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Late Miocene palaeobiogeography of the Mediterranean-Atlantic Region: An analysis based on shelf ostracod assemblages of the Northwestern Morocco

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ABSTRACT

A Late Miocene palaeobiogeographic framework of the Mediterranean-Atlantic Region, based on a comparative study of the continental shelf ostracod assemblages collected from a section in the Saïss Basin, northwestern Morocco, is proposed. Distribution data and statistical analyses allowed to identify six palaeoecoregions. Five of these units, that is South European Atlantic Shelf, Saharan Upwelling, Adriatic Sea, Western Mediterranean and Alboran Sea, were identified according to the ecoregions used in modern biogeographic frameworks. For the easternmost part of the Proto-Mediterranean basin a "Late Miocene Southeastern Mediterranean" palaeoecoregion is proposed. The Tortonian-Messinian palaeobiogeography of the so-called "Miocene European-West African Province", preceding the onset of the Messinian Salinity Crisis, was under the influence of the relationships between Atlantic and Proto-Mediterranean biota in tropical, subtropical and possibly warm temperate waters.

1. Introduction

During the Late Miocene the Rifian Corridor filled wedge-top and foredeep basins associated with the orogeny that affected the western margin of former Tethys Ocean, resulting from the Africa-Iberia convergence (Andrieux et al., 1971; Vergés and Fernàndez, 2012). The palaeogeography of the Rifian Corridor, an important Mediterranean-Atlantic seaway during the late Tortonian and the early Messinian, has been extensively studied to define the sequence of events which led to the closure of the proto-Mediterranean basin, the onset of the Messinian Salinity Crisis (proposed by Manzi et al., 2013 at 5.971 Ma) and the birth of the modern Mediterranean Sea (Capella et al., 2018). The lowermost deposits outcropping in the South Rifian Corridor consist of middle Tortonian sediments (10.57–8.37 Ma; Capella et al., 2018), and the closure of this seaway has been dated 6.9–7.1 Ma (Capella et al., 2018), pre-dating the Messinian Salinity Crisis.

The Oued El Kell Section (Fig. 1) consists of sediments deposited in the early Messinian, approximately during the time period between the last phases of the South Rifian Corridor and the beginning of the Mediterranean Salinity Crisis, and in the Late Pliocene coastal Atlantic Moroccan waters. It is located in the north-western part of the Saïss Basin, a foreland depression which extended westward into the Gharb Basin, opened during the Late Miocene and presently situated between the Rifian orogen and the middle Atlas (Charrière, 1984; Charrière and Saint-Martin, 1989; Capella et al., 2018).

Neogene ostracod assemblages of the Rifian Corridor have been investigated in a relatively few studies, dealing with the Tortonian, Messinian and Pliocene sediments of Zemmour, Gharb, Saïss, Rabat and Melilla-Nador regions (Carbonel and Cirac, 1978; Carbonel, 1980; Carbonel et al., 1981a, 1981b; Cirac and Peypouquet, 1983; Bouab and Boutakiout, 1986), including the Bou Regreg composite section (Bossio et al., 1976; Benson et al., 1991) that yielded taxa characteristic of deep marine (psychrospheric), shelf to marginal palaeoenvironments. Ostracods are unfortunately not figured in the above-mentioned papers. SEM micrographs have been reported by Bouab (1992) in an unpublished thesis on north-eastern Moroccan ostracod assemblages, and ink drawings of relatively good quality by Kili (1993, unpublished) who studied the Tortonian, Messinian and Pliocene assemblages of the South Rifian

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Corridor (Gharb, Saïss an Taounate basins). Investigations considering morphological variability of some ostracod species recorded in Neogene sediments from northern Morocco have been carried out by Ducasse and Cirac (1981), Tölderer-Farmer (1985) and Bouab (1987).

There is general agreement among researchers that the progressive shrinkage of the Tethys (the term "Neo-Tethys" is also used to denote this Mesozoic-Cenozoic ocean; v. Şengör, 2015) led to the formation of the Proto-Mediterranean Basin, through the progressive closure of the connections with the Indo-Pacific and with the Paratethys during the Miocene (Rögl, 1998; Meulenkamp et al., 2000; Popov et al., 2004; Hüsing et al., 2009), creating the conditions for the Messinian Salinity Crisis and the subsequent Pliocene re-establishment of marine environments in the new formed Mediterranean Sea. The similarity of ecological traits of the shelf marine environments of the North-western Africa, Southwestern Europe and Mediterranean, in the Late Miocene as well as in recent times, led many (palaeo)biogeographers to regard these areas as a single province.

Marine geographic classifications were proposed using various kinds of information such as climate, water masses, ocean currents, etc. (v. Table 1 in Lourie and Vincent, 2004). With regard to bioprovinces, we consider the most direct approach that based on faunal distribution (Ekman, 1953; Briggs, 1974) which enables a comparative analysis between present and past bioregions by means of fossil assemblages.

Since the first half of the nineteenth century, zoologists tried to summarize the available data with the aim to describe the worldwide geographic distribution of specific marine taxa. Through the use of crustacean zoogeography, Milne Edwards (1838) distinguished a "région Celtique", extending from the Strait of Gibraltar to the English Channel and, possibly, to Iceland, from a "région mediterranéenne".

In their pioneering work, Forbes, 1856; Forbes and Godwin-Austen, 1859; Woodward, 1856 identified a Lusitanian Province and a Mediterranean Province, despite the fact that the latter was, in the authors' opinion, "not entitled to take rank as an independent marine (bio) province". These authors divided the Mediterranean "Province" into Western and Eastern sectors, separating the north ("warm temperate") from the south ("outer tropical" in Hall Jr, 1964) through the winter and summer isotherms.

Different bioprovince boundaries (Table 1, Fig. 2) were subsequently identified. Ortmann (1896) defined a "Guinea Subregion", extending from the northern boundary of the Namib to the Gibraltar Strait, a "mediterrane Subregion" and an "atlantisch-boreale Subregion", from the Gibraltar Strait to the Arctic Ocean.

Ekman (1953), used a "Mediterranean-Atlantic fauna" to identify a zoogeographic area (corresponding to the "warm temperate Mediterranean-Atlantic Region" of Briggs, 1974) including three regions: i) the Mediterranean Sea, ii) the Lusitanian region, extending

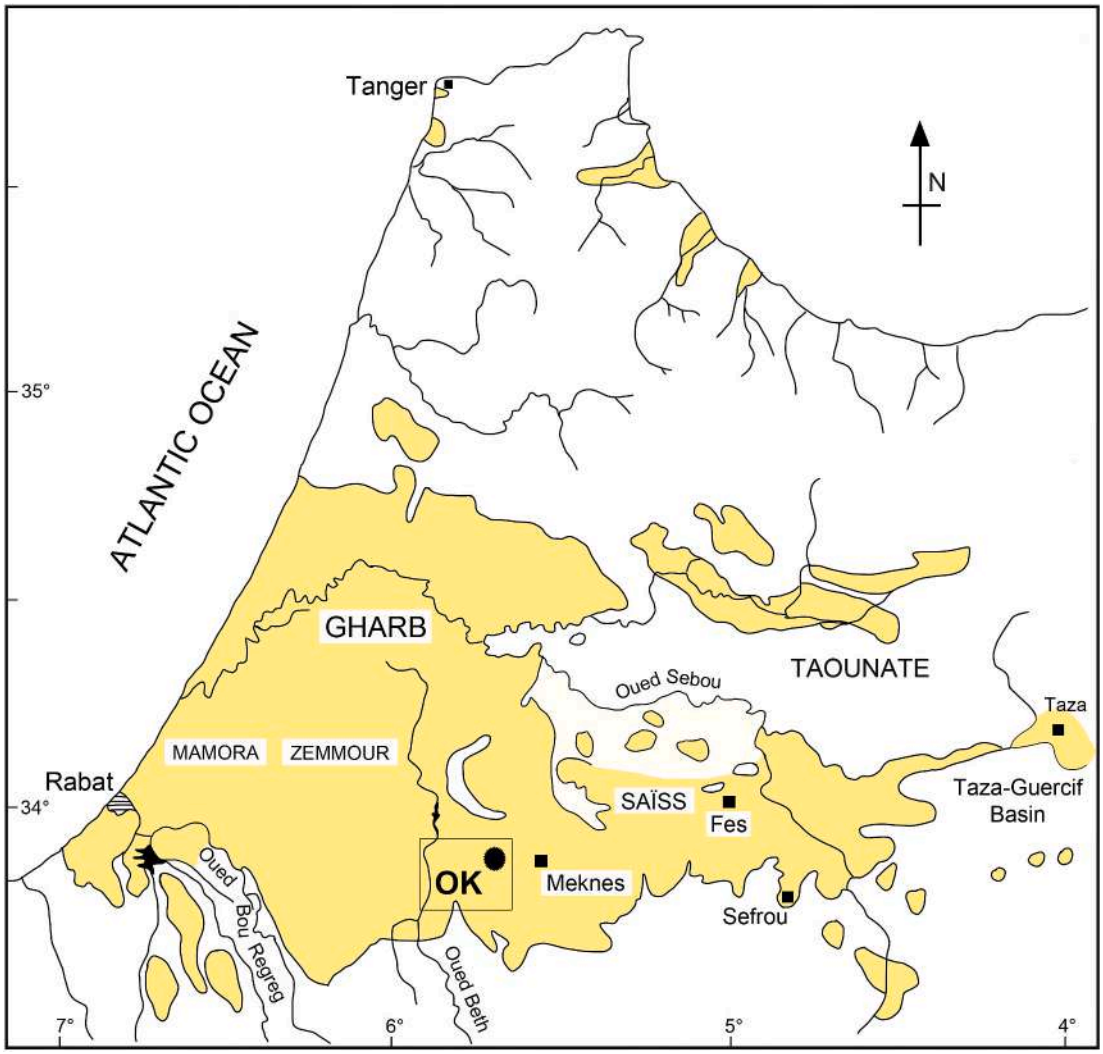
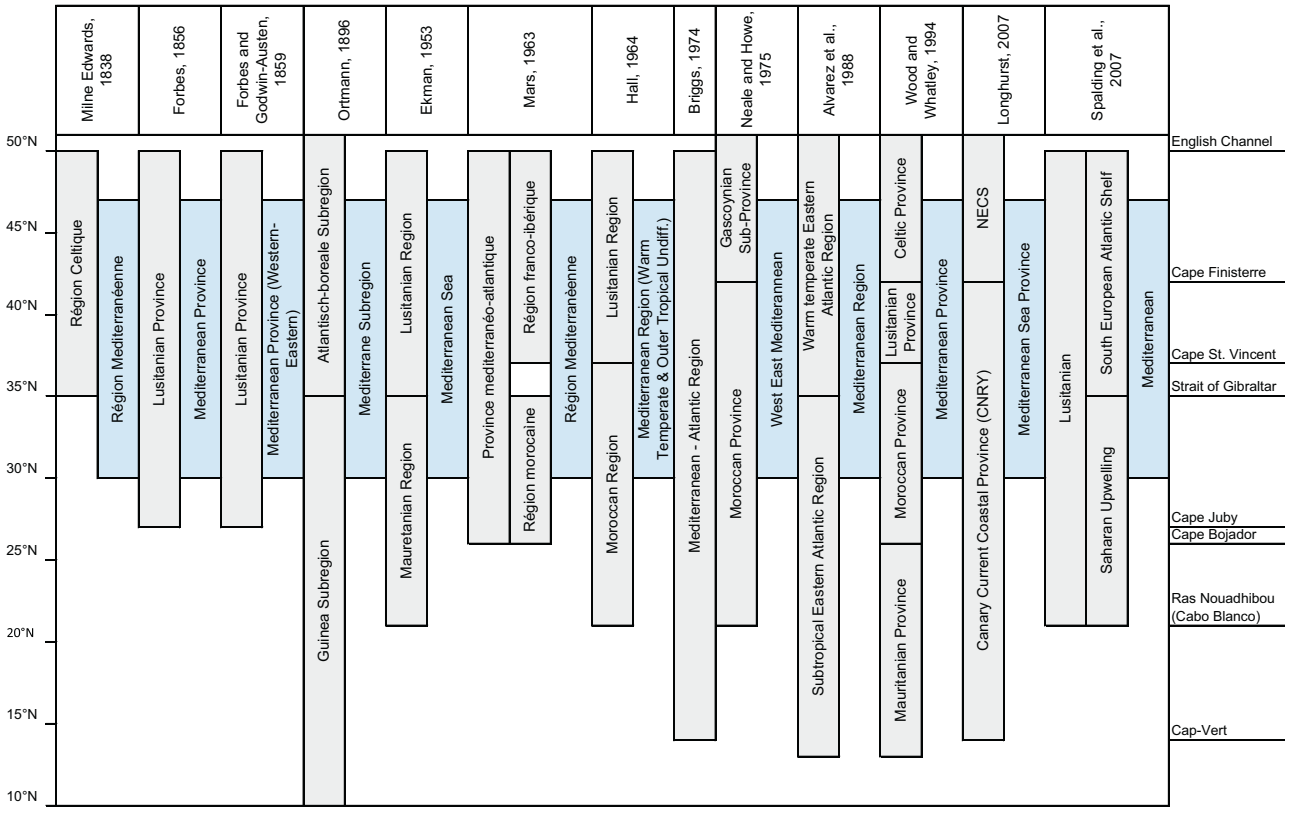


Fig. 1. Location of the study section; OK = Oued El Kell Section. Modified from Barbieri and Ori (2000). The shaded area marks the outcrops of the Neogene-Quaternary basins in northwestern Morocco.

Table 1
Schematic outline of some classic and modern biogeographic subdivisions of the Mediterranean-Atlantic area.



from the Strait of Gibraltar to the western entrance of the English Channel and iii) the Mauretanian (sic) region, from the Strait of Gibraltar to Ras Nouadhibou (Cap Blanc, Cabo Blanco).

Some researchers, however, did not acknowledge the biogeographic value of the Strait of Gibraltar or of the English Channel. Mars (1963), for example, recognised a "Province méditerranéo-atlantique" extending from Cape Bojador to the English Channel. It was subdivided in a "région franco-ibérique", from Cape St. Vincent to the English Channel, a "région méditerranéenne", including the Mediterranean and the Gulf of Cádiz, and a "région morocaine", from Cape Bojador to the north-western Morocco, just to the south of Cape Spartel. Hall Jr (1964) assigned the Lusitanian region and the northern parts of the Mediterranean to the Warm temperate shallow-water marine climatic zone; the Moroccan region and the southern parts of the Mediterranean were included in the Outer tropical shallow-water marine climatic zone.

A different point of view has been expressed in studies describing a wide Mediterranean-Atlantic Region where the whole Mediterranean, the coastal waters of north-western African and the Iberian Peninsula form the "Lusitania(n) Province" (Hayden et al., 1984; Golikov et al., 1990; Briggs, 1995; Briggs and Bowen, 2012).

Longhurst (2007) identified, within the Atlantic Coastal Biome, a Northeast Atlantic Shelves Province (NECS) which included the western Europe continental shelf from Cape Finisterre (Spain) to Jutland (Denmark), and a Canary Current Coastal Province (CNRY) from Cape Finisterre to Cap-Vert (Senegal), considering the Mediterranean Sea - Black Sea Province (MEDI) as part of the Atlantic Westerly Winds Biome; Alvarez et al. (1988) recognised in the Northeastern Atlantic three phytogeographic regions: the Subtropical Eastern Atlantic region, the Mediterranean region and the Warm temperate Eastern Atlantic region.

Zoogeographic provinces based on the distribution of benthic ostracods were proposed by Neale and Howe (1975) who separated western and eastern Mediterranean, and placed at Cape Finisterre the boundary between Moroccan and Celtic (Gascoynian) provinces. A study based on water-mass characteristics and distribution of ostracod genera was conducted by Wood and Whatley (1994), who identified ten provinces between the Niger Delta and the Barents Sea. The authors identified a Moroccan province, extending from Cape Bojador to Cape St. Vincent, and a Lusitanian province, with Cape Finisterre as northern boundary. In the Celtic Province were included north Iberian and French Atlantic waters: consequently, the Lusitanian province was narrowed between 37° 1′ N and 42° 52′ N.

In contrast to most other biogeographic subdivisions, the biogeographic system developed by Spalding et al. (2007) recognised within the Mediterranean seven different ecoregions, thus offering a useful palaeobiogeographical interpretative tool for the study of the relationship between Upper Miocene ostracod assemblages of the (Proto)Mediterranean-Atlantic area. In this biogeographic framework the Mediterranean Sea Province included seven ecoregions: Adriatic Sea (30), Aegean Sea (31), Levantine Sea (32), Tunisian Plateau/Gulf of Sidra (33), Ionian Sea (34), Western Mediterranean (35) and Alboran Sea (36). The Lusitanian Province consisted of the South European Atlantic Shelf (27), Saharan Upwelling (28) and Azores Canaries Madeira (29) ecoregions. Both Lusitanian Province and Mediterranean Sea Province were included in the Temperate Northern Atlantic Realm. An even greater number of Mediterranean biogeographic units were identified by other workers such as Bianchi et al. (2012), who described twelve sectors within the Mediterranean. Such a detailed model is not suitable for our purposes because the insufficient number of studies on Upper Miocene ostracods in some of these sectors. Our knowledge about the distribution of ostracod species in the Mediterranean and in the Proto-Mediterranean led us to prefer the biogeographic system developed by Spalding et al. (2007) for the comparison between Late Miocene

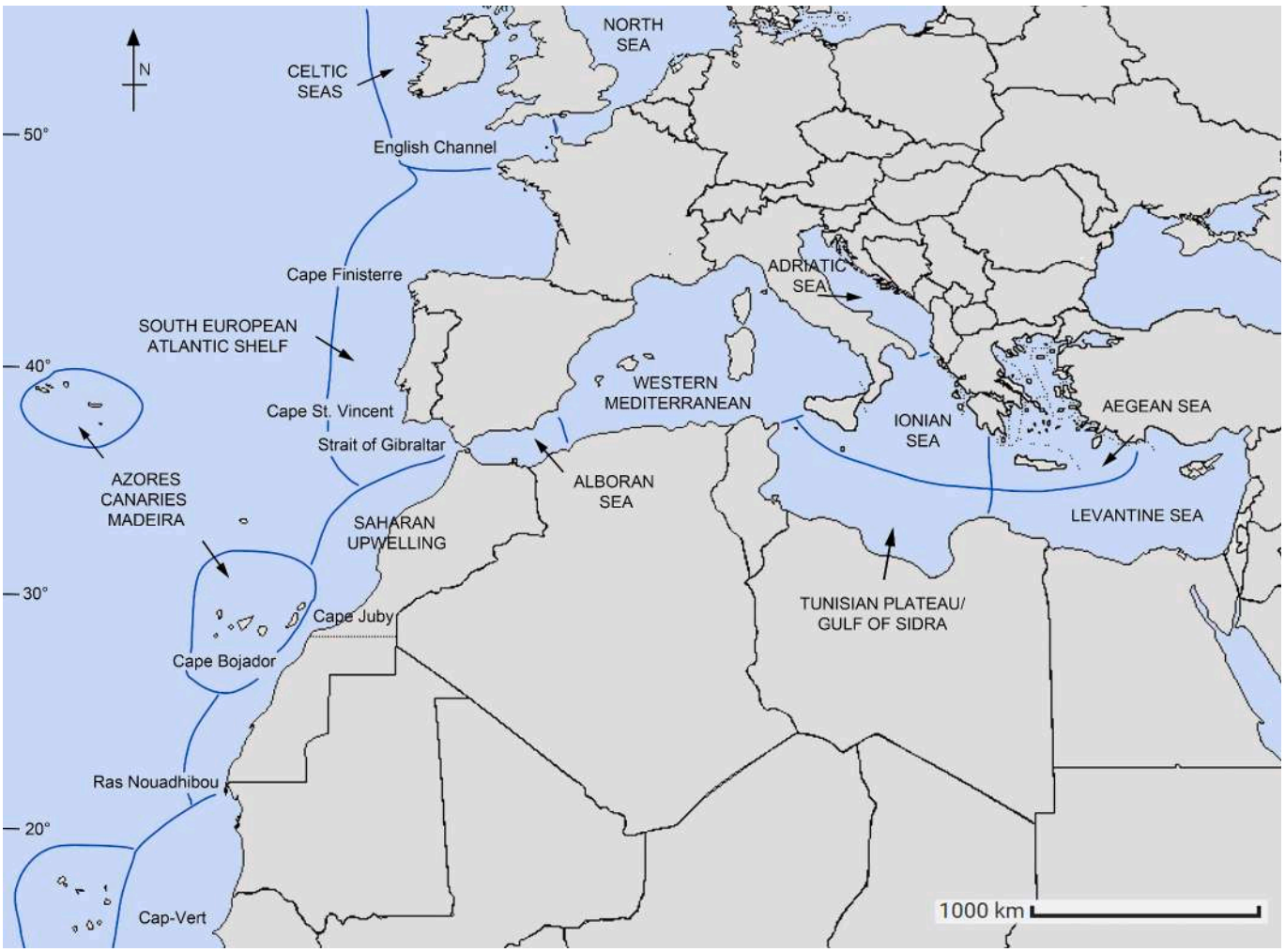


Fig. 2. Map of ecoregions identified by Spalding et al. (2007).

associations of the Mediterranean-Atlantic region. Consequently, without going into the merits of the nomenclatural debate concerning biogeographic units (Cecca and Westermann, 2003), we have adopted the classification of Spalding et al. (2007), where it is stated that "ecoregions are the smallest-scale units in the Marine Ecoregions of the World" and the term "province" is referred to the higher hierarchical level (v. Spalding et al., 2007, p. 575, for complete definitions). In our opinion is more appropriate, in the studies on fossil biotas, to use the terms "palaeoecoregion" and "palaeoprovince" due to the methodological differences between biogeography and palaeobiogeography.

The comparison of our material with the available literature showed that all the shelf ecoregions where Upper Miocene ostracod assemblages included at least ten species common to the Oued El-Kell Messinian faunas, are located within the Temperate Northern Atlantic Realm.

2. Palaeobiogeography and climate of the Mediterranean-Atlantic area in the Late Miocene

The configuration of tectonic plates of the (Proto)Mediterranean-Atlantic area in the Late Miocene was approximately similar to the present, and the distribution of shelf taxa was influenced by the formation and disappearance of marine seaways, for example the Betic and the Rifian corridors, and barriers to the migration of species, such as the closure of the Gibraltar area that led to the Messinian Salinity Crisis. On the other hand, during the Neogene climate was a major driving factor in taxa distribution in the Eastern Atlantic-Proto-Mediterranean area, as highlighted by common occurrence of tropical and subtropical genera and species (Monegatti and Raffi, 2010).

Compared to present day, Miocene climate was generally warmer and the global mean surface temperatures were higher [from ~5.3 °C to 11.5 °C, according to Burls et al., 2021] than preindustrial, with a cooling trend from the Burdigalian-Langhian Miocene Climate Optimum to the Late Miocene (Zachos et al., 2001).

The ocean temperatures during the Messinian probably reached near-modern values, whereas the sea surface temperatures in the Northern Hemisphere, in the latitudinal range 30°-50° N, were slightly warmer than today, both in the Mediterranean Sea and in the eastern Atlantic (Tzanova et al., 2015; Herbert et al., 2016; Super et al., 2020).

In the Late Miocene a marked lowering of the sea surface temperatures was probably confined to high-latitude waters (Super et al., 2020) and, despite this, during the summer the Arctic Ocean was ice-free (Stein et al., 2016). The climate of the upper part of the Messinian was characterized by some glacial stages, the most prominent being TG12, TG14, TG20 and TG22 (Shackleton et al., 1995) all included in the time range 5.5–5.8 Ma (Krijgsman et al., 2004; van den Berg et al., 2015).

The complex Neogene climatic history of the Mediterranean-Atlantic region showed a transition of the tropical Early-Middle Miocene bioprovinces towards cooler environments (Lauriat-Rage et al., 1993). In the Proto-Mediterranean, the Paleogene tethyan tropical biota, showing Indo-west Pacific affinity, were replaced, due to the progressive closure of the Sues Isthmus, by tropical biota with Atlantic affinity. In the Atlantic Moroccan region and in the Mediterranean area the shift from tropical to subtropical climate occurred during the Tortonian-Messinian transition (Sierro, 1985; Benson et al., 1991). Palaeoclimatic

reconstructions based on Upper Miocene carbonate, with special regards to scleractinian corals, highlighted the presence of warm temperate assemblages (Bosellini and Perrin, 2008; Martín et al., 2010). The Messinian Salinity Crisis caused the disappearing of the marine tropical biota and the Mediterranean, at the beginning of the Pliocene, was repopulated by subtropical Atlantic species (Bianchi et al., 2012).

According to Silva and Landau (2007) the tropical Miocene European-West African Province (MEWAP, in Ávila et al., 2016) included both the present day Mediterranean-Moroccan Province (i.e. ecoregions 28–36 in Spalding et al., 2007) and the Franco-Iberian Province (roughly equivalent to ecoregion 27 in Spalding et al., 2007). In the Early and middle Pliocene the Mediterranean-Moroccan Province was still tropical, whereas the biota of the Franco-Iberian Province showed subtropical features.

Monegatti and Raffi (2007, 2010) hypothesized, on the basis of mollusc assemblages, that during the late Messinian the tropical-subtropical transition withdrew from 48° N to 37–38° N. These boundaries correspond approximately to the present day subtropical-warm temperate and warm temperate-cool temperate transitions, respectively along the Portuguese and Breton coasts.

In sum, previous investigations suggest that the Late Miocene represented a transitional and still not well defined phase of palaeoclimatic and palaeobiogeographic change, displaying the presence of both tropical, subtropical and warm temperate assemblages, due to different reactions to climatic variations in different taxonomic groups.

The finding of rich, diversified and well preserved Messinian assemblages typical of shelf palaeoenvironment, provided us the opportunity to compare the Late Miocene ostracod distribution with the biogeography of the Mediterranean-Atlantic region as attested by recent investigations, with the aim of defining palaeogeographic units in the last phases of the Tethys, just before the Messinian Salinity Crisis.

3. Stratigraphic framework

The Oued El Kell Section crops out approximately 15 km west of Meknes, in the western side of the Saïss Basin, northwestern Morocco. The marly sediments outcropping in the lower part of the section pertain to the Lower Akrech Sequence (v. Barbieri and Ori, 2000, Fig. 4). The Messinian sediments were deposited in a shallow basin on the Atlantic side of the restricted or just closed South Rifian Corridor, whereas the Piacenzian levels formed in a bay located at about 100 km from the Gibraltar Strait, the only Pliocene seaway passage between Atlantic and Mediterranean. The foraminiferal assemblages of the Oued El Kell Section have been studied by Barbieri and Ori (2000), who placed the lower part of the section (samples OK 1-OK 11) in the (sub)tropical subzone M13b (*Globigerinoides extremus/Globorotalia plesiotumida-Globorotalia lenguaensis* Interval Subzone; 8.3–6.0 ma), and the following three samples (OK 12-OK 14) in the Ml4 *Globorotalia lenguaensis-Globorotalia tumida* Interval Zone (6.0–5.6 Ma) (Berggren et al., 1995; v. also Fig. 29.10 in Hilgen et al., 2012). All the 14 Miocene samples pertain to the Mt. 10 (6.9–5.6 Ma), *Globorotalia conomiozea/Globorotalia mediterranea - Globorotalia sphericomiozea* Interval Zone defined by Berggren et al. (1995; v. also Fig. 29.10 in Hilgen et al., 2012). The uppermost part of the section pertains to the Zammour Sequence and has been assigned by Barbieri and Ori (2000) to the Pl3 = *Globorotalia margaritae-Sphaeroidinellopsis seminulina* (3.58–3.12 Ma, Berggren et al., 1995) Interval Zone, in the Piacenzian (Late Pliocene). Between the Messinian and the Piacenzian sediments was present a hiatus of about 2.4 Ma (Barbieri and Ori, 2000).

Barbieri and Ori (2000) assigned, on the basis of benthic foraminifer assemblages, the palaeoenvironment of the Messinian sediments of the Oued El Kell Section to the "middle neritic zone" (biofacies B4a), with an estimated palaeodepth in the range 30–100 m, approximately corresponding with the "coastal circalittoral zone" (étage circalittoral côtier) defined for the recent Atlantic Moroccan Shelf by Bayed and Glémarec (1987). For the Piacenzian part of the section an inner neritic zone (0–30 m), approximately corresponding with the infralittoral zone of Bayed and Glémarec (1987) has been suggested (biofacies B7; Barbieri and Ori, 2000).

4. Material and methods

Nineteen sediment samples were collected from the 49 m that make up the Oued El Kell Section for ostracod assemblage analysis (Fig. 3). The same samples were previously studied by Barbieri and Ori (2000), who investigated the biostratigraphy and the palaeoenvironment of various Atlantic outcrops by means of foraminiferal assemblages. The samples OK 1-OK 14 are of Messinian age, and the uppermost five samples (OK 16-OK 19) pertain to the Late Pliocene (Piacenzian). The sample OK 15 was lost and was not considered in the study of ostracod assemblages. They were oven-dried (150 to 250 g dried weight), disaggregated and washed through 230 and 120 mesh sieves (63 and 125 μm, respectively). The residue was examined under binocular light microscope and all the ostracod valves were picked from the coarsest fraction (>125 μm). SEM micrographs (Figs. 4–5) of the majority of the taxa were carried out for an accurate comparison with the species described and figured in the available literature, with special regards for Neogene Mediterranean and eastern Atlantic studies (Appendix 1). Problems of synonymy (e.g., multiple specific names used for morphotypes, assignment of the same species to different genera, etc.) and morphological variability were carefully considered (e.g., *Sagmatocythere versicolor*, Figs. 5.K-L) but not discussed in detail herein. Detailed taxonomic studies on this material are in progress. The records of well figured shells under various generic and specific names, were indicated in Appendix 2.

Palaeobiogeographic analyses have been performed on the Messinian taxa of the Oued El Kell section. The species recorded both in the Messinian sediments of Oued El Kell and in previous investigations

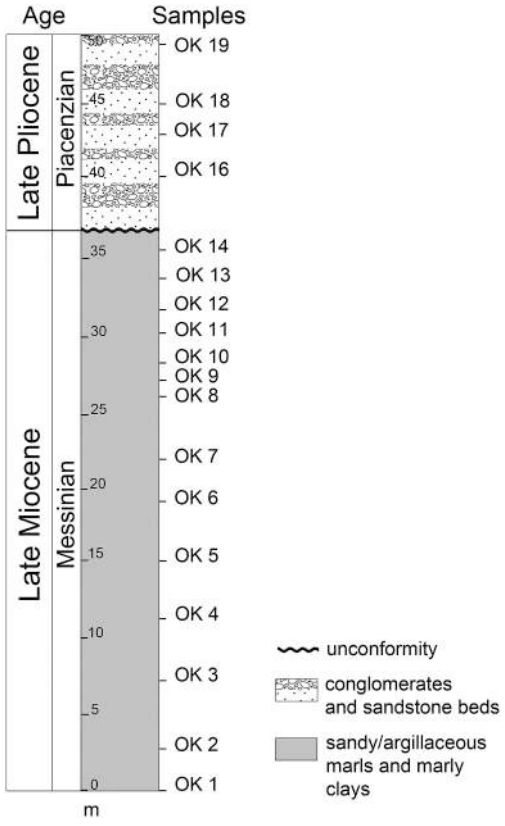


Fig. 3. Oued El Kell Section, age and position of samples OK1 to OK19 (modified after Barbieri and Ori, 2000).

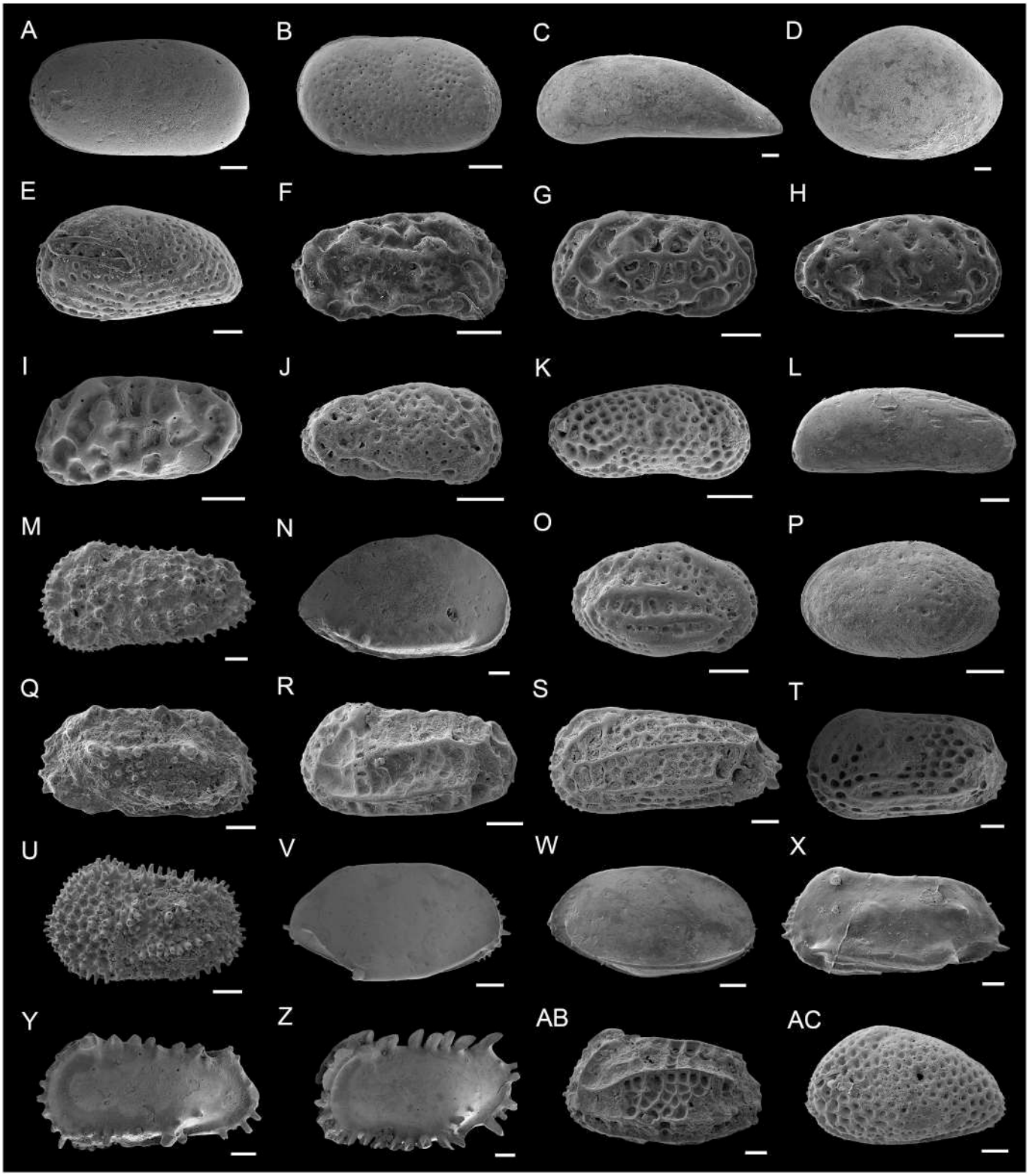


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Fig. 4. **A.** *Cytherella inaequalis* Moyes, 1965, left valve, sample OK 12, ABMC 2023/088; **B.** *Cytherella scutulum* Ruggieri, 1976, left valve, sample OK 4, ABMC 2023/004; **C.** *Paracypris* sp. Carbonnel and Courme-Raoult, 1997, left valve, sample OK 9, ABMC 2023/033;**D.** *Bairdoppilata conformis* (Terquem, 1878), left valve, sample OK 12, ABMC 2023/081; **E.** *Cytheridea acuminata* Bosquet, 1852, left valve, sample OK 17, ABMC 2023/070; **F.** *Callistocythere crispata* (Brady, 1868), right valve, sample OK 12, ABMC 2023/038; **G.** *Callistocythere flavidofusca* (Ruggieri, 1950), left valve, sample OK 13, ABMC 2023/169; **H.** *Callistocythere producta* Aruta, 1983, right valve, sample OK 6, ABMC 2023/171; **I.** *Callistocythere tetradactyla* Ciampo, 1984, left valve, sample OK 6, ABMC 2023/121; **J.** *Callistocythere* aff. *vidua* Ciampo, 1986, right valve, sample OK 3, ABMC 2023/063; **K.** *Leptocythere foveolata* Moyes, 1965, right valve, sample OK 18, ABMC 2023/138; **L.** *Pontocythere turbida* (Müller, 1894), right valve, sample OK17, ABMC 2023/052; **M.** *Acanthocythereis hystrix* (Reuss, 1850), left valve, sample OK 5, ABMC 2023/009; **N.** *Bosquetina carinella* (Reuss, 1850), right valve, sample OK 16, ABMC 2023/137; **O.** *Buntonia robusta* Ruggieri, 1954, right valve, sample OK 6, ABMC 2023/016; **P.** *Rectobuntonia posteropunctata* (Moyes, 1965), right valve, sample OK 8, ABMC 2023/023; **Q.** *Carinocythereis whitei* (Baird, 1850), right valve, sample OK 2, ABMC 2023/177; **R.** *Cistacythereis caelatura* Uliczny, 1969, left valve, sample OK 8, ABMC 2023/018; **S.** *Cistacythereis emaciata* (Brady, 1867), left valve, sample OK 8, ABMC 2023/010; **T.** *Olimfalunia plicatula* (Reuss, 1850), left valve, sample OK 13, ABMC 2023/116; **U.** *Henryhowella asperrima* (Reuss, 1850), left valve, sample OK 6, ABMC 2023/049; **V.** *Carinovalva aquila* (Ruggieri, 1972), RV, sample OK 7, ABMC 2023/159; **W.** *Carinovalva testudo* (Namias, 1900), right valve, sample OK 6, ABMC 2023/005; **X.** *Ruggieria tetraptera* (Seguenza, 1880), left valve, sample OK 12, ABMC 2023/015; **Y.** *Pterygocythereis coronata* (Roemer, 1838), left valve, sample OK 7, ABMC 2023/157; **Z.** *Pterygocythereis jonesii* (Baird, 1850), left valve, sample OK 9, ABMC 2023/132; **AB.** *Chrysocythere cataphracta* Ruggieri, 1962, left valve, sample OK 13, ABMC 2023/053; **AC.** *Senesia triangularis* (Oertli, 1956), left valve, sample OK 17, ABMC 2023/051. Scale bars = 100 μm.

dealing with Upper Miocene assemblages in the Atlantic-Mediterranean region were considered. Redonian occurrences (Maybury and Whatley, 1980, 1984; Maybury, 1985, 1990), formerly assigned to the Pliocene have been considered cautiously of Messinian age (an extensive discussion can be found in Monegatti and Raffi, 2010). Analyses were performed with and without the Redonian data to see if the results would change. Species present in the studied sediments and in Pliocene-Quaternary assemblages, but not previously recorded in Miocene assemblages (e.g., *Callistocythere flavidofusca*, Fig. 4.G), nonmarine species (e.g., *Ilyocypris gibba*, Fig. 5.AC) and previously unknown species (e.g., *Callistocythere* aff. *vidua*, Fig. 4.J) were not taken into account. Occurrences of Late Miocene species not supported by figures, were left out of the analysis.

All the Late Miocene sites with ostracod species in common with the assemblages found in the Messinian part of the Oued El Kell section were placed in the ecoregions defined by Spalding et al. (2007). Statistical analysis were performed on the presence/absence data of the ecoregions where Upper Miocene ostracod assemblages included at least ten species common to the Oued El-Kell Messinian assemblages.

The Cluster Analysis and Principal Component Analysis, based on binary data (presence/absence), were performed using the freeware PAST version 4.06b (Hammer et al., 2001). The Euclidean distance measure and paired group algorithm were used for Clustering (Q-mode).

5. Results

A total of 6823 ostracod valves (one carapace counted as two valves) were collected from the Messinian part of the section (Table 2). Ostracod assemblages included 143 species, 75 definitively or tentatively classified, 17 left in open nomenclature, and 51 with affinitive status due to the poorly preserved material, to the absence of adult specimens or because they are still undescribed.

Sixty-one of these species (Table 3) were known from Upper Miocene deposits located in the Mediterranean-Atlantic area, in nine of the ecoregions identified by Spalding et al. (2007), all included in the Lusitanian (ecoregions 27 and 28) and Mediterranean Sea (ecoregions 30–36) provinces, within the Temperate Northern Atlantic Realm. A small number of species were previously recorded in the Late Miocene of the Western Atlantic [for example *Kangarina abyssicola*, a cosmopolitan ostracod figured by Bold Bold, 1963 from Trinidad], of the Azores [*Aurila semilunata*, reported by Meireles et al., 2012 as *A.* sp.] and of Gabon [*Buntonia robusta*, *Henryhowella asperrima*, *Ruggieria tetraptera* (Bold Bold, 1966, 1968)]. Unfortunately, in these areas data are scarce and consequently the ostracods of the ecoregions 29 (Azores Canaries Madeira), 66 (Southwestern Caribbean) and 85 (Gulf of Guinea South) were not taken into account. The studies on Tortonian-Messinian ostracods of more distant regions (e.g., Irizuki, 1994; Yamaguchi et al., 2012) showed no species in common with the assemblages reported herein.

None of the 61 species used for palaeobiogeographic analysis were present in all the ecoregions. *R. tetraptera*, occurring in eight ecoregions, had the widest distribution, followed by *Acanthocythereis hystrix*, *Callistocythere crispata* and *Cytheridea acuminata*, present in seven ecoregions. Seven species (*Aurila anterocostata*, *Bosquetina carinella*, *Buntonia* aff. *obesa*, *Palmoconcha extendata*, *Rectobuntonia posteropunctata*, *Sagmatocythere grateloupiana* and *Semicytherura cornubiensis*, Table 3) occurring in Late Miocene African and European Atlantic areas, were not present in the Late Miocene Proto-Mediterranean basin. *Cimbaurila vitrocincta* and *Cistacythereis caelatura* were endemic to Moroccan Late Miocene waters. *Leptocythere foveolata* and *Mutilus labiatus* were present in the Atlantic waters and in the westernmost areas of the Proto-Mediterranean basin. Eight species, not found north of Sicily, were confined to the southern part of the Proto-Mediterranean and to the North-African Atlantic: *Bairdoppilata conformis, Carinovalva aquila, Chrysocythere cataphracta, Cytheropteron vespertilio, Eucytherura mistrettai, Paijenborchella solitaria, Paracypris* sp. and *Pulaviella geometra.*

Some species, present in the Atlantic and in the western-central part of the Proto-Mediterranean did not occur in the Aegean and Levantine seas. They are: *Aurila impressa, A. semilunata, B. conformis, Callistocythere tetradactyla, Carinovalva testudo, Cytheropteron latum, C. vespertilio, Graptocythere polyptycha, H. asperrima, Krithe oertlii, S. versicolor, S. tenuis, Semicytherura furcilla* and *S. microwallacei.*

The following species were not reported from any of the four southeastern Mediterranean ecoregions (31–34): *Argilloecia pera, Callistocythere producta, Cytherella scutulum, Cytheropteron ruggierii, Eucytherura protracta, E. mistrettai, Loxoconcha reticulopunctata, K. abyssicola, Hemicytherura videns, Flexus tenuicarinatus, Monoceratina oblita, M. labiatus, Palmoconcha dertobrevis, Pterygocythereis jonesii, P. geometra, Sagmatocythere napoliana, Semicytherura foeda* and *Senesia triangularis.* This last species was also absent from the Adriatic area.

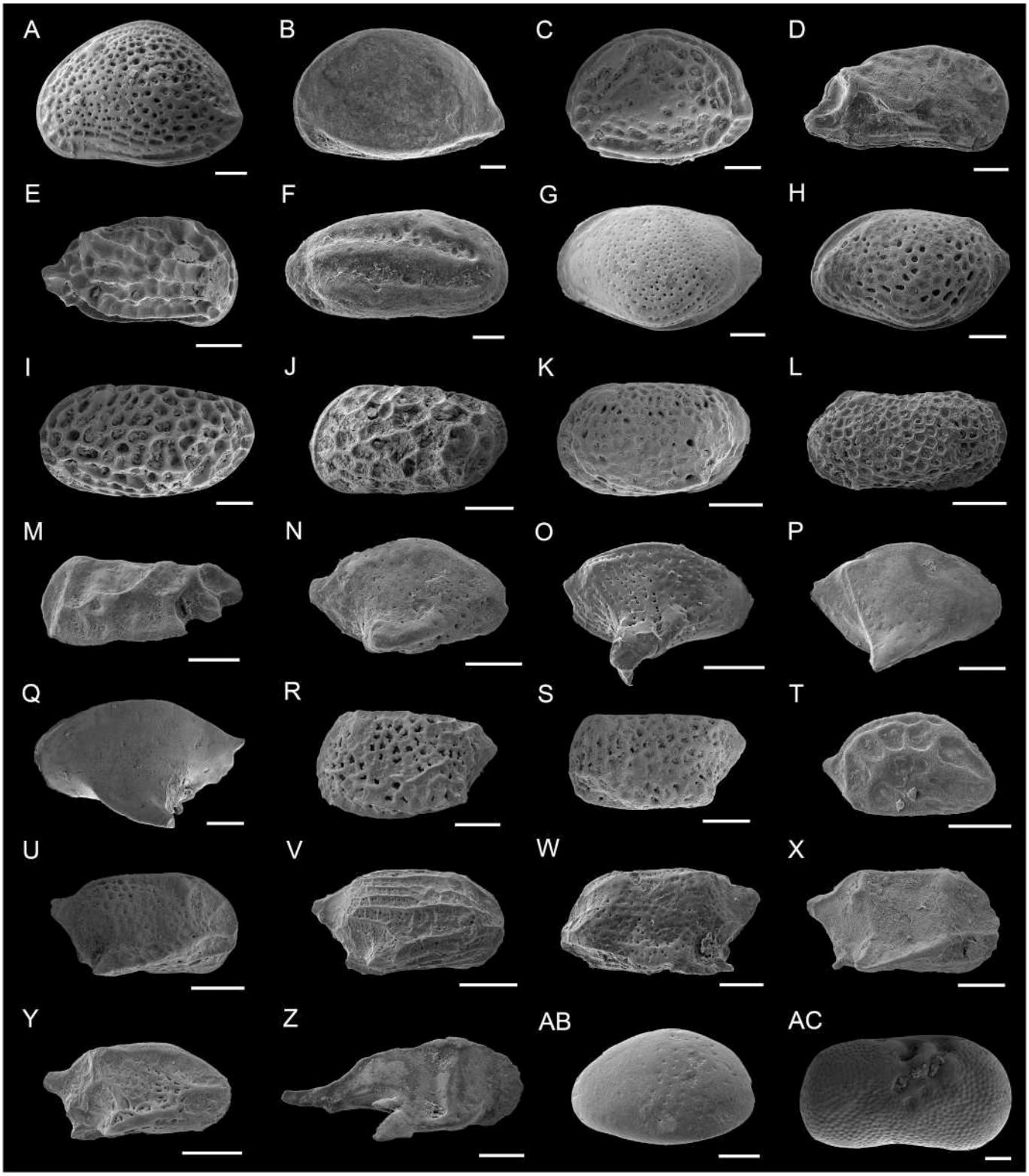
6. Statistical analysis

We found that the best results were obtained with the biogeographic framework of Spalding et al. (2007). Analyses performed with and without Redonian occurrences revealed similar results. For this reason, and for the sake of brevity, we reported only the former analysis.

The cluster analysis generated the dendrogram shown in Fig. 6 and the Principal Component Analysis (PCA) ordination diagram was reported in Fig. 7.

The cluster analysis was performed on the presence/absence data of the species present in the Oued El Kell Messinian assemblages and previously reported from late Miocene successions of the Mediterranean-Atlantic Region. The dendrogram could be cut at different levels to produce different palaeobiogeographic groups.

At low cut-off levels (euclidean distance 5.75 ÷ 5.28), the South European Atlantic Shelf (27) was grouped apart. Western Mediterranean (30) and Adriatic Sea (35) were grouped using slightly higher cut-off values (distance 5.28 ÷ 4.80). With a distance 4.80 ÷ 4.50 the cluster tree showed that the ecoregions 27, 30 and 35 were individually discriminated and the southwestern units, i.e. the Saharan Upwelling



(caption on next page)

Fig. 5. **A.** *Aurila impressa* Ruggieri, 1977, left valve of carapace, sample OK 18, ABMC 2023/168; **B.** *Aurila semilunata* (Seguenza, 1880), left valve, sample OK 14, ABMC 2023/071; **C.** *Cimbaurila vitrocincta* (Ruggieri, 1950), left valve, sample OK 18, ABMC 2023/115; **D.** *Caudites calceolatus* (Costa, 1853), right valve of carapace, sample OK 17, ABMC 2023/183; **E.** *Mutilus labiatus* Moyes, 1965, right valve, sample OK 12, ABMC 2023/156; **F.** *Flexus tenuicarinatus* (Capeder, 1902), right valve, sample OK 16, ABMC 2023/165; **G.** *Palmoconcha dertobrevis* (Ruggieri, 1967), left valve, sample OK 7, ABMC 2023/030; **H.** *Palmoconcha extendata* (Bassiouni, 1962), left valve, sample OK 13, ABMC 2023/166; **I.** *Sagmatocythere grateloupiana* (Bosquet, 1852), left valve, sample OK 17, ABMC 2023/096; **J.** *Sagmatocythere napoliana* (Puri, 1963), left valve, sample OK 10, ABMC 2023/185; **K.** *Sagmatocythere versicolor* (Müller, 1894) morph. 1, left valve, sample OK 3, ABMC 2023/155; **L.** *Sagmatocythere versicolor* (Müller, 1894) morph. 2, left valve, sample OK 9, ABMC 2023/056; **M.** *Paracytheridea triquetra* (Reuss, 1850), left valve, sample OK 9, ABMC 2023/026; **N.** *Cytheropteron latum* Müller, 1894, right valve, sample OK 3, ABMC 2023/025; **O.** *Cytheropteron monoceros* Bonaduce et al., 1976, right valve, sample OK 7, ABMC 2023/083; **P.** *Cytheropteron sulcatum* Bonaduce et al., 1976, right valve, sample OK 7, ABMC 2023/027; **Q.** *Cytheropteron vespertilio* (Reuss, 1850), left valve, sample OK 18, ABMC 2023/153; **R.** *Eucytherura mistrettai* Sissingh, 1972, left valve, sample OK 7, ABMC 2023/017; **S.** *Eucytherura protracta* Ruggieri, 1962, left valve, sample OK 3, ABMC 2023/140; **T.** *Hemicytherura videns* (Müller, 1894), right valve, sample OK 5, ABMC 2023/003; **U.** *Semicytherura alifera* Ruggieri, 1959, right valve, sample OK 3, ABMC 2023/098; **V.** *Semicytherura aviculaecaput* Aiello and Szczechura, 2004, right valve, sample OK 6, ABMC 2023/028; **W.** *Semicytherura cornubiensis* Maybury, 1985 *nomen nudum*, left valve, sample OK 17, ABMC 2023/180; **X.** *Semicytherura foeda* Ciampo, 1986, right valve, sample OK 8, ABMC 2023/019; **Y.** *Semicytherura furcilla* Aiello and Szczechura, 2004, right valve, sample OK 7, ABMC 2023/008; **Z.** *Paijenborchella solitaria* Ruggieri, 1962, right valve, sample, OK 9, ABMC 2023/042; **AB.** *Pulaviella geometra* (Ruggieri, 1962), left valve, sample OK 3, ABMC 2023/014; **AC.** *Ilyocypris gibba* (Ramdohr, 1808), right valve, sample OK 18, ABMC 2023/108. Scale bars = 100 μm.

Table 2
Total number of valves collected in the Messinian samples of the Oued El Kell Section (one carapace = two valves).

	Messinian													
samples	OK 1	OK 2	OK 3	OK 4	OK 5	OK 6	OK 7	OK 8	OK 9	OK 10	OK 11	OK 12	OK 13	OK 14
distance above the base section (m)	0	3	7	11	15	19	22	26	27	28	30.5	32	34	36.5
number of valves	54	203	853	135	294	771	954	628	1875	402	14	223	223	194
total								6823						

(28) and Alboran Sea (36), formed a cluster separated from the southeastern Mediterranean units (31–34). With a higher cutoff level (distance 4.50 ÷ 4.35) the cluster tree displayed five isolated ecoregions (27, 28, 30, 35, 36) and one cluster including the southeastern Mediterranean ecoregions (31–34). The latter cut-off level was chosen (Fig. 6, distance 4.40) so as to highlight six clusters, corresponding to six Late Miocene palaeoecoregions.

In the Principal Component Analysis the nine considered ecoregions were plotted in the two-dimensional space based on scores on the first two principal components. The first axis accounted for the 23.56% of the variance and the second axis for the 18.64% (Axis 1: eigenvalue = 3.04, Axis 2: eigenvalue = 2.41). The former was mainly related with the palaeoecological conditions (especially temperature and, possibly, salinity) characteristic of the southeastern Proto-Mediterranean, and the latter with the separation of Atlantic and Proto-Mediterranean basins. The diagram showed that the southeastern Mediterranean ecoregions 31–34 were grouped in the left part of the diagram. The Mediterranean units 30, 35 and 36 showed positive values for both first and second components. The Atlantic ecoregions (27 and 28) loaded on the negative side of the second axis. The Saharan Upwelling (28) displayed positive values for first component, whereas South European Atlantic Shelf unit (27) was located approximately on the second axis.

Both the distribution of the above mentioned, selected species, and the results of the statistical analysis have led to the identification of six Proto-Mediterranean-Atlantic Late Miocene ecoregions, reported in Fig. 8.

7. Taxonomic notes and distribution

Brief taxonomic notes and Late Miocene palaeogeographic distribution of the main species.

It has to be noted that reports not supported by figures were not considered.

Acanthocythereis hystrix (Reuss, 1850). Fig. 4.M. 1850 *Cypridina hystrix* Reuss, p. 47, pl. 10, Fig. 6. A species showing a certain morphologic variability and a wide palaeogeographic distribution. Reported from the Southern Spain by González-Regalado and Ruiz, 1990 (as *A.* aff. *hystrix*); Ruiz and Gonzalez-Regalado, 1996; Romero et al., 2021, Northern Morocco (Bouab, 1992; Kili, 1993), Southern Turkey (Avşar et al., 2006; Darbaş and Nazik, 2010), Tunisia (Bonaduce et al., 1992), Lybia (van Hinte et al., 1980; Gammudi, 1990; Gammudi and Keen, 1993), Italy (Ciampo, 1980, as *Acanthocythereis* sp.; Ruggieri, 1962, 1963, as *Trachyleberis hystrix*; Aruta, 1983; Bonaduce and Russo, 1985), Algeria (Sissingh, 1972b; Carbonnel and Courme-Raoult, 1997; Babinot and Boukli-Hacene, 1998).

Argilloecia pera Ciampo, 1986. 1986 *Argilloecia pera* Ciampo, p. 50, pl. 16, Figs. 3–4. A rare species, previously recorded only in Upper Miocene assemblages from Italy by Ciampo, 1986; Dall'Antonia, 2003 (as *Argilloecia tenuis*).

Aurila anterocostata Harrison et al., 2000. 2000 *Aurila anterocostata* Harrison, Maybury and Whatley, pp. 45–46, pl. 5, Figs. 11–12, pl. 6, Figs. 1–5, pl. 11, Figs. 8–9, pl. 12, Fig. 10. An Atlantic species, described from the Redonian of the Northwestern France (Harrison et al., 2000).

Aurila impressa Ruggieri, 1977. Fig. 5.A. 1977 *Aurila* (*Aurila*) *convexa impressa* Ruggieri, p. 177–180, pl. 1, Figs. 1, 5, text-Figs. 1–2. Originally described as a subspecies of *A. convexa*, this species was reported from Italy (Ruggieri, 1962, as *Mutilus punctatus;* Ruggieri, 1977; Aruta, 1983; Bonaduce and Russo, 1985; Dall'Antonia and Bossio, 2001), northwestern France (Maybury, 1985, as *A. convexa*), northeastern Morocco (Bouab, 1992, as *A.* cf. *punctata*) and Tunisia (Bonaduce et al., 1992).

Aurila semilunata (Seguenza, 1880). Fig. 5.B. 1880 *Cythere semilunata* Seguenza, p. 125, pl. 12, Fig. 7. Ruggieri, 1963 redescribed the Seguenza's species from the Late Miocene of southern Italy. The presence of the species in Upper Miocene deposits from the Azores, in northeastern Atlantic, was shown by Meireles et al., 2012 (as *Aurila* sp.).

Bairdoppilata conformis (Terquem, 1878). Fig. 4.D. 1878 *Bairdia subdeltoidea* var. *conformis* Terquem, p. 93, pl. 10, fig. 17. Occurrences of this species in Upper Miocene northern African assemblages were reported by van Hinte et al., 1980 (as *B.* sp. 2), from Lybia, by Babinot and Boukli-Hacene, 1998 (as *Neonesidea* sp. aff. *corpulenta*) from Algeria, and by Kili, 1993 (as *Bairdoppilata rhomboidalis*) from Morocco.

Bosquetina carinella (Reuss, 1850). Fig. 4.N. 1850 *Cypridina carinella* Reuss, p. 76, pl. 10, Fig. 10. Uncommon in the Late Miocene, *B. carinella* was found by Ruiz and Gonzalez-Regalado, 1996, in southern Spain.

Buntonia aff. *obesa* Ciampo, 1986. An undescribed species reported as *B. textilis* by Ruiz and Gonzalez-Regalado, 1996, from southern Spain.

Callistocythere crispata (Brady, 1868). Fig. 4.F. 1868 *Cythere crispata* Brady, p. 221, pl. 14, figs. 14–15. Reported under different specific names, due to variability of the shell sculpture, from Italy by Ruggieri, 1962, 1967; Aruta, 1983; Dall'Antonia and Bossio, 2001 (as *C. pallida*);

Table 3
Species used for statistical analyses and occurrences in deposits located in the ecoregions identified by Spalding et al. (2007). South European Atlantic Shelf (27), Saharan Upwelling (28), Adriatic Sea (30), Aegean Sea (31), Levantine Sea (32), Tunisian Plateau/Gulf of Sidra (33), Ionian Sea (34), Western Mediterranean (35) and Alboran Sea (36).

species	ecoregions (Spalding et al., 2007)								
	27	28	30	31	32	33	34	35	36
Acanthocythereis hystrix (Reuss, 1850)	●	●			●	●	●	●	●
Argilloecia pera Ciampo, 1986			●						
Aurila anterocostata Harrison et al., 2000	●								
Aurila impressa Ruggieri, 1977	●		●			●		●	●
Aurila semilunata (Seguenza, 1880)							●		
Bairdoppilata conformis (Terquem, 1878)		●				●			●
Bosquetina carinella (Reuss, 1850)	●								
Buntonia aff. *obesa* Ciampo, 1986	●								
Callistocythere crispata (Brady, 1868)	●	●	●		●	●		●	●
Callistocythere producta Aruta, 1983			●					●	
Callistocythere tetradactyla Ciampo, 1984	●	●	●			●			●
Carinocythereis whitei (Baird, 1850)	●		●	●	●			●	●
Carinovalva aquila Ruggieri, 1972				●					
Carinovalva testudo (Namias, 1900)	●	●				●		●	●
Caudites calceolatus (Costa, 1853)			●		●	●			●
Chrysocythere cataphracta Ruggieri, 1962		●			●	●		●	●
Cimbaurila vitrocincta (Ruggieri, 1950)		●							
Cistacythereis caelatura Uliczny, 1969		●							●
Cistacythereis emaciata (Brady, 1867)		●		●		●	●	●	●
Cytherella inaequalis Moyes, 1965	●	●		●		●			●
Cytherella scutulum Ruggieri, 1976	●							●	●
Cytheridea acuminata (Bosquet, 1852)			●	●	●	●	●	●	●
Cytheropteron latum Müller, 1894	●						●	●	●
Cytheropteron ruggierii Pucci, 1956			●					●	
Cytheropteron vespertilio (Reuss, 1850)							●		
Eucytherura mistrettai Sissingh, 1972								●	
Eucytherura protracta Ruggieri, 1962			●					●	●
Flexus tenuicarinatus (Capeder, 1902)	●	●	●					●	●
Graptocythere polyptycha Reuss, 1850			●			●		●	●
Hemicytherura defiorei Ruggieri, 1953			●	●				●	●
Hemicytherura videns (Müller, 1894)	●	●	●						
Henryhowella asperrima (Reuss, 1850)	●	●				●		●	●
Ionicythere parva (Seguenza, 1880)			●		●	●		●	
Kangarina abyssicola (Müller, 1894)	●		●					●	●

Table 3 (*continued*)

species	ecoregions (Spalding et al., 2007)								
	27	28	30	31	32	33	34	35	36
Krithe oertlii Dieci and Russo, 1967		●	●				●	●	
Leptocythere foveolata Moyes, 1965	●								●
Loxoconcha reticulopunctata Ciampo, 1986	●		●						
Monoceratina oblita Bonaduce et al., 1976			●						
Mutilus labiatus Moyes, 1965	●	●							●
Olimfalunia plicatula (Reuss, 1850)	●		●	●		●		●	●
Paijenborchella solitaria Ruggieri, 1962				●				●	
Palmoconcha dertobrevis (Ruggieri, 1967)	●		●					●	
Palmoconcha exendata (Bassiouni, 1962)	●								
Paracypris sp. Carbonnel and Courme-Raoult, 1997								●	
Paracytheridea triquetra (Reuss, 1850)	●		●	●	●			●	●
Pontocythere turbida (Müller, 1894)	●				●				●
Pterygocythereis coronata (Roemer, 1838)	●			●					
Pterygocythereis jonesii (Baird, 1850)	●	●						●	
Pulaviella geometra (Ruggieri, 1962)								●	
Rectobuntonia posteropunctata (Moyes, 1965)	●								
Ruggieria tetraptera (Seguenza, 1880)	●	●	●		●	●	●	●	●
Sagmatocythere grateloupiana (Bosquet, 1852)	●								
Sagmatocythere napoliana (Puri, 1963)			●						●
Sagmatocythere tenuis (Ciampo, 1980)	●						●	●	
Sagmatocythere versicolor (Müller, 1894)	●	●	●				●	●	●
Semicytherura cornubiensis Maybury, 1985 *nomen nudum*	●								
Semicytherura foeda Ciampo, 1986							●		
Semicytherura furcilla Aiello and Szczechura, 2004	●					●			
Semicytherura microwallacei Maybury, 1985 *nomen nudum*	●						●		
Senesia triangularis (Oertli, 1956)	●	●						●	●
Xestoleberis prognata Bonaduce and Danielopol, 1988	●	●			●		●	●	

by Ciampo, 1986 (as *C. aurita*), Atlantic side of France by Moyes, 1965 (as *C. rugosa*), northern Morocco by Nachite et al., 2006 (as *Callistocythere* sp. 2); Bouab, 1992 (as *C. littoralis*), Tunisia by Bonaduce et al., 1992 (as *C.* aff. *macilenta*), Algeria by Carbonnel and Courme-Raoult, 1997 (as *C. aspera*), and southern Turkey by Babinot, 2002 (as *C.* sp. 3).

Callistocythere tetradactyla Ciampo, 1984. Fig. 4.I. 1984 *Callistocythere tetradactyla* Ciampo, p. 252, pl. 2, Figs. 1–2. Described from

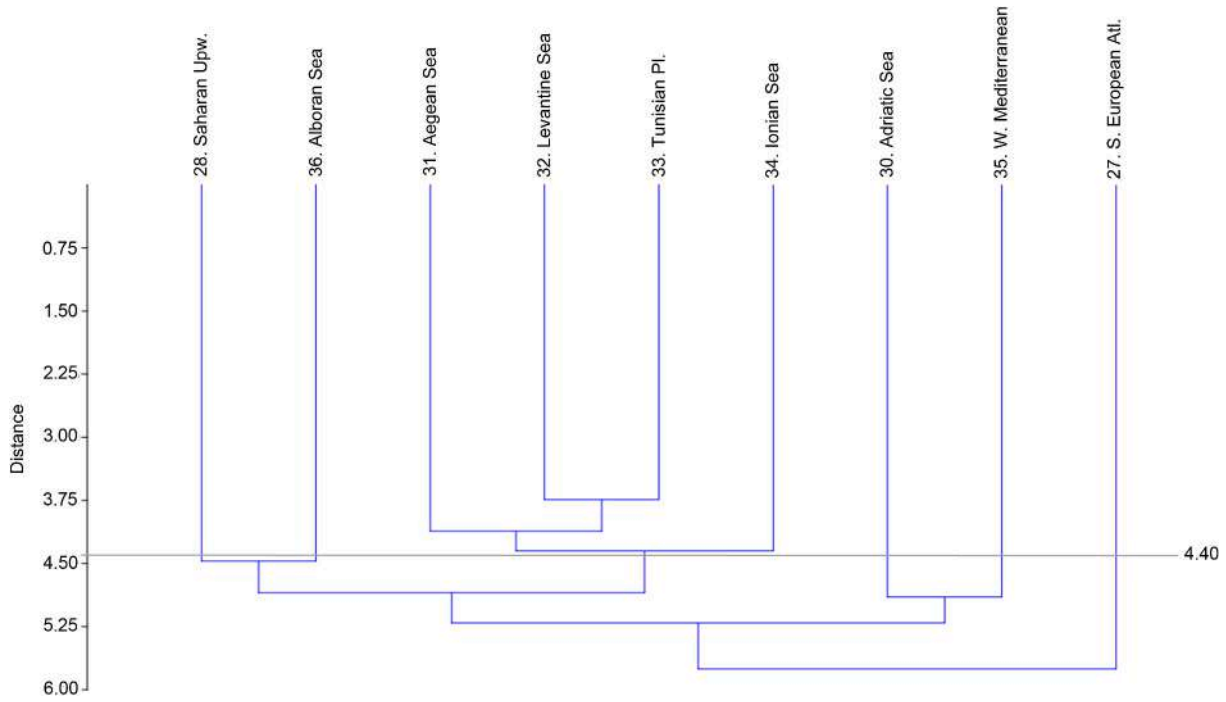


Fig. 6. Cluster analysis performed on the presence/absence data of 61 selected Messinian species in the Late Miocene of the Mediterranean Atlantic Region, using the "ecoregions" identified by Spalding et al. (2007): South European Atlantic Shelf (27), Saharan Upwelling (28), Adriatic Sea (30), Aegean Sea (31), Levantine Sea (32), Tunisian Plateau/Gulf of Sidra (33), Ionian Sea (34), Western Mediterranean (35) and Alboran Sea (36).

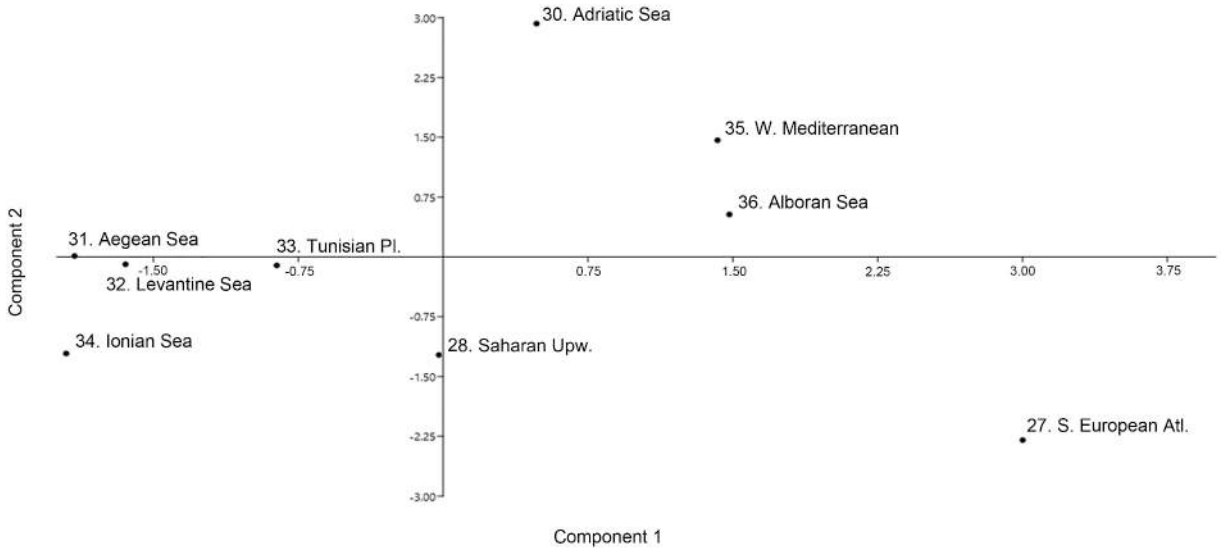


Fig. 7. Scatter plot from Principal Component Analysis (PCA) plotting first and second principal components performed on the presence/absence data of 61 selected Messinian species in the Late Miocene of the Mediterranean Atlantic Region, using the "ecoregions" identified by Spalding et al. (2007): South European Atlantic Shelf (27), Saharan Upwelling (28), Adriatic Sea (30), Aegean Sea (31), Levantine Sea (32), Tunisian Plateau/Gulf of Sidra (33), Ionian Sea (34), Western Mediterranean (35) and Alboran Sea (36).

Tortonian successions of northern Italy and found in Lybia by van Hinte et al., 1980 (as *C.* sp.2) and El-Waer, 1988 (as *C.* sp.), in Portugal by Nascimento, 1988 (as *C. oertlii*), and in Morocco by Bouab, 1992 and Kili, 1993 (as *C. oertlii*).

Carinocythereis whitei (Baird, 1850). Fig. 4.Q. 1850 *Cythereis whitei* Baird, p. 175, pl. 20, Fig. 3. Occurrences: Italy (Ruggieri, 1962 and Dieci and Russo, 1965a, 1965b, both as *C. carinata*), Crete (Sissingh, 1972a, as *C. carinata*), France (Carbonnel, 1969, as *C. carinata,* and Maybury, 1985, as *C.* sp. cf. *C. carinata*), northeastern Morocco (Bouab, 1992, as *C. carinata*), southern Spain (Ruiz and Gonzalez-Regalado, 1996), Algeria (Babinot and Boukli-Hacene, 1998), southern Turkey (Faranda et al., 2013, as *Occlusacythereis occlusa*).

Carinovalva aquila (Ruggieri, 1972). Fig. 4.V. 1972 *Lixouria aquila* Ruggieri, p. 102, Figs. 3–4, 6–7. Rare in the Late Miocene, being recorded only by Sissingh (1972a) in Crete, as *Incongruellina keiji*.

Carinovalva testudo (Namias, 1900). Fig. 4.W. 1900 *Cythere testudo* Namias, p. 104, pl. 15, figs. 14–15. A species characteristic of western and central part of the MEWAP during the Late Miocene. Reported from France by Moyes, 1965 (as *Ruggieria carinata*); Carbonel, 1985 (as *C. carinata*); Carbonnel and Courme-Raoult, 1997 (as *Dahomeya*

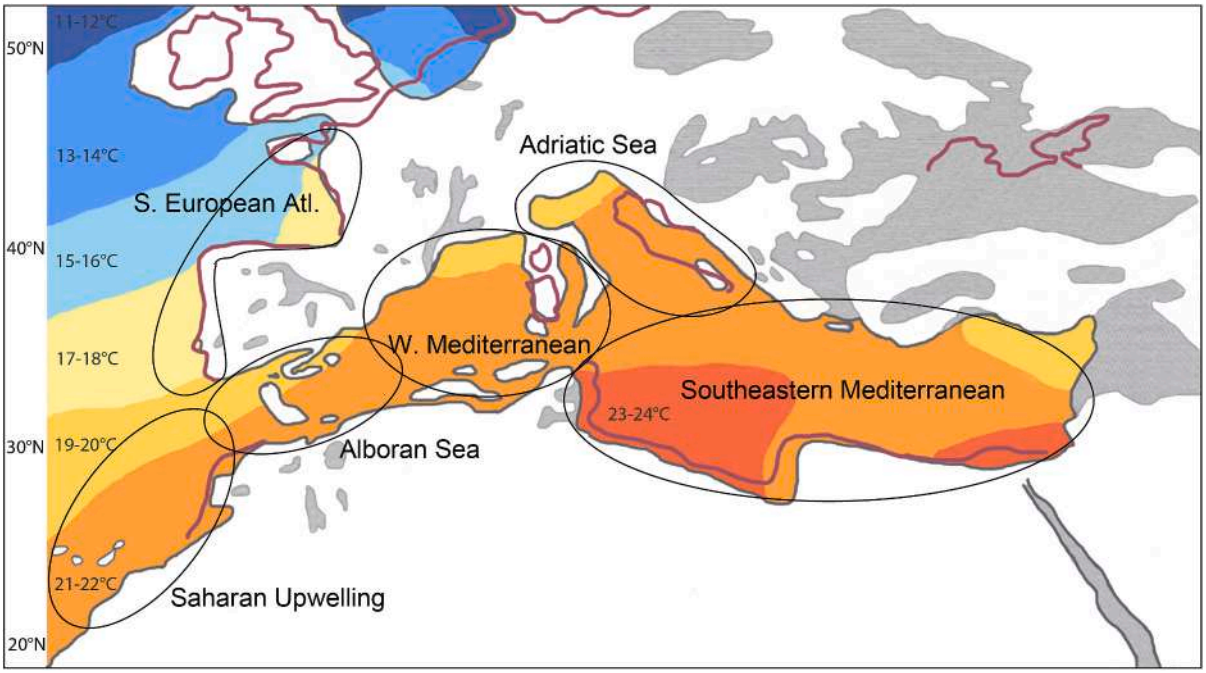


Fig. 8. Late Miocene palaeoecoregions identified by distribution data and statistical analyses. South European Atlantic Shelf, Saharan Upwelling, Adriatic Sea, Western Mediterranean and Alboran Sea correspond with the ecoregions discerned by Spalding et al. (2007); Southeastern Mediterranean palaeoecoregion includes the Aegean Sea, Levantine Sea, Tunisian Plateau/Gulf of Sidra and Ionian Sea ecoregions (Spalding et al., 2007). Palaeogeographic map modified after Meulenkamp and Sissingh, 2003; Miocene sea surface temperature reconstructions modified after Burls et al., 2021, are intended as an approximate guide only.

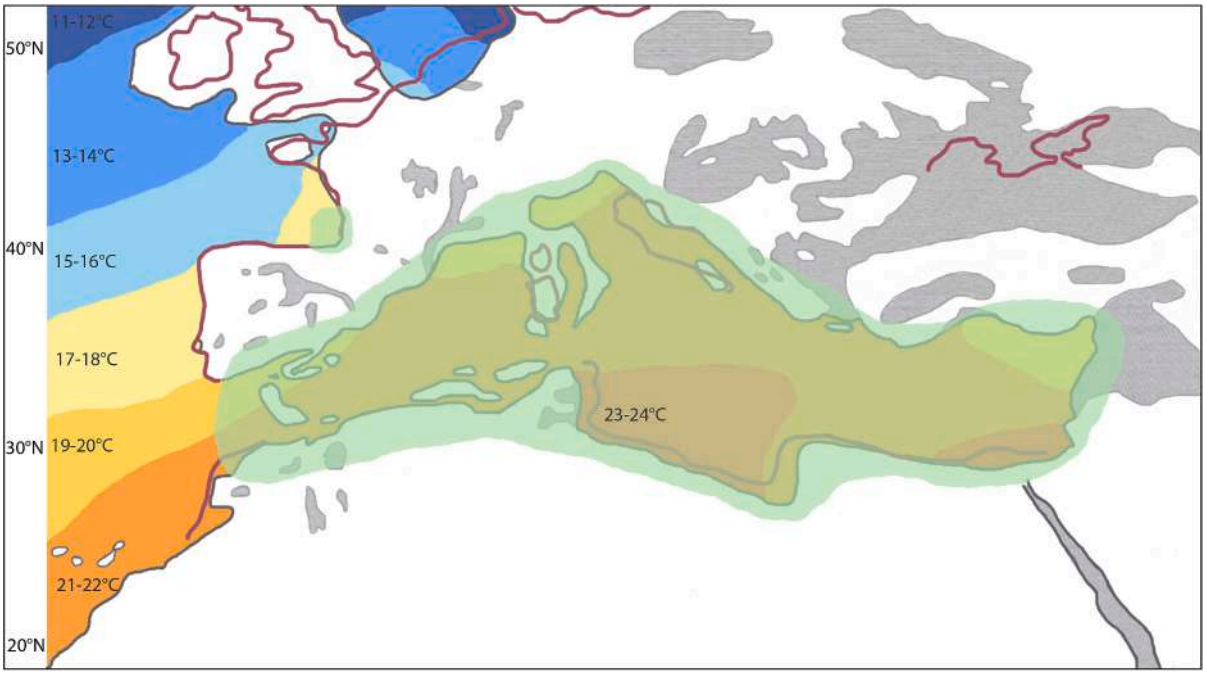


Fig. 9. Late Miocene distribution of *Ruggieria tetraptera* (Seguenza, 1880) in Proto-Mediterranean Atlantic area. Palaeogeographic map modified after Meulenkamp and Sissingh, 2003; Miocene sea surface temperature reconstructions modified after Burls et al., 2021, are intended as an approximate guide only.

carinata), from Sicily byAruta, 1983, from Lybia by El-Waer, 1988 (as *C. carinata*), from Morocco by Kili, 1993 (as *Incongruellina unicostulata*), from Algeria by Babinot and Boukli-Hacene, 1998 (as *C. marginata*), and from Spain by Keen, 2004 (as *C. carinata*).

Caudites calceolatus (Costa, 1853). Fig. 5.D. 1853 *Cytherina calceolata* Costa, p. 185, pl. 16, fig. 14. The present is the first Late Miocene report outside the Proto-Mediterranean, where the species was found by Russo, 1969 (as *C.* sp. 1) and Miculan, 1992 (as *C.* cf. *mediterranensis*) in northern Italy, by El-Waer, 1991 (as *Caudites* sp.) in Lybia, by Bouab, 1992, in northeastern Morocco, by Babinot, 2002 (as *C. mediterranensis*) and Donat, 2009 (as *C. orientalis*) in southern Turkey.

Chrysocythere cataphracta Ruggieri, 1962. Fig. 4.AB. 1962 *Chrysocythere cataphracta* Ruggieri, p. 26, pl. 2, Figs. 11–13. A termophilic species, reported by Carbonnel (1992), from the Late Miocene of

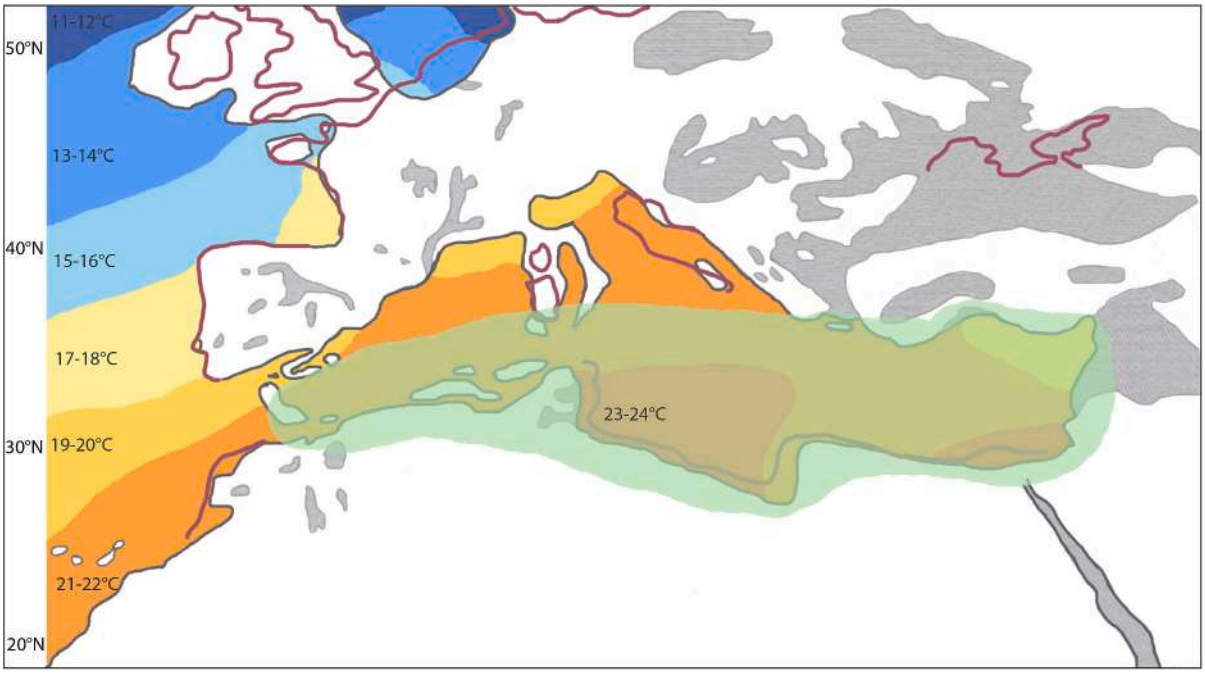


Fig. 10. Late Miocene distribution of *Chrysocythere* in Proto-Mediterranean Atlantic area.
Palaeogeographic map modified after Meulenkamp and Sissingh, 2003; Miocene sea surface temperature reconstructions modified after Burls et al., 2021, are intended as an approximate guide only.

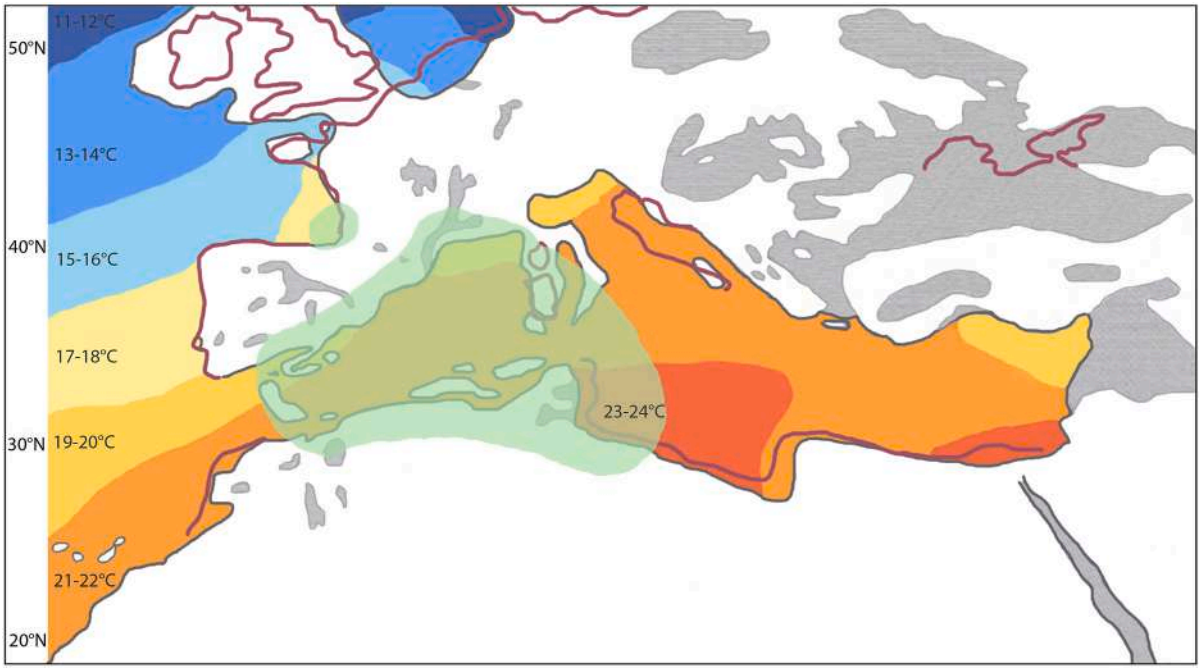


Fig. 11. Late Miocene distribution of *Carinovalva testudo* (Namias, 1900) in Proto-Mediterranean Atlantic area. Palaeogeographic map modified after Meulenkamp and Sissingh, 2003; Miocene sea surface temperature reconstructions modified after Burls et al., 2021, are intended as an approximate guide only.

Senegal. It was confined in the southern part of the MEWAP, as shown by the findings of Ruggieri, 1962; Aruta, 1983, from Sicily, Sissingh, 1972b; Babinot and Boukli-Hacene, 1998, from Algeria, Doruk, 1973 (as *C. paradisus*) from southern Turkey, Gammudi, 1990; El-Waer, 1991; Gammudi and Keen, 1993, from Lybia, Bonaduce et al., 1992 (as *C. paradisus*).

Cimbaurila vitrocincta (Ruggieri, 1950). Fig. 5.C. 1950 *Hemicythere cimbaeformis vitrocincta* Ruggieri, p. 42, text-figs. 23–25, pl. 1, Fig. 9. A species endemic, in the Late Miocene, of Moroccan waters, as shown by the reports of Ducasse and Cirac, 1981; Bouab, 1992 (both as *Mutilus venetiensis*).

Cistacythereis caelatura Uliczny, 1969. Fig. 4.R. 1969 *Cistacythereis caelatura* Uliczny, p. 82, pl. 6, Figs. 1–3, pl. 16, fig. 18. The species was present, during the Late Miocene, only in Moroccan area, as displayed by Bouab, 1992; Kili, 1993, (both as *C. cebrenidos*).

Cistacythereis emaciata (Brady, 1867). Fig. 4.S. 1867 *Cythere emaciata* Brady, p. 210. A species relatively common in Upper Miocene sediments from the central-southern areas of the MEWAP. Occurrences: Algeria, in

Sissingh, 1972b (as *Falunia ruida*); Carbonnel and Courme-Raoult, 1997 (as *Hiltermannicythere* sp.1 aff. *emaciata*), southern Italy, in Aruta, 1983 (as *Hiltermannicythere* aff. *H. rubra*); Bonaduce and Russo, 1985 (as *Hiltermannicythere* sp.), northern Morocco, in Bouab, 1987 (as *Falunia* ? *rugosa*); Bouab, 1992 (as *C. rubra*); Kili, 1993 (as *Falunia*? *rugosa*); Nachite and Bekkali, 2010 (as *Hiltermannicythere emaciata*), Lybia, in El-Waer, 1991 (as *C. qabilatshurfahensis*), Tunisia, in Bonaduce et al., 1992 (as *Hiltermannicythere* sp. 1 aff. *emaciata*), Crete, in Faranda et al., 2008 (as *C. rubra*).

Cytherella inaequalis Moyes, 1965. Fig. 4.A. 1965 *Cytherella inaequalis* Moyes, p. 9, pl. 1, Figs. 3–5. Described from Atlantic French successions by Moyes, 1965, and figured from Upper Miocene assemblages from Crete by Sissingh, 1972a (as *Cytherella* sp.) and Faranda et al., 2008 (as *C.* gr. *vulgata*), Morocco, by Bouab, 1992 (as *C. compressa*); Kili, 1993, Tunisia, by Bonaduce et al., 1992 (as *C.* sp. 1 ex gr. *vulgata*).

Cytherella scutulum Ruggieri, 1976. Fig. 4.B. 1976 *Cytherella scutulum* Ruggieri, p. 95, text-Fig. 6. An uncommon species, occurring in the south-western part of the Late Miocene MEWAP. It is reported from Sicily, by Aruta, 1983 (as *C. pulchella*), Morocco, by Bouab, 1992 (as *C. pulchella*), and southern Spain, by Ruiz and Gonzalez-Regalado, 1996 (as *C. circumpunctata*).

Cytheridea acuminata Bosquet, 1852. Fig. 4.E. 1852 *Cytheridea Mülleri* var. *acuminata* Bosquet, p. 39. We recognised a moderate morphological variability of this specie. *C. acuminata* was commonly found in the Upper Miocene ostracod assemblages of Turkey (e.g., Öğrünç and Nazik, 1998), and is reported from Crete (Sissingh, 1972a; Faranda et al., 2008), Lybia (van Hinte et al., 1980), Italy (Dieci and Russo, 1967; Aruta, 1983, as *C. acuminata neapolitana*; Bonaduce and Russo, 1985, as *C. josephinae*), Algeria (Guernet et al., 1984; Babinot and Boukli-Hacene, 1998, as *C. arca*), Greece (Mostafawi, 1990; Karakitsios et al., 2017) Morocco (Bouab, 1992), and Tunisia (Bonaduce et al., 1992; Temani et al., 2020, both as *C. arca*).

Cytheropteron latum Müller, 1894. Fig. 5.N. 1894 *Cytheropteron latum* Müller, p. 300, pl. 20, Figs. 3, 9, pl. 21, Figs. 10–14. Occurrences: Sicily (Aruta, 1983; Ciampo, 1986, as *C.* aff. *latum*), northwestern France (Maybury, 1985, as *C. praenodosum*) and northeastern Morocco (Bouab, 1992, as *C. alatum*).

Cytheropteron ruggierii Pucci, 1956. 1956 *Cytheropteron ruggierii* Pucci, p. 170, pl. 1, Figs. 5–6, text-Fig. 2. Recorded in Algeria by Sissingh, 1972b (as *Cytheropteron* sp.) and in northern Italy by Ciampo, 1986 (as *C.* aff. *rotundatum*).

Cytheropteron vespertilio (Reuss, 1850). Fig. 5.Q. 1850 *Cypridina vespertilio* Reuss, p. 81, pl. 11, Fig. 10. A rare species, occurring in the Late Miocene only in northern Italy (Ruggieri, 1967).

Eucytherura mistrettai Sissingh, 1972a. Fig. 5.R. 1972a *Eucytherura mistrettai* Sissingh, p. 140. A rare species, reported, in the Late Miocene, only by Sissingh, 1972b from Algeria (as *E. ruggierii*).

Eucytherura protracta Ruggieri, 1962. Fig. 5.S. 1962 *Eucytherura protracta* Ruggieri, p. 55, pl. 6, Fig. 12. Described from the Tortonian of Sicily, the species was found in northern Italy by Miculan, 1992 and in Morocco by Bouab, 1992 (as *Eucytherura* sp. 2).

Flexus tenuicarinatus (Capeder, 1902). Fig. 5.F. 1902 *Cythere tenuicarinata* Capeder, p. 15, pl. 1, fig. 34. Characteristic of the central and western areas of the Late Miocene MEWAP, *F. tenuicarinatus* was recorded in Italy by Ruggieri, 1962 (as *Eucytheretta* sp. aff. *E. triebeli*); Dieci and Russo, 1965a, 1965b (as *F. triebeli*); Russo, 1969; Ruggieri, 1992, in France by Moyes, 1965 (as *Eucytheretta* aff. *triebeli*); Carbonnel, 1969 (as *F. triebeli*); Maybury, 1985 (as *F.* aff. *triebeli*), and in Morocco by Bouab, 1992; Kili, 1993 (both as *Cytheretta triebeli*).

Graptocythere polyptycha Reuss, 1850. 1850 *Cypridina polyptycha* Reuss, p. 83, pl. 10, fig. 22. Occurrences: northern Italy (Dieci and Russo, 1965a, 1965b, as *Hemicythere* (?) *polyptycha*; Ascoli, 1968, as *Climacoidea* aff. *polyptycha*; Miculan, 1992, as *G. hscripta*), Tunisia (Bonaduce et al., 1992), northeastern Morocco (Bouab, 1992, as *Pachycaudites h-scripta*) and Algeria (Carbonnel and Courme-Raoult, 1997, as *G. hscripta*).

Hemicytherura defiorei Ruggieri, 1953. 1953 *Hemicytherura defiorei* Ruggieri, p. 50, text-Figs. 8, 11–13. The species was reported from Italy by Dieci and Russo, 1965a, 1965b; Aruta, 1983, France, by Carbonnel, 1969, Morocco, by Bouab, 1992, and Algeria, by Babinot and Boukli-Hacene, 1998.

Hemicytherura videns (Müller, 1894). Fig. 5.T. 1894 *Cytheropteron videns* Müller, p. 303, pl. 20, Figs. 2, 8, pl. 21, figs. 15–16, 18. Present in Upper Miocene assemblages from France (Moyes, 1965; Maybury, 1985, as *H.* cf. *videns*), northern Italy (Ciampo, 1986; Miculan, 1992 (as *Hemicytherura* sp. 1) and Morocco (Nachite and Bekkali, 2010).

Henryhowella asperrima (Reuss, 1850). Fig. 4.U. 1850 *Cypridina asperrima* Reuss, p. 74, pl. 10, Fig. 5. A Tethyan species, widely

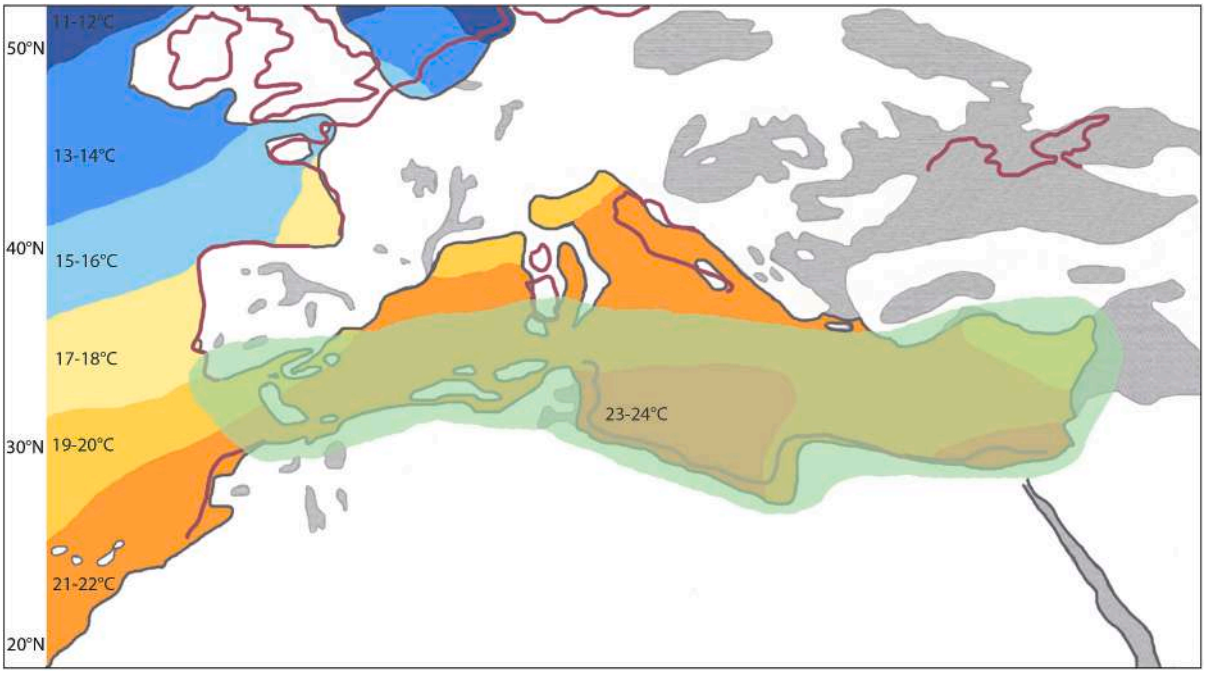


Fig. 12. Late Miocene distribution of *Acanthocythereis hystrix* (Reuss, 1850) in Proto-Mediterranean Atlantic area. Palaeogeographic map modified after Meulenkamp and Sissingh, 2003; Miocene sea surface temperature reconstructions by Burls et al., 2021, are intended as an approximate guide only.

distributed in the Neogene. Occurrences: Spain (Cita et al., 1980; González-Regalado and Ruiz, 1990; Aranki et al., 1992; Ruiz and Gonzalez-Regalado, 1996), Morocco (Bouab, 1992; Kili, 1993; Nachite et al., 2006), Tunisia (Bonaduce et al., 1992), Algeria (Carbonnel and Courme-Raoult, 1997; Babinot and Boukli-Hacene, 1998). Outside the MEWAP *H. asperrima* was reported from the Late Miocene of Gabon (Bold Bold, 1966, 1968).

Ionicythere parva (Seguenza, 1880). 1880 *Cythere parva* Seguenza, p. 325, pl. 17, fig. 28. Reported from the Late Miocene of Italy, by Aruta, 1983 (as *Cytheromorpha reticulata*); Ciampo, 1986 (as *Cytheromorpha golnarae*), Tunisia, by Bonaduce et al., 1992 (as *I. punctatissima*), and Turkey, by Donat, 2009 (as *Callistocythere mediterranea*).

Kangarina abyssicola (Müller, 1894). 1894 *Cytheropteron abyssicolum* Müller, p. 302, pl. 20, Figs. 5–11, pl. 21, Figs. 6–9. This is a cosmopolitan species, figured by Bold (1963) from the Late Miocene of Trinidad. In the Late Miocene MEWAP it was restricted to the central-western areas, being reported from Italy (Ruggieri, 1962; Dieci and Russo, 1965a, 1965b, both as *K. abyssicola coarctata)*, France (Carbonnel, 1969, as *K. abyssicola coarctata*, and Maybury, 1985), and Morocco (Bouab, 1992).

Krithe oertlii Dieci and Russo, 1967. 1967 *Krithe oertlii* Dieci and Russo, p. 15, pl. 1, Figs. 7–8, pl. 3, Figs. 7–8.

Described from the Tortonian of northern Italy, the species is reported from Sicily by Ciampo, 1980 (as *Krithe* sp. 1), Morocco, by Kili, 1993 (as *K. citae*), and Algeria by Carbonnel and Courme-Raoult, 1997 (as *K. aquilonia*).

Leptocythere foveolata Moyes, 1965. Fig. 4.K. 1965 *Leptocythere foveolata* Moyes, p. 30, pl. 2, Fig. 12. During the Late Miocene the species was present in the western part of the MEWAP, being recorded from France by Moyes, 1965, and Maybury, 1985 (as L. *pliocenica*), and from Morocco by Bouab, 1992 (as *Leptocythere*? sp. 1).

Loxoconcha reticulopunctata Ciampo, 1986. 1986 *Loxoconcha reticulopunctata* Ciampo, p. 88, pl. 4, Figs. 5–6. Described from the northern Italy by Ciampo, 1986, the species was previously figured from France by Moyes, 1965 (as. L. *punctatella*).

Monoceratina oblita Bonaduce et al., 1976. 1976 *Monoceratina oblita* Bonaduce et al., p. 117, pl. 70, Figs. 1–8, text-fig. 45. The presence of *M. oblita* in Upper Miocene sediments was displayed by Dall'Antonia, 2003, from the Tremiti Islands, Italy.

Mutilus labiatus Moyes, 1965. Fig. 5.E. 1965 *Mutilus labiatus* Moyes, p. 101, pl. 13, Figs. 7–10. In the Late Miocene the species was present in the western part of the paleoprovince. *M. labiatus* was reported from France by Moyes, 1965; Ducasse and Cirac, 1981; Bouab, 1992 (both as *M. retiformis*).

Olimfalunia plicatula (Reuss, 1850). Fig. 4.T. 1850 *Cypridina plicatula* Reuss, p. 84, pl. 10, fig. 23. A species showing high morphological variability, reported from France by Moyes, 1965, Portugal, by Nascimento, 1988, Italy, by Dieci and Russo, 1965a, 1965b (as *Falunia plicatula*); Dall'Antonia and Bossio, 2001 (as *Capsacythere sicula*), Crete, by Sissingh, 1972a (as *F. plicatula*); Faranda et al., 2008 (as *Celtia clatrata*), Tunisia, by Bonaduce et al., 1992 (as *C. sicula*), and Algeria, by Babinot and Boukli-Hacene, 1998 (as *C.* sp. aff. *sicula*).

Paijenborchella solitaria Ruggieri, 1962. Fig. 5.Z. 1962 *Paijenborchella solitaria* Ruggieri, p. 54, pl. 6, Fig. 9. Described from the Tortonian of the Sicily, the species was figured by Sissingh, 1972a, from the Late Miocene of Crete.

Palmoconcha dertobrevis (Ruggieri, 1967). Fig. 5.G. 1967 *Loxoconcha dertobrevis* Ruggieri, p. 376, figs. 39–41. Occurrences: Italy, Ruggieri, 1967 (as L. *dertobrevis*); Aruta, 1983 (as *Loxoconcha agilis*); Algeria, Sissingh, 1972b (as *L. dertobrevis*), and France, Maybury, 1985 (as *P. subrugosa*).

Palmoconcha extendata (Bassiouni, 1962). Fig. 5.H. 1962 *Loxoconcha extendata* Bassiouni, p. 60, pl. 9, Figs. 7–9, text-Fig. 3. Found in the Late Miocene only by Maybury, 1985 (as *Palmoconcha* sp. 1), from northwestern France.

Paracypris sp. Carbonnel and Courme-Raoult, 1997. Fig. 4.C.1997 *Paracypris* sp., p. 15, pl. 1, fig. 17. A possibly still undescribed species, figured by Carbonnel and Courme-Raoult, 1997, from the Late Miocene of Algeria.

Paracytheridea triquetra (Reuss, 1850). Fig. 5.M. 1850 *Cypridina triquetra* Reuss, p. 82, pl. 10, fig. 19. A species showing a remarkable intraspecific variability, reported from France by Moyes, 1965; Maybury, 1985 (as *P. fossarotunda*), Crete by Sissingh, 1972a (as *Paracytheridea* sp.), Italy by Ruggieri, 1962 (as *P. bovettensis*); Ruggieri, 1977 (as *P.* sp. cfr. *triquetra*); Aruta, 1983 (as *Paracytheridea* sp.); Miculan, 1992 (as *Paracytheridea* sp. 1), Algeria by Babinot and Boukli-Hacene, 1998, and Turkey by Babinot, 2002 (as *P.* aff. *triquetra*).

Pontocythere turbida (Müller, 1894). Fig. 4.L. 1894 *Cytheridea turbida* Müller, p. 361, pl. 30, figs. 28, 31–33, 40–45, 47. Upper Miocene shells conspecific with the Oued El Kell specimens were figured from France by Maybury, 1985 (as *P.* cf. *turbida*), Algeria, by Babinot and Boukli-Hacene, 1998, and Turkey, by Donat, 2009 (as *P. elongata*).

Pterygocythereis coronata (Roemer, 1838). Fig. 4.Y. 1838 *Cytherina coronata* Roemer, p. 518, pl. 6, fig. 30. Rarely found in the Late Miocene, being reported from Crete by Sissingh, 1972a, and from France by Maybury, 1985, both as *P. ceratoptera.*

Pterygocythereis jonesii (Baird, 1850). Fig. 4.Z. 1850 *Cythereis Jonesii* Baird, p. 175, pl. 20, Fig. 1. Late Miocene occurrences were from central and western sectors of the paleoprovince: Aruta, 1983 (Sicily); Nascimento, 1988 (Portugal); Guernet, 1990 (Morocco); Ruiz and Gonzalez-Regalado, 1996 (Spain).

Pulaviella geometra (Ruggieri, 1962). Fig. 5.AB. 1962 *Xestoleberis geometra* Ruggieri, p. 62, pl. 7, fig. 19. The present is the first Atlantic record of this very rare species, described from the Tortonian of Sicily.

Rectobuntonia posteropunctata (Moyes, 1965). Fig. 4.P. 1965 *Buntonia posteropunctata* Moyes, p.78, pl. 9, Figs. 5–7. A Late Miocene eastern Atlantic endemic species, described by Moyes from northwestern France.

Ruggieria tetraptera (Seguenza, 1880). Fig. 4.X. 1880 *Cythere tetraptera* Seguenza, p. 125, pl. 12, Fig. 9. Common in Late Miocene European-West African Palaeoprovince, the species was reported from Italy (Ruggieri, 1962; Ruggieri, 1963 Dieci and Russo, 1965a, 1965b; Ruggieri, 1967; Aruta, 1983), France (Moyes, 1965), Algeria (Sissingh, 1972b), Lybia (Gammudi, 1990; El-Waer, 1991; Gammudi and Keen, 1993), Tunisia (Bonaduce et al., 1992), Morocco (Kili, 1993; Nachite and Bekkali, 2010) Spain (Ruiz and Gonzalez-Regalado, 1996), Turkey (Donat, 2009; Şafak, 2019). Bold (1966, 1968) figured the species from the Late Miocene of Gabon.

Sagmatocythere grateloupiana (Bosquet, 1852). Fig. 5.I. 1852 *Cythere grateloupiana* Bosquet, p. 81, pl. 4, Fig. 3. During the Late Miocene the species was endemic to eastern Atlantic, being reported from northwestern France by Maybury, 1985 (as *Kuiperiana grateloupiana*); Maybury, 1990 (as *Loxocorniculum grateloupianum*), Portugal, by Nascimento, 1988 (as *Loxoconcha* (*Sagmatocythere*) *grateloupiana*), and Spain, by Ruiz et al., 1999 (as *S. napoliana*).

Sagmatocythere napoliana (Puri, 1963). Fig. 5.J. 1963 *Loxoconcha napoliana* Puri, p. 5. Rare in the Late Miocene, *S. napoliana* was reported from northern Italy by Ciampo, 1984 (as *Loxoconcha crispa*) and from northwestern Morocco by Bouab, 1992 (as *Loxoconcha mediterranea*).

Sagmatocythere tenuis (Ciampo, 1980). 1980 *Loxoconcha moncharmonti tenuis* Ciampo, p. 19, pl. 3, Fig. 1. Recorded in the Late Miocene from Sicily, by Ciampo, 1980; Aruta, 1983 (both as L. *moncharmonti tenuis*), northwestern France, Maybury and Whatley, 1984; Maybury, 1985 (both as *S. pseudomultifora*), Greece, by Mostafawi, 1990.

Sagmatocythere versicolor (Müller, 1894). Figs. 5.K, 5.L. 1894 *Loxoconcha versicolor* Müller, p. 346, pl. 27, Fig. 4, pl. 28, Figs. 5, 10. A species with a relatively high degree of morphological variability, found in Italy by Ruggieri, 1962; Aruta, 1983 (both as *Loxoconcha variesculpta*); Ciampo, 1986 (as *S. oblonga*), Algeria, by Sissingh, 1972b (as L. *variesculpta*), Spain, by Cita et al., 1980 (as *L. variesculpta*), northwestern France by Maybury, 1985 (as *Kuiperiana* aff. *subovata*), Morocco, by Bouab, 1992 (as *Loxoconcha carinata*); Nachite and Bekkali, 2010 (as *S. multiflora*).

Semicytherura cornubiensis Maybury, 1985 *nomen nudum*. Fig. 5.W. 1985 *Semicytherura cornubiensis* Maybury, p. 113, pl. 6, figs. 15–17, pl. 46, Fig. 2. This rare species was described and figured (unpublished) from the Redonian of the northwestern France.

Semicytherura foeda Ciampo, 1986. Fig. 5.X. 1986 *Semicytherura foeda* Ciampo, p. 98, pl. 8, Fig. 10. The present is the first Atlantic record of this rare species, described from southern Italy.

Semicytherura furcilla Aiello and Szczechura, 2004. Fig. 5.Y. 2004 *Semicytherura furcilla* Aiello and Szczechura, p. 46, pl. 11, Figs. 4–5. The species was recorded from northwestern France by Maybury, 1985 (as *Semicytherura* sp. 1 Yassini, 1979) and from Tunisia by Bonaduce et al., 1992 (as *Cytheropteron rarum*).

Semicytherura microwallacei Maybury, 1985 *nomen nudum*. 1985 *Semicytherura cornubiensis* Maybury, p. 130, pl. 8, Figs. 8–12. The species, described and figured (unpublished) from the Redonian of the northwestern France, was also reported from Sicily by Ciampo, 1980 (as *Semicytherura* sp. 1).

Senesia triangularis (Oertli, 1956). Fig. 4.AC. 1956 *Hemicythere* ? *triangularis* Oertli, p. 95, pl. 13, figs. 348–354. Late Miocene occurrences: France, by Carbonnel, 1969 (as *Hemicythere triangularis*); Carbonnel and Courme-Raoult, 1997; Maybury, 1985 (as *Aurila* ? sp. 10), Algeria, by Guernet et al., 1984 (as *S.* aff. *triangularis*), and Morocco, by Kili, 1993 (as *Hemicythere triangularis*).

Xestoleberis prognata Bonaduce and Danielopol, 1988. 1988 *Xestoleberis prognata* Bonaduce and Danielopol, p. 381, pl. 3, figs. a-c, pl. 1, figs. g-h. The variability of *X. prognata,* frequently confused with similar species*,* was described in Abate et al., 1994. It was reported from Italy by Aruta, 1983 (as *Xestoleberis* sp. 16), Portugal by Nascimento, 1988 (as *X. glabrescens*), Greece, by Mostafawi, 1990 (as *Xestoleberis* sp.), Morocco, by Kili, 1993 (as *X. glabrescens*), Spain, by Ruiz and Gonzalez-Regalado, 1996, Turkey, by Öğrünç and Nazik, 1998 (as *X. glabrescens*); Donat, 2009 (as *X. reymenti*).

8. Discussion

In the Mediterranean-Atlantic Region (sensu Ekman, 1953 and Briggs, 1974), the Late Miocene was an interval of intense and discontinuous palaeogeographic and climatic change, under the combined influence of the convergence between the European and African plates and the Late Miocene global cooling.

On the one hand, palaeobiogeographic reconstructions, mainly based on molluscan distribution (Brébion, 1981; Le Lœuff and von Cosel, 1998; Silva and Landau, 2007), considered the "Miocene European-West African Province" (MEWAP, in Ávila et al., 2016) as a tropical "biogeographic entity, extending from north-western France to western Angola" (Vermeij, 2011) and bordered to the north by a narrow subtropical belt corresponding to the English Channel area. On the other, recent studies (Tzanova et al., 2015; Herbert et al., 2016; Super et al., 2020) have suggested a transition from the tropical/subtropical (sensu Monegatti and Raffi, 2010; approximately corresponding to the inner/outer tropical as defined by Hall, 1964) waters of the Middle Miocene to the Messinian subtropical/warm temperate climate, approximately similar to the present-day conditions. It should also be considered that during the late Tortonian the south-Rifian area was characterized by a number of subtropical taxa (e.g., Alvinerie et al., 1992).

The majority of the ostracods occurring in the Messinian assemblages of the Oued El Kell Section was assigned to extant, cosmopolitan genera (i.a. *Argilloecia*, *Aurila, Eucytherura, Krithe, Loxoconcha, Sagmatocythere, Semicytherura, Xestoleberis*), whereas only a small number of species were placed in extinct genera (e.g., *Flexus*, *Graptocythere, Pulaviella*) or genera living in tropical and subtropical environments (e.g., *Carinovalva*, *Chrysocythere*, *Ruggieria*) and not present in the Mediterranean-Atlantic Region. No endemic genus was recognised. Our interest was focused on the possible identification of palaeobiogeographic Late Miocene units within the north-eastern part of the MEWAP, through the distribution data of a well-defined group of ostracod species occurring in the Messinian of Atlantic Morocco. The results showed that in the Late Miocene was possible to discern five of the nine considered ecoregions (South European Atlantic Shelf, Saharan Upwelling, Adriatic Sea, Western Mediterranean and Alboran Sea), whereas the four south-eastern Mediterranean ecoregions (Aegean Sea, Levantine Sea, Tunisian Plateau/Gulf of Sidra and Ionian Sea) should be regarded as a single palaeoecoregion, herein proposed as "Late Miocene Southeastern Mediterranean Palaeoecoregion".

It would have been desirable to treat the Tortonian-Messinian transition, but the low level of biostratigraphic age resolution of most of the studies prevented us from discriminating Tortonian and Messinian distribution data and, consequently, from detecting possible changes in the palaeobiogeographic set-up.

The class Ostracoda includes thousands of living and fossil benthic species showing limited dispersal capabilities due to the lack of a pelagic larval stage, which is probably one of the reasons why ostracod assemblages generally show a high level of endemicity in comparison, as with benthic foraminifera (e.g., Andreu and Tronchetti, 1996; Gebhardt, 2003; Savelieva et al., 2017; Aiello et al., 2018). The high (palaeo) biogeographic potential of ostracod taxa could be underestimated due to the paucity and inhomogeneity of the distribution data and to taxonomic uncertainties, and the present study is an attempt to evaluate an approach where identification at species level of a limited, but well documented number of species was used for palaeobiogeographic analyses. The comparison with the distributional data of the ostracod genera reported by Wood and Whatley (1994) for the Eastern Atlantic environments provided some insights into the palaeoclimatic setting of the MEWAP. Three of the genera occurring in the Oued El Kell assemblages, *Carinovalva, Chrysocythere* and *Ruggieria,* presently restricted to the tropical African shelf, lived in the warm waters of the MEWAP. The distribution of these genera during the Late Miocene (Appendix 2) highlighted some significant differences. *Ruggieria* was encountered in the entire Proto-Mediterranean-Atlantic Region (Fig. 9), whereas *Chrysocythere* was not present in its northern parts (Fig. 10) and *Carinovalva* did not occur in the easternmost areas. The distribution of *Chrysocythere* was probably due to its thermophilic nature: the presence of this genus suggested that at least in the southern part of the MEWAP, during the Late Miocene, the sea surface temperatures were similar to those of today's Gulf of Guinea. *Carinovalva testudo* (Fig. 11) was possibly an Atlantic species unable to live in easternmost, warmest and high salinity (Meijer et al., 2004; Kontakiotis et al., 2022) waters of the Proto-Mediterranean. Consequently, a subtropical/tropical affinity for this species was inferred. The wide distribution of *R. tetraptera*, also found in the Late Miocene of the northwestern France, probably in a subtropical-temperate palaeoenvironment, suggested that climatic change was not the only cause of the subsequent (Pliocene-Pleistocene) disappearance of the genus above 15 north latitude. In addition, we noted the peculiar distribution of *A. hystrix* (Fig. 12), presently living in the Mediterranean Sea, which was limited, in the Late Miocene, to the southern areas of the MEWAP. *A. hystrix* lives today in the Adriatic Sea (Bonaduce et al., 1976) and consequently could not be regarded as a tropical species. Nonetheless, due to its Late Miocene distribution, the hypothesis of a shift of climatic preferences during the Pliocene-Pleistocene should be considered. Alternatively, we could not exclude that the morphological variability of *A. hystrix* hides two or more cryptospecies with different ecological propensities.

9. Conclusions

The results of the present study provided evidence for the presence of six Late Miocene palaeoecoregions in the Proto-Mediterranean-Atlantic Region. Five of these palaeobiogegraphic units corresponded to the South European Atlantic Shelf, Saharan Upwelling, Adriatic Sea, Western Mediterranean and Alboran Sea ecoregions defined by Spalding et al. (2007); the sixth palaeoecoregion, herein proposed as "Late Miocene Southeastern Mediterranean Palaeoecoregion", included the

Aegean Sea, Levantine Sea, Tunisian Plateau/Gulf of Sidra and Ionian Sea ecoregions (Spalding et al., 2007). These palaeobiogeographic units were recognised using the distribution data of a selected number of ostracod species identified in the Messinian assemblages from the Atlantic section of Oued El Kell, in northwestern Marocco. In comparison with palaeobiogeographic reconstructions based on molluscan assemblages, ostracod species allowed a more detailed zonation, and the MEWAP appeared as a puzzle of tropical-subtropical palaeoecoregions rather than a single, tropical "biogeographic entity". The Late Miocene palaebiogeography of the shelf areas of the Proto-Mediterranean-Atlantic Region was under the influence of tropical, subtropical and temperate sea surface temperatures, and under the effect of the more or less wide connections between the Atlantic Ocean and the Proto-Mediterranean Basin, and their biota. We believe that investigations based on fossil ostracod assemblages from biostratigraphically well defined sedimentary sequences, and performed paying special attention to distribution data and taxonomic issues at the species level, could greatly improve our knowledge of the complex palaeobiogeographic evolution of the Mediterranean-Atlantic area during the Cenozoic.

CRediT authorship contribution statement

Giuseppe Aiello: Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Roberta Parisi:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Roberto Barbieri:** Investigation, Data curation, Resources. **Diana Barra:** Writing – review & editing, Supervision, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A

List of species
▲ species previously reported from Upper Miocene deposits of the Mediterranean-Atlantic Region, used for statistical analyses
■ species not previously reported from Upper Miocene deposits of the Mediterranean-Atlantic Region
● probably undescribed species
✱ non-marine species
Acanthocythereis hystrix (Reuss, 1850) ▲
Aglaiocypris sp. ●
Argilloecia pera Ciampo, 1986 ▲
Aurila anterocostata Harrison et al., 2000 ▲
Aurila convexa (Baird, 1850) *s.l.* ■
Aurila impressa Ruggieri, 1977 ▲
Aurila semilunata (Seguenza, 1880) ▲
Aurila aff. *prasina* Barbeito-Gonzalez, 1971 ●
Bairdoppilata conformis (Terquem, 1878) ▲
Basslerites sp. ●
Bosquetina carinella (Reuss, 1850) ▲
Buntonia aff. *obesa* Ciampo, 1986 ▲
Buntonia robusta Ruggieri, 1954 ■
Callistocythere crispata (Brady, 1868) ▲
Callistocythere flavidofusca (Ruggieri, 1950) ■
Callistocythere producta Aruta, 1983 ▲
Callistocythere tetradactyla Ciampo, 1984 ▲
Callistocythere aff. *badia* (Norman, 1862) ●
Callistocythere aff. *montana* Doruk, 1980 ●
Callistocythere aff. *rastrifera* (Ruggieri, 1953) ●
Callistocythere aff. *vidua* Ciampo, 1986 ●
Callistocythere sp. 2 ●
Callistocythere sp. C ●
Carinocythereis whitei (Baird, 1850) ▲
Carinovalva aquila (Ruggieri, 1972) ▲
Carinovalva testudo (Namias, 1900) ▲
Caudites calceolatus (Costa, 1853) ▲
Chrysocythere cataphracta Ruggieri, 1962 ▲
Cimbaurila vitrocincta (Ruggieri, 1950) ▲
Cistacythereis caelatura Uliczny, 1969 ▲
Cistacythereis emaciata (Brady, 1867) ▲
Cluthia aff. *keiji* Neale and Howe, 1975 ●

Cyamocytheridea aff. *dertonensis* Ruggieri, 1958 ●
Cyprideis ? *torosa* (Jones, 1850) ✱
Cyprideis sp. 1 ✱
Cytherella inaequalis Moyes, 1965 ▲
Cytherella scutulum Ruggieri, 1976 ▲
Cytherella sp. Carbonnel and Courme-Raoult, 1997 ●
Cytheretta aff. *semipunctata* (Bornemann, 1855) ●
Cytheridea acuminata Bosquet, 1852 ▲
Cytheromorpha aff. *nana* Bonaduce et al., 1976 ●
Cytheropteron latum Müller, 1894 ▲
Cytheropteron monoceros Bonaduce et al., 1976 ■
Cytheropteron ruggierii Pucci, 1956 ▲
Cytheropteron sulcatum Bonaduce et al., 1976 ■
Cytheropteron vespertilio (Reuss, 1850) ▲
Cytheropteron aff. *bifidum* Colalongo and Pasini, 1980 ●
Darwinula sp. ✱
Eucypris sp. 1 ●
Eucythere aff. *curta* Ruggieri, 1975 ●
Eucytherura mistrettai Sissingh, 1972a, 1972b ▲
Eucytherura protracta Ruggieri, 1962 ▲
Eucytherura aff. *lamina* Ciampo, 1986 ●
Eucytherura aff. *poliphylla* Ruggieri, 1962 ●
Flexus tenuicarinatus (Capeder, 1902) ▲
Graptocythere polyptycha Reuss, 1850 ▲
Grinioneis aff. *haidingeri* Reuss, 1850 ●
Heliocythere aff. *vejhonensis* (Prochazka, 1893) ●
Hemicytherura defiorei Ruggieri, 1953 ▲
Hemicytherura videns (Müller, 1894) ▲
Henryhowella asperrima (Reuss, 1850) ▲
Heterocythereis aff. *albomaculata* (Baird, 1838) ✱
Heterocypris sp. ✱
Ilyocypris gibba (Ramdohr, 1808) ✱
Ionicythere parva (Seguenza, 1880) ▲
Kangarina abyssicola (Müller, 1894) ▲
Krithe oertlii Dieci and Russo, 1967 ▲
Leptocythere foveolata Moyes, 1965 ▲
Leptocythere aff. *multipunctata* (Seguenza, 1883) ●
Loculicytheretta sp. ●
Loxoconcha ? *punctatella* (Reuss, 1850) ●
Loxoconcha reticulopunctata Ciampo, 1986 ▲
Loxoconcha aff. *aspidis* Bonaduce et al., 1992 ●
Loxoconcha aff. *maghrebensis* Carbonnel and Courme-Raoult, 1997 ●
Loxoconcha aff. *rhomboidea* (Fischer, 1855) ●
Microcytherura aff. *dianae* Aiello and Szczechura, 2004 ●
Microcytherura aff. *nigrescens* Müller, 1894 ●
Microcytherura sp. 1 ●
Microxestoleberis aff. *xenomys* (Barbeito-Gonzalez, 1971) ●
Monoceratina oblita Bonaduce et al., 1976 ▲
Mutilus labiatus Moyes, 1965 ▲
Neocytherideis aff. *cribrata* Ciampo, 1986 ●
Occultocythereis ? *scipionis* Bonaduce et al., 1992 ●
Olimfalunia plicatula (Reuss, 1850) ▲
Paijenborchella solitaria Ruggieri, 1962 ▲
Palmoconcha dertobrevis (Ruggieri, 1967) ▲
Palmoconcha extendata (Bassiouni, 1962) ▲
Palmoconcha sp. 1●
Paracypris sp. Carbonnel and Courme-Raoult, 1997 ▲
Paracytheridea triquetra (Reuss, 1850) ▲
Paracytheromorpha aff. *rimafossa* Maybury and Whatley, 1980 ●
Paradoxostoma aff. *acuminatum* Müller, 1894 ●
Paradoxostoma sp. ●
Phlyctenophora aff. *affinis* (Schneider, 1953) ●
Phlyctocythere ? *pellucida* (Müller, 1894) ●
Pontocypris pallida (Müller, 1894) ■
Pontocypris ? *frequens* (Müller, 1894) ●
Pontocypris aff. *serrata* (Müller, 1894) ●

Pontocythere turbida (Müller, 1894) ▲
Potamocypris sp. ✱
Procytherideis aff. *complicata* (Ruggieri, 1953) ●
Procytherideis aff. *cubspiralis* (Brady et al., 1874) ●
Propontocypris ? *succinea* (Müller, 1894) ●
Propontocypris aff. *declivis* (Müller, 1894) ●
Pseudopsammocythere aff. *reniformis* (Brady, 1868) ●
Pterygocythereis coronata (Roemer, 1838) ▲
Pterygocythereis jonesii (Baird, 1850) ▲
Pulaviella geometra (Ruggieri, 1962) ▲
Rectobuntonia aff. *miranda* Bonaduce et al., 1976 ●
Rectobuntonia posteropunctata (Moyes, 1965) ▲
Ruggieria aff. *monastirensis* Bonaduce et al., 1992 ●
Ruggieria tetraptera (Seguenza, 1880) ▲
Sagmatocythere grateloupiana (Bosquet, 1852) ▲
Sagmatocythere napoliana (Puri, 1963) ▲
Sagmatocythere tenuis (Ciampo, 1980) ▲
Sagmatocythere versicolor (Müller, 1894) ▲
Semicytherura alifera Ruggieri, 1959 ■
Semicytherura aviculaecaput Aiello and Szczechura, 2004 ■
Semicytherura cornubiensis Maybury, 1985 *nomen nudum* ▲
Semicytherura foeda Ciampo, 1986 ▲
Semicytherura furcilla Aiello and Szczechura, 2004 ▲
Semicytherura microwallacei Maybury, 1985 *nomen nudum* ▲
Semicytherura ? *paradoxa* (Müller, 1894) ●
Semicytherura ? *superba* Ciampo, 1986 ●
Semicytherura aff. *acuminata* (Müller, 1894) ●
Semicytherura aff. *acuta* (Müller, 1894) ●
Semicytherura aff. *angulata* (Brady, 1868) ●
Semicytherura aff. *dispar* (Müller, 1894) ●
Semicytherura aff. *duracina* Witte, 1993 ●
Semicytherura aff. *intorta* (Terquem, 1878) ●
Semicytherura aff. *nigrescens* (Baird, 1838) ●
Semicytherura aff. *omorfa* (Barbeito-Gonzalez, 1971) ●
Semicytherura aff. *rara* (Müller, 1894) ●
Semicytherura aff. *turbulenta* Ciampo, 1986 ●
Semicytherura sp. ●
Senesia triangularis (Oertli, 1956) ▲
Syrtica aff. t*orpida* Bonaduce et al., 1992 ●
Urocythereis sp. ●
Xestoleberis prognata Bonaduce and Danielopol, 1988 ▲
Xestoleberis aff. *decipiens* Müller, 1894 ●
Xestoleberis aff. *dispar* Müller, 1894 ●
Xestoleberis aff. *intumescens* Müller, 1894 ●
Xestoleberis aff. *piriformis obliqua* Terquem, 1878 ●
Xestoleberis aff. *plana* Müller, 1894 ●

Appendix B

Reports of the studied species, under various generic and specific names during the Late Miocene. Only figured species have been considered.

species	references	area	ecoregion
Acanthocythereis hystrix (Reuss, 1850)	González-Regalado and Ruiz, 1990 (as *A.* aff. *hystrix*); Ruiz and Gonzalez-Regalado, 1996; Romero et al., 2021	Huelva, Spain	27
	Kili, 1993	Rifian Corridor, Morocco	28
	Avşar et al., 2006; Darbaş and Nazik, 2010	Southern Turkey	32
	Bonaduce et al., 1992	Gulf of Gabès, Tunisia	33
	Gammudi, 1990; Gammudi and Keen, 1993	Sirt Basin, Libya	33
	van Hinte et al., 1980	Pelagian Platform, Lybia	33
	Ciampo, 1980 (as *Acanthocythereis* sp.)	Southern Sicily, Italy	34
	Ruggieri Ruggieri, 1963 (as *Trachyleberis hystrix*)	Ionian Calabria, Italy	34
	Aruta, 1983	Northern Sicily, Italy	35
	Bonaduce and Russo, 1985	Sardinia, Italy	35
	Carbonnel and Courme-Raoult, 1997 (as *Trachyleberis hystrix*)	Sidi ali ben Toumi, Algeria	35

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species	references	area	ecoregion
	Ruggieri, 1962 (as *Trachyleberis hystrix*)	Central Sicily, Italy	35
	Sissingh, 1972b	Carnot, Algeria	35
	Babinot and Boukli-Hacene, 1998	Tessala, Algeria	36
	Bouab, 1992	North-eastern Morocco	36
Argilloecia pera Ciampo, 1986	Ciampo, 1986	Northern Italy	30
	Dall'Antonia, 2003 (as *A. tenuis*)	Tremiti, Italy	30
Aurila anterocostata Harrison et al., 2000	Harrison et al., 2000	Northwestern France	27
Aurila impressa Ruggieri, 1977	Maybury, 1985 (as *A. convexa*)	Northwestern France	27
	Ruggieri, 1977 (as *A. convexa impressa*)	Northern Italy	30
	Bonaduce et al., 1992	Gulf of Gabès, Tunisia	33
	Dall'Antonia and Bossio, 2001	Lampedusa, Italy	33
	Aruta, 1983 (as *A. convexa impressa*)	Northern Sicily, Italy	35
	Bonaduce and Russo, 1985	Sardinia, Italy	35
	Ruggieri, 1962 (as *Mutilus punctatus*)	Central Sicily, Italy	35
	Bouab, 1992 (as *A.* cf. *punctata*)	Northeastern Morocco	36
Aurila semilunata (Seguenza, 1880)	Ruggieri Ruggieri, 1963	Ionian Calabria, Italy	34
Bairdoppilata conformis (Terquem, 1878)	Kili, 1993 (as *B. rhomboidalis*)	Rifian Corridor, Morocco	28
	van Hinte et al., 1980 (as *B.* sp. 2)	Pelagian Platform, Lybia	33
	Babinot and Boukli-Hacene, 1998 (as *Neonesidea* sp. aff. *corpulenta*)	Tessala, Algeria	36
Bosquetina carinella (Reuss, 1850)	Ruiz and Gonzalez-Regalado, 1996	Huelva, Spain	27
Buntonia aff. *obesa* Ciampo, 1986	Ruiz and Gonzalez-Regalado, 1996 (as *B. textilis*)	Huelva, Spain	27
Callistocythere crispata (Brady, 1868)	Moyes, 1965 (as *C. rugosa*)	Aquitaine, France	27
	Nachite et al., 2006 (as *C.* sp. 2)	Northwestern Morocco	28
	Ciampo, 1986 (as *C. aurita*); Ruggieri, 1967 (as *C. pallida*)	Northern Italy	30
	Babinot, 2002 (as *C.* sp. 3)	Southern Turkey	32
	Bonaduce et al., 1992 (as *C.* aff. *macilenta)*	Gulf of Gabès, Tunisia	33
	Dall'Antonia and Bossio, 2001 (as *C. pallida*)	Pelagian Archipelago, Italy	33
	Aruta, 1983 (as *C. pallida*)	Northern Sicily, Italy	35
	Carbonnel and Courme-Raoult, 1997 (as *C. aspera*)	Sidi ali ben Toumi, Algeria	35
	Ruggieri, 1962 (as *C. pallida, C. rotundata* and *C. ennensis*)	Central Sicily, Italy	35
	Bouab, 1992 (as *C. littoralis*)	Northeastern Morocco	36
Callistocythere producta Aruta, 1983	Ciampo, 1986	Northern Italy	30
	Aruta, 1983	Northern Sicily, Italy	35
Callistocythere tetradactyla Ciampo, 1984	Nascimento, 1988 (as *C. oertlii*)	Bacia do Tejo, Portugal	27
	Kili, 1993 (as *C. oertlii*)	Rifian Corridor, Morocco	28
	Ciampo, 1984	Northern Italy	30
	El-Waer, 1988 (as *C.* sp.)	Northwestern Lybia	33
	van Hinte et al., 1980 (as *C.* sp. 2)	Pelagian Platform, Lybia	33
	Bouab, 1992 (as *C. oertlii*)	Northeastern Morocco	36
Carinocythereis whitei (Baird, 1850)	Maybury, 1985 (as *C.* sp. cf. *C. carinata*)	Northwestern France	27
	Ruiz and Gonzalez-Regalado, 1996	Huelva, Spain	27
	Dieci and Russo, 1965a, 1965b (as *C. carinata*)	Northern Italy	30
	Sissingh, 1972a (as *C. carinata*)	Crete, Greece	31
	Faranda et al., 2013 (as *Occlusacythereis occlusa*)	Southern Turkey	32
	Carbonnel, 1969 (as *C. carinata*)	Rhône Valley, France	35
	Ruggieri, 1962 (as *C. carinata*)	Central Sicily, Italy	35
	Babinot and Boukli-Hacene, 1998	Tessala, Algeria	36
	Bouab, 1992 (as *C. carinata*)	North-eastern Morocco	36
Carinovalva aquila (Ruggieri, 1972)	Sissingh, 1972a (as *Incongruellina keiji*)	Crete, Greece	31
Carinovalva testudo (Namias, 1900)	Carbonel, 1985 (as *C. carinata*)	South-western France	27
	Keen, 2004 (as *C. carinata*)	Carmona, Spain	27
	Moyes, 1965 (as *Ruggieria carinata*)	Aquitaine, France	27
	Kili, 1993 (as *Incongruellina unicostulata)*	Rifian Corridor, Morocco	28
	El-Waer, 1988 (as *C. carinata*)	Northwestern Lybia	33
	Aruta, 1983	Northern Sicily, Italy	35
	Carbonnel and Courme-Raoult, 1997 (as *Dahomeya carinata*)	Rhône Valley, France	35
	Babinot and Boukli-Hacene, 1998 (as *C. marginata*)	Tessala, Algeria	36
Caudites calceolatus (Costa, 1853)	Russo, 1969 (as *C.* sp. 1); Miculan, 1992 (as *C.* cf. *mediterranensis)*	Northern Italy	30
	Babinot, 2002 (as *C. mediterranensis*); Donat, 2009 (as *C. orientalis*)	Southern Turkey	32
	El-Waer, 1991 (as *C.* sp.)	Northwestern Lybia	33
	Bouab, 1992	North-eastern Morocco	36
Chrysocythere cataphracta Ruggieri, 1962	Kili, 1993	Rifian Corridor, Morocco	28
	Doruk, 1973 (as *C. paradisus*)	Southern Turkey	32
	Bonaduce et al., 1992 (as *C. paradisus*)	Gulf of Gabès, Tunisia	33
	El-Waer, 1991	Northwestern Lybia	33
	Gammudi, 1990; Gammudi and Keen, 1993	Sirt Basin, Libya	33
	Aruta, 1983	Northern Sicily, Italy	35
	Ruggieri, 1962	Central Sicily, Italy	35
	Sissingh, 1972b	Carnot, Algeria	35
	Babinot and Boukli-Hacene, 1998	Tessala, Algeria	36
Cimbaurila vitrocincta (Ruggieri, 1950)	Ducasse and Cirac, 1981 (as *Mutilus venetiensis*)	Northwestern Morocco	28
	Bouab, 1992 (as *Mutilus venetiensis*)	North-eastern Morocco	36
Cistacythereis caelatura Uliczny, 1969	Kili, 1993 (as *C. cebrenidos*)	Rifian Corridor, Morocco	28
	Bouab, 1992 (as *C. cebrenidos*)	North-eastern Morocco	36

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species	references	area	ecoregion
Cistacythereis emaciata (Brady, 1867)	Kili, 1993 (as *Falunia* ? *rugosa*)	Rifian Corridor, Morocco	28
	Nachite and Bekkali, 2010 (as *Hiltermannicythere emaciata*)	North-western Morocco	28
	Faranda et al., 2008 (as *C. rubra*)	Crete	31
	Bonaduce et al., 1992 (as *Hiltermannicythere* sp. 1 aff. *emaciata)*	Gulf of Gabès, Tunisia	33
	El-Waer, 1991 (as *C. qabilatshurfahensis*)	Northwestern Lybia	33
	Mostafawi, 1990 (as *Hiltermannicythere* sp.)	Kythira, Greece	34
	Aruta, 1983 (as *Hiltermannicythere* aff. *H. rubra*)	Northern Sicily, Italy	35
	Bonaduce and Russo, 1985 (as *Hiltermannicythere* sp.)	Sardinia, Italy	35
	Carbonnel and Courme-Raoult, 1997 (as *Hiltermannicythere* sp.1 aff. *emaciata*)	Sidi ali ben Toumi, Algeria	35
	Sissingh, 1972b (as *Falunia ruida*)	Carnot, Algeria	35
	Babinot and Boukli-Hacene, 1998 (as *Hiltermannicythere* sp. aff. *rugosa*)	Tessala, Algeria	36
	Bouab, 1987 (as *Falunia* ? *rugosa*); Bouab, 1992 (as *C. rubra*)	North-eastern Morocco	36
Cytherella inaequalis Moyes, 1965	Moyes, 1965	Aquitaine, France	27
	Kili, 1993	Rifian Corridor, Morocco	28
	Sissingh, 1972a (as *C.* sp.); Faranda et al., 2008 (as *C.* gr. *vulgata*)	Crete	31
	Bonaduce et al., 1992 (as *C.* sp. 1 ex gr. *vulgata)*	Gulf of Gabès, Tunisia	33
	Bouab, 1992 (as *C. compressa*)	North-eastern Morocco	36
Cytherella scutulum Ruggieri, 1976	Ruiz and Gonzalez-Regalado, 1996 (as *C. circumpunctata*)	Huelva, Spain	27
	Aruta, 1983 (as *C. pulchella*)	Northern Sicily, Italy	35
	Bouab, 1992 (as *C. pulchella*)	North-eastern Morocco	36
Cytheridea acuminata Bosquet, 1852	Dieci and Russo, 1967	Northern Italy	30
	Sissingh, 1972a; Faranda et al., 2008	Crete	31
	Karakitsios et al., 2017	North Aegean, Greece	31
	Öğrünç and Nazik, 1998; Avşar et al., 2006; Şafak and Heybeli, 2008; Darbaş and Nazik, 2010; Şafak and Nurlu, 2018; Şafak, 2019	Southern Turkey	32
	Bonaduce et al., 1992 (as *C. arca)*	Gulf of Gabès, Tunisia	33
	Temani et al., 2020 (as *C. arca)*	Eastern Tunisia	33
	van Hinte et al., 1980	Pelagian Platform, Lybia	33
	Mostafawi, 1990	Kythira, Greece	34
	Aruta, 1983 (as *C. acuminata neapolitana*)	Northern Sicily, Italy	35
	Bonaduce and Russo, 1985 (as *C. josephinae*)	Sardinia, Italy	35
	Babinot and Boukli-Hacene, 1998 (as *C. arca*)	Tessala, Algeria	36
	Bouab, 1992	North-eastern Morocco	36
	Guernet et al., 1984	Oran, Algeria	36
Cytheropteron latum Müller, 1894	Maybury, 1985 (as *C. praenodosum*)	Northwestern France	27
	Ciampo, 1986 (as *C.* aff. *latum*)	Southern Sicily, Italy	34
	Aruta, 1983	Northern Sicily, Italy	35
	Bouab, 1992 (as *C. alatum*)	North-eastern Morocco	36
Cytheropteron ruggierii Pucci, 1956	Ciampo, 1986 (as *C.* aff. *rotundatum*)	Northern Italy	30
	Sissingh, 1972b (as *C.* sp.)	Carnot, Algeria	35
Cytheropteron vespertilio (Reuss, 1850)	Ruggieri, 1967	Northern Italy	30
Eucytherura mistrettai Sissingh, 1972a, 1972b	Sissingh, 1972b (as *E. ruggierii*)	Carnot, Algeria	35
Eucytherura protracta Ruggieri, 1962	Miculan, 1992	Northern Italy	30
	Ruggieri, 1962	Central Sicily, Italy	35
	Bouab, 1992 (as *E.* sp. 2)	North-eastern Morocco	36
Flexus tenuicarinatus (Capeder, 1902)	Maybury, 1985 (as *F.* aff. *triebeli*)	Northwestern France	27
	Moyes, 1965 (as *Eucytheretta* aff. *triebeli*)	Aquitaine, France	27
	Kili, 1993 (as *Cytheretta triebeli*)	Rifian Corridor, Morocco	28
	Dieci and Russo, 1965a, 1965b (as *F. triebeli*); Russo, 1969; Ruggieri, 1992	Northern Italy	30
	Ruggieri, 1962 (as *Eucytheretta* sp. aff. *E. triebeli*)	Central Sicily, Italy	35
	Carbonnel, 1969 (as *F. triebeli*)	Rhône Valley, France	35
	Bouab, 1992 (as *Cytheretta triebeli*)	North-eastern Morocco	36
Graptocythere polyptycha Reuss, 1850	Dieci and Russo, 1965a, 1965b (as *Hemicythere* (?) *polyptycha*); Ascoli, 1968 (as *Climacoidea* aff. *polyptycha*); Miculan, 1992 (as *G. hscripta*)	Northern Italy	30
	Bonaduce et al., 1992	Gulf of Gabès, Tunisia	33
	Carbonnel and Courme-Raoult, 1997 (as *G. hscripta*)	Northern Algeria	35
	Bouab, 1992 (as *Pachycaudites h-scripta*)	North-eastern Morocco	36
Hemicytherura defiorei Ruggieri, 1953	Dieci and Russo, 1965a, 1965b	Northern Italy	30
	Faranda et al., 2008	Crete	31
	Aruta, 1983	Northern Sicily, Italy	35
	Carbonnel, 1969	Rhône Valley, France	35
	Babinot and Boukli-Hacene, 1998	Tessala, Algeria	36
	Bouab, 1992	North-eastern Morocco	36
Hemicytherura videns (Müller, 1894)	Maybury, 1985 (as *H.* cf. *videns*)	Northwestern France	27
	Moyes, 1965	Aquitaine, France	27
	Nachite and Bekkali, 2010	North-western Morocco	28
	Ciampo, 1986; Miculan, 1992 (as *H.* sp. 1)	Northern Italy	30
Henryhowella asperrima (Reuss, 1850)	González-Regalado and Ruiz, 1990; Ruiz and Gonzalez-Regalado, 1996	Huelva, Spain	27
	Kili, 1993	Rifian Corridor, Morocco	28
	Nachite et al., 2006	Northwestern Morocco	28
	Bonaduce et al., 1992	Gulf of Gabès, Tunisia	33
	Carbonnel and Courme-Raoult, 1997	Sidi ali ben Toumi, Algeria	35

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species	references	area	ecoregion
	Aranki et al., 1992	El Castillo de la Duquesa, Spain	36
	Babinot and Boukli-Hacene, 1998	Tessala, Algeria	36
	Bouab, 1992	North-eastern Morocco	36
	Cita et al., 1980	Almanzora, Spain	36
Ionicythere parva (Seguenza, 1880)	Ciampo, 1986 (as *Cytheromorpha golnarae*)	Northern Italy	30
	Donat, 2009 (as *Callistocythere mediterranea*)	Southern Turkey	32
	Bonaduce et al., 1992 (as *I. punctatissima*)	Gulf of Gabès, Tunisia	33
	Aruta, 1983 (as *Cytheromorpha reticulata*)	Northern Sicily, Italy	35
Kangarina abyssicola (Müller, 1894)	Maybury, 1985	Northwestern France	27
	Dieci and Russo, 1965a, 1965b (as *K. abyssicola coarctata*)	Northern Italy	30
	Carbonnel, 1969 (as *K. abyssicola coarctata*)	Rhône Valley, France	35
	Ruggieri, 1962 (as *K. abyssicola coarctata*)	Central Sicily, Italy	35
	Bouab, 1992	North-eastern Morocco	36
Krithe oertlii Dieci and Russo, 1967	Kili, 1993 (as *K. citae*)	Rifian Corridor, Morocco	28
	Ciampo, 1986 (as *K. pernoides*); Dieci and Russo, 1967	Northern Italy	30
	Ciampo, 1980 (as *K.* sp. 1)	Southern Sicily, Italy	34
	Carbonnel and Courme-Raoult, 1997 (as *K. aquilonia*)	Sidi ali ben Toumi, Algeria	35
Leptocythere foveolata Moyes, 1965	Moyes, 1965	Aquitaine, France	27
	Maybury, 1985 (as L. *pliocenica*)	Northwestern France	27
	Bouab, 1992 (as *L.*? sp. 1*)*	North-eastern Morocco	36
Loxoconcha reticulopunctata Ciampo, 1986	Moyes, 1965 (as L. *punctatella*)	Aquitaine, France	27
	Ciampo, 1986	Northern Italy	30
Monoceratina oblita Bonaduce et al., 1976	Dall'Antonia, 2003	Tremiti, Italy	30
Mutilus labiatus Moyes, 1965	Moyes, 1965	Aquitaine, France	27
	Ducasse and Cirac, 1981 (as *M. retiformis*)	Northwestern Morocco	28
	Bouab, 1992 (as *M. retiformis*)	North-eastern Morocco	36
Olimfalunia plicatula (Reuss, 1850)	Moyes, 1965	Aquitaine, France	27
	Nascimento, 1988	Bacia do Tejo, Portugal	27
	Dieci and Russo, 1965a, 1965b (as *Falunia plicatula*)	Northern Italy	30
	Sissingh, 1972a (as *Falunia plicatula*); Faranda et al., 2008 (as *Celtia clatrata*)	Crete	31
	Bonaduce et al., 1992 (as *Capsacythere sicula)*	Gulf of Gabès, Tunisia	33
	Dall'Antonia and Bossio, 2001 (as *Capsacythere sicula)*	Lampedusa, Italy	33
	Carbonnel and Courme-Raoult, 1997 (as *Falunia plicatula*)	Sidi ali ben Toumi, Algeria	35
	Babinot and Boukli-Hacene, 1998 (as *Capsacythere* sp. aff. *sicula*)	Tessala, Algeria	36
Paijenborchella solitaria Ruggieri, 1962	Sissingh, 1972a	Crete	31
	Ruggieri, 1962	Central Sicily, Italy	35
Palmoconcha dertobrevis (Ruggieri, 1967)	Maybury, 1985 (as *P. subrugosa*)	Northwestern France	27
	Ruggieri, 1967 (as *Loxoconcha dertobrevis*)	Northern Italy	30
	Aruta, 1983 (as *Loxoconcha agilis*)	Northern Sicily, Italy	35
	Sissingh, 1972b (as *Loxoconcha dertobrevis*)	Carnot, Algeria	35
Palmoconcha extendata (Bassiouni, 1962)	Maybury, 1985 (as *P.* sp. 1)	Northwestern France	27
Paracypris sp. Carbonnel and Courme-Raoult, 1997	Carbonnel and Courme-Raoult, 1997	Sidi ali ben Toumi, Algeria	35
Paracytheridea triquetra (Reuss, 1850)	Maybury, 1985 (as *P. fossarotunda*)	Northwestern France	27
	Moyes, 1965	Aquitaine, France	27
	Ruggieri, 1977 (as *P.* sp. cfr. *triquetra*); Miculan, 1992 (as *P.* sp. 1)	Northern Italy	30
	Sissingh, 1972a (as *P.* sp.)	Crete	31
	Babinot, 2002 (as *P.* aff. *triquetra)*	Southern Turkey	32
	Aruta, 1983 (as *P.* sp.)	Northern Sicily, Italy	35
	Ruggieri, 1962 (as *P. bovettensis*)	Central Sicily, Italy	35
	Babinot and Boukli-Hacene, 1998	Tessala, Algeria	36
Pontocythere turbida (Müller, 1894)	Maybury, 1985 (as *P.* cf. *turbida*)	Northwestern France	27
	Donat, 2009 (as *P. elongata*)	Southern Turkey	32
	Babinot and Boukli-Hacene, 1998	Tessala, Algeria	36
Pterygocythereis coronata (Roemer, 1838)	Maybury, 1985 (as *P. ceratoptera*)	Northwestern France	27
	Sissingh, 1972a (as *P. ceratoptera*)	Crete	31
Pterygocythereis jonesii (Baird, 1850)	Nascimento, 1988	Bacia do Tejo, Portugal	27
	Ruiz and Gonzalez-Regalado, 1996	Huelva, Spain	27
	Guernet, 1990 (as *P.* cf. *jonesii*)	North-western Morocco	28
	Aruta, 1983	Northern Sicily, Italy	35
Pulaviella geometra (Ruggieri, 1962)	Ruggieri, 1962 (as *Xestoleberis geometra*)	Central Sicily, Italy	35
Rectobuntonia posteropunctata (Moyes, 1965)	Moyes, 1965 (as *Buntonia posteropunctata*)	Aquitaine, France	27
Ruggieria tetraptera (Seguenza, 1880)	Moyes, 1965	Aquitaine, France	27
	Ruiz and Gonzalez-Regalado, 1996	Huelva, Spain	27
	Kili, 1993	Rifian Corridor, Morocco	28
	Nachite and Bekkali, 2010	North-western Morocco	28
	Dieci and Russo, 1965a, 1965b; Ruggieri, 1967	Northern Italy	30
	Donat, 2009; Şafak, 2019	Southern Turkey	32
	Bonaduce et al., 1992	Gulf of Gabès, Tunisia	33
	El-Waer, 1991	Northwestern Lybia	33
	Gammudi, 1990; Gammudi and Keen, 1993	Sirt Basin, Libya	33
	Ruggieri Ruggieri, 1963	Ionian Calabria, Italy	34

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species	references	area	ecoregion
	Aruta, 1983	Northern Sicily, Italy	35
	Ruggieri, 1962	Central Sicily, Italy	35
	Sissingh, 1972b	Carnot, Algeria	35
	Babinot and Boukli-Hacene, 1998 (as *Ruggieria bicarinata*)	Tessala, Algeria	36
Sagmatocythere grateloupiana (Bosquet, 1852)	Maybury, 1985 (as *Kuiperiana grateloupiana*); Maybury, 1990 (as *Loxocorniculum grateloupianum*)	Northwestern France	27
	Ruiz et al., 1999 (as *S. napoliana*)	Huelva, Spain	27
	Nascimento, 1988 (as *Loxoconcha* (*Sagmatocythere*) *grateloupiana*)	Bacia do Tejo, Portugal	27
Sagmatocythere napoliana (Puri, 1963)	Ciampo, 1984 (as *Loxoconcha crispa*)	Northern Italy	30
	Bouab, 1992 (as *Loxoconcha mediterranea*)	North-eastern Morocco	36
Sagmatocythere tenuis (Ciampo, 1980)	Maybury and Whatley, 1984 (as *S. pseudomultifora*); Maybury, 1985 (as *S. pseudomultifora*)	Northwestern France	27
	Ciampo, 1980 (as *Loxoconcha moncharmonti tenuis*)	Southern Sicily, Italy	34
	Mostafawi, 1990	Kythira, Greece	34
	Aruta, 1983 (as *Loxoconcha moncharmonti tenuis*)	Northern Sicily, Italy	35
Sagmatocythere versicolor (Müller, 1894)	Maybury, 1985 (as *Kuiperiana* aff. *subovata*)	Northwestern France	27
	Nachite and Bekkali, 2010 (as *S. multiflora*)	North-western Morocco	28
	Ciampo, 1986 (as *S. oblonga*)	Northern Italy	30
	Ciampo, 1986 (as *S. oblonga*)	Ionian Calabria, Italy	34
	Aruta, 1983 (as *Loxoconcha variesculpta*)	Northern Sicily, Italy	35
	Ruggieri, 1962 (as *Loxoconcha variesculpta*)	Central Sicily, Italy	35
	Sissingh, 1972b (as *Loxoconcha variesculpta*)	Carnot, Algeria	35
	Bouab, 1992 (as *Loxoconcha carinata*)	North-eastern Morocco	36
	Cita et al., 1980 (as *Loxoconcha variesculpta*)	Almanzora, Spain	36
Semicytherura cornubiensis Maybury, 1985 *nomen nudum*	Maybury, 1985	Northwestern France	27
Semicytherura foeda Ciampo, 1986	Ciampo, 1986	Ionian Calabria, Italy	34
Semicytherura furcilla Aiello and Szczechura, 2004	Maybury, 1985 (as *S.* sp. 1 Yassini, 1979)	Northwestern France	27
	Bonaduce et al., 1992 (as *Cytheropteron rarum*)	Gulf of Gabès, Tunisia	33
Semicytherura microwallacei Maybury, 1985 *nomen nudum*	Maybury, 1985	Northwestern France	27
	Ciampo, 1980 (as *S.* sp. 1)	Southern Sicily, Italy	34
Senesia triangularis (Oertli, 1956)	Maybury, 1985 (as *Aurila*? sp. 10)	Northwestern France	27
	Kili, 1993 (as *Hemicythere triangularis*)	Rifian Corridor, Morocco	28
	Carbonnel, 1969 (as *Hemicythere triangularis*); Carbonnel and Courme-Raoult, 1997	Rhône Valley, France	35
	Guernet et al., 1984 (as *S.* aff. *triangularis*)	Oran, Algeria	36
Xestoleberis prognata Bonaduce and Danielopol, 1988	Nascimento, 1988 (as *X. glabrescens*)	Bacia do Tejo, Portugal	27
	Ruiz and Gonzalez-Regalado, 1996	Huelva, Spain	27
	Kili, 1993 (as *X. glabrescens*)	Rifian Corridor, Morocco	28
	Öğrünç and Nazik, 1998 (as *X. glabrescens*); Donat, 2009 (as *X. reymenti*)	Southern Turkey	32
	Mostafawi, 1990 (as *X.* sp.)	Kythira, Greece	34
	Aruta, 1983 (as *X.* sp. 16)	Northern Sicily, Italy	35

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