Mediterranean Corals Through Time: From Miocene to Present

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Agostina Vertino, Jarosław Stolarski,
Francesca R. Bosellini, and Marco Taviani

Abstract

Stony corals, especially scleractinians, are a recurrent component of the benthic fauna of the Mediterranean basin and its Mesozoic-to-Cenozoic precursors. Both morphological and geochemical features of coral skeletons place these organisms among the most important natural paleoarchives of the Mediterranean geological history. The present day low diversity of the Mediterranean scleractinian fauna (25 genera and only 33 species) strikingly contrasts with its high diversity in the Early-Middle Miocene (over 80 genera and hundreds of species). The decline in coral richness has occurred since the late Middle Miocene onwards. This impoverishment trend was not linear, but abrupt in shallow-water environments during and immediately after the Late Miocene and more gradual since the Pliocene onwards. At the end of the Miocene, the Mediterranean coral fauna underwent a drastic modification that led to the disappearance of almost all zooxanthellate corals and the well-established shallow-water coral-reef province. However, the generic diversity of azooxanthellate and deep-water corals did not undergo significant modifications, that were instead much stronger at the end of the Pliocene and of the Pleistocene. Indeed, before the Calabrian stage, all remnant Indo-Pacific-like azooxanthellate genera disappeared and a clear NE Atlantic affinity was established, whereas at the Pleistocene – Holocene boundary, there was a clear reduction in psychrospheric deep-water taxa. The causes that led to the impoverishment of the Mediterranean coral fauna diversity are complex and not all fully understood. However, there is a clear link between the coral diversity decrease, the gradual northward shift outside the tropical belt of the Mediterranean region, and the major climate modifications on a global scale during the last 20 million years.

Keywords

Corals • Scleractinia • Mediterranean • Neogene • Pleistocene • Recent • Climate

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A. Vertino (✉)
Department of Earth and Environmental Sciences,
University of Milano-Bicocca, Piazza della Scienza 4,
20126, Milan, Italy
e-mail: agostina.vertino@unimib.it

J. Stolarski
Institute of Paleobiology, Polish Academy of Sciences,
Twarda 51/55, 00-818 Warsaw, Poland
e-mail: stolacy@twarda.pan.pl

F.R. Bosellini
Department of Chemical and Geological Sciences,
University of Modena and Reggio Emilia,
L.go S.Eufemia 19, 41100 Modena, Italy
e-mail: francesca.bosellini@unimore.it

M. Taviani
Institute of Marine Sciences, National Research Council
(ISMAR-CNR), Bologna, via Gobetti 101, 40129 Bologna, Italy

Biology Department, Woods Hole Oceanographic Institution,
266 Woods Hole Road, Woods Hole, MA 02543, USA
e-mail: marco.taviani@bo.ismar.cnr.it

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Introduction

“Coral” is a popular term used to refer to marine animals in the class Anthozoa (phylum Cnidaria) that typically form colourful and fascinating colonies. More properly, the locution “stony corals” (Cairns et al. 1999) is instead used to indicate those cnidarians that form calcified skeletons and that belong to both the class Anthozoa (order Scleractinia and subclass Octocorallia *partim*) and Hydrozoa (family Stylasteridae).

This paper is mostly focused on the stony coral representatives of the order Scleractinia, whose evolutionary history dates back to the Paleozoic (Stolarski et al. 2011), though it is mostly known from its sudden Mesozoic appearance about 240 Ma (Roniewicz and Morycowa 1993). Scleractinians produce an aragonite skeleton, with some possible exceptions in the Cretaceous (Stolarski et al. 2007), and comprise the main reef-building organisms of both shallow and deep modern seas. They have long been used for reconstructing the history of oceans and seas, mainly because they can build large carbonate structures (“reefs”) which are well preserved in the geological record, and because most extant reef-building scleractinian species are restricted to tropical shallow marine waters (Veron 1995, 2000) thus having a distinct climatic significance (Rosen 1999). Indeed reef-building zooxanthellate scleractinians, i.e., living in symbiosis with the unicellular algae zooxanthellae (e.g., Stanley and van de Schootbrugge 2009), thrive in the modern euphotic zone of the circum-global latitude belt comprised between 35–40°N and about 35°S where the lowest mean annual sea-surface temperature is around 16 °C (Rosen 1999). Azooxanthellate scleractinians, deprived of photosymbionts, are almost as rich in species as the zooxanthellate ones (711 *vs* 777 species, Roberts et al. 2009) and also include frame-building taxa which function as primary engineers of extensive carbonate bioconstructions. However they are much less known than the tropical cousins because they thrive in dark, cold (mostly 4–8 °C) and generally deep (up to > 1,000 m) oceanic waters (e.g. Freiwald et al. 2004).

Zooxanthellate (z-) and azooxanthellate (az-) corals have been a recurrent component of the benthic fauna of the Mediterranean basin and its Mesozoic-to-Cenozoic precursors. Being particularly sensitive to environmental modifications, they have undergone several changes in both diversity, reef-building capacity and geographic distribution through time. However, despite the spectacular record in Cenozoic deposits of peri-Mediterranean regions, the history of Mediterranean corals (in particular azooxanthellate ones) is still poorly understood.

This contribution provides a critical overview of Miocene to Recent Mediterranean corals, with special emphasis on the az-scleractinian genera distribution through space and time (Figs. 14.1–14.3). Our inferences are based on literature review and analysis of fossil and modern coral specimens held in the collections of several institutions (Museum of Paleontology and Botanical Garden, University of Modena and Reggio Emilia, IPUM; “G. Gemmellaro” Museum of Palaeontology and Geology, University of Palermo, MPG-P; Museum of Paleontology, University of Catania, MP-C; Museum of Natural History, Turin University, MN-T; Museum of Paleontology, Sapienza University of Rome, MP-R; Departement of Earth Sciences, University Milano-Bicocca, DES-M; Institute of Marine Sciences – CNR, Bologna; Muséum National d’Histoire Naturelle, Paris; Smithsonian National Museum of Natural History, Washington D.C., NMNH). We present and briefly discuss the most relevant aspects related to the presence in the Mediterranean basin of both zooxanthellate and azooxanthellate coral taxa during about the last 20 million years. The distinction between z- and az-coral genera presented in this paper follows the criteria proposed by Wilson and Rosen (1998) and Perrin and Bosellini

Fig. 14.1 Map showing the Mediterranean Sea and the location of the Miocene to Pleistocene outcrops containing the fossil azooxanthellate scleractinian corals (az-corals) mentioned in the text. Colouring of stratigraphic units (*colours of stars*) follows the Commission for the Geological Map of the World (http://www.ccgm.org; see also http://www.stratigraphy.org)

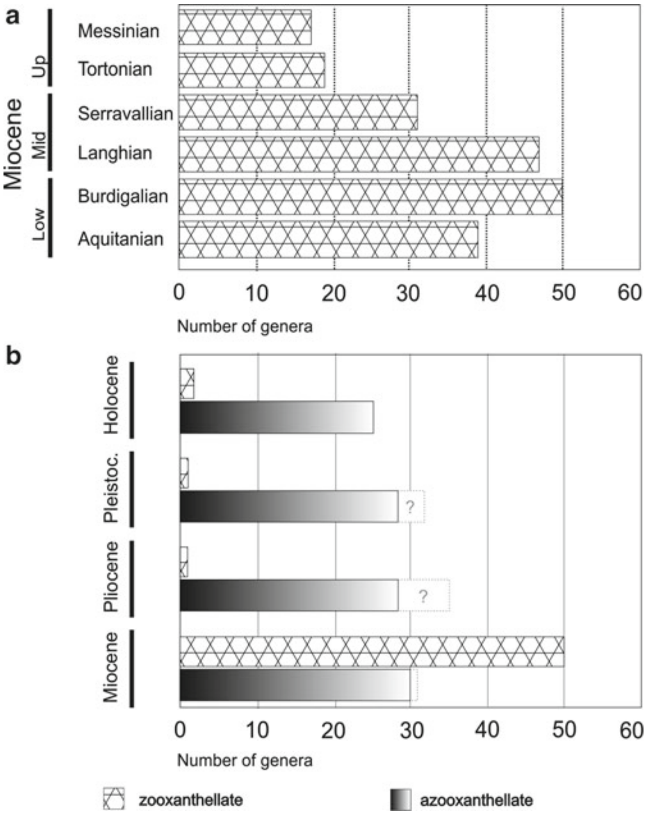

Fig. 14.2 Abundance of genera of zooxanthellate scleractinian corals during the Miocene (**a**) and of both zooxanthellate and azooxanthellate scleractinian corals from Miocene to Holocene (**b**). *White* histograms with *grey dotted lines* and *question marks* indicate taxa mentioned in previous works and whose occurrence needs to be verified (Fig. 14.2a modified after Bosellini and Perrin 2008)

(2012) for fossil corals. Although zooxanthellae are not preserved in the fossil record as body fossils (Stanley and Helmle 2010), we infer with some confidence their former presence in the coral tissues based upon actualistic assumption made at the generic systematic level.

Our work aims to highlight the importance of fossil corals as a natural archive of information on the history of the Mediterranean basin, and to foster the need for more studies related to both taxonomic and stratigraphic aspects of Neogene-Pleistocene coral deposits from peri-Mediterranean regions. In fact, most information on Neogene corals, and in particular azooxanthellate ones, dates back to the first half of the twentieth century, therefore both the stratigraphy of coral-bearing deposits and the taxonomy at the species level is in need of a comprehensive review. Some recent overviews of Oligo-Miocene Mediterranean z-corals (Bosellini and Perrin 2008; Perrin and Bosellini 2012), of Pleistocene az-scleractinians (Vertino 2003), and this study represent a first step towards critical revision of fossil Mediterranean corals, but there is still a long road ahead.

Mediterranean Coral Fauna in the Miocene

Early-Middle Miocene

Aquitanian z-corals are documented from a number of localities (e.g., Chevalier 1961; Perrin and Bosellini 2012), but their diversity seems to be modest. Az-corals from the same stage are instead virtually unknown except for the occasional records of *Desmophyllum*, *Phyllangia* and some rhizangiid corals (Chevalier 1961; Oosterban 1988; Cahuzac and Chaix 1993, 1996).

The Burdigalian-Langhian seems to have been a particularly favorable time for corals. They have been reported from several localities (review in Chevalier 1961; Bosellini and Perrin 2008; Perrin and Bosellini 2012) and in northern Italy alone (mostly in the Turin Hills deposits) over 70 scleractinian genera, including z- and az-corals, have been recorded. The Burdigalian shallow-water bioconstructions were of moderate lateral extension, with Porites and Tarbellastraea as the most common genera associated with *Favites*, *Montastraea*, *Favia*, *Solenastrea*, *Siderastrea*, *Thegioastrea*, *Caulastraea*, *Goniopora* and *Stylophora* (Perrin and Bosellini 2012). These corals were found in shallow-water mixed carbonate-siliciclastic sediments as well as in mass-gravity dominated deposits (e.g., Turin Hills localities), mixed with deeper-water az-corals. Langhian z-coral deposits document a Middle-Miocene latitudinal expansion of true coral reefs and reef complexes, followed by a contraction during the Serravallian, when z-corals apparently disappear from distinct areas such as the Aquitaine Basin, Catalonia, Corsica, Sardinia, Gulf of Suez and Central Paratethys (Perrin et al. 1998; Perrin and Bosellini 2012). These local environmental deteriorations are reflected in a strong decrease of z-coral genera between Langhian and Serravallian (Bosellini and Perrin 2008; Fig. 14.2a).

The Early-Middle Miocene also represents a flourishing time interval for Mediterranean az-corals. So far 30 genera and 7 subgenera can be certainly ascribed to this time period (Figs. 14.2–14.3), and the occurrence of further taxa (mentioned in nineteenth and early twentieth century literature) needs to be verified. Early-Middle Miocene az-corals have been recorded from several peri-Mediterranean regions (Fig. 14.1). However, the most diverse fauna examined so far pertains to Burdigalian-Langhian deposits from northern Italy (Turin Hills), where exceptionally large morphotypes, such as *Balanophyllia* specimens over 10 cm in length (Zuffardi-Comerci 1932; Chevalier 1961; A. Vertino pers. obs.), are rather common. More than half of the Early-Middle Miocene az-scleractinian genera are colonial and morphologically indistinguishable from taxa living today in (i) infralittoral (e.g., *Astrangia*, *Cladangia*, *Cladocora*, Fig. 14.4c, d, *Culicia*, *Madracis* "*pharensis*-like"), (ii)

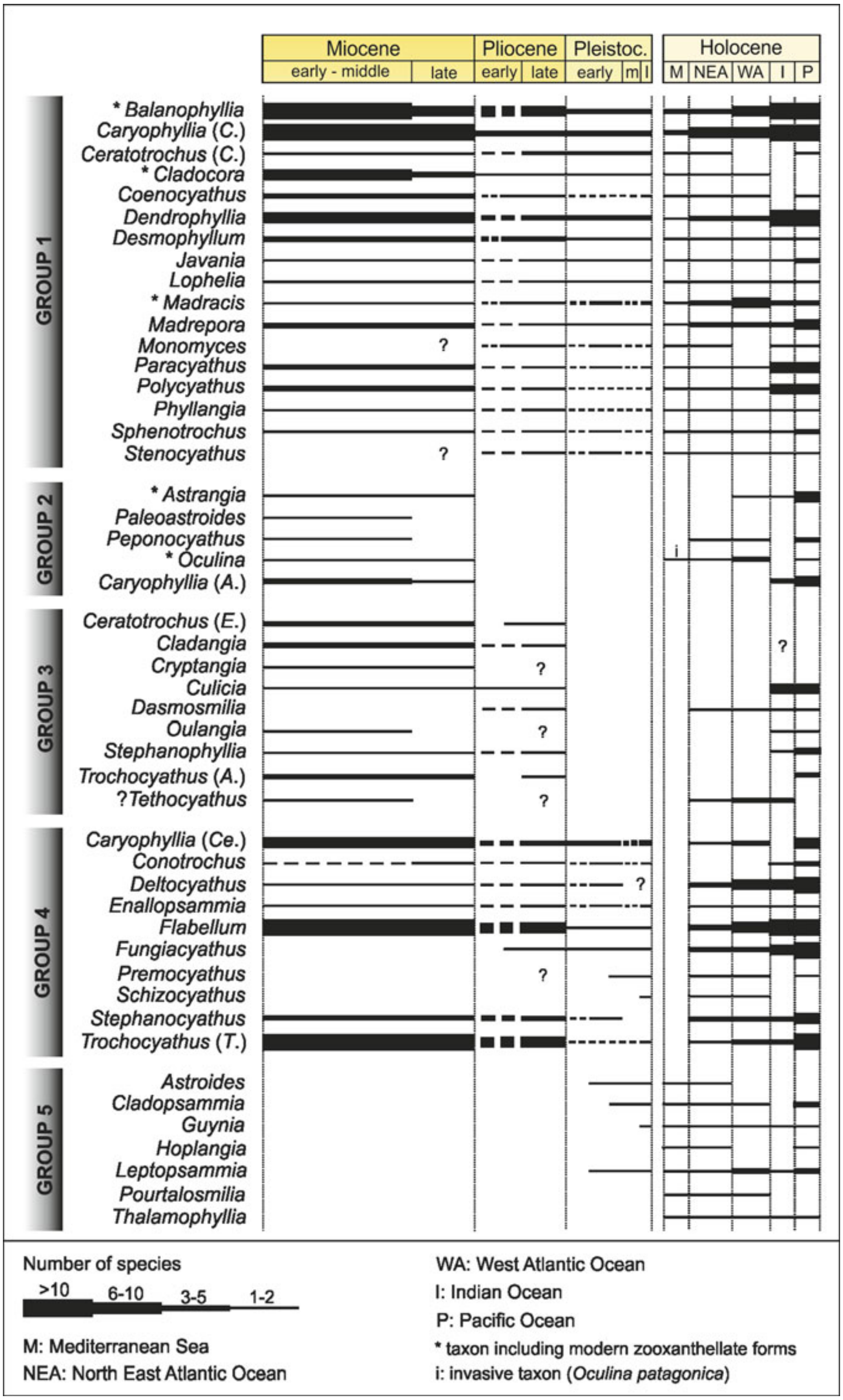

Fig. 14.3 List of Miocene to Recent Mediterranean azooxanthellate scleractinian genera and subgenera recognized so far. Taxa assigned to five main groups in line with their presence in the Mediterranean through time. *Group 1*: present since the Miocene or at least the Early Pliocene; *group 2*: disappeared after the Miocene; *group 3*: disappeared after the Pliocene; *group 4*: disappeared after the Pleistocene; *group 5*: currently living in the Mediterranean and not known before the Pleistocene or Holocene. Present distribution (and symbiotic status) of corals in the Mediterranean Sea, East–west Atlantic, Indian and Pacific oceans as stated in Zibrowius 1980; Vertino 2003; Roberts et al. 2009. Extant genera and subgenera, with exception of *Caryophyllia* (*Ceratocyathus*), according to Cairns and Kitahara 2012. Stratigraphy after the International Chronostratigraphic Chart 2012 (http://www.stratigraphy.org). *Dotted lines* and *question marks* refer to fossil occurrences documented only in ancient literature and in need of taxonomic confirmation.

circalittoral to epibathyal (e.g., *Coenocyathus*, *Dendrophyllia*, Fig. 14.4e, f, *Polycyathus*) and (iii) preferentially or exclusively bathyal environments (e.g., *Lophelia*, *Madrepora*, Fig. 14.4h, *Enallopsammia*). Most solitary corals are instead typical of lower circalittoral to bathyal environments (such as *Desmophyllum*, Fig. 14.4a, b) with exceptions of some species belonging to the genera *Balanophyllia* and *Caryophyllia* that are morphologically close to shallow-water species. Specimens resembling the typical azooxanthellate frame-building species *Lophelia pertusa* and *Madrepora oculata* (Fig. 14.4h) are relatively common but present only as isolated fragments. Among the genera and subgenera known so far, the only extinct ones are *Paleoastroides*, *Cryptangia* and *Ceratotrochus* (*Edwardsotrochus*), although the last genus has been recorded in the Mediterranean throughout the Pliocene

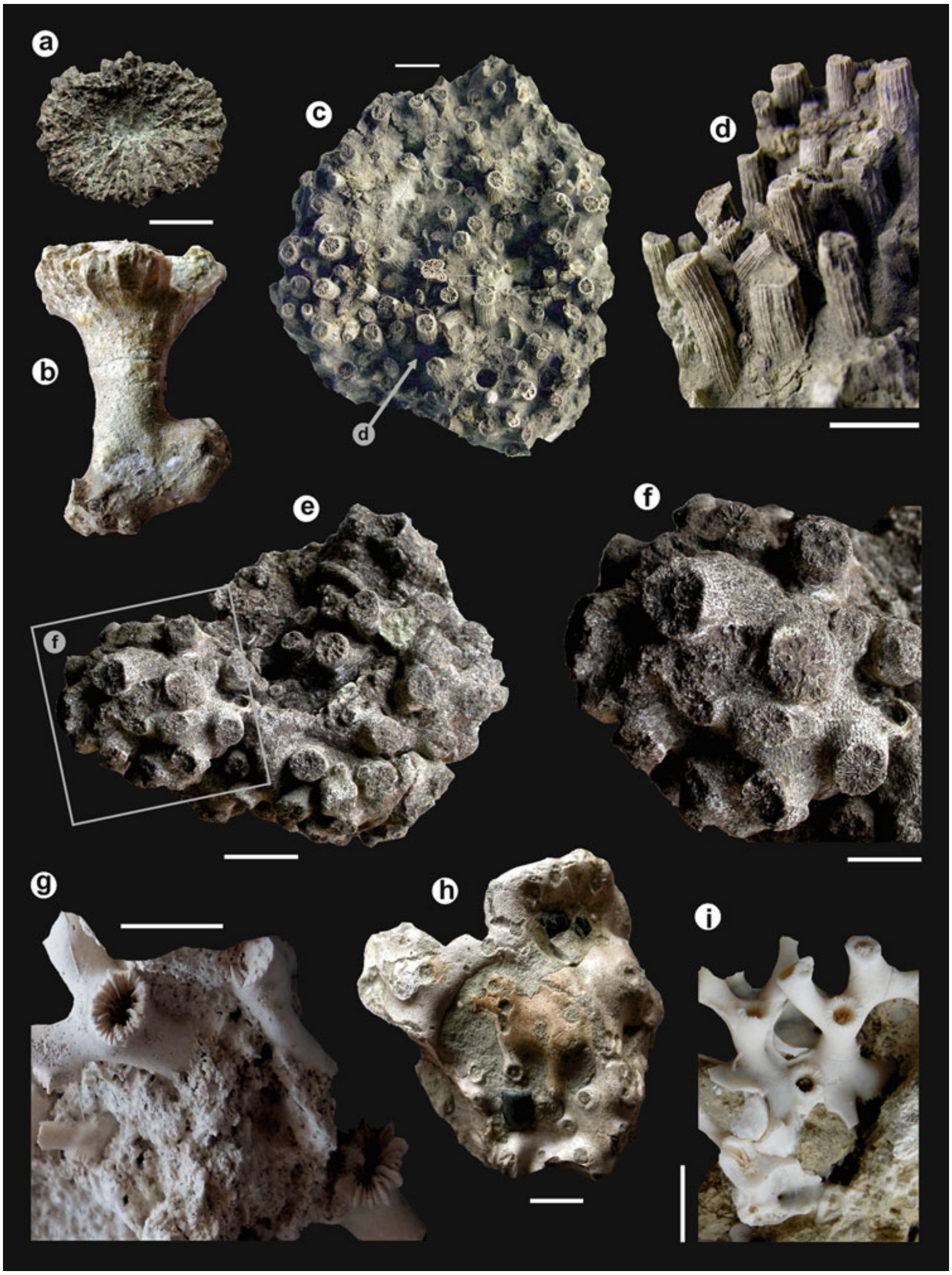

Fig. 14.4 Fossil examples of scleractinian corals persistent in the Mediterranean from Miocene to Recent (group 1, see Fig. 14.3): *Desmophyllum* cf. *dianthus* (**a**, **b**), Baldissero, Turin Hills, Miocene, MNH-T/10369; *Cladocora* cf. *caespitosa* (**c**, **d**), "Argille Azzurre Fm", Castell'Arquato, Pliocene, IPUM/16925 (specimen figured in Montanaro 1931, Tav IV, Fig. 14.6); *Dendrophyllia* sp. (**e**, **f**), Rio Batteria, Turin Hills, Miocene, MNH-T/10360; *Lophelia pertusa* (**g**), Gravitelli, Messina, Pleistocene, MP-C/VIPlC3; *Madrepora oculata* (**h**), Sciolze, Turin Hills, Miocene, MNH-T/10072, (**i**), La Montagna, Messina, Pleistocene, MP-C/VIPlC4. Scale bars equal 10 mm, only in (**e**) equals 20 mm

(Figs. 14.3; 14.5c, f). Almost all Early-Middle Miocene az-scleractinian genera still exist in modern Indian and/or Pacific waters, around 70 % in the NE Atlantic and only 50 % in the modern Mediterranean (Fig. 14.3). It is noteworthy that the following six taxa *Caryophyllia* (*Acanthocyathus*), *Conotrochus*, *Culicia*, *Oulangia*, *Trochocyathus* (*Aplocyathus*) (14.5a, b) *Stephanophyllia*, (Fig. 14.5e) are today exclusive to Indo-Pacific regions and that most of the very common and diverse genera of Early-Middle Miocene deposits, such as *Balanophyllia*, *Dendrophyllia*, *Flabellum* (14.5h–j), *Trochocyathus* (*Trochocyathus*) are among the most diverse genera in

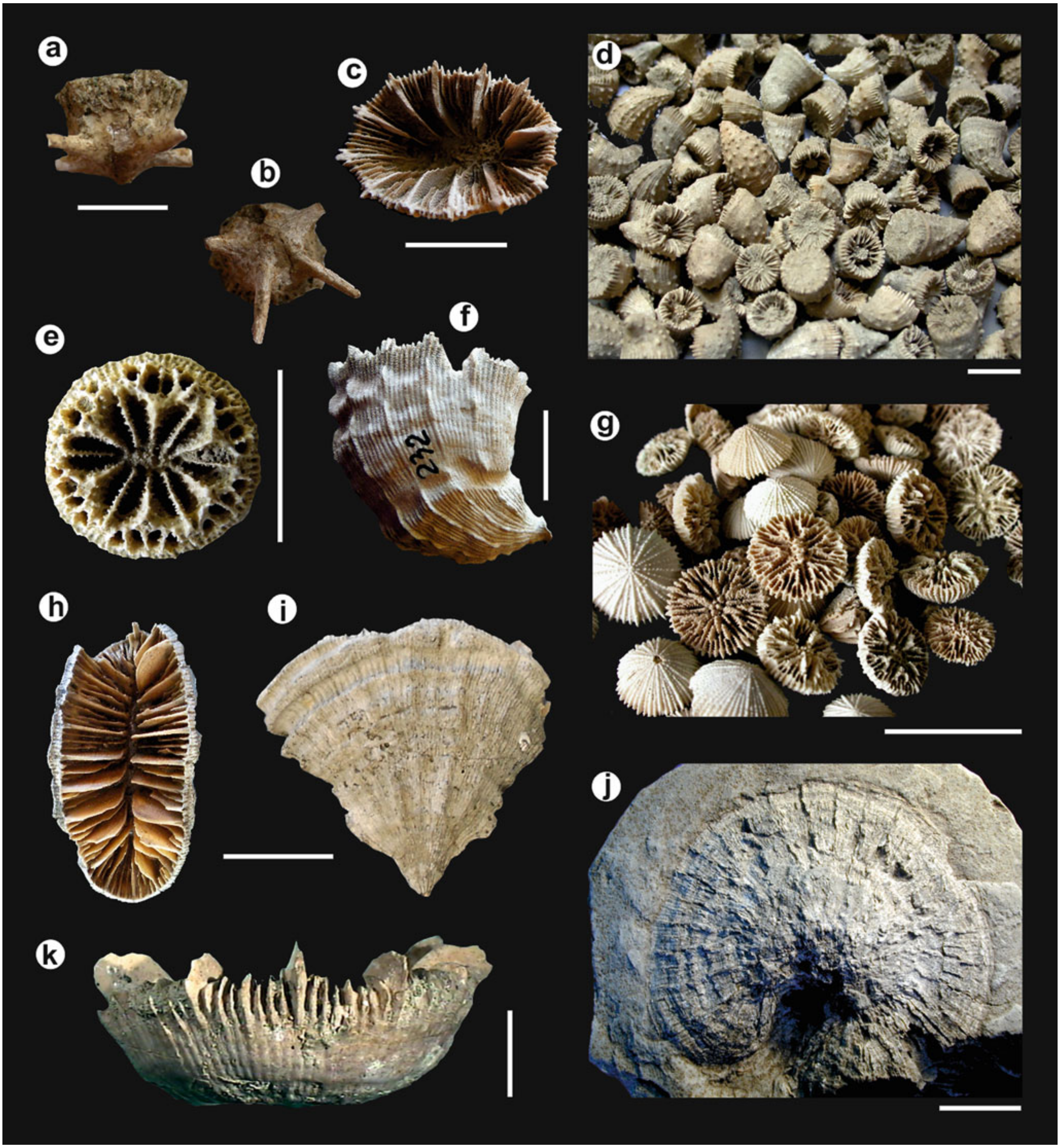

Fig. 14.5 Fossil examples of Miocene to Pleistocene scleractinian corals extinct in the Mediterranean. *Trochocyathus* (*Aplocyathus*) *armatus*, (**a**, **b**), Grangia, Turin Hills, Miocene, MNH-T/10689; *Ceratotrochus* (*Edwardsotrochus*) *duodecimcostatus*, (**c**, **f**), Civiciano, Siena basin, Pliocene, DES-M/VIPlC1; *Trochocyathus multispinosus* (**d**), Tortona, Miocene, IPUM/32352; *Stephanophyllia elegans* (**e**), Tortona, Miocene, IPUM/16851; *Deltocyathus italicus*, Tortona, Miocene, IPUM/32390; *Flabellum avicula* (**h**, **i**), Chero, Piacenza, Pliocene, IPUM/16937; *Flabellum vaticani* (**j**), Cava Lanciani, Vaticano, Rome, Pliocene, MP-R/3638 (very similar to modern *F. knoxi* specimens, held in the Smithsonian NMNH and collected in the south Pacific at c. 420 m depth); *Stephanocyathus elegans* (**k**), Messina, Pleistocene, MPG-P/547. Scale bars equal 10 mm in (**a**–**g**, **k**) and 20 mm in (**h**–**j**)

modern Indo-Pacific waters (Fig. 14.3). Among the extant genera, only *Peponocyathus* seems to disappear from the proto-Mediterranean before the Tortonian stage.

Late Miocene

Z-coral reefs were abundant and well developed during the late Tortonian and Messinian in several peri-Mediterranean regions (southeastern Spain, the Balearic Islands, Italy, Sicily, Algeria, and Morocco), in particular the western Mediterranean (Martín and Braga 1994; Brachert et al. 1996; Braga et al. 1996; Martín et al. 2010). However, with respect to the Serravallian, the northern limit of Tortonian z-coral assemblages is shifted to the south (Perrin and Bosellini 2012) and the reef-building scleractinians are much less diverse than in the past reaching typically two to four genera (mostly *Tarbellastrea*, *Porites*, *Siderastrea* and *Solenastrea*) per locality. The reef belt shrinks further during the Messinian when very low-diversity reefs (typically dominated by the genera *Porites* and *Siderastrea*) are especially frequent in the western part of the Mediterranean basin (review in Bosellini and Perrin 2008 and Perrin and Bosellini 2012). From west to east they occurred in: Morocco (Ben-Moussa et al. 1989; Saint Martin and André 1992; Saint Martin and Cornée 1996; Rouchy et al. 2003), Spain (Esteban and Giner 1980; Rheinhold 1995; Esteban et al. 1978; Braga 1996; Sánchez-Almazo et al. 2001; Vennin et al. 2004; Martín et al. 2010), Baleares (Pomar 1991), Algeria (Saint Martin 1996), peninsular Italy (Bossio et al. 1996; Bosellini et al. 2001, 2002; Bosellini 2006; Romano et al. 2007), Sicily and Pelagian islands (Catalano 1979; Pedley and Grasso 1994; Pedley 1996; Buccheri et al. 1999; Moissette et al. 2002), Malta (Saint Martin and André 1992), Crete (Brachert et al. 2006), Cyprus (Follows 1992), and Turkey (Karabiyikoğlu et al. 2005). In general, the subtropical Messinian reef corals formed under mesotrophic to oligotrophic conditions (Bosellini et al. 2002; Romano et al. 2007) at an estimated temperature of around 16–17 °C (Bosellini and Perrin 2008). Despite their low diversity, the framebuilding capacity of z-corals in this period was particularly high, with the formation of true and large reef structures (including quite many fringing reef complexes) within both pure carbonate and mixed carbonate-siliciclastic settings (Pomar and Hallock 2007; Perrin and Bosellini 2012). Corals display a large suite of growth habits, up to aberrant forms. Reefs differ greatly even in the same geographic location both horizontally and vertically showing distinct ecological succession along a paleobathymetric gradient, suggested to be partly controlled by variations in sea-level and related changes in hydrodynamic energy and light conditions (e.g., Pomar 1991; Bosellini et al. 2001, 2002; Vennin et al. 2004) or by sediment supply (Rheinhold 1995). For any event, the further deterioration of Messinian seawater caused a stop to such coral growth in the Mediterranean with last ‘reefs’ being represented by microbialites (Esteban and Giner 1980; Riding et al. 1991a, b; Moissette et al. 2002; Roveri et al. 2009) and *Halimeda* and vermetid constructions (e.g., Braga et al. 1996; Bosellini et al. 2002). Interestingly small bioconstructions, up to 3 m high and up to 10 m across, commonly associated with oolitic bars and large microbial carbonate mounds were still present in the Messinian post-evaporitic Terminal Complex (Sorbas Member; Western Mediterranean) and characterized by only *Porites* (Esteban and Giner 1977; Riding et al. 1991a, b; Calvet et al. 1996; Braga and Martin 2000; Roveri et al. 2009; Martín et al. 2010). The final act of the Messinian Salinity Crisis (MSC) seems to have swept away most if not all stenoecious marine biota from the Mediterranean (Taviani 2002, 2004, and references therein). However, the main cause of the disappearance of the Mediterranean z-coral reef province at the end of the Miocene appears to be only secondarily linked with the MSC. Indeed, the cause of the diversity decrease of Mediterranean z-coral reefs, very evident after the Serravallian (Bosellini and Perrin 2008) and throughout the Late Miocene (Martín et al. 2010), has been mostly related to (i) the closure of the open marine seaway through Middle East (Bosellini and Perrin 2008) and (ii) the decreasing seawater surface temperature linked with the gradual northward shift of the Mediterranean region outside the tropical belt (e.g., Rosen 1999; Perrin 2002; Bosellini and Perrin 2008; Martín et al. 2010).

Concerning Late Miocene a–z corals, most occurrences are found in northern Apennine localities, such as Tortona, Stazzano, S. Agata, Monte Baranzone, Montegibbio (De Angelis 1894; Simonelli 1896; Montanaro 1929; Zuffardi-Comerci 1937; Chevalier 1961; Corselli 2001), and in Sicily (Cafici 1883; Alemagna 1936) and pertain to the Tortonian stage. They are particularly rich in solitary forms such as *Balanophyllia*, *Ceratotrochus multispinosus* (Fig. 14.5d), *Ceratotrochus* (*Edwardsotrochus*) *duodecimcostatus*, *Deltocyathus italicus* (Fig. 14.5g), *Flabellum* and *Stephanophyllia* (Fig. 14.5e). Some Middle Miocene genera have not been recorded so far in Late Miocene deposits (Fig. 14.3) but this is possibly an artefact resulting from the scantiness of suitable outcrops of Tortonian to Messinian age. An exceptional case is represented by the lower Messinian taphocoenosis at Carboneras in the Spanish Betic Cordillera (Barrier et al. 1991). The benthic assemblage here is quite diverse (calcified sponges, cnidarians, molluscs and stalked crinoids) and contains numerous scleractinians (14 species at least, belonging to 13 genera) including Mediterranean extant genera such *Madrepora*, *Dendrophyllia*, *Desmophyllum*, *Caryophyllia*, *Javania*, *Balanophyllia* and *Flabellum*.

Truly cold-water coral bioconstructions (*Lophelia-Madrepora* dominated), comparable to the modern ones, have not been recorded so far in Late Miocene peri-Mediterranean outcrops. However, framestones and/or rudstones dominated by azooxanthellate colonial corals (*Dendrophyllia* and/or *Oculina*) have been identified in southern Italy (Mastandrea et al. 2002).

Coral Responses to a Cooling Mediterranean: From the Pliocene to the Glacial Ages

The end of the Miocene corresponds to the disappearance of the tropical/subtropical coral reef province and almost all zooxanthellate coral genera from the Mediterranean (Chevalier 1961; Rosen 1999; Bosellini and Perrin 2008; Martín et al. 2010; Perrin and Kiessling 2010; Perrin and Bosellini 2012 and reference therein). On a global scale, the beginning of the Pliocene marks a strong decrease in coral diversity and, for tropical shallow-water coral reefs, the establishment of a latitudinal belt comparable to that in the Holocene (Perrin and Kiessling 2010).

Pliocene

The Pliocene shallow-water coral fauna is less diverse with respect to the Miocene, lacking almost all zooxanthellate colonial corals with the only certain exception of the species *Cladocora caespitosa* (e.g., Aguirre and Jiménez 1998; Dornbos and Wilson 1999). Montanaro (1931) mentions *Siderastraea* and *Plesiastraea* from the Pliocene of northern Italy ("Astiano di Riorzo", Emilia Romagna region, Italy) but this occurrence needs to be verified. Typical shallow-water (< 50 m water depth) Pliocene taxa are colonial *Cladangia*, *Cladopsammia*, *Culicia*, *Madracis* and *Policyathus* and some species of solitary *Balanophyllia* and *Caryophyllia*. However the majority of the scleractinian genera known so far from Pliocene deposits are solitary forms preferentially or exclusively living in modern circalittoral to bathyal environments (De Angelis 1893, 1894, 1895; Osasco 1895; Simonelli 1895, 1896; Zuffardi-Comerci 1927, 1937; Montanaro 1931; Dieni and Omenetto 1960; Chevalier 1961; Russo 1980; Corselli 1997). In particular, the marine Piacenzian clayey deposits from northern Italy (Argille Azzurre Fm: Montanaro 1931; Zuffardi-Comerci 1937; Spadini 2012 pers. comm.) host abundant specimens of the genus *Flabellum*, the subgenus *Edwardsotrochus* (Fig. 14.5c, f) and dendrophylliids that may reach very large size as their Miocene counterparts. Very well preserved specimens of *Flabellum* (*F. siciliense*) and *Stephanophyllia* occur also in coarser Pliocene sediments, such as the bioclastic sands and calcarenites of Altavilla Milicia in Sicily (MPl 5 in age according to Ruggieri and D'Arpa 2004). The presence of deep-water frame-building genera, such as the colonial *Lophelia* and *Madrepora* (known in the nineteenth and early twentieth century literature as *Lophohelia* and *Amphihelia*, *Diplohelia*, respectively), the solitary gregarious *Desmophyllum* and some dendrophylliids (*Enallopsammia*, *Dendrophyllia*), is ascertained in the middle Pliocene from northern Italy (unpublished data), but their occurrence in several other Italian outcrops (e.g. Seguenza 1864, 1880; De Angelis 1894; Simonelli 1895, 1896; Montanaro 1931; Zuffardi-Comerci 1932; Chevalier 1961) needs to be corroborated with careful stratigraphic and taxonomic studies. Moreover deep-sea coral-bearing deposits dominated by *Madrepora*, *Lophelia*, *Desmophyllum* are reported as "Upper Pliocene" from several outcrops in southern Italy (e.g. Barrier 1984, 1987; Roux et al. 1988; Barrier et al. 1989) and Rhodes (Hanken et al. 1996). However, some of the Italian deposits have been recently ascribed to the Calabrian stage (Vertino 2003). Notably, the colonial az-scleractinian *Coenocyathus* is recorded from a Pliocene deep-water chemoherm in the Stirone river, northern Apennines (Monegatti et al. 2001).

The Indo-Pacific affinity recognized for the Miocene coral fauna is still discernible in Mediterranean Pliocene assemblages, though the number of species of several genera appears to be reduced (Fig. 14.3). Indeed, taxa living today exclusively in Indo-Pacific waters, such as *Culicia*, *Stephanophyllia*, and less commonly *Caryophllia* (*Acantocyathus*) and *Trochocyathus* (*Aplocyathus*), are known from several Pliocene Italian deposits and also from southern Spain and France, northern Africa, Greece (e.g., Chevalier 1961; Chaix and Cahuzac 2005; Vertino 2003; Martinell and Domènech 2009). Moreover the genera *Balanophyllia*, *Dendrophyllia*, *Trochocyathus* and *Flabellum* are still diverse in Pliocene outcrops and include species very similar to those in the modern Indo-Pacific (e.g., Fig. 14.5j).

Pleistocene

Similarly to what has been observed for shallow-water molluscs by Monegatti and Raffi (2010), climate variations during and at the end of the Pliocene seem to have had a strong impact on the diversity of both shallow- and deep-water az-corals. The data collected so far implies that the Pleistocene coral fauna is much more similar to the modern NE Atlantic than to the Pliocene one. Before the beginning of the Pleistocene (i) the typical "Indo-Pacific" genera and subgenera (*Culicia*, *Stephanophyllia*, *Acantocyathus* and *Aplocyathus*) seem to disappear in the Mediterranean and (ii) the diversity of dendrophylliids and of the very common Mio-Pliocene genera *Flabellum* and *Trochocyathus* remarkably decreased (Fig. 14.3). All genera and almost all species known from Pleistocene deposits of peri-Mediterranean regions live (or are very similar to species living) today in the NE Atlantic Ocean. Actually the genera *Astroides*, *Cladopsammia*, *Guynia*, *Leptopsammia* and *Schizocyathus* have not been recorded so far in Mediterranean deposits older than Pleistocene. However, they could have been misidentified and, regarding small-sized species such as *Guynia* and *Schizocyathus*, overlooked in Mio-Pliocene deposits.

The Pleistocene scleractinians known so far from the Mediterranean can be placed into four groups according to their environmental distribution: (1) Infralittoral, photophilous, e.g., *Cladocora caespitosa* (Bernasconi et al. 1997; Titschack et al. 2008; Peirano et al. 2004, 2009; Antonioli et al. 2009; Drinia et al. 2010; references therein), *Balanophyllia europaea* (e.g. Barrier et al. 1990) and sciaphilous, e.g., *Astroides calycularis* (Zibrowius 1995), *Cladopsammia rolandi*; (2) Infralittoral to upper circalittoral; preferentially on overhangs and caves above 50 m water depth, e.g., *Caryophyllia inornata*, *Hoplangia durotrix*, *Leptopsammia pruvoti*; (3) Lower circalittoral to bathyal, e.g., *Caryophyllia clavata*, *C. smithii*, *Ceratotrochus magnaghi*, *Paracyathus pulchellus* (Vertino 2003 and reference therein); (4) Preferentially or exclusively bathyal, e.g., *Caryophyllia coronata*, *Caryophyllia* (*Ceratocyathus*) *elegans*, *Desmophyllum dianthus*, *Flabellum messanense*, *Fungiacyathus* aff. *fragilis*, *Lophelia pertusa* (Fig. 14.4g), *Madrepora oculata* (Fig. 14.4i), *Stephanocyathus elegans* (Fig. 14.4k) (Di Geronimo 1979; Vertino 2003; Di Geronimo et al. 2005; Titschack and Freiwald 2005; Taviani et al. 2011a, b). In the Calabrian stage (*G. cariacoensis* Zone, Vertino 2003), as well as in the Late Pleistocene (Remia and Taviani 2005; McCulloch et al. 2010; Taviani et al. 2011a, b), bathyal corals displaying a high frame-building potential (above all *L. pertusa*, *M. oculata*, *D. dianthus*) created extensive carbonate bioconstructions aligned with extant "cold-water coral reefs" from the modern ocean (e.g. Freiwald et al. 2004; Roberts et al. 2009). The most striking example of cold-water coral communities in the Early Pleistocene Mediterranean is represented by the spectacular coral framestones and rudstones cropping out along the margins of the Messina Strait (southern Italy, Seguenza 1864, 1873–1877, 1880; Di Geronimo 1987; Barrier et al. 1989, 1996; Zibrowius 1987, 1991; Roux et al. 1988; Di Geronimo et al. 2005; Vertino 2003). The abundance of still-submerged fossil cold-water corals (CWC), mostly ascribed to the Late Pleistocene (either predating or postdating the last glacial maximum: Taviani and Colantoni 1984; Taviani et al. 2005b; McCulloch et al. 2010; Angeletti and Taviani 2011; Taviani et al. 2011a, b) implies that better conditions than those today did exist in the very recent past of the Mediterranean for the settlement and maintenance of Atlantic-type frame-building CWC.

Present Coral Fauna: NE Atlantic Relict

The last remarkable modification that led to the modern composition of the Mediterranean coral fauna occurred at the end of the Pleistocene. The investigations carried out so far on Holocene benthic communities show that nine scleractinian genera (*Conotrochus*, *Deltocyathus*, *Enallopsammia*, *Flabellum*, *Fungiacyathus*, *Pemocyathus*, *Schizocyathus*, *Stephanocyathus*, *Trochocyathus*), the subgenus *Caryophyllia* (*Ceratocyathus*) and over 15 species (Vertino 2003) disappeared at the end of the Pleistocene (Fig. 14.3). Interestingly, most of these Pleistocene taxa are morphologically indistinguishable from species that live today in very deep and cold waters of the NE Atlantic (e.g. *Fungiacyathus fragilis*, *Caryophyllia sarsiae*, *C. ambrosia*, *Premocyathus polymorphus*, *Aulocyathus atlanticus*, *Stephanocyathus elegans*, *Flabellum alabastrum*, *Schizocyathus fissilis*, *Balanophyllia caryophylloides*, *Enallopsammia rostrata*).

In total 25 genera and 33 species live today in the Mediterranean Sea, most of them on hard substrates of the continental shelf (Zibrowius 1980). Only *Sphenotrochus andrewianus*, typical species of the "biocoenosis of coarse-grained sands and fine gravels under bottom currents (SGCF)", and the morphotypes "clavus" and "vermiformis" of the two circalittoral to epibathyal species *Caryophyllia smithii* and *Stenocyathus vermiformis*, respectively, are restricted to mobile substrates. The modern shallow-water coral fauna is very similar to the Pleistocene one; in fact, all infralittoral Pleistocene photophilous and sciafilous species are still present in modern Mediterranean waters, although the geographic distribution and/or development of some colonial species appears to be highly reduced. For instance, *Astroides calycularis*, at present known only in rocky coastal areas of the southwestern Mediterranean, had a wider geographic distribution during Pleistocene interglacial periods (when the superficial water temperature was probably higher) being found as fossil in several localities of the northern Mediterranean (Zibrowius 1995). Moreover *C. caespitosa* (Fig. 14.6b), the only zooxanthellate bioconstructor coral of the modern Mediterranean, forms still extensive banks near the Tunisian coast, in the Aegean (Laborel 1961; Zibrowius 1980; Peirano et al. 1998) and Adriatic Sea (Kružić et al. 2012), but seemed to be much more flourishing in warmer periods of the Pliocene and Pleistocene. *Oculina patagonica* represents another remarkable difference between the modern infralittoral Mediterranean coral fauna and Pleistocene one. This is indeed a

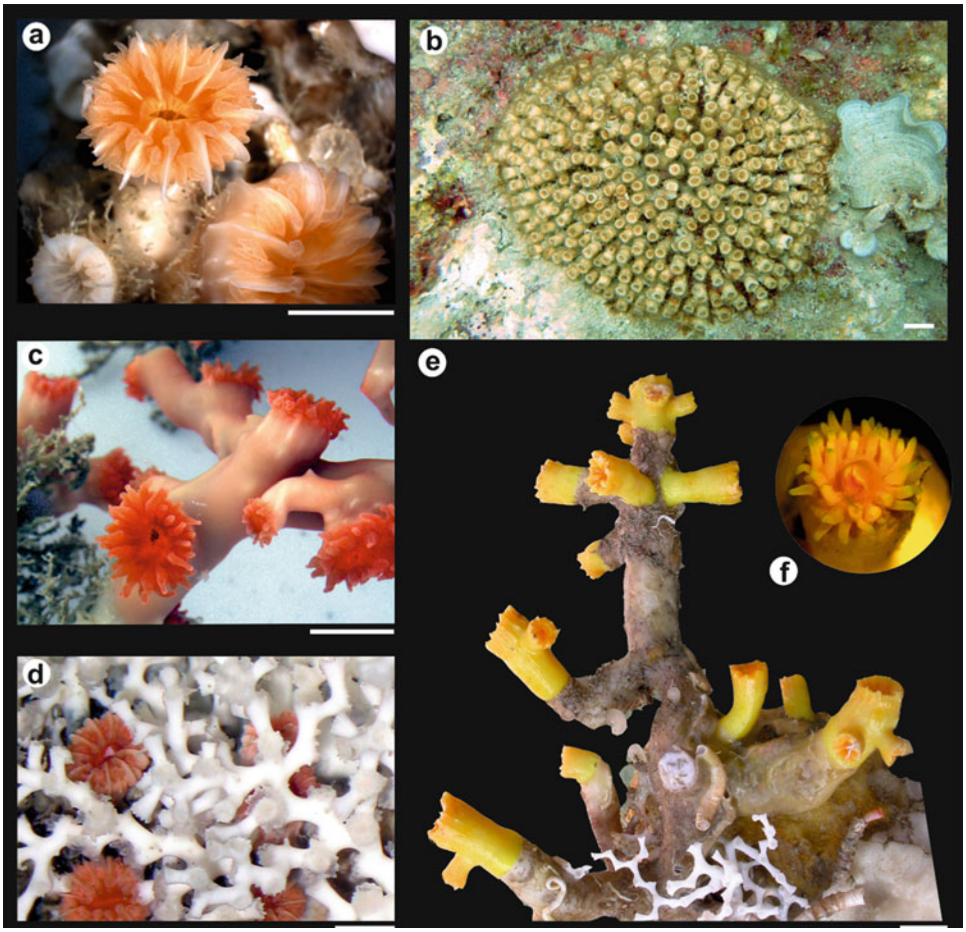

Fig. 14.6 Examples of modern (living) Mediterranean scleractinian corals. Solitary, gregarious, azooxanthellate *Desmophyllum dianthus* (**a**); colonial zooxanthellate *Cladocora caespitosa* (**b**); colonial azooxanthellate *Lophelia pertusa* (**c**), *Madrepora oculata* (**d**, *white*; corals with *red* polyps represent *Desmophyllum*) and *Dendrophyllia cornigera* (**e**, **f**). With exception of *Cladocora*: (Porto Cesareo, 11.5 m depth) all photographed specimens were collected in the bathyal environment (at ca. 600 m water depth) of the Mediterranean Sea during the M70-1 cruise, 2006, from the SML province (**a**, **c**) and the Bari Canyon (**d**–**f**). Scale bars equal 10 mm in (**a**–**c**), 20 mm in (**d**)

non-native invasive zooxanthellate species of recent introduction in the Mediterranean (60–70 years?) which today is widely known throughout the basin: Italy (Liguria), France (Marseille), Spain (Algeciras to Catalonia, Alboran, Cabrera and Columbretes), Algeria and Tunisia, Egypt (Alexandria area), Israel, Lebanon, Turkey, Greece (Zibrowius 1992; Sartoretto et al. 2008).

Apart from the exceptions mentioned above, the diversity of infralittoral to circalittoral and circalittoral to epibathyal corals (ecological groups "2" and "3" described in the previous paragraph) seems to be unchanged from the Pleistocene onwards. Instead, as mentioned above, the modern bathyal coral community is notably different than the Pleistocene one, lacking all cold stenothermic species which live today in the neighbouring NE Atlantic bathyal bottoms at temperature lower than 10 °C (Vertino 2003 and references therein). The extensive *Lophelia*-dominated bioconstructions, which characterized the Pleistocene Mediterranean and are the main components of the still growing NE Atlantic banks and giant mounds (comprehensive review in Freiwald et al. 2004; Roberts et al. 2009), underwent a strong regression at the end of the Pleistocene. Nevertheless, well-developed frame-building CWC communities are still present on Atlantic-like mounds, in terms of extension and biodiversity, of some locations of the western Mediterranean (Alboran Sea) (Lo iacono et al. in press). Moreover, bathyal *Madrepora*-dominated communities still thrive in the Ionian Sea, on the top and upper flanks of the small Santa Maria di Leuca (SML) mounds (e.g., Taviani et al. 2005a; Savini and Corselli 2010; Vertino et al. 2010a; Fig. 14.6a, c), as well as along flanks of canyons, fault escarpments and overhangs in several other localities of the Mediterranean Sea (Freiwald et al. 2009; Orejas et al. 2009; Gori et al. 2013; Sanfilippo et al. 2012; Fig. 14.6d–f).

Finally, it is worth mentioning the role as "secondary building" that the genus *Dendrophyllia* has been playing since at least the Early Miocene in the (proto-) Mediterranean. This genus is present in the modern basin with two species, *D. ramea* and *D. cornigera*, which differ in geographical and depth distribution (Zibrowius 1980, 2003; Salomidi et al. 2010). In the Mediterranean *D. ramea* is commonly observed around 30–40 m water depth whereas *D. cornigera* has a much wider bathymetric and geographic distribution. Indeed, the latter species has been recorded alive from around 80 up to 730 m water depth and it is rather common in bathyal communities (Zibrowius 1980; Freiwald et al. 2009; Mastrototaro et al. 2010; Vertino et al. 2010a; Salomidi et al. 2010), locally associated to the frame-building corals *M. oculata* and *L. pertusa*. *D. cornigera* can be considered as a community-structuring species because it can build very large colonies and, at certain places, its broken branches can create peculiar rubble facies which host diverse epi- and endofauna communities (Rosso et al. 2010; Vertino et al. 2010a; Taviani et al. 2011a, b). Likely, most of the *D. cornigera* rubble facies which characterize today the bathyal seafloor of several Mediterranean regions dates back to the Late Pleistocene implying, as already pointed out by Blanc et al. (1959) and Zibrowius (1980), a greater development of this species in the recent geological past of the basin. Remarkably, comparable dendrophylliid-dominated facies have been recorded so far both in Miocene (Mastandrea et al. 2002; Bosellini et al. 1999) and Early Pleistocene outcrops from southern Italy (Vertino 2003).

Corals Other than Scleractinians

Calcified corals also include anthozoans in the subclass Octocorallia and hydrozoans of the family Stylasteridae that secrete a calcitic skeleton. Their fossil history is comparatively poor with respect to scleractinians. Nevertheless, they are consistently cited in the paleontological literature. Bathyal representatives of the octocoral family Isididae (mostly the genus *Keratoisis*) have been recorded from the Miocene (e.g. De Angelis and Neviani 1897; Barrier et al. 1991; Zuffardi-Comerci 1932), Pliocene (Simonelli 1895) and Plio-Pleistocene (e.g. Seguenza 1864; Di Geronimo 1979, 1987; Fois 1990; Barrier et al. 1996; Vertino 2003; Di Geronimo et al. 2005) of the Mediterranean basin. Moreover, octocoral holdfasts referred to as Primnoidae have been recognized in the Miocene coral collection from the Turin Hills (Museum of Natural History, Turin University), in Plio-Pleistocene outcrops from southern Italy (Di Geronimo 1979; Grasshoff and Zibrowius 1983; unpublished data) and submerged deposits from the eastern Mediterranean of presumable Pleistocene age. Among octocorals, the genus *Corallium* has also been recorded several times in Miocene to Pleistocene outcrops of peri-Mediterranean regions (e.g., Zuffardi-Comerci 1927, 1932; Chevalier 1961; Barrier et al. 1991; Vertino et al. 2010b). Finally, a rich stylasterid fauna (14 species in at least 8 genera: *Calyptopora*, *Conopora*, *Crypthelia*, *Distichopora*, *Lepidopora*, *Pliobothrus*, *Stenohelia*, *Stylaster*) characterizes the lower Messinian taphocoenosis of Carboneras (Barrier et al. 1991), and *Errina* and *Stenohelia* have been collected from the Pleistocene of southern Italy (Di Geronimo et al. 2005). It is worth remarking that, with exception of the sytlasterid *Errina*, all coral genera mentioned in this paragraph are absent in the modern Mediterranean. Similarly to what has happened to scleractinians, Mediterranean octocorals and stylasterids underwent an abrupt diversity decrease in shallow waters at the end of the Miocene and in deep-waters at the end of the Pleistocene.

Corals as Palaeoceanographic Archives

In recent years a growing attention has been granted to certain corals as potential palaeoceanographic archives because of their encoding of seawater signals (temperature, nutrients, pH) within their carbonate skeleton. One of the reasons for the current success in oceanographic reconstructions relies upon the original aragonite composition of the exoskeleton in scleractinians that permits precise age assessment using U-series dating. Corals can be used to decipher oceanographic signals at various time scales from decadal to millennia (e.g., Schrag and Linsley 2002; Stirling and Andersen 2009; Thompson et al. 2011). Regarding specifically the Mediterranean basin, this technique has been applied thus far to both shallow- and deep-water Pleistocene to Holocene scleractinians using stable (oxygen, carbon, boron) and radiogenic (strontium and neodymium) isotopes and/or trace elements (Montagna et al. 2005, 2011a, b; Silenzi et al. 2005; López Correa et al. 2010; Trotter et al. 2011). In the shallow water environment, the prime candidate has been the zooxanthellate colonial coral *Cladocora caespitosa* that appears to be a reliable archive of seawater surface temperature (Peirano et al. 2004; Silenzi et al. 2005; Montagna et al. 2007, 2008a, b, 2011a), pH (Trotter et al. 2011) and pre- and post-bomb surface radiocarbon. Simultaneously, growing attention has been devoted to the geochemical screening of bathyal taxa to determine their reliability as oceanographic recorders. The solitary coral *Desmophyllum dianthus* has been shown to store decipherable information in its aragonitic exoskeleton (Montagna et al. 2005). In particular, it has been demonstrated that the P/Ca ratio of the skeletal aragonite of this quasi-cosmopolitan species is linearly correlated to the ambient seawater phosphorus concentration (Montagna et al. 2006; Anagnostou et al. 2011). Nonetheless, most of the geochemical signals are modified by the coral physiology during the biomineralization processes, complicating the paleoclimate reconstruction (Meibom et al. 2008; Brahmi et al. 2012). Culturing experiments and geochemical studies at fine scale resolution of Mediterranean corals are required to provide reliable evidence for these interpretations.

Regarding intermediate bathymetric situations in the water column (basically lower circalittoral to epibathyal benthic habitats), not much attention has been paid in evaluating such corals in the Mediterranean (i.e. *Dendrophyllia* spp, and *Caryophyllia* spp.). Geochemical applications to calcitic corals are still rather rare, although some attention has been given to fossil Isididae and both recent and fossil *Corallium* (Vielzeuf et al. 2008; Montagna et al. 2011b).

Current geochemical research on Mediterranean corals targets the Li/Mg ratio (Montagna et al. 2009) and neodymium isotopes (^{143}Nd/^{144}Nd: Montagna et al. 2011b) as reliable proxies for seawater temperature independent from 'vital effects' and water mass circulation, respectively.

Biodiversity of Tomorrow

What factors may shape the future Mediterranean coral diversity? Ocean acidification poses a direct threat to marine calcifiers, above all aragonitic corals, including those in the Mediterranean (Montagna et al. 2008a). On the other hand, recent studies on both shallow and deep water corals seem to document a certain resilience of scleractinians (at least azooxanthellate ones) to increasing temperature (Caroselli et al. 2012) and decreasing seawater pH, indicating that no extinction is foreseen in the near future (Rodolfo-Metalpa et al. 2011; Maier et al. 2012; McCulloch et al. 2012a, b).

Non-native invasion by coral species (e.g., *Oculina patagonica*) has already affected the aboriginal Mediterranean fauna. The warming trend of Mediterranean seawater might pave the road to the coming and successful establishment of true tropical corals, likely from the Red Sea as Lessepsian migrants. This issue has been considered by Por (2009) who makes the point that the Levantine Basin is already presenting a thermal status conducive to the maintenance of scleractinians such *Stylophora pistillata* and *Siderastrea savignyiana*, an argument conforming to the concept of the Godot basin introduced by Taviani 2002; Oliverio and Taviani 2003. However, the hydrological conditions prevailing in the Suez maritime connection between the two seas, and the relatively short larval life of corals seems to limit this migration (Por 2009). Although in the near future some subtropical-tropical corals may eventually settle in the Mediterranean, it is arguable that the expected cooling imported by the next ice age would be so detrimental as to cause their extinction (Chap. 16 by Sabelli and Taviani, this volume).

Discussion and Final Remarks

Data collected so far have led us to categorize the known Miocene to Recent az-scleractinian genera and subgenera in five main groups (Fig. 14.3). The first one includes the so-called "persistent" taxa, those that have lived in the Mediterranean since the Miocene or, at least, the Early Pliocene (some examples shown in Fig. 14.4). Almost all members of this group today show a very wide geographic distribution, and many of them have undergone a clear diversity decline at species level since the late Miocene. Interestingly, the most diverse Miocene genera (dendrophylliids and *Caryophyllia*) correspond to the most diverse ones of the Indo-Pacific Oceans. Groups 2, 3, 4 comprise the "extinct" taxa, which disappeared from the Mediterranean at the end of the Miocene, Pliocene or Pleistocene (some examples are shown in Fig. 14.5). Group 2 includes genera and subgenera that seem to disappear at the end of the Miocene, with exception of the recent alien species *Oculina patagonica*. Group 3 comprises taxa that were extinct in Mediterranean waters at the end of the Pliocene whereas to group 4 belong the taxa (mostly bathyal) which disappeared at the end of the Pleistocene. Finally, in group 5 we have gathered those genera that have been almost unknown in the fossil record so far or recorded only not earlier than the Pleistocene Calabrian stage.

On the whole, the Mediterranean scleractinian diversity has clearly diminished since the Late Miocene. This trend was not linear but abrupt in shallow-water environments during and immediately after the Late Miocene and more gradual from the Pliocene onwards. Indeed, at the end of the Miocene, the Mediterranean coral fauna underwent a drastic modification that led to the disappearance of the well established shallow-water coral-reef province. The generic diversity of azooxanthellate and deep-water corals did not undergo evident modifications, that were instead much stronger at the end of the Pliocene and of the Pleistocene (Fig. 14.3).

Summarizing, we can assert with confidence that the Mediterranean coral fauna composition has undergone three major modifications since the late Miocene:

- Miocene – Pliocene boundary: (a) disappearance of the "Mediterranean z-coral reef province" and of almost all z-genera; (b) species diversity decrease of most az-coral genera.
- Pliocene – Pleistocene boundary (or at least before the Calabrian stage) (a) diversity decrease at the genus level, (b) disappearance of Indo-Pacific-like taxa; (c) clear outline of Atlantic affinity.
- Pleistocene – Holocene boundary: strong diversity decrease at the genus level with disappearance of deep-

water taxa living today at very low temperature (< 10 °C) in the neighbouring NE Atlantic.

The causes of these three major changes and of the general coral diversity decrease since the Serravallian are not fully understood. However, there seems to be a clear link between the Mediterranean coral diversity demise and the major climate modifications on a global scale during the last 20 million years. In particular, the decrease of z-coral genera since the late Middle Miocene (Bosellini and Perrin 2008) seems to correspond with the gradual cooling and re-establishment of a major ice-sheet on Antarctica after the late Middle Miocene climatic optimum (Zachos et al. 2001). Moreover, the differences between the Piacenzian (Late Pliocene) and Calabrian (Early Pleistocene) az-coral diversity (Fig. 14.3) could be related to the main oceanographic modifications that were driven by the major expansion of the Northern Hemisphere ice sheets at ca. 2.7 Ma (Shackleton et al. 1984; Dwyer et al. 1995). It is worth remarking that the decrease in Mediterranean coral diversity from the late Miocene on has been also ascribed to oceanographic modifications triggered by the gradual northward shift outside the tropical belt of the Mediterranean region (e.g. Rosen 1999; Perrin 2002; Bosellini and Perrin 2008; Martín et al. 2010).

The disappearance of the stenothermic bathyal corals at the end of the Pleistocene is still under debate; however, it has been generally ascribed to the shift from psychrosphere to thermosphere conditions of the Mediterranean Sea as a consequence of the transition from glacial to interglacial age. Indeed, the extensive development of Mediterranean framebuilding CWC communities as well as the presence of psychrospheric bathyal species (scleractinian and other groups of organisms) has been often related to glacial periods (Corselli 2001; Taviani et al. 2005b). Nevertheless, the absence of abundant cold-water corals in the Mediterranean during the Last Glacial Maximum (McCulloch et al. 2010) implies that, during glacial periods, bathyal corals did not thrive in this basin if other important environmental conditions, such as nutrition, oxygenation (Fink et al. 2012), low sedimentation rate, were not optimal.

As mentioned above this contribution represents a first step towards a better understanding of the evolutionary history of Mediterranean corals. In order to make a proper use of the extraordinary Cenozoic record of the peri-Mediterranean regions and of the corals as paleoenvironmental indicators, paleontological data needs to be combined with updated regional geological and stratigraphical information. Furthermore, taxonomic review at the species level is essential to improve our knowledge of the Mediterranean coral fauna and, as a consequence, the geological history of this basin.

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