C. R. Palevol 12 (2013) 245–255

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General palaeontology, systematics and evolution (Palaeobiogeography)

The Late Miocene coldspot of z-coral diversity in the Mediterranean: Patterns and causes

Le « point froid » de diversité des coraux symbiotiques au cours du Miocène supérieur en Méditerranée : patrons et causes

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ARTICLE INFO

Article history:
Received 11 February 2013
Accepted after revision 28 May 2013
Available online 20 August 2013

Presented by: Philippe Taquet

Keywords:
Late Miocene
Mediterranean
Corals
Biodiversity
Messinian
Tortonian
Salinity Crisis

Mots clés :
Miocène supérieur
Méditerranée
Coraux
Biodiversité
Messinien
Tortonien
Crise de Salinité

ABSTRACT

The Late Miocene distribution and diversity of zooxanthellate-like corals in the Mediterranean are analyzed in their paleobiogeographical framework, using our REEFCORAL database. The Late Miocene Mediterranean pool reached 20 z-coral genera. Although this fauna could build flourishing reef ecosystems during the Early Messinian, it was a relict fauna with severely limited speciation that lived on the edge of its ecological requirements in terms of solar energy and temperature range. Most z-coral genera, because they had long stratigraphic ranges and had survived previous extinctions, were able to adapt to the Messinian environments, which were unusual for such biotas. Hence, *Porites*, the most widespread genus in the region and also the most dominant in ecological assemblages, was the best equipped to cope with the drastic changes related to the Messinian Salinity Crisis.

RÉSUMÉ

La distribution et la diversité des coraux symbiotiques méditerranéens au cours du Miocène supérieur sont analysées dans leur contexte paléobiogéographique, grâce à notre base de données REEFCORAL. Cette faune comprend 20 genres. Il est montré que la faune de coraux symbiotiques du Miocène supérieur méditerranéen, bien que capable d'édifier des écosystèmes récifaux florissants au cours du Messinien inférieur, correspond à une faune relique à spéciation fortement réduite et vivant à la limite de leurs exigences écologiques en termes d'éclairement et de température. La plupart des genres de coraux symbiotiques, grâce à leur large répartition stratigraphique dans la région, ont acquis une capacité d'adaptation à des conditions environnementales telles que celles du Messinien. Ainsi, *Porites*, le genre le plus répandu dans cette région et aussi le plus abondant dans les assemblages écologiques, était le mieux pourvu pour faire face aux importants changements environnementaux liés à la Crise de Salinité Messinienne.

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http://dx.doi.org/10.1016/j.crpv.2013.05.010

1. Introduction

Deciphering how regional diversity is linked to patterns of past taxonomic richness and its distribution in the area, and to ongoing adaptation of taxa to new and evolving environmental conditions, can be regarded as a major step towards an integrated understanding of the spatiotemporal framework in which the relationship between species richness and environment is embedded (Ricklefs, 2006, 2007). As a window on deep time, paleontology can explore such relationships on a variety of scales.

The low diversity of Late Miocene coral reefs and reef-coral assemblages in the Mediterranean region is well known and has been emphasized by many authors, becoming a typical feature of Late Miocene Mediterranean reefs (see Buchbinder, 1996; Chevalier, 1962a; Esteban, 1996; Esteban et al., 1996; Pedley, 1996a, 1996b; for reviews). Causes explaining this diversity have been implicitly linked to the increasing influence of abiotic conditions leading to the Mediterranean Messinian Salinity Crisis, favoring the influence of contemporary environment rather than the heritage of previous regional taxonomical richness.

In past decades, detailed descriptions and analyses of Messinian coral reef outcrops in the region have produced many data. These were accompanied by substantial improvements of our knowledge of Mediterranean paleogeography (Piller et al., 2007; Popov et al., 2004; Rögl, 1999; Sissingh, 2001) and the geodynamical context of the Messinian Salinity Crisis (Braga et al., 2006; Hüsing et al., 2010; Iaccarino and Bossio, 1999; Martín et al., 1989; van Assen et al., 2006). Synthetic works on the evolution of Cenozoic reefs on a global scale (Kiessling, 2006; Perrin, 2002; Perrin and Kiessling, 2010) have complemented those on Mediterranean z-corals during the Oligocene-Miocene (Bosellini and Perrin, 2008, 2010; Perrin and Bosellini, 2012).

The aim of this paper is to assess and discuss the diversity patterns of z-coral communities in the Mediterranean during the Late Miocene (Tortonian-Messinian) in the framework of the Mediterranean history including the Miocene geodynamical and climatic context, together with the Cenozoic evolution of scleractinian corals in the region.

2. Methodological approach and material

2.1. The REEFCORAL database

The REEFCORAL database (Bosellini and Perrin, 2008, 2010; Perrin and Bosellini, 2012) groups information relative to coral assemblages occurring in Oligocene and Miocene outcrops of the circum-Mediterranean area. This database comprises data extracted from three different sources: most of recent published literature, data provided by the study of coral collections in museums, in particular the collections of the MNHN in Paris, and our own coral collections. Stratigraphic data associated with each coral occurrences have been updated and homogenized and systematic revisions of some coral genera were done before entering information in the database. A symbiotic status was attributed to each genus following the uniformitarian approach discussed in Perrin and Bosellini (2012).

REEFCORAL currently provides information on more than 3200 coral occurrences from 332 localities in the circum-Mediterranean region. One hundred and fifty-eight genera are represented, 103 of them having a zooxanthellate or unknown symbiotic status (see details in Perrin and Bosellini (2012), Table 2, p. 6–7).

2.2. The Late Miocene dataset

The Late Miocene dataset comprises 20 coral genera, all of them with an unequivocal zooxanthellate-like symbotic status.

One hundred and fifty-three Upper Miocene localities are represented in REEFCORAL, including 83 in the Tortonian and 110 in the Messinian with 40 localities common to both stages. When the number of sites is weighted by the duration of each stage according to the 2012 Geological Time Scale (Gradstein et al., 2012), the number of z-coral localities per million years is three times more important in the Messinian than in the Tortonian, attesting to the prosperous expansion of z-coral communities during the Messinian, in particular during the lower part of this stage.

2.3. Biases and reliability

Three potential types of biases may affect the analysis of data extracted from the REEFCORAL database:

- biases related to spatial heterogeneity of data, with some areas potentially more investigated than others;
- temporal bias resulting from stratigraphic uncertainties and difficulties of dating with precision shallow-water carbonate rocks of this age;
- taxonomic bias, which in REEFCORAL has been minimized by homogenization of data and revision of some genera and also by considering coral genera rather than species, the latter being much more subjective than the first.

Biases have been already identified and discussed in previous papers (Bosellini and Perrin, 2008, 2010; Perrin and Bosellini, 2012). In addition, spatial and temporal heterogeneity of data has been analyzed in detail for the entire database (Oligocene-to-Miocene time interval) by Perrin and Bosellini (2012). In particular, the east-west disparity of data reported by these authors and due to a relative lack of data in the eastern regions, is also noticeable in the Late Miocene while the spatial disparity between the northern and southern margins of the Mediterranean Basin is less apparent for this interval than for the entire Oligocene-Miocene.

Finally, the two rarefaction curves established respectively for the Tortonian and Messinian z-coral genera (Fig. 1) show that the sampling size corresponding to data contained in REEFCORAL is significantly representative of the taxonomic richness in the Mediterranean region.

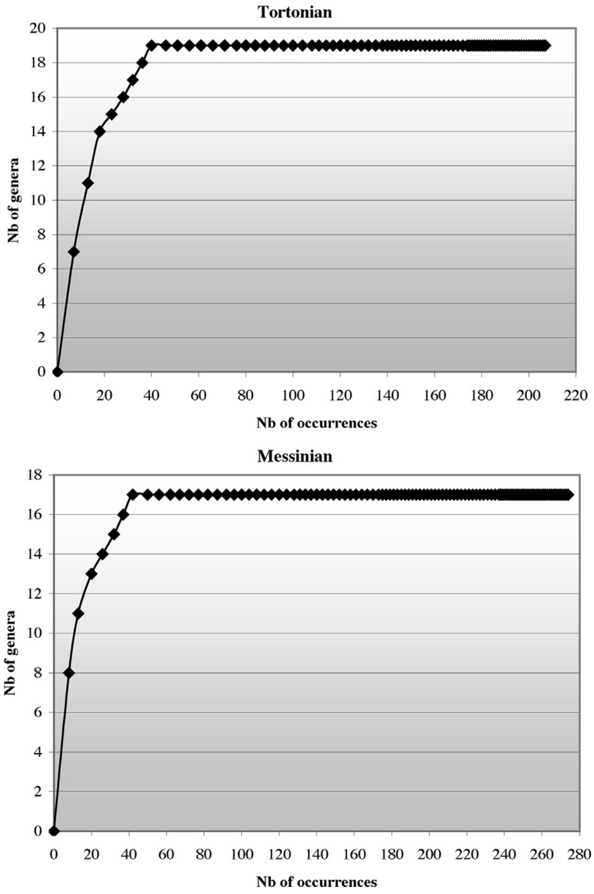

Fig. 1. Rarefaction curves of z-coral genera in the Mediterranean region, respectively for the Tortonian and the Messinian time interval according to the REEFCORAL database.

Fig. 1. Courbes de raréfaction des genres de coraux symbiotiques de la région Méditerranéenne, respectivement pour le Tortonien et pour le Messinien, selon la base de données REEFCORAL.

3. Spatial patterns of z-coral distribution in the paleogeographical context of the Mediterranean

3.1. Tortonian

During the Tortonian, Mediterranean z-coral assemblages extended to a latitude of about 44°N (Fig. 2), which represents the global northern limit of z-coral communities at that time (Perrin, 2002). It should be noted however that the septentrional limit of coral reef development did not reach 40°N. Tortonian z-coral assemblages occurred in the entire Mediterranean basin, except in the Paratethys (Fig. 2), where non-marine water conditions prevailed during this stage (Popov et al., 2004). In the eastern Mediterranean, z-coral assemblages, including reefs, are known from Cyprus, southern Turkey and Crete (Baron-Szabo, 1995; Brachert et al., 2006; Follows, 1992; Follows et al., 1996; Hayward, 1982; Hayward et al., 1996; Karabiyikoglu et al., 1999, 2005; Kroeger et al., 2006; Tsaparas and Marcopoulou-Diacantoni, 2005) and in the Sirt Basin in Libya (Hladil et al., 1991). Generic richness in this area varies from 12 genera on the northern margin to 3 along the southern shelf, although the latter is represented by only one site. Reef buildups, including patch reefs and coral thickets, developed during the Tortonian in the area formed by the Hyblean shelf, Malta, and Lampedusa Island (André et al., 2002; Grasso and Pedley, 1985; Grasso et al., 1982; Pedley, 1979, 1983, 1996a, 1996b; Pedley et al., 1992). Despite the relative diversity of reefal settings and the significant number of coral localities and research work, the number of z-coral genera reported in this area remains rather modest. The opening of the Tyrrhenian Sea provided a large set of suitable substrates for the flourishing of oligospecific z-coral communities (9 genera reported for the area), some of which formed fringing reefs and reef complexes. In the lower part of the Rhône Valley, a few low-diversity coral communities were able to evolve despite frequent inputs of siliciclastics. In the western part of the Mediterranean, the presence of the Betic and Rifean open seaways favored the expansion of two reef alignments, respectively developed along the southern coasts of Betics and Balearic promontory and along the margin of North Africa (Bonnet, 1997; Braga et al., 1990; Chevalier, 1962a, 1962b; Lopez Buendia, 1992; Mankiewicz, 1995; Martín et al., 1989; Santisteban and Taberner, 1988; Soria et al., 1999). Along the eastern Atlantic margin, a few sites bearing z-coral communities have been reported in Portugal. These assemblages were not forming reefs and consisted of only one z-coral genus (Chevalier, 1964).

3.2. Messinian

In the Messinian (Fig. 3), the latitudinal range of z-corals was slightly restricted, and there was a significant decrease of generic richness in the northernmost localities. In addition, z-corals disappeared from localities exposed to cooler waters, such as the Atlantic coast of Portugal. In the southern Rhône Valley, the settings favorable for coral growth during the Middle-Late Miocene, such as the Lower Rhône Archipelago, disappeared in the Messinian (Sissingh, 2001). In the eastern Mediterranean, the number of reported sites bearing z-coral assemblages together with generic diversity decreased along the southern margin of Greece and Turkey, while Messinian *Porites* reefs occurred along the Mediterranean coast of Israël (Buchbinder, 1996). In the Adriatic Sea, low-diversity z-coral communities developed on the Apulian carbonate platform with small coralgal *Porites* patch reefs along the northern coast and a fringing reef complex on the southern shelf (Bosellini et al., 2001, 2002; Danese, 1999). The eastern shelves of Tunisia and Malta were still bearing some reef and non-reef low-diversity z-coral communities during the Early Messinian. In the opening Tyrrhenian Sea, Messinian z-coral assemblages were well developed along the Sicilian Calabrian arc at the entrance of this narrow gulf but also at its northern end, where the well-known Rosignano reef complex occurred (Bossio et al., 1996; Chevalier, 1959, 1962a). In the western Mediterranean, numerous reef complexes thrived along the two Betics-Balearic Islands (Brachert et al., 2001, 2002; Braga and Martín, 1996; Calvet et al., 1996; Dabrio et al., 1981; Esteban and Giner, 1980; Franseen and Mankiewicz, 1991; Franseen et al., 1993; Garcin, 1987; Mankiewicz, 1996; Martín and Braga, 1994; Martín

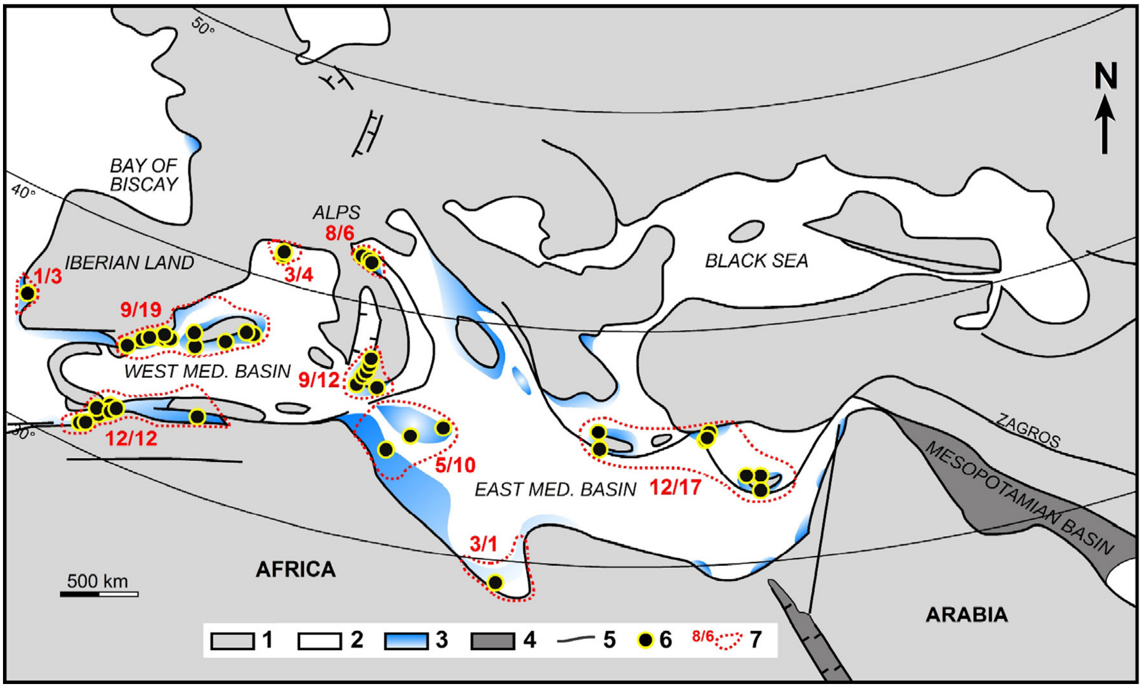

Fig. 2. Paleogeographic map showing the distribution of Tortonian z-coral communities together with the distribution of main carbonate platforms (data extracted from the REEFCORAL database). 1: continental environments; 2: shelves; 3: carbonate platforms; 4: evaporitic sedimentation; 5: synsedimentary faults; 6: z-coral assemblages; 7: z-coral generic richness (first number) and number of localities (second number) in the area bounded by the dotted line. Paleogeographic map re-drawn and modified from Popov et al. (2004).

Fig. 2. Carte paléogéographique montrant la distribution des assemblages de coraux symbiotiques et celle des plates-formes carbonatées au Tortonien (données extraites de REEFCORAL). 1 : milieux continentaux ; 2 : plateaux continentaux ; 3 : plates-formes carbonatées ; 4 : sédimentation évaporitique ; 5 : failles synsédimentaires ; 6 : assemblages de coraux symbiotiques ; 7 : richesse générique des coraux symbiotiques (premier chiffre) et nombre de sites (second chiffre) dans la zone délimitée par la ligne en pointillé. Carte paléogéographique redessinée et modifiée d'après Popov et al. (2004).

et al., 1997; Perrin et al., 1995; Pomar, 1991; Reinhold, 1995; Riding et al., 1991) and North African reef alignments (Chaix et al., 1986; Chevalier, 1962a; Elhamzaoui and Lachkhem, 1994; Saint-Martin, 1984, 1987, 1996; Saint-Martin and Cornée, 1996; Saint-Martin et al., 1995).

4. Z-coral generic richness of the Mediterranean Late Miocene

4.1. *The Late Miocene generic pool and spatiotemporal fluctuation of diversity*

The Late Miocene pool of z-corals in the Mediterranean is represented by 20 genera, including 19 in the Tortonian (of which one genus is not recorded in the Messinian) and 17 in the Messinian (Fig. 4). Four genera (*Porites*, *Tarbellastrea*, *Solenastrea* and *Siderastrea*) have a large geographical distribution in the Mediterranean region during the entire Late Miocene. The two first genera have a widespread spatial distribution because they are represented in 25% of the Tortonian localities and even more than 30% of the Messinian localities for *Porites*. In terms of taxonomic composition of assemblages in individual habitats, these genera correspond to the dominant and abundant taxa. *Porites* is the sole z-coral genus in some Messinian coral buildups. The frequency of geographical distributions of *Platygyra* and *Favites* shows frequent occurrences during the whole Late Miocene. *Montastraea* and *Thegioastrea*, which are fairly common in the Tortonian, have a highly restricted geographical distribution in the Messinian, while the reverse is documented for *Acanthastrea*. The other genera remain rare, being represented by only one or two occurrences in the Late Miocene.

4.2. *Spatiotemporal fluctuation of the generic richness during the Late Miocene*

All 20 Late Miocene Mediterranean z-coral genera are known in the circum-Mediterranean region before the beginning of the Tortonian except *Mioscapophyllia*, a rare genus recorded from a unique Tortonian-Messinian locality in Morocco (Chevalier, 1962a, 1962b) and unknown elsewhere. According to our REEFCORAL database, three genera that were already rare in the Tortonian became extinct in the Messinian. In addition, the geographical distributional patterns of some genera show slight changes and rebalancing between the Tortonian and Messinian, as for example the geographic spread of *Porites*, and the marked spatial restriction of *Thegioastrea* and *Montastraea*. It should be noted also that the rare coral-bearing facies that have been dated with certainty from the Late Messinian correspond to small monogeneric coral buildups formed by *Porites* (Braga et al., 2006; Martín et al., 1999; Riding et al., 1991). So, with the current state of knowledge, and keeping in mind

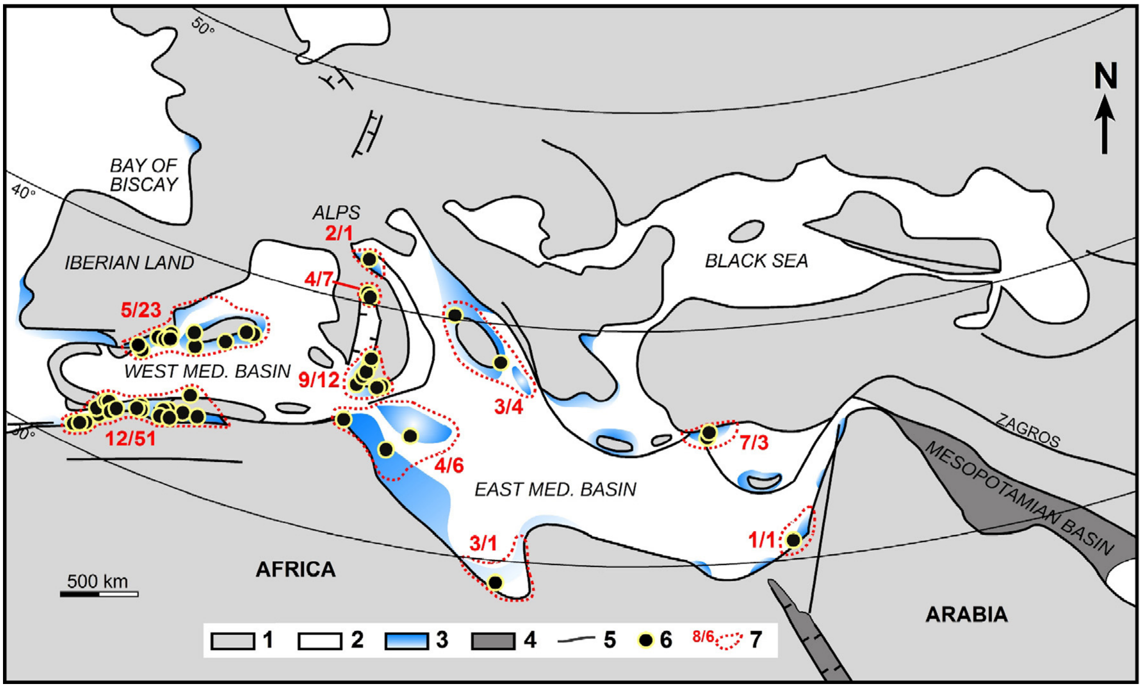

Fig. 3. Paleogeographic map showing the distribution of Messinian z-coral communities together with the distribution of main carbonate platforms (data extracted from the REEFCORAL database). Same legend as Fig. 2. Paleogeographic map re-drawn and modified from Popov et al. (2004).

Fig. 3. Carte paléogéographique montrant la distribution des assemblages de coraux symbiotiques et celle des plates-formes carbonatées au Messinien (données extraites de REEFCORAL). Même légende que la Fig. 2. Carte paléogéographique redessinée et modifiée d'après Popov et al. (2004).

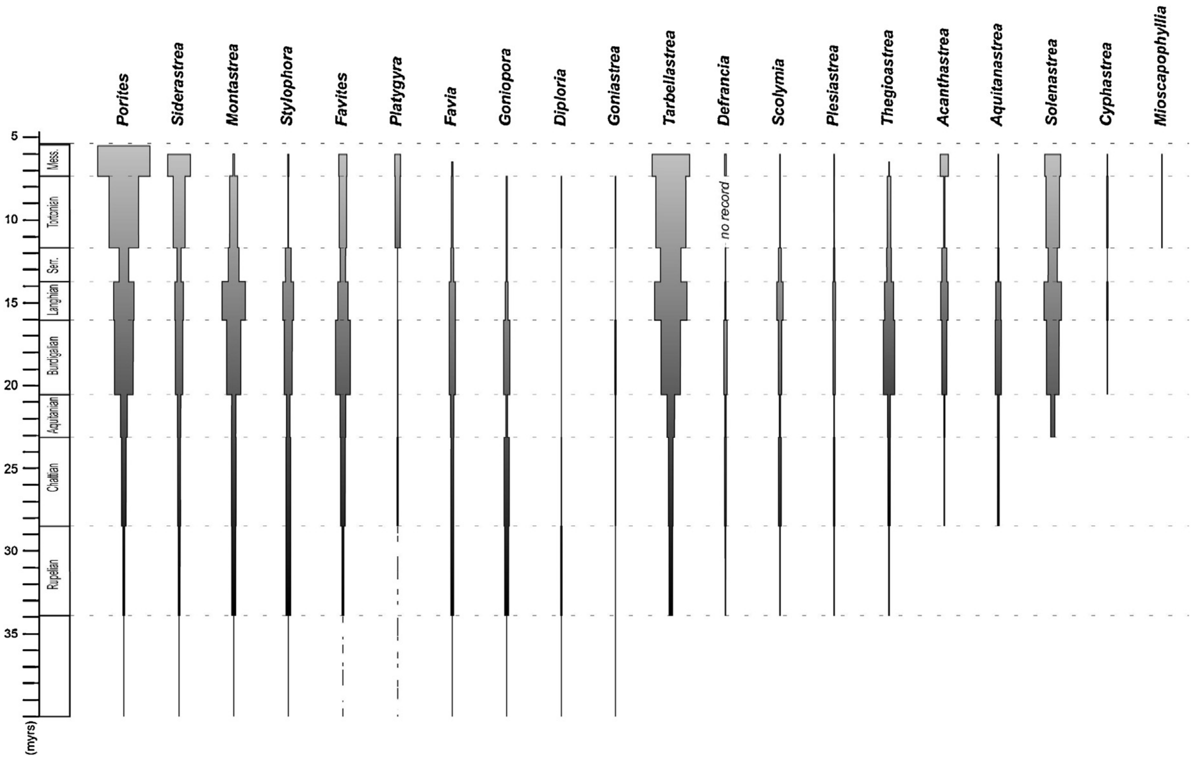

Fig. 4. Relationship between the temporal range in the mesogean realm and the number of occurrences for each z-coral genus represented in the Upper Miocene of the Mediterranean region.

Fig. 4. Relation entre la répartition stratigraphique dans le domaine mésogéen et le nombre d'occurrences pour chaque genre de coraux symbiotiques présents dans le Miocène supérieur de la région Méditerranéenne.

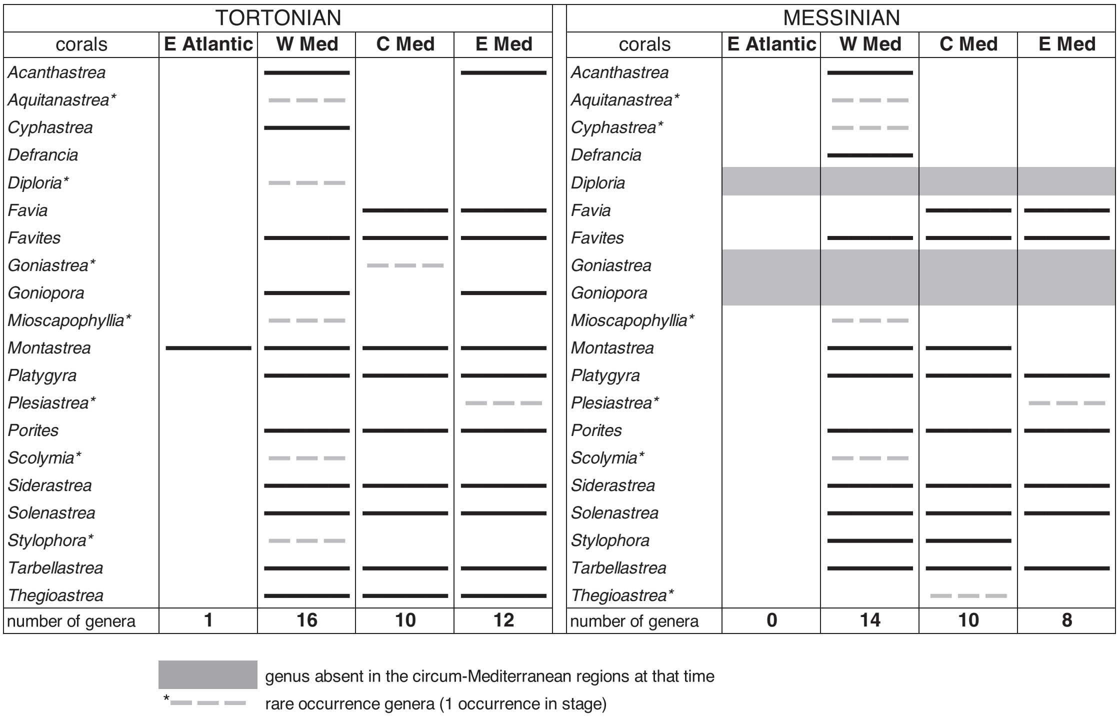

Fig. 5. Distribution of Late Miocene z-coral genera in Mediterranean subregions during the Tortonian and during the Messinian respectively. The central Mediterranean area encompasses the localities from Malta, Tunisia, Corsica and Italy, excepted the Apulian Shelf which was part of the eastern Mediterranean during the Late Miocene.

Fig. 5. Distribution des genres de coraux symbiotiques du Miocène supérieur dans les sous-régions méditerranéennes respectivement au cours du Tortonien et du Messinien. La sous-région de Méditerranée centrale comprend les localités de Malte, Tunisie, Corse et Italie, exceptées celles de la plaque apulienne, qui, au cours du Miocène supérieur, faisait partie du bassin de la Méditerranée orientale.

the difficulty of dating with precision the carbonate rocks of this age, z-coral diversity in the Upper Messinian was probably limited to the sole genus *Porites*.

The geographic distributional pattern of z-coral genera during the Late Miocene shows no clear preferential occurrence of any particular genus in a particular area of the Mediterranean and no differentiation between the eastern and western Mediterranean (Fig. 5), because genera apparently endemic to one subregion are rare (known from only one or two localities). Our results indicate however that areas with the highest generic diversity in the Tortonian (i.e. South Turkey, Calabria–Sicily, Betics-Balearic Islands, and North African shelf) are maintained during the Messinian as major sources of z-coral biodiversity (Figs. 2 and 3).

4.3. Temporal ranges of the different Late Miocene genera in the circum-Mediterranean realm

We examined in detail the relationships between the temporal range of the concerned z-coral genera in the region and their geographical expansion, represented by the number of occurrences of each coral genus present in the Upper Miocene of the Mediterranean area (Figs. 4 and 6). Half the genera forming the Late Miocene z-coral fauna of the Mediterranean were already present in the region during the Eocene (Fig. 4). Regarding the number of occurrences as a function of the temporal range of genera in the Mesogean region since the Eocene, more than half of the occurrences are long-range genera (temporal ranges Eocene-to-Messinian and Eocene-to-Tortonian), both in the Tortonian and in the Messinian (Fig. 6). In addition, a large proportion of occurrences (85% for the Tortonian, and 83% for the Messinian) results from genera present in the area since the Eocene or the Early Oligocene. The significant contribution of Aquitanian-Messinian range genera (more than 11% and 10% respectively for the Tortonian and for the Messinian) is in large part caused by the appearance of *Solenastrea* from the Aquitanian in the region, one of the widespread genera of the Mediterranean Late Miocene (Fig. 6).

With the exception of *Solenastrea*, the most widespread genera (*Porites*, *Siderastrea*, *Tarbellastrea*) tend to have a long temporal range in the region, dating back from the Eocene or Early Oligocene (Fig. 4). Genera having a frequent geographical distribution during the Late Miocene, such as *Platygyra*, *Favites*, *Montastraea* and *Thegioastrea*, also have a quite long temporal range in the region, where they are present since the Eocene or Early Oligocene (Fig. 4).

Variations in the number of occurrences through time for any given z-coral represent the changing number of sites colonized by this genus, and therefore, the rate of spatial expansion or decline of the genus considered. Expansion rates of the widespread and frequent genera occur through a gradual spatial expansion from stage to stage, except during the Serravallian. This is well marked

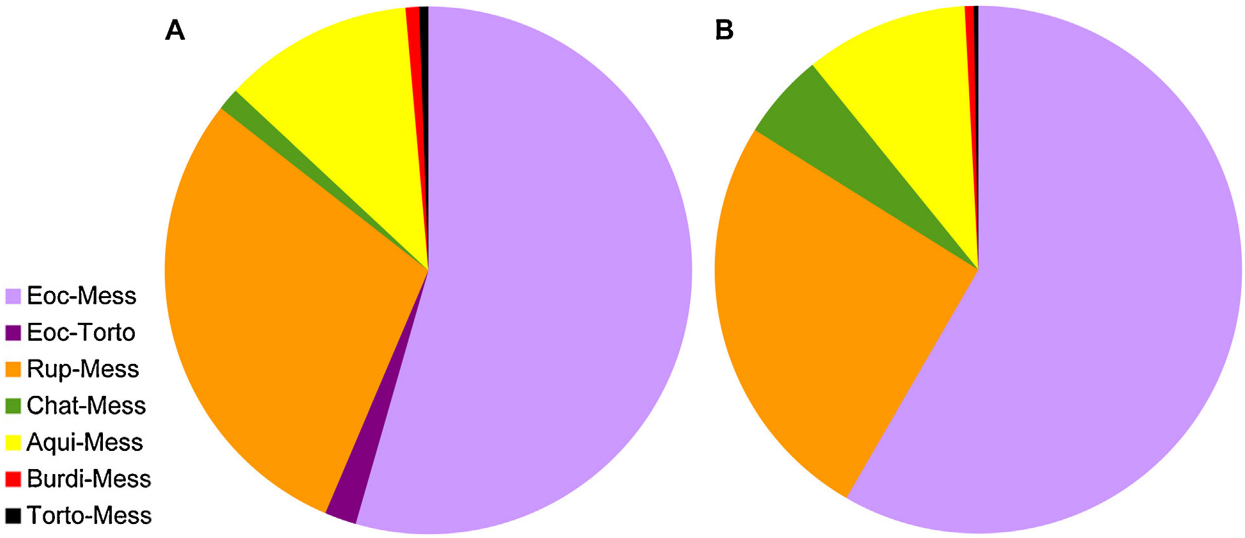

Fig. 6. Percentage of z-coral occurrences, respectively in the Tortonian and in the Messinian, according to the temporal range of genera in the Mesogean region. Temporal ranges of genera are indicated by the different colors. Eoc-Mess: Eocene to Messinian; Eoc-Torto: Eocene to Tortonian; Rup-Mess: Rupelian to Messinian; Chat-Mess: Chattian to Messinian; Aqui-Mess: Aquitanian to Messinian; Burdi-Mess: Burdigalian to Messinian; Torto-Mess: Tortonian to Messinian.

Fig. 6. Pourcentage d'occurrences, respectivement dans le Tortonien et le Messinien, en fonction de la répartition stratigraphique dans la région mésogéenne. Les répartitions stratigraphiques des genres sont indiquées par les différentes couleurs. Eoc-Mess : Eocène à Messinien ; Eoc-Torto : Eocène à Tortonien ; Rup-Mess : Rupélien à Messinien ; Chat-Mess : Chattien à Messinien ; Aqui-Mess : Aquitanien à Messinien ; Burdi-Mess : Burdigalien à Messinien ; Torto-Mess : Tortonien à Messinien.

for *Porites*, *Siderastrea*, *Tarbellastrea*, *Solenastrea*, and *Platygyra* (Fig. 4). The Middle Miocene, including the Miocene Climatic Optimum and the subsequent Middle Miocene climatic transition, represents a major change in the Cenozoic climatic evolution and an important step in the re-organization of the global climatic system (Flower and Kennett, 1994). In the circum-Mediterranean region, the upper part of the Serravallian corresponds to a general deterioration of environmental conditions favorable for z-corals and a related restriction of suitable habitats for development of z-coral communities; hence all genera show a decrease of their spatial distribution at that time (see Perrin and Bosellini, 2012, for detail). Some other genera show a gradual spatial expansion to a maximum, followed by a gradual decrease (*Montastraea*, *Stylophora*, *Favites*, *Favia*, *Goniopora*, *Scolymia*, *Plesiastrea*, *Thegioastrea*, *Aquitanastrea*). These genera declined but survived until the Late Miocene (Fig. 4). The remaining genera are either too rare to be analyzed (*Diploria*, *Goniastrea*, *Cyphastrea*, *Mioscapophyllia*) or have a potentially incomplete record, such as *Defrancia* and possibly *Acanthastrea* (Fig. 4).

5. Discussion

5.1. Spatial patterns

Analysis of the geographic distribution of z-coral genera during the Late Miocene does not show any clear differentiation between eastern and western Mediterranean provided that noise produced by the spatial heterogeneity of data resulting from different levels of investigation between areas is heeded. A similar pattern was found for the entire Oligocene-to-Miocene time interval with no evidence of biogeographic subprovinces in the circum-Mediterranean region for the z-coral fauna, which has been explained by the long-distance dispersal potential of coral larvae compared to the scale of the Mediterranean at that time (Perrin and Bosellini, 2012).

It should be noted however that areas with relatively higher generic richness in the Tortonian are maintained as important sources of z-coral richness during the Early Messinian. This trend is further enhanced along the Betics-Balearic and North African Messinian coral reef alignments extending from the edges of the Alboran Sea westward. The high number of reefs and reef complexes around the Alboran Sea during the Messinian may result from several causes:

- the highest level of investigation in the western Mediterranean, especially in western North Africa (Morocco and Algeria) and southern Spain, compared to the eastern Mediterranean areas;
- the tectonic activity in the Betics and North Morocco that created topographic highs favourable to the settlement of coral reefs;
- the presence of open marine waters either for a slightly longer time in this zone close to the Atlantic Ocean compared to areas more to the east, or continuously in small basins of the Alboran Sea.

Such basins could have acted as potential sanctuaries for open marine biotas during the Messinian Salinity Crisis, permitting the survivorship of the z-coral genus *Porites*, and the growth of *Porites* patch reefs in marginal basins after the crisis (Braga et al., 1995, 2006; Martín et al., 1993, 1999; Riding et al., 1991, 1998).

Furthermore, the increasing number of reef ecosystems from the beginning of the Tortonian to the end of the Early Messinian has also to be replaced in the global context of the increasing carbonate production from reef ecosystems from the beginning to the end of the Miocene. There was indeed a global Early to Late Miocene increase in reef volume related to reef expansion in the Indo-Pacific and also to a lesser degree in the Mediterranean, although the Late Miocene z-corals thrive at the northern limit of the reef belt (Perrin, 2002; Perrin and Kiessling, 2010).

5.2. The Late Miocene generic pool: heritage of the Mediterranean history

The Mediterranean Late Miocene pool of z-corals is represented by 20 genera, which is of comparable size to the present-day z-coral diversity of the Caribbean where a total of 25 genera is commonly assessed.

From our analysis, it appears that the so-often reported Tortonian-to-Messinian coral decline corresponds to the loss of only three rare coral genera at the end of the Tortonian. Moreover, this reduction of coral generic richness from the Tortonian to the Messinian is corrupted by potential biases, including the difficulty of defining the Tortonian-Messinian boundary in the carbonate sections bearing coral facies, which classically extend from the Upper Tortonian to the Lower Messinian, and the discovery of rare taxa within assemblages largely dominated by one or two genera. More significant is the occurrence of monogeneric *Porites* buildups at the top of Messinian carbonate platforms, in association with the development of particular microbial-rich facies, forming altogether the Terminal Carbonate Complex (Esteban, 1979), which in the western Mediterranean has been considered as coeval or even postdating the basinal evaporitic deposits.

The Mediterranean z-coral pool already overcame several reductions in the Early-Late Serravallian and Serravallian-Tortonian boundary (Bosellini and Perrin, 2008). These decreases of faunal diversity are related to global and regional climatic causes, mainly the long-term cooling resulting from the slow migration of the Mediterranean realm northwards outside of the tropical-subtropical belt. Higher frequency climatic fluctuations, such as cooling of sea-surface temperatures leading to the deposit of temperate carbonates in the Early Tortonian (Betzler et al., 1997, 2000), or glacial-to-interglacial cycles in the Latest Tortonian and Early Messinian (Brachert et al., 1996, 1998, 2001; Martín and Braga, 1994) have no perceptible effects on z-coral diversity at the regional scale. In addition, the closure of the seaway through the Middle East ended the potential faunal exchange with the Indo-Pacific coral fauna and consequently limited the genetic pool of z-corals within the Mediterranean (Perrin and Bosellini, 2012). Thus, the Late Miocene Mediterranean z-coral fauna, although having the capacity to build well-developed reef ecosystems during the Early Messinian, was a relict fauna with highly limited speciation (only one genus originated in the Tortonian), living on the edge of their ecological requirements in terms of light (as reduced incidence of solar energy at these latitudes) and temperature ranges. When compared to their previous counterparts, the Late Miocene z-coral ecosystems are characterized by:

- major differences in the structure of coral communities, resulting from a lower taxonomic richness and the large dominance of the genus *Porites*;
- the preserved capacity of building 3D reef structures similar to earlier Oligocene-Miocene 3D-shallow-water framework reefs (e.g. Chattian: Bosellini, 2006; Bosellini and Russo, 1992; Langhian-Earliest Serravallian: Perrin, 2000; Perrin et al., 1998).

In this sense, they differ from modern high-latitude *Porites*-dominated communities, which do not form 3D reef framework (Halfar et al., 2005).

Most genera comprising the Late Miocene z-coral fauna have a long temporal range in the Mediterranean region, where their first appearance dates to the beginning of the Oligocene or from the Eocene or even earlier. In a previous study concerning the Oligocene-Miocene z-coral fauna of the circum-Mediterranean region, we demonstrated that the most widespread genera tend to have a long temporal range while the spatially restricted genera have a moderate to short stratigraphic range because widely distributed taxa have a better chance of surviving extinction (Perrin and Bosellini, 2012). Additionally, the potential ability of individual taxa to adapt to varied or new conditions is probably enhanced for long-term range genera. This would explain why these Late Miocene Mediterranean z-corals were still able to flourish at these relatively high latitudes for tropical fauna. For the same reason, *Porites*, the most widespread genus and also the most dominant within ecological assemblages, was the best equipped, and hence the only one, to survive the Salinity Crisis. The high capacity of this genus to adapt efficiently to a wide spectrum of ecological conditions is still observable in modern reef settings and is particularly well demonstrated by the presence of high-latitude monospecific *Porites* coral communities (Halfar et al., 2005).

6. Conclusions

Z-coral diversity and distribution in the Mediterranean region resulted from a combination of long-term evolution of the Mediterranean taxonomic pool (historical biogeography), long-term climatic trend towards cooler sea-surface temperatures and reduction of light resulting from the northwards migration of the whole region, and short-term tectonic events producing changes in environmental conditions.

Some areas, such as the two reef-coral alignments bordering the northern and southern margins of the Alboran Sea, preferentially acted as sources of z-coral diversity during the Late Miocene.

The Late Miocene pool, which is represented by about 20 genera, corresponds to a relict fauna, isolated from the global z-coral genetic pool since the Early Miocene and with highly limited speciation. This Mediterranean fauna also corresponds to the highest latitude z-coral assemblages of their time, which were living on the edge of their ecological requirements in terms of solar energy and temperature ranges.

At the regional scale, there is no significant difference between the Tortonian and the Messinian z-coral fauna. The most important faunal change is the maintenance of only one genus, *Porites*, in facies ending the Messinian carbonate platforms (TCC) and coeval or even postdating the Salinity Crisis in the marginal basins close to the Alboran Sea.

Most genera comprising the Late Miocene z-coral fauna have a long temporal range in the region which certainly contributed to provide them a good ability of adaptation to a wide range of abiotic conditions, and hence to cope with environmental and climatic conditions unusual for such type of tropical-subtropical biotas.

Acknowledgements

This work is a contribution to the CNRS project PICS 4723 "Carbonate Production from Greenhouse to Icehouse Earth System: changing patterns of reef ecosystems and z-coral communities during the Eocene-Miocene climatic transition". Two anonymous reviewers are thanked for their valuable suggestions which helped in improving the manuscript.

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