



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 Centroiherian 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 Centroeibérico 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, epicontinental 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.

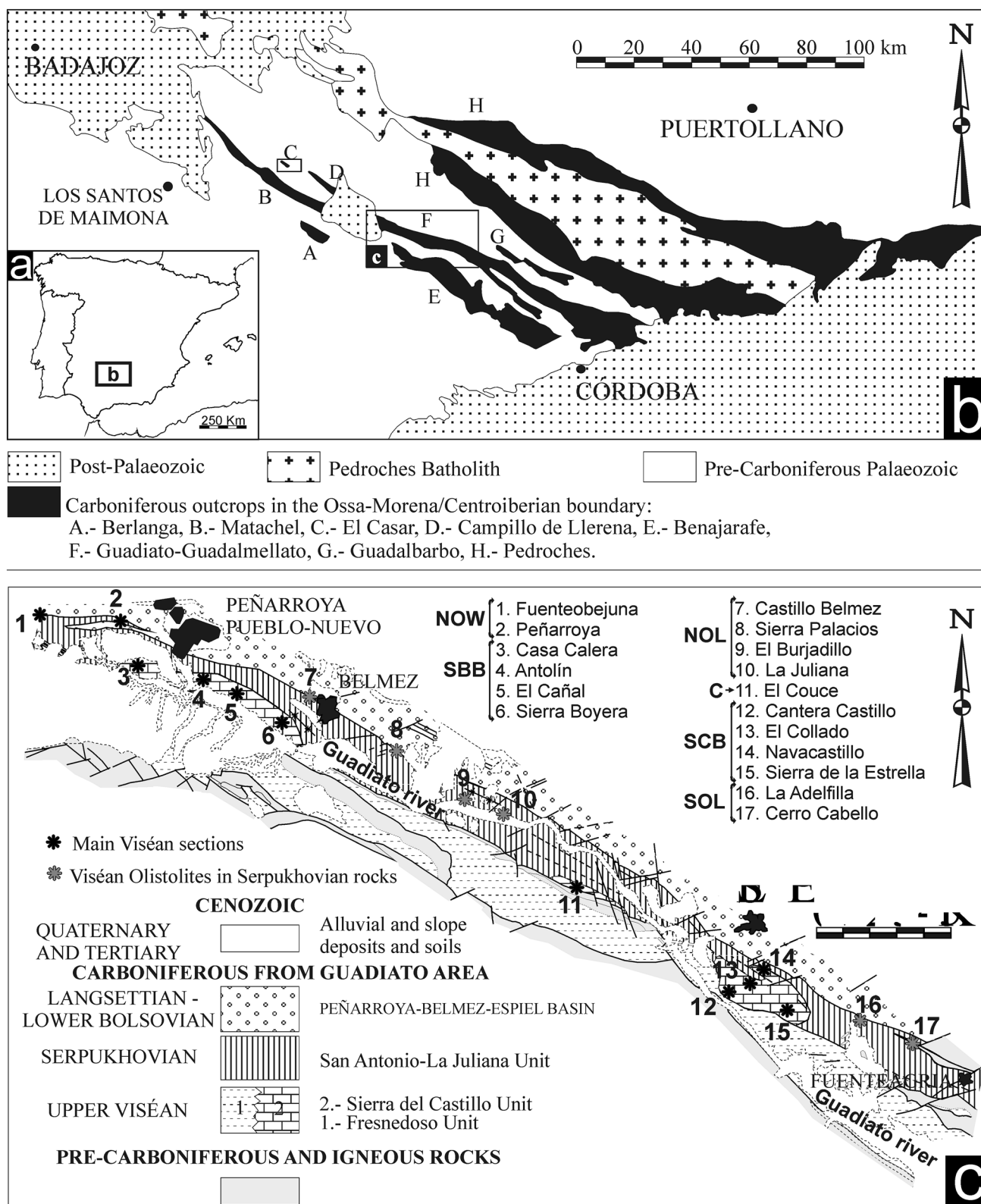
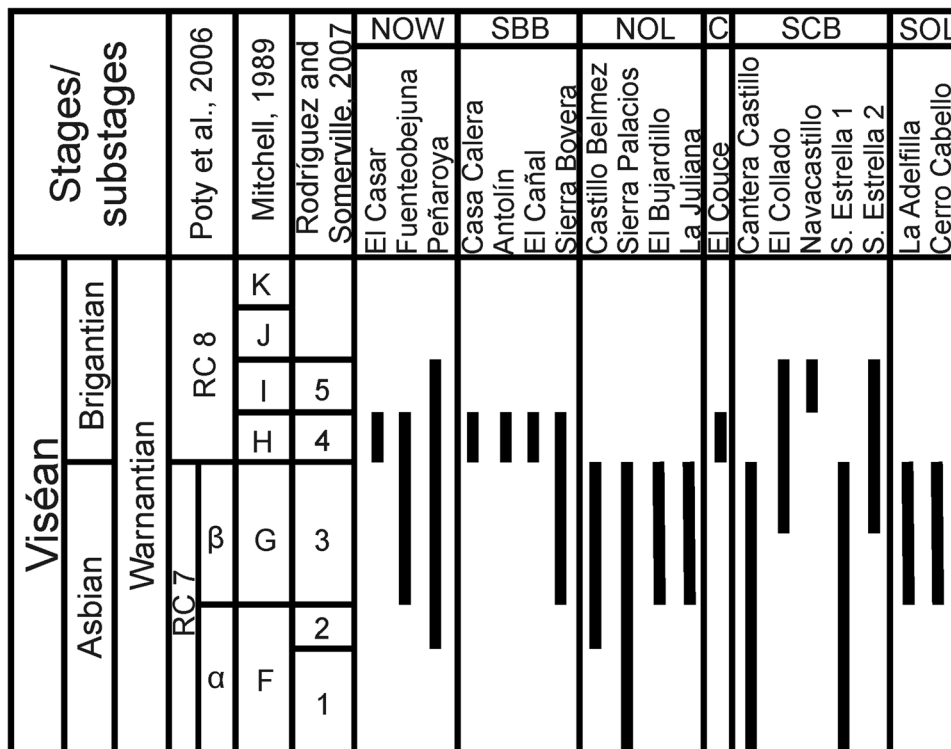


Fig. 1 Location maps of the El Guadiato Area and the studied outcrops. **a** Location of the El Guadiato Area and Los Santos de Maimona in Spain. **b** Regional map and location of the El Guadiato Area

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 Viséan, also in Ossa Morena) and from Kingscourt (late Viséan, 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 volgenae*) 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.

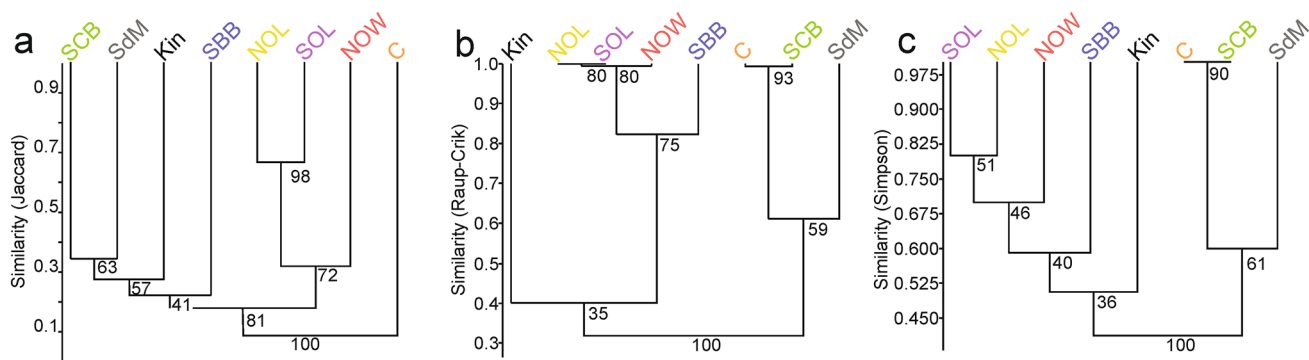


Fig. 3 Paired Group (UPGMA) Hierarchical Cluster analyses, including all outcrops and all rugose coral species. Different clusters correspond to different similarity indices: **a** Jaccard, **b** Raup-Crick, **c** Simpson. NOW: Northwestern outcrops; SBB: Sierra Boyera

Block; NOL: Northern Olistoliths; C: El Couce Outcrop; SCB: Sierra del Castillo Block; SOL: Southern Olistoliths; SdM: Los Santos de Maimona; Brt: Britain

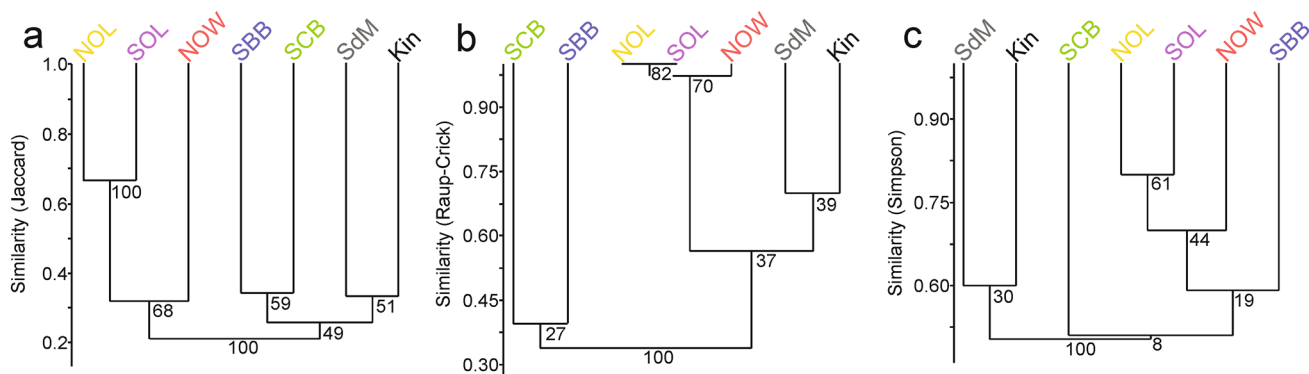


Fig. 4 Paired Group (UPGMA) Hierarchical Cluster analyses, after removing deeper water environments and undissected rugose corals. Different clusters correspond to different similarity indices: **a** Jaccard, **b** Raup-Crick, **c** Simpson. Abbreviations as in Fig. 3

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 Northern 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 undissected 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 Kingscourt 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 Kingscourt.

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 differentiates two groups along Axis 1: Kingsncourt, 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.

Kingsncourt 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.

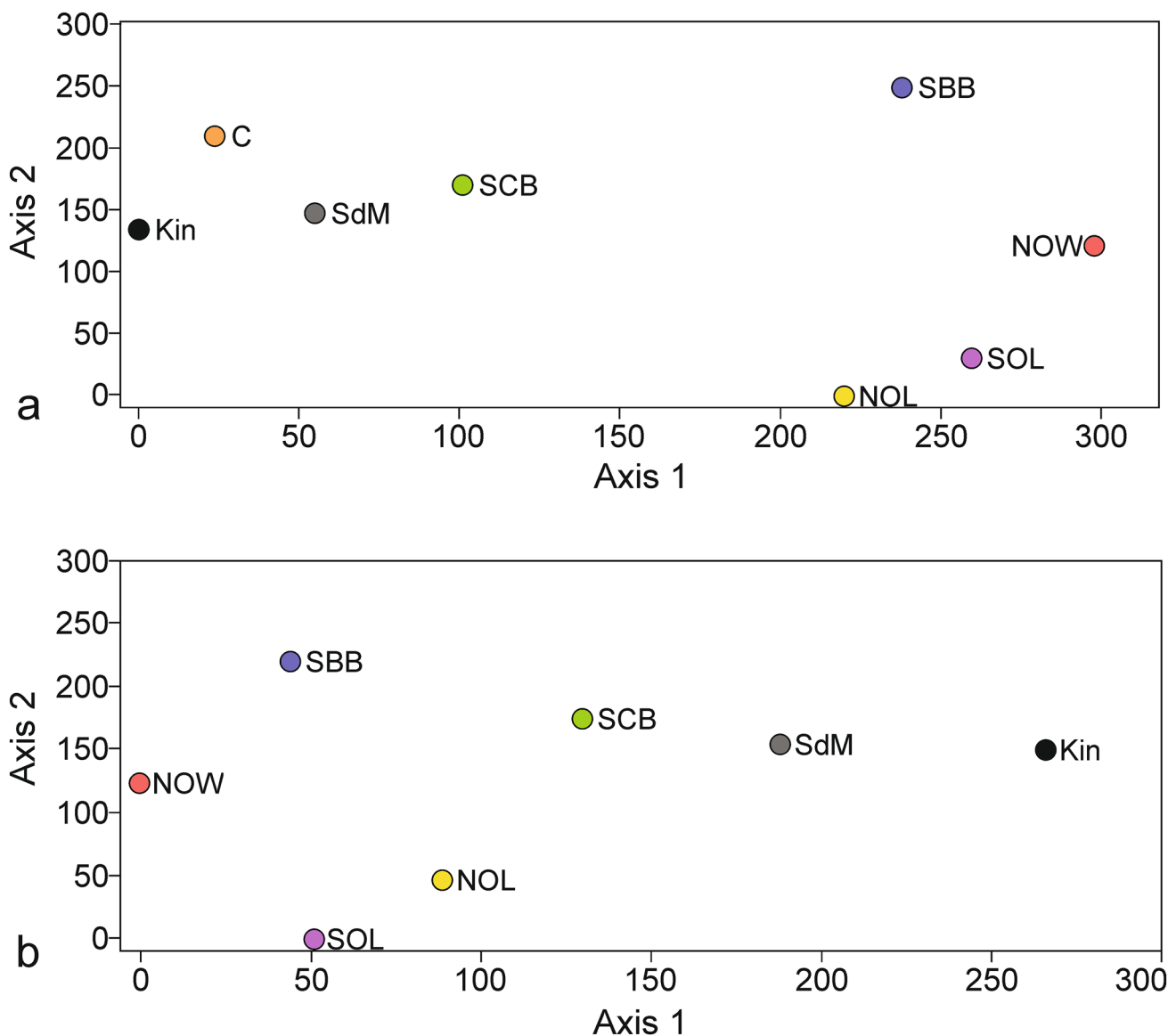


Fig. 5 Detrended Correspondence Analyses: **a** All outcrops and all rugose coral species; **b** Shallow water outcrops, undissepimented rugose corals not included. Abbreviations as in Fig. 3

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 Couce'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.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1007/s41513-022-00194-3>.

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Data availability All the specimens included in this study are stored in the collection of the Area of Palaeontology of the Department of Geology, Stratigraphy and Palaeontology of the Complutense University of Madrid.

Code availability Not applicable.

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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