**
Aulina	**M**							**S**	**-**	**-**	**ASME**	**E**
Auloclisia	**SD**					**S**	**AC**	**-**	**AGC**	**GSE**	**EG**	
Aulokoninckophyllum	**SDF**			**A**	**A**	**A**	**A**	**A S**	**AGSM**	**GSCM**	**GSCE**	**G**
Aulophyllum	**SD**								**AGSCE**	**AGSCE**	**AGSE**	**AG**
Axoclisia	**SD**					**A**	**-**	**-**	**AGSCE**	**G**		
Axophyllum	**SD**				**A**	**AE**	**AC**	**AC**	**AGSC**	**AGSM**	**GSM**	**GSEM**
Barytichisma	**SU**										**E**	
Bathybalva	**SU**	**C**										
Biphyllum	**SD**									**C**		
Bothrophyllum	**SD**								**AGC**	**GCS**	**SCE**	**S**
Bifossularia	**SD**	**C**	**C**	**AC**	**A C**	**A SC**	**A**	**A**	**ACEG**			
Bradyphyllum	**SU**					**C**	**-**	**-**	**A**	**GCM**		
Calmiussiphyllum	**SD**			**AE**								
Calophyllum	**SU**					**C**	**-**	**-**	**C**			
Campophyllum	**SD**	**ACE**	**-**	**-**	**-**	**-**	**-**	**-**	**C**			
Caninia	**SD**	**ACE**	**AC**	**AC**	**AC**	**AC**	**AC**	**AE**	**AGSCE**	**AGSC**	**AC**	**E**
Caninophyllum	**SD**		**E**	**ACE**	**A**	**A**	**A**	**AE**	**AGSC**	**ACE**	**SE**	
Caninostrotion	**SD**											**M**
Carruthersella	**SD**					**A C**	**AC**	**C**	**-**	**ACS**	**S**	
Ceriodotia	**F**					**E**	**E**					
Claviphyllum	**SU**	**C**	**C**	**C**	**C**	**-**	**-**	**-**	**G**	**GCE**	**GCE**	
Clinophyllum	**SU**						**C**					

Clisiophyllum	SD	C	-	-	A C	A C	AC	ACE	AGSC	AGSCEM	AGSCEM	G
Commutia	SU	C										
Conilophyllum	SD	ACE										
Corphalia	SD				E		A					
Corwenia	F								GE	AGE	GCE	GE
Cravenia	SU			A	A	AGS	A	-	AG			
Cryptophyllum	SU						A	-	-	GE		
Cyathaxonia	SU	AC	ACE	ACE	ACE	ACE	ACE	ACE	AGCE	AGCEM	GE	GE
Cyathoclisia	SD		E	AE	ACE	ASC	E	E				
Delepinella	SD			A	A	A						
Diaschophyllum	SD										S	
Dibunophyllum	SD						A S	A SC	AGSCE	AGSCEM	AGSCEM	GSE
Diphyphyllum	F							A	AGCE	AGSCM	AGSCEM	GSEM
Dorlodotia	F				AE	AE	AC	E	-	E		
Drewerelasma	SU	C	-	-	C	C						
Effigies	SU										C	
Enniskillenia	SU									AE		
Eostrotion	SD	C	AC	AC	C	-	-	-	-	--	E	
Espielia	F								GSM	G		
Fasciculophyllum	SU		A	A	A	A	A	-	-	-	C	
Gangamophyllum	SD								AGEC	GSECM	GSECM	GSEM
Guadiatia	F									A	G	
Haplolasma	SD					AE	AE	ASE	AGSE	AGSCM	SM	S
Hapsiphyllum	SU			A	-	C	-	-	-	-	E	
Hebukophyllum	SD	C										
Heterostrotion	F			A								
Hettonia	SD					C						
Howthia	F				A							
Kabakovitchiella	SU	C										
Keyserlingophyllum	SD		C	A C	C	C						
Kizilia	SD	A	-	-	-	-	-	A	AGSC	GSM	GSEM	
Koninckonaotum	SD									C		
Koninckophyllum	SD				A	AS	AC	AS C	AGSC	AGSCEM	ASCEM	GSE
Koninckophyllum (colonial)	F								A	A		
Laccophyllum	SU	C	-	-	-	C						
Leonardophyllum	SU											M
Lithostrotion	M						AS	ASC	AGSCE	AGSCEM	AGSCEM	GSEM
Lonsdaleia	F								E	ASEM	ASECM	EM
Lophophyllidium	SU					A	-	S	-	C	C	

Lophophyllum	**SD**	C	AC	A	C	-	-	-	C			
Lublinophyllum	**F**								C	AC	C	
Lytvophyllum	**SD**											E
Melanophyllidium	**F**									M	M	
Merlewoodia	**SD**				A	AS	-	-	A	A		
Mirka	**SD**									C	C	
Morenaphyllum	**SD**									G	G	
Nemistium	**F**								GE	ACEM	SM	
Neoclisiophyllum	**SD**					A						
Neokoninckophyllum	**SD**									C		
Nervophyllum	**SD**								C	CE	E	E
Nina	**SD**									E	E	E
Nominoephyllum	**SU**					A						
Orionastraea	**M**								E	ACE		
Ostravaia	**SU**										C	
Palaeosmilia	**SD**				A	ASC	ASC	ASCE	AGSCE	AGSCEM	AGSCEM	GSEM
Palastraea	**M**								GE	AGSCEM	AGSM	GS
Pareynia	**SD**							S	AGS	SM	GS	
Pentaphyllum	**SU**	C	-	A	C	ASC	C	-	AC	C		
Proheterelasma	**SU**			A	A	A	A	A				
Protolonsdaleia	**F**											
Pseudoaulina	**M**										S	S
Pseudocaninia	**SD**								C	C		
Pseudoclaviphyllum	**SU**									E		
Pseudouralinia	**SD**					C						
Pseudozaphrentoides'	**SD**								AGSC	AGSCEM	AGSCM	
Richrathina	**SU**					C						
Rhopalolasma	**SU**				A C							
Rotiphyllum	**SU**	C	C	A C	AC	AC	AC	AC	AGC	GCM	GC	
Rozkowskia	**SD**							C	-	C		
Rylstonia	**SD**	C	-	A	A SC	ASC	AC	A	AG	A GSCE	E	
Sabolia	**SD**						A	A				
Saharaphrentis	**SU**									S		
Saleelasma	**SU**	A	A	A	C							
Schoenophyllum	**F**										E	E
Semenoffia	**SD**			A	-	-	-	-	AGM			
Serraphyllum	**FM**										M	
Silesamplus	**SU**										C	
Siphonodendron	**F**					SC	ACE	ASCE	AGSCE	AGSCEM	AGSCEM	GSE

Siphonophyllia	**SD**	ACE	ACE	AE	AES	AGSCE	ASC	ASC	AGSCE	AGSM	GCSM	
Slimoniphyllum	**SD**									AC	CE	
Sochkineophyllum	**SU**	C	-	-	-	-	-	-	G	G		
Solemnophyllum	**SD**					A	A					
Solenodendron	**F**			A	A S	A	AC	-	AGCE	AGM	GC	G
Spirophyllum	**SD**					AC	A	-	AGC	CE	GC	
Stelechophyllum	**M**									E		
Sychnoelasma	**SU**	C	ACE	ACE	ACE	AGSCE	ACE	CE				
Syringaxon	**SU**	C	-	-	-	A	-	-	-	M		
Tachylasma	**SU**									C	CE	
Thysanophyllum	**F**									AM	A	
Thuriantha	**SU**	C										
Tizraia	**F**								G	GS	GS	
Turbinatocaninia	**SD**								C	E	ACE	E
Ufimia	**SU**	C	-	-	C	C	C	-	GC	GCS	GCE	
Uralinia	**SD**	A	AE	AE	CE	C						
Variaxon	**SU**										E	
Vassiljukia	**M**						E					
Viseaulina	**SD**								A			
Vojnimitor	**SU**										M	
Vojnovskytes	**SU**									M	M	
Zakowia	**SD**									C	C	
Zaphrentites	**SU**	AC	ACE	ACE	ACE	ASC	C	-	GC	AGSCE	AGSCE	G
Zaphrentoides	**SU**					C	-	-	G			
Zaphriphyllum	**SD**				S	S						
Zaphrufimia	**SU**									AGC	CE	E
Total genera		**28**	**17**	**31**	**37**	**50**	**41**	**34**	**61**	**77**	**71**	**34**
New genera		**17**	**5**	**14**	**12**	**19**	**8**	**5**	**35**	**27**	**11**	**4**
Extinct genera		**4**	**16**	**0**	**6**	**6**	**17**	**12**	**8**	**11**	**17**	**41**
Total assumed		**28**	**27**	**39**	**46**	**60**	**57**	**56**	**70**	**81**	**71**	**34**
New genera assumed		**17**	**5**	**12**	**9**	**17**	**7**	**2**	**20**	**17**	**11**	**4**
Extinct genera assumed			**6**	**0**	**2**	**3**	**10**	**3**	**6**	**6**	**21**	**41**
		RC1	RC2	RC3	RC4α	RC4β	RC5	RC6	RC7	RC8	Pen.	Arn.