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Integrating Aegean Last Interglacial faunas into the Mediterranean palaeobiogeographic framework: New evidence from Karpathos (Greece)

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ABSTRACT: The Last Interglacial (LIG) or Marine Isotope Stage (MIS) 5e, spanning 129 to 116 kyrs ago, is recognised as one of the warmest periods in the Quaternary, with global sea surface temperatures (SSTs) 1°C–2°C higher than today, sea levels 5–10 m above the current level and biogeographical range expansion of specific tropical species into the Mediterranean. We present new stratigraphic, palaeoecological and palaeobiogeographic data from the uplifted marine terraces of Kastellos Bay, Karpathos (Aegean Sea, Greece). Detailed sedimentological analysis reveals that the so-called "Tyrrhenian" terrace comprises multiple depositional cycles, with only the uppermost bed attributable to MIS 5e. From this unit, we document 64 molluscan taxa, including members of the "Senegalese fauna" and several species not previously reported from Greek LIG deposits. Ecological affinities of the assemblage indicate a heterogeneous infralittoral environment with mean annual SSTs of around 20°C, consistent with other Mediterranean records. By revising and integrating Greek species lists into a Mediterranean–Atlantic framework, we demonstrate that the Aegean Ecoregion forms a key link between eastern and western Mediterranean faunas and shares affinities with the Saharan Upwelling region. These results refine the palaeobiogeographic interpretation of tropical species dispersal into the Mediterranean and highlight the need for robust chronological calibrations of Greek LIG sites to improve reconstructions of faunal dynamics under warm climate scenarios.

KEYWORDS: marine terrace; MIS 5e; molluscs; palaeobiogeography; palaeoecology; Pleistocene

Introduction

The Last Interglacial (LIG) or Marine Isotope Stage (MIS) 5e (129–116 kyrs; Shackleton et al., 2020), also known as the Tyrrhenian in the Mediterranean (Gignoux, 1913), is regarded as one of the warmest interglacial periods in the Quaternary. During MIS 5e, global mean sea surface temperatures (SSTs) were 1°C to 2°C higher than present-day values (Hoffman et al., 2017; Shackleton et al., 2020), and because of an important ice-cap retreat, the sea level was approximately +5 to +10 m higher than today (Antonioli, 2012; Dutton and Lambeck, 2012; Sanchez Goni et al., 2012; Dutton et al., 2015). The LIG is often viewed as a good analogue for understanding the current climate change and faunal alternations driven by global warming (Overpeck et al., 2006; Rohling et al., 2008; Siddall and Valdes, 2011; Antonioli et al., 2017; Fischer et al., 2018; Albano et al., 2024; Antoine et al., 2024).

As temperature is one of the main factors driving marine species distributions (e.g., Raffi et al., 1985; Hoegh-Guldberg and Bruno, 2010; Doney et al., 2012), studying fossilised marine molluscan faunas can provide insights into the temperature ranges of specific localities (e.g., Melo et al., 2023; Santagati et al., 2024). Additionally, fossil data accumulated from a peculiar region hint at ecosystem changes that might happen in the near future due to global warming (Scarponi et al., 2022; Albano et al., 2024; Antoine et al., 2024).

In the eastern Atlantic, there are two main hypothesised routes of dispersal for the restricted number of tropical species that expanded their latitudinal ranges to higher latitudes in the Northern Hemisphere during the final phase of glacial Termination 2 and the early stages of MIS 5e, that is, the inception of the Last Interglacial period (Ávila, 2005; Ávila et al., 2009, 2015, 2019; Muhs et al., 2014; Meco et al., 2022; Melo et al., 2023).

The first hypothesis proposes an archipelagic route, either in a continuous stepping-stone fashion or in a "saltational mode" skipping some archipelagos, with species originating in the Cabo Verde Archipelago and migrating northward along the

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Macaronesian archipelagos: from Cabo Verde to the Canaries, then the Selvagens, then Madeira. Some species may have entered the Mediterranean, while others reached and colonised the Azores (Meco, 1977; Gerber et al., 1989; García-Talavera, 1990, 1999; Callapez and Soares, 2000; García-Talavera and Sánchez-Pinto, 2001; Meco et al., 2002; Ávila et al., 2009, 2015; Cabero, 2009; Martín-González et al., 2016, 2019; Melo et al., 2022a, 2022b).

The second hypothesis involves dispersal along the African coastline, originating in the tropical/Senegalese area and progressing northward via creeping or larval dispersal during periods of reduced upwelling, eventually entering and colonising the Mediterranean region (e.g., see the extreme scenario of Albano et al., 2024).

In the Mediterranean region, the LIG or MIS 5e is frequently identified by marine terrace deposits found along the coastlines (e.g., Anapliotis, 1966; Ferranti et al., 2006; Roberts et al., 2009). These deposits contain fossil representatives of the so-called "Senegalese fauna" (Gignoux, 1913), which includes warm-water molluscan species such as *Thetystrombus latus* (Gmelin, 1791), and serves as a palaeoclimatic indicator of the widespread warm and tropical conditions that prevailed at that time in the Mediterranean (e.g., Zazo, 1999; Muhs et al., 2015; Bulian et al., 2025).

Thetystrombus latus (Gmelin, 1791), along with other warm-water mollusc species, disappeared from the Mediterranean after the LIG as conditions became unfavourable for their survival. These widespread cycles of distributional expansion, followed by retraction of marine biogeographical units (Hall, 1964; Petuch, 2004), have been documented by palaeontologists at multiple sites, contributing to biogeographical models (see the literature in Melo et al., 2023). Such findings are essential for identifying similarities and differences between Pleistocene and modern Ecoregions.

The concept of Marine Ecoregions was first introduced by Spalding et al. (2007) to classify shallow marine regions with depths between 0 and 200 m. These Ecoregions are defined as areas with "relatively homogeneous species composition, clearly distinct from adjacent systems" (Spalding et al., 2007) (these Ecoregions are shown in Fig. 6 for reference). Today, the Mediterranean Sea is divided into seven marine Ecoregions, each characterised by distinct oceanographic and topographic features, as well as relatively homogeneous species composition (Tsirintanis et al., 2022). A diversity gradient is observed from S to N and from SE to NW, with the relatively species-poor Levantine Sea contrasting with the more species-rich Western Mediterranean (Coll et al., 2012; Agiadi et al., 2024). Marine Ecoregions are further grouped into Provinces (Hall, 1964; Raffi et al., 1985; Spalding et al., 2007; Freitas et al., 2019), which broadly reflect the taxonomic composition in these areas.

According to Spalding et al. (2007), with corrections and updates by Freitas et al. (2019), the Mediterranean Ecoregions, together with the Macaronesian archipelagos, are included in the Lusitanian biogeographic Province, which extends from the Brittany Peninsula southwards to Cap Blanc on the Nouadhibou Peninsula. Within Macaronesia, Freitas et al. (2019) recognised two distinct ecoregions: the Azores Ecoregion and the Webbnesia Ecoregion (comprising Madeira, Selvagens and the Canary Islands). In contrast, the colder Celtic Seas, North Sea and Baltic Sea Ecoregions are included in the Northern European Seas biogeographic Province (Spalding et al., 2007). The warm and tropical Cabo Verde Archipelago constitutes a distinct biogeographic subprovince (sensu Freitas et al., 2019), which, together with the Sahelian Upwelling ecoregion, belongs to the West African Transition biogeographic Province. This province marks the transition to the Gulf of Guinea biogeographic Province further south, at the border of Senegal and Guinea-Bissau. Therefore, while *Thetystrombus latus* and the rest of the "Senegalese fauna" no longer occur in the Mediterranean, they are still found in the West African Transition biogeographic Province, across both of its subprovinces (e.g., Amorosi et al., 2014; Muhs et al., 2015), thus serving as palaeobiogeographic markers.

While recent studies, such as the global data set integration by Melo et al. (2023), have broadened our understanding of biogeographical shifts during MIS 5e in the Atlantic Ocean, the eastern Mediterranean remains underrepresented, particularly the Aegean Sea. This gap is significant, as data from the Aegean region could offer insights into the historical distribution and eventual disappearance of tropical species. Despite numerous studies in Greece over the past century that identified Tyrrhenian deposits containing the "Senegalese fauna" (e.g., Mitzopoulos, 1933; Anapliotis and Georgiadou-Dikeoulia, 1967), much of this work has been overlooked due to language barriers and outdated nomenclature. Incorporating these overlooked data sets is essential for filling knowledge gaps, particularly for understanding species' geographic range expansions and contractions in the Mediterranean (Ávila et al., 2008), which is crucial for predicting how ongoing climate change may affect future marine biodiversity.

In this work, we investigate the faunal composition of a Tyrrhenian terrace (Anapliotis, 1961, 1966; Barrier, 1979) in the Aegean Sea in Karpathos, focusing on its ecological and palaeobiogeographical affinities. On a broader scale, we seek to understand the biogeographical dynamics of the eastern Mediterranean during the LIG, when tropical species could only migrate through the Strait of Gibraltar, and the region showed a well-established biodiversity gradient. Additionally, we aim to integrate Greek datasets into the global Pleistocene map of LIG localities, ensuring that the species are verified and updated with current taxonomic standards.

Geological background

The island of Karpathos is located in the forearc of the eastern Hellenic subduction zone, where the African plate obliquely moves to the northeast below the Aegean–Anatolian plate (Fig. 1) (e.g., Christodoulou, 1968; Aubouin et al., 1976; Barrier, Müller, et al., 1979; Jolivet et al., 2013; Veliz-Borel et al., 2024). It is composed of a stack of allochthonous, carbonate, ophiolitic and turbiditic, Triassic to Miocene units of the Hellenic Chain, unconformably sealed by localised Upper Miocene to Pleistocene deposits (e.g., Christodoulou, 1968; Davidson-Monett, 1974; Aubouin et al., 1976; Barrier, Müller, et al., 1979; Bonneau, 1984; Fytrolakis, 1989; Kokkalas and Doutsos, 2004; van Hinsbergen et al., 2005; Jolivet et al., 2013; Pantopoulos and Zelilidis, 2014; Moissette et al., 2017; Cordey and Quillévéré, 2019). The island underwent severe vertical motions, which are testified by uplifted marine abrasion surfaces up to 400 m asl (above present sea level), uplifted relicts of fossiliferous marine terraces that are supposed to have deposited during the Late Pleistocene and Holocene terrestrial deposits. These deposits rest unconformably above both the basement and the Neogene to Pleistocene deposits (e.g., Barrier, Müller, et al., 1979; Veliz-Borel et al., 2024). Based on the presence of *Thetystrombus latus* (Gmelin, 1791) [also known from the old literature as *Strombus bubonius* Lamarck, 1822], the Upper Pleistocene marine deposits of Karpathos were considered as Tyrrhenian in age (MIS 5e) (Anapliotis, 1961, 1966; Barrier, 1979). Such presumably Tyrrhenian marine terraces are most regularly exposed and show the most complete and fossiliferous lithological successions in the south-east of the island in the Kastellos Bay area (Fig. 1). Veliz-Borel et al. (2024) studied

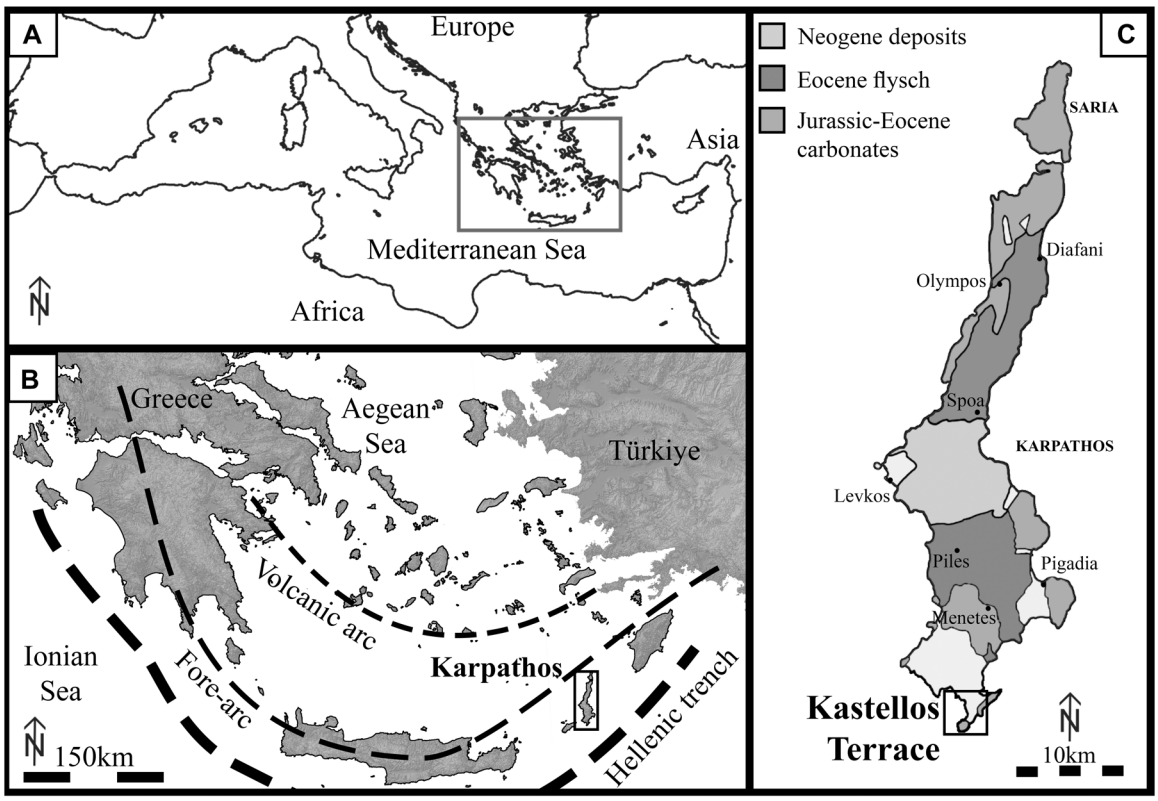


Figure 1. Simplified maps of the study area. (A) Location of the Aegean Sea in the Mediterranean; (B) location of Karpathos in the Hellenic forearc and simplified geodynamic context; and (C) location of the study area in Karpathos (from Moissette et al., 2017, simplified from Barrier and Angelier, 1981).

recent deposits above uplifted marine terraces devoid of marine associated sediments. We focus just below on carbonate layers of the terraces.

Material and methods

Field investigations

Along the southeastern coast of Karpathos, in the Kastellos area, an investigation was conducted on a Pleistocene "Tyrrhenian" outcrop (35.405000° N, 27.142833° E), where one section was described in detail and shown to correspond to a composite terrace (Fig. 1). The study documents the stratigraphy and involves collecting samples from the carbonate and sandy layers in the upper part of the section. Depositional environments were determined by using both textural features and faunal content in carbonate beds (Flügel, 2004), and associated sedimentary structures observable in field following the database of Merzeraud (2017). All together, these observations allow to depict sedimentary cycles (transgressive-regressive cycles) indicative of the relative sea-level variations (Merzeraud, 2017).

U–Th dating

Samples were collected at different levels of the composite "Tyrrhenian" terrace and two of them were dated using the U–Th method, after X-Ray investigations (at Montpellier University) to find aragonitic samples. One *Thetystrombus* shell was dated at the GEOMAR Helmholtz Centre for Ocean Research Kiel, after dissolution, using an AXIOM multi-collector inductively coupled plasma mass spectrometer (MC-ICP-MS) (Fietzke et al., 2005), and a *Cladocora* coral sample was dated though laser ablation coupled to an MC-ICP-MS (Neptune+ instrument of the AETE-ISO platform in Montpellier; Condomines et al., 2023).

Sample preparation and species identification

A variety of species from different horizons were recovered. Large specimens (>2 mm) of all taxa were extracted from the strata, some of which were heavily cemented, with stratigraphic position and context carefully documented. Because much of the uppermost layer was cemented, additional fossils were collected directly from the terrace surface. Whenever possible, at least 10 L of non-cemented material was gathered from selected spots at the top of the horizon, with all fossils retained. From these samples, bulk sediment (c. 500 g) was processed to recover small specimens, using practical rather than standardised criteria. As the objective was a qualitative rather than quantitative assessment, no preliminary analyses were performed to determine the minimum sample mass, a limitation that may constrain direct comparisons with other MIS 5e studies (Ávila, 2005).

Specimens were not sieved, in order to preserve fragile fossils, and the residues were instead examined under a stereomicroscope. This approach enabled recovery of small molluscs, including delicate taxa. Typical species assemblages were defined, and any changes in their composition were observed and analysed (Fig. 3). As reported in previous studies of Greek fossil faunas (Koskeridou and Thivaiou, 2012; Thivaiou et al., 2019; Psarras et al., 2021, 2022, 2023), we identified the species using a combination of morphological and colour pattern characteristics seen under UV light (e.g., Crippa and Masini, 2022). When necessary, in order to make the patterns visible, we bleached certain Conidae specimens in sodium hypochlorite for 24 hours, then washed them with water and allowed them to dry. Because the faunas from the Pleistocene are primarily composed of species that still exist today, we identified the fossil specimens by consulting previous scientific literature (e.g., Mitzopoulos, 1933; Cuerda, 1957; Anapliotis, 1961, 1966; Dekkers, 2008; Chirli and Linse, 2011; Chakroun and Zaghbib-Turki, 2017; Santagati et al., 2024).

Additionally, we checked the updated nomenclature of the species identified, by using online databases (e.g., WoRMS—World Register of Marine Species 2025; MolluscaBase, 2025).

Photography

The Conidae specimens were photographed under UV, following the methodology outlined by Psarras et al. (2022, 2023), as comprehensively described in Crippa and Masini (2022). The rest of the fauna was photographed under natural light, as their morphology was enough to clearly identify them. A CANON EOS-70D camera equipped with an EFS 15–85 mm image stabiliser ultrasonic lens was utilised, with an additional x4 magnification lens applied when needed. The photos were captured with reduced exposure levels and a small aperture to better highlight the UV colours. Multiple shots were taken at various focus points and later merged and blended (Auto-Align Layers, Auto-Blend Layers) using Adobe Photoshop, where individual image white balance, levels, tone and contrast were also adjusted (e.g., Hendricks, 2015, 2018; Adobe Inc, 2025; see Crippa and Masini, 2022, for more details). The UV photographs were captured under a UV light with a 365 nm wavelength. Two Convoy S2 + UV flashlights were positioned diagonally on either side of the specimen, with the original glass replaced by a ZWB2 filter to block any visible light from the flashlight. When necessary, specimens were photographed using a LEICA M165 C stereoscope and a LEICA IC90 E camera.

Species list update

For the extensive nomenclatural update of the species found in Greece and the update of other Mediterranean fauna, we used the lists of past authors. For the Greek faunas, we used previous studies that analysed various "Tyrrhenian" localities in Greece, such as Corinth, Perachora and the islands of Karpathos, Strofades, Armathia and Crete (Mitzopoulos, 1933; Psarianos, 1961; Anapliotis, 1961, 1963a, 1963b, 1966; Anapliotis and Georgiadou-Dikeoulia, 1967; Georgiades-Dikeoulia and Marcopoulou-Diacantoni, 1976; Angelier et al., 1977). Six species that were misidentified as Indo-Pacific species, as, for example, *Nassarius conoidalis* (Deshayes, 1833)) in Georgiades-Dikeoulia and Marcopoulou-Diacantoni (1976), were excluded from the species list. The composite lists of species in Greece have been compiled and are included in the Supplementary Material. Furthermore, for the rest of the Mediterranean, we updated the presence/absence list from Melo et al. (2023) based on other studies (Cuerda, 1957; Vera-Peláez et al., 2004; Zenetos et al., 2005; Amorosi et al., 2014; Galili et al., 2016; Chakroun and Zaghbib-Turki, 2017; Manousis, 2023; Santagati et al., 2024). The specimens collected during this study are stored at the National and Kapodistrian University of Athens, Museum of Geology and Paleontology, Invertebrate Collection, with catalogue numbers MGPA-000090000 to MGPA-000090365.

Palaeoecology and palaeobiogeography

To reconstruct the palaeoenvironmental conditions of the locality, we inferred the ecological preferences (e.g., temperature, depth) of the fossil species based on the documented tolerances of their modern representatives. While we are aware of the potential limitations of this actualistic approach, including the possibility of long-term adaptation or niche evolution since the LIG, the method remains a robust framework for palaeoenvironmental interpretation (i.e., Monegatti and Raffi, 2001; Meco et al., 2002; Meco, 2008; Garilli, 2011; Ávila et al., 2015, 2016; Psarras et al., 2024; Santagati et al., 2024). We used these palaeoecological affinities to compare the temperature tolerances of the species found in the assemblage. The mean temperature ranges provide insight into preferred temperature levels of the fauna. To ascertain the depth ranges, SST ranges, and SST means of the collected species, we used data from the Ocean Biodiversity Information System (OBIS, 2025). We downloaded the SST and depth values from the OBIS database and carefully checked them using the software R (v4.1.2; R Core Team, 2024). Specimens without depth values or those collected from land were disregarded, focusing only on specimens collected at documented depths.

Additionally, data sets containing taxa with invalid names (e.g., *Strombus latus* and *Strombus alatus*) were carefully reviewed, and incorrect data sets were excluded or polished. Assignation to a specific biogeographic region (similar to Santagati et al., 2024) was carried out using the distribution maps extracted from WoRMS and MolluscaBase (WoRMS—World Register of Marine Species, 2025; MolluscaBase, 2025) by checking the documented distribution of each species. The refined data sets were then used to calculate the mean annual SST ranges, depth ranges and preferred temperature ranges of the fauna (see Supplementary Material). However, it is worth considering that some taxa (especially small-sized ones, or those with complex taxonomy such as Turridae s.l. and Rissoidae) may not have occurrences covering the entire actual range or accurate identification among the limitations of this approach, with consequent underrepresentation of the actual range and temperature and biogeographic affinity. This species list and associated temperature ranges were subsequently used to verify the biostratigraphic age of the locality. Many of the identified species show distinct stratigraphic occurrences in the Mediterranean over the last 150 ka. Furthermore, the temperature ranges in which these species thrive today provide an indication of the SST conditions required during the deposition of the Senegalese species (see examples in Muhs et al., 2015). The reconstruction of palaeoenvironments at the Kastellos Bed 5 relied on the Mediterranean benthic bionomy framework (Pérès and Picard, 1964; Picard, 1965; Pérès, 1967), applied to the ecological preferences of the identified taxa.

Non-metric multidimensional scaling

The species lists of Melo et al. (2023) and the revised species lists from Greece were analysed using non-metric multidimensional scaling (nMDS) based on the Bray–Curtis dissimilarity index. Since the nMDS was performed on Presence–Absence data, the results were identical to the nMDS based on the Sørensen (Dice) index. A hierarchical cluster analysis was then performed using the Bray–Curtis dissimilarity index and the paired group (UPGMA) method in the software PAST 4.06b (Hammer et al., 2001).

Abbreviations

LIG, Last Interglacial; MIS 5e, Marine Isotope Stage 5e; SST, sea surface temperatures; asl, above sea level;

Ecoregions of the Northern European Seas Province: BS, Baltic Sea; CS, Celtic Sea; NS, North Sea.

Ecoregions of the Lusitanian Province: ADS, Adriatic Sea; AEG, Aegean Sea; ALS, Alboran Sea; AZO, Azores Archipelago, Webbnesia Ecoregion, which includes the archipelagos of Madeira (MAD), Selvagens (SEL) and Canary Islands (CAN) (Freitas et al., 2019); BLS, Black Sea; IOS, Ionian Sea; LES, Levantine Sea; SAU, Saharan Upwelling; SEAS, South European Atlantic Shelf; TUP, Tunisian Plateau/Gulf of Sindra; and WEM, Western Mediterranean.

Ecoregions of the West African Transition Province: CAB, Cabo Verde; SU, Sahelian Upwelling.

Ecoregions of the Gulf of Guinea Province: GGC, Gulf of Guinea Central; GGI, Gulf of Guinea Islands; GGS, Gulf of Guinea South; GGU, Gulf of Guinea Upwelling; and GGW, Gulf of Guinea West.

MGPA, Museum of Geology and Paleontology of the National and Kapodistrian University of Athens, Greece.

Results

Lithostratigraphy and fauna of the Kastellos "Tyrrhenian" terrace

The Kastellos deposits crop out between 10 and 15 m asl. They comprise five sedimentary beds (1 to 5) organised into three superimposed sedimentary cycles bounded by erosional surfaces (Fig. 2). From bottom to top:

- *Deposits of the lowest cycle*, which are 1.70 m thick and rest upon eroded Pliocene marls (Zachariasse et al., 2008). These deposits include beds 1 to 3. Bed 1 is a coarse-grained limy conglomerate with pebbles eroded from the basement and rhodoliths, topped by a submarine hard ground underlined by *Lithophaga*-type borings. Bed 2 is a bioturbated sandy bioclastic limestone with bivalves including Pectinidae, *Cerastoderma* sp., *Callista* sp., *Spondylus* sp. and *Glycymeris* sp., as well as gastropods including *Gibbula* sp., other unidentified Trochidae and *Anomia* sp. Bed 2 changes upward into bioturbated coarse-grained bioclastic limestones of bed 3 with broken shells of bivalves and gastropods, among which are *Callista* sp., *Glycymeris* sp., Veneridae and *Homalopoma* sp., as well as serpulid worms of the genus *Ditrupa* sp. The top of bed 3 is a stripped surface with dm-wide erosional channels.
- *Deposits of the intermediate cycle*, which are found in the 1 m thick bed 4. They consist first of very coarse-grained bioclastic limestones infilling the underlying channels, with pebbles eroded from the basement and molluscs. Bioturbated coarse-grained bioclastic limestones occur above with cross beddings and abundant molluscs, bryozoans, and rare in situ *Cladocora caespitosa* coral colonies. Mollusc fauna includes *Cardita calyculata*, *Homalopoma* sp., *Glycymeris* sp., Trochidae, *Callista* sp., *Capulus* sp. and *Papillicardium* sp. The top of bed 4 is marked by a sharp surface and a sudden change in facies at the transition to bed 5.
- *Deposits of the upper cycle*, which are found in the 0.4 m thick bed 5. It consists of a packstone with sparse *Cladocora caespitosa* colonies and well-preserved and abundant gastropods (*Thetystrombus latus*) and bivalves (*Glycymeris* sp., *Spondylus gaederopus*).

Beds 1 to 3 constitute part of a transgressive–regressive sedimentary cycle with foreshore deposits topped by a hard ground (bed 1) and upward changing into upper shoreface deposits crosscut by an erosional surface. Bed 4 displays a similar organisation, with a transgressive lag in its lowermost part changing upward into upper shoreface, high-energy deposits. Sedimentation abruptly changes in bed 5 with low-energy marine deposits from an inner sheltered platform. Consequently, the so-called Kastellos terrace comprises three superimposed terrace deposits, all previously considered as a single Tyrrhenian deposit (Anapliotis, 1961, 1966).

Species list and inventory of species reported for the first time

Past studies in Karpathos have identified 38 species of bivalves and gastropods (Anapliotis, 1961, 1966), whose taxonomy is presently revised (Fig. 3). Our detailed analysis of the fauna contained in bed 5 of the Kastellos terrace has uncovered 64 species, 23 of which have already been mentioned in previous studies (see Supplementary Material). While we found 41 species that had never been mentioned before in Karpathos, we did not find 15 of the species mentioned by these previous studies (see Supplementary Material). Along with the molluscan fauna, we found a very small bone (0.5 cm) of a vertebrate animal, very few benthic foraminifera, three small otoliths, sea urchin spikes, five Dentaliidae specimens, many rhodophyte clumps and corals of *Cladocora caespitosa*, one *Flabellum* sp. and two more unidentified solitary corals.

We identified the distinct representatives of the "Senegalese fauna" (Gignoux, 1913) *Thetystrombus latus* (Gmelin, 1791), *Polinices lacteus* (Guilding, 1834) and *Hyotissa hyotis* (Linnaeus, 1758) = *Hyotissa mcgintyi* (Harry, 1985) (see discussion) (Fig. 3).

Furthermore, two species are identified as fossils from global LIG strata for the first time: *Babelomurex cariniferus* (G. B. Sowerby II, 1834) and *Mitromorpha karpathoensis* (Nordsieck, 1969). Also, the specimens of *Conus* (*Lautoconus*) *ventricosus* Gmelin, 1791 are considered here as the stratigraphic subspecies *Conus* (*Lautoconus*) *ventricosus rhodesensis* Psarras et al., 2024, according to Psarras et al. (2024). No specimens of *Conus* (*Chelyconus*) *ermineus* Born, 1778 were identified, as the flat spired specimens, previously assumed to be characteristic of *Conus* (*Chelyconus*) *ermineus* Born, 1778, present patterns similar to *Conus* (*Lautoconus*) *ventricosus* Gmelin, 1791.

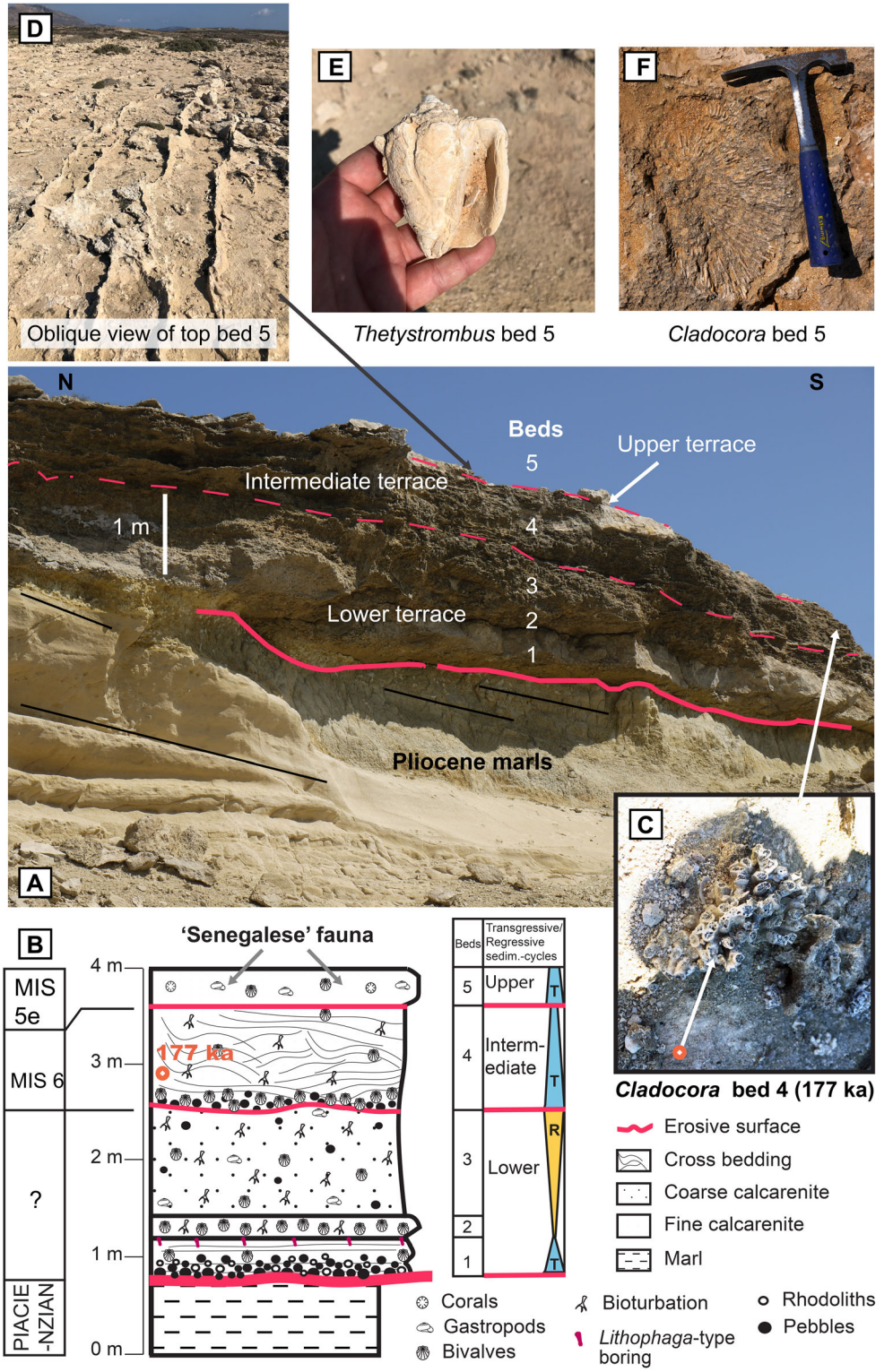
Age determination

A *Cladocora caespitosa* coral colony was collected in life position in bed 4 (Fig. 2). Uranium–Thorium dating yielded a reliable age of 177 ± 3 ka (Table in Fig. 2(G)). The negligible ^{232}Th content rules out detrital contamination and significant initial ^{230}Th contribution, while the measured (^{234}U/^{238}U) ratio closely matches that of seawater. Unfortunately, the *Cladocora caespitosa* colonies in the overlying bed 5 underwent severe diagenesis and were unsuitable for dating. Consequently, U/Th analyses were carried out on a fragment of the central columnar part of an aragonitic *Thetystrombus latus* in bed 5. An apparent U/Th age of *ca* 90 ka was obtained. Even if this age seems to be consistent with the age of the underlying bed 4, it is not considered robust because U isotope ratios in the sample indicate open system behaviour. In the Kastellos area, U/Th ages on mollusc shells were previously provided by Barrier (1979), who reported an age of 120 ka for a terrace at +5 m asl and an age of 260 ka for a +45 m asl terrace. However, the dated shells were also affected by similar open-system processes and their ages cannot be considered as truly reliable.

The presence of fossil molluscs from the "Senegalese fauna," which today inhabit regions with higher SSTs than those of the Mediterranean, suggests that past climate conditions were significantly warmer. Their presence has consistently been used as an indicator for the LIG due to their temperature preferences (Muhs et al., 2015; Santagati et al., 2024). In spite of uncertainty in its age, bed 5 is obviously younger than bed 4 dated at 177 ± 3 ka. According to Muhs et al. (2015), the only time period in the Mediterranean, after MIS 7 (~240 ka) (Zazo, 1999), when this fauna could have thrived is during MIS 5e or the LIG. In view of the age constraint and the presence of *Thetystrombus latus* and the Senegalese fauna, we can confidently attribute the studied terrace (Bed 5 only) to MIS 5e.

Palaeoenvironments of Kastellos Terrace bed 5

The fossil assemblage from bed 5 of the Kastellos terrace includes 64 taxa represented by 347 specimens. Molluscs dominate, but corals, crustaceans, echinoids, foraminifera and



G Sample	U (ppm)	(^{234}U/^{238}U)	(^{230}Th/^{238}U)	Age (ka)	(^{234}U/^{238}U)$_i$
Cladocora coral Bed 4	3.6 ± 0.2	1.090 ± 0.003	0.891 ± 0.006	177 ± 3	1.148 ± 0.004

Figure 2. Kastellos terraces. (A) Field view of the studied outcrop in the Bay of Kastellos. (B) Lithostratigraphy of the studied outcrop with reconstructed transgressive–regressive cycles. (C) Branching *Cladocora* coral colony in life position in bed 4, dated at 177 ± 3 ka. (D) Oblique view of the surface of bed 5. (E) *Tethystrombus latus* specimen collected in bed 5. (F) Massive *Cladocora* coral colony found in life position in bed 5. (G) U–Th Data for *Cladocora* coral in bed 4, obtained through LA-MC-ICP-MS (method described in Condomines et al., 2023). The results are the weighted averages of 8 analyses of coral branches. (^{238}U/^{232}Th) activity ratios are higher than 7000, and no correction of initial ^{230}Th is necessary. The age and its 2σ error are calculated using the IsoPlotR programme (Vermeesch, 2018). [Color figure can be viewed at wileyonlinelibrary.com]

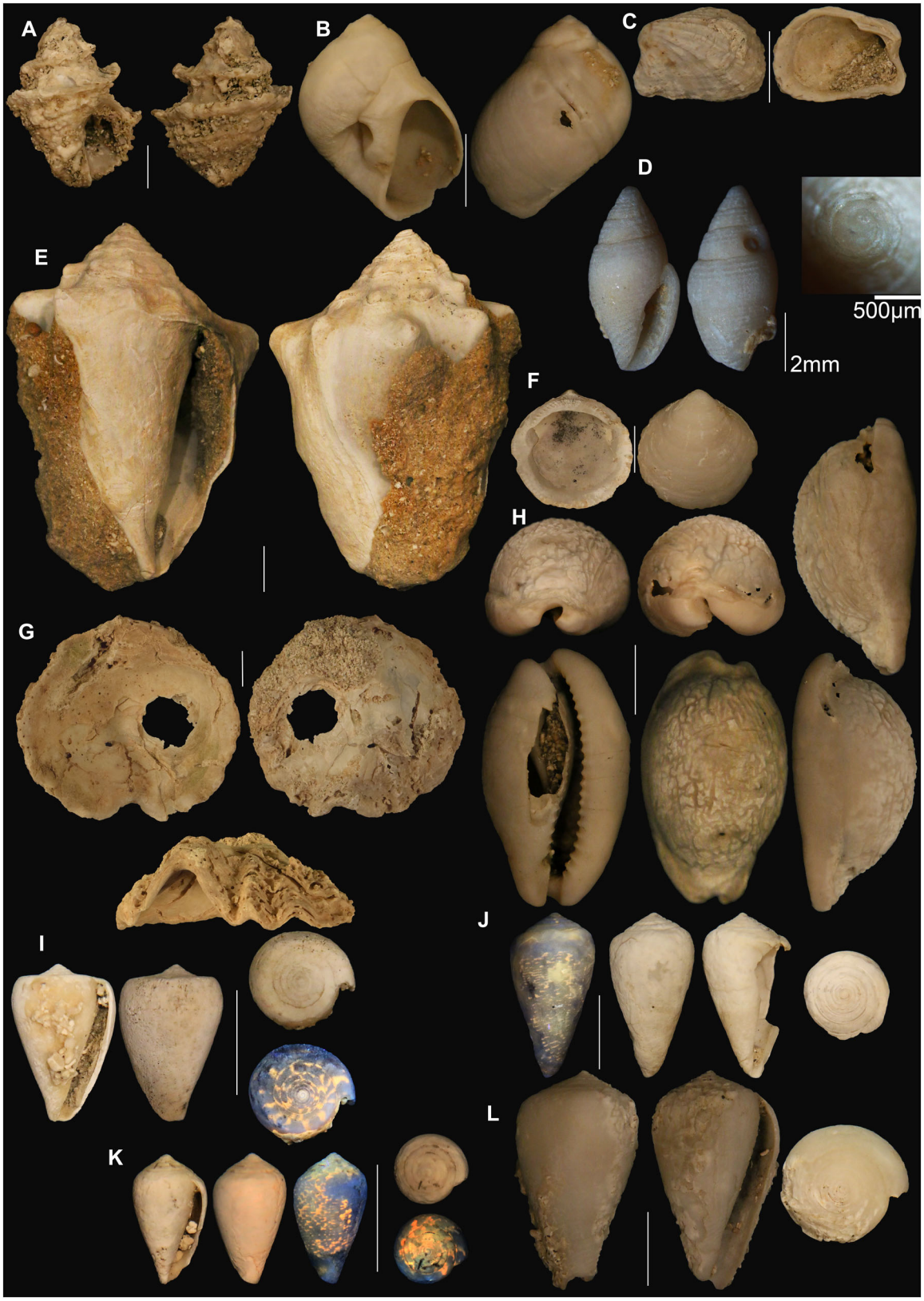


Figure 3. Selected species from the Tyrrhenian of Karpathos, under natural and UV (I, J, K) light. A – *Babelomurex cariniferus* (G. B. Sowerby II, 1834). B – *Polinices lacteus* (Guilding 1834). C – *Cardita rufescens* Lamarck, 1819. D – *Mitromorpha karpathoensis* (Nordsieck, 1969). E – *Thetystrombus latus* (Gmelin, 1791). F – *Glycymeris pilosa* (Linnaeus, 1767). G – *Hyotissa mcgintyi* (Harry, 1985). H – *Luria lurida* (Linnaeus, 1758). I–L – *Conus* (*Lautoconus*) *ventricosus rhodesensis* Psarras et al., 2024. Scale bars = 1 cm. [Correction made on 14 November 2025, after first online publication: Figure caption 3B has been amended at the request of the corresponding author.] [Color figure can be viewed at wileyonlinelibrary.com]

rhodoliths are also present. The collection strategy—targeting larger specimens and examining loose sediment fractions under a stereoscope—was aimed at a qualitative assemblage assessment rather than quantitative community analysis. Low specimen counts for many taxa preclude the definition of discrete palaeobiocoenoses, and yet, the combined ecological preferences of the recovered species provide a reliable framework for palaeoenvironmental interpretation (Pérès and Molinier, 1957; Pérès and Picard, 1964; Pérès, 1967; Gamulin-Brida, 1967; Blanc, 1968). Such an approach has

long been applied in palaeoecological studies across the region (e.g., Dominici, 2001; Nielsen et al., 2006; Moissette et al., 2007, 2013, 2017; Koskeridou et al., 2009, 2013, 2019).

Overall, the assemblage reflects a heterogeneous shallow marine environment within the infralittoral zone, structured as a mosaic of microhabitats.

Rhodoliths and stable substrates

Abundant rhodoliths (Rhodophyta, $N = 9$) indicate moderate-energy conditions where movement prevents sediment burial, forming complex habitats for nestling bivalves like *Cardita calyculata* ($N = 4$) and *Acar clathrata* ($N = 3$). Solitary corals (*Flabellum siciliense* $N = 1$, *Caryophyllia* sp. $N = 2$) and the corallivorous muricid *Babelomurex cariniferus* ($N = 1$) point to the availability of stable substrates with corals, while *Hyotissa mcgintyi* ($N = 5$), besides being a warm-water indicator, confirms rocky surfaces.

Vegetated, photophilic environments

Grazers such as *Rissoa membranacea* ($N = 13$) and *Alvania* spp. ($N = 17$) point to the presence of photophilic algae, consistent with modern infralittoral assemblages. The large strombid *Thetystrombus latus* ($N = 4$) and detritivore *Cerithium vulgatum* ($N = 13$) point to organic-rich vegetated bottoms. *Pinna nobilis* ($N = 1$), *Lima lima* ($N = 3$) and *Tricolia pullus* ($N = 5$) suggest seagrass meadows and sheltered stable substrates. *Patella caerulea* ($N = 10$) indicates rocky substrates in the intertidal to shallow subtidal zone.

High-energy coarse detritic bottoms

Shallow-burrowing *Glycymeris bimaculata* ($N = 5$) and *G. pilosa* ($N = 9$) indicate sandy–gravelly settings influenced by waves and currents, a community well recognised in Mediterranean benthic zonation. Hard-substrate taxa such as *Spondylus gaederopus* ($N = 4$), *Chama gryphoides* ($N = 9$) and *Striarca lactea* ($N = 2$) reveal nearby rocky outcrops or gravels embedded within the detritic facies.

Sheltered sandy–muddy bottoms

Deposit-feeding bivalves like *Moerella donacina* ($N = 5$) and fragile taxa such as *Loripinus fragilis* ($N = 2$) and *Barbatia barbata* ($N = 1$) indicate lower energy, fine-grained settings rich in organic matter. Benthic foraminifera are also consistent with this habitat. Carnivorous gastropods *Neverita josephinia* ($N = 2$) and *Polinices lacteus* ($N = 4$), predators of infaunal bivalves, support this interpretation.

Complete list of species from the LIG of Greece

The nomenclatural update of the species found in Greece yielded 244 taxa in total, 113 species of bivalves and 131 species of gastropods (see Supplementary Material). From this list, past studies had identified some extra "Senegalese" faunal elements (Gignoux, 1913) such as *Monoplex trigonus* (Gmelin, 1791) (in Mitzopoulos, 1933; Anapliotis, 1963a), *Anadara geissei* (Kobelt, 1891) (in Mitzopoulos, 1933) and *Cymbula safiana* (Lamarck, 1819) (in Angelier et al., 1977) that are not mentioned anywhere else in the literature. While we did not find these species at the AMPG, we provisionally retained them in our lists, as they might have expanded their geographic ranges into the Mediterranean, along with the rest of the "Senegalese fauna."

For the first time, the LIG mollusc faunas of Greece are compiled into a single data set and classified within the Aegean Sea Ecoregion (Spalding et al., 2007). Nearly all studied localities in Greece are unequivocally within the Aegean. However, the Perachora locality presents a challenge, as it lies within the Gulf of Corinth (Mitzopoulos, 1933). Although Spalding et al. (2007) place the modern Gulf of Corinth within the Ionian Sea Ecoregion, evidence suggests that during the LIG, the Gulf functioned as a corridor between the Ionian and Aegean Seas (Roberts et al., 2009, fig. 9(g)). Given this transitional role and the proximity of Perachora findings (Mitzopoulos, 1933) to the Aegean, we classify the LIG samples from the Corinth area as belonging to the Aegean Ecoregion.

The mollusc fauna of the LIG Aegean Ecoregion is similar to those of the Ionian Sea and Western Mediterranean Ecoregions (Fig. 4). Additionally, newly incorporated data from the Tunisian, Levantine and Ionian Ecoregions (Supplementary Material) further highlight that Mediterranean Ecoregions differ from those of the Atlantic during MIS 5e (Fig. 4). Among non-Mediterranean regions, the Saharan Upwelling Ecoregion is the only one that shows similarities to the Mediterranean Ecoregions (Fig. 4 and Table 1). The Ionian Sea and the Western Mediterranean Ecoregions apparently show the highest biodiversity, while the Tunisian plateau shows the lowest biodiversity. Furthermore, the Ionian Sea and the Western Mediterranean Ecoregions share many common species (e.g., *Alvania beanii* (Hanley in Thorpe, 1844), *Bittium reticulatum* (da Costa, 1778), *Hexaplex trunculus* (Linnaeus, 1758)), though those species are widespread in the Mediterranean today (WoRMS—World Register of Marine Species 2025).

Some unique species are found in only one Ecoregion during the LIG:

Saharan Upwelling Ecoregion: *Anadema macandrewii* (Mörch, 1868) and *Marginella glabella* (Linnaeus, 1758), species not present today in the Mediterranean (WoRMS—World Register of Marine Species 2025).

Western Mediterranean Ecoregion: *Alvania mamillata* Risso, 1826, *Bittium lacteum* (R. A. Philippi, 1836), *Leufroyia concinna* (Scacchi, 1836) and *Tritia incrassata* (Strøm, 1768), species widespread today in the Mediterranean (WoRMS—World Register of Marine Species 2025).

Tunisian Plateau/Gulf of Sidra Ecoregion: *Galeodea echinophora* (Linnaeus, 1758) and *Tritia neritea* (Linnaeus, 1758), species widespread today in the Mediterranean (WoRMS—World Register of Marine Species 2025).

Ionian Sea Ecoregion: *Aplus dorbignyi* (Payraudeau, 1826), *Episcomitra cornicula* (Linnaeus, 1758) and *Haedropleura septangularis* (Montagu, 1803), species widespread today in the Mediterranean (WoRMS—World Register of Marine Species 2025).

Aegean Sea Ecoregion: *Babelomurex cariniferus* (G. B. Sowerby II, 1834), *Mitromorpha karpathoensis* (Nordsieck, 1969) and *Tritia varicosa* (W. Turton, 1825), species widespread today in the Mediterranean (WoRMS—World Register of Marine Species 2025).

Levantine Sea Ecoregion: *Volvarina mitrella* (Risso, 1826) and *Alvania colossophilus* Oberling, 1970, from which the first is widespread today in the Mediterranean and the second is only found in eastern Mediterranean.

Discussion

Depth estimation and palaeoenvironment

The Kastellos Bed 5 assemblage broadly resembles Mediterranean biocoenoses as defined by Pérès and Picard (1964), though

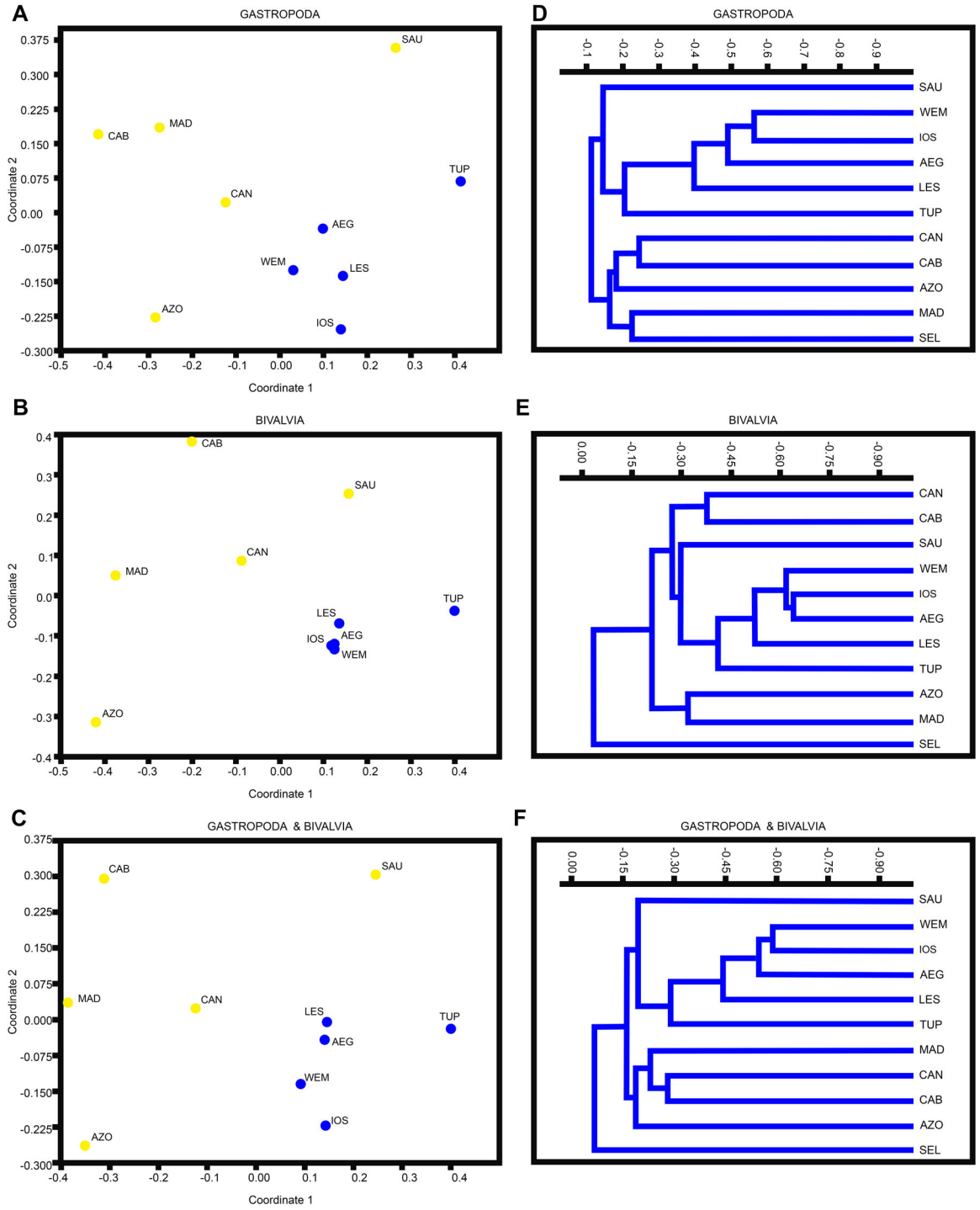


Figure 4. Non-metric multidimensional scaling (A-C) and Hierarchal cluster analysis (D) of the updated species lists of Melo et al. (2023) found in each Ecoregion of the East Temperate Northern Atlantic Realm of Spalding et al. (2007), with corrections from Freitas et al. (2019). A–C: nMDS tests (Sørensen (Dice) index) on Gastropoda (A), Bivalvia (B) and mixed faunal elements (C). In all three graphs, the East Atlantic Ecoregions (yellow) are clearly defined from the Mediterranean ones (blue). Selvagens archipelago (SEL) was not included in those graphs, as its distance from the rest disrupted the nMDS outcome. D–F: Graph of cluster analysis displays the relations between the faunas of each Ecoregion on Gastropoda (D), Bivalvia (E) and mixed faunal elements (F). Distances were calculated using Bray–Curtis and paired group (UPGMA). East Atlantic Ecoregions: Azores Archipelago (AZO), Madeira Archipelago (MAD), Selvagens Archipelago (SEL), Canary Archipelago (CAN), Cabo Verde Archipelago (CAB) and Saharan Upwelling (SAU). Mediterranean Ecoregions: Western Mediterranean (WEM), Tunisian Plateau/Gulf of Sidra (TUP), Ionian Sea (IOS), Aegean Sea (AEG) and Levantine Sea (LES). [Color figure can be viewed at wileyonlinelibrary.com]

the absence of key diagnostic taxa prevents a direct attribution. Nevertheless, the ecological diversity of the fauna points to a dynamic coastal setting shaped by both stable and shifting substrates, organic enrichment and variable energy regimes.

A. Evidence for a shallower depth (10–20 m, infralittoral). Several taxa indicate deposition within the well-illuminated infralittoral zone. The abundance of *Patella caerulea* points to close proximity to the shoreline, as limpets are characteristic inhabitants of the mediolittoral and upper infralittoral. Photophilic environments are further supported by grazers such as *Rissoa membranacea* ($N = 13$), *Tricolia pullus* ($N = 5$) and *Alvania* spp. ($N = 17$), which thrive on algae and seagrass. Together, these elements strongly suggest that shallow, vegetated habitats formed an important component of the Kastellos palaeoenvironment.

B. Evidence for greater depth (~20–30 m, lower infralittoral). Other components of the assemblage point to slightly deeper conditions. Rhodoliths, while capable of forming from nearshore shallows to >100 m depth (e.g., Rendina et al., 2020), typically develop most extensively in the lower infralittoral to upper circalittoral (15–40 m) in the Mediterranean (e.g., Basso et al., 2017). Their occurrence here is consistent with such settings, though recent studies (Pierri et al., 2024, and references therein) confirm that rhodolith beds can also occur in very shallow water (<2 m). Solitary corals (*Flabellum siciliense*, *Caryophyllia* sp.) represent relatively deeper water element, as these taxa commonly appear at the lower limit of the infralittoral (~20–25 m). Finally, scaphopods (Dentaliidae) are frequent in detritic bottoms of infralittoral–circalittoral transitions (20–40 m).

Synthesis

The assemblage reflects a mosaic of microhabitats across the infralittoral zone (Fig. 5). The abundance of unequivocal shallow-water taxa suggests deposition within the deeper infralittoral, while the presence of corals, rhodoliths and scaphopods is best explained by slightly deeper conditions at ~20–25 m. Local topography likely played a role, with seagrass and limpets inhabiting shallower highs (5–15 m) and rhodoliths and corals occupying adjacent depressions (15–25 m). Minor storm-induced reworking could have mixed shells across these settings, producing the assemblage now preserved. Taken together, the evidence indicates that Kastellos Terrace Bed 5 has deposited in a low-energy environment at a depth of approximately ~15–30 m within the infralittoral (Fig. 5). This assemblage reflects habitat heterogeneity and depth–range overlap within the infralittoral, permitting both shallow-infralittoral and lower infralittoral taxa to occur together.

Table 1. Total species per region.

	SAU	WEM	TUP	IOS	AEG	LES
Gastropods	44	230	27	218	131	110
Bivalves	39	101	35	105	113	65
SUM	83	331	62	323	244	175

AEG, Aegean Sea; IOS, Ionian Sea; LES, Levantine Sea and Cyprus; SAU, Saharan Upwelling; TUP, Tunisian Plateau/Gulf of Sindra; and WEM, Western Mediterranean.

Faunal characteristics

While the fauna is almost identical to that found today in the Aegean Sea, the main distinction is the presence of *Polinices lacteus* (Guilding, 1834) and *Thetystrombus latus* (Gmelin, 1791). One might expect to find *Conus* (*Chelyconus*) *ermineus* Born, 1778, a species commonly used as a key indicator in Tyrrhenian localities (e.g., Muhs et al., 2015). However, despite studying several flat-spired specimens under UV light, which were previously considered as morphotypes of *C. ermineus*, we did not find any specimen with the characteristic colour patterns of *Conus* (*Chelyconus*) *ermineus* Born, 1778. This suggests that the presence of this taxon, which can only be detected with UV light (Psarras et al., 2024), has yet to be confirmed in the Mediterranean region. The Conidae specimens from Karpathos provided information about the morphological and pattern variations (Fig. 3(I)–(L)) of *Conus* (*Lautoconus*) *ventricosus rhodesensis* Psarras et al., 2024. While the specimens showed a range of morphological forms, from flat-spired to very elongated spires, their patterns remained consistent and closely matched those described by Psarras et al. (2024) for the Pleistocene subspecies of Rhodes.

Furthermore, while the name *Hyotissa hyotis* (Linnaeus, 1758) has been applied to oysters with "saw-toothed" shell margins in the eastern Atlantic and the Mediterranean from the Pliocene to the Pleistocene (e.g., Zazo et al., 2003; Amorosi et al., 2014; Khalili and Vinn, 2023; Santagati et al., 2024; Gaaloul et al., 2025), many of these records may represent

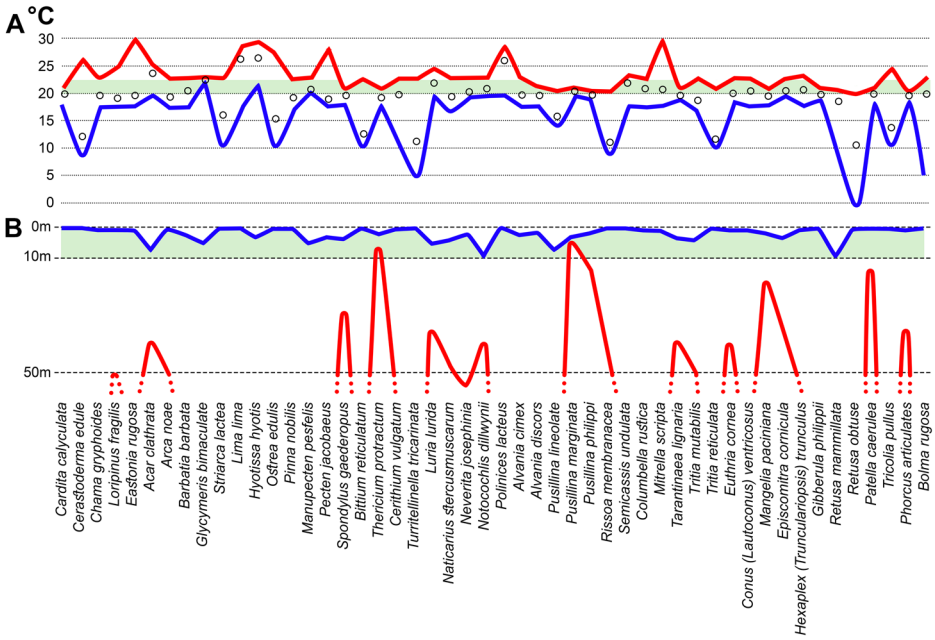


Figure 5. Minimum and maximum temperature and depth ranges for 50 out of the 64 species studied herein. (A) Temperature ranges for the studied species (blue = min temperature tolerance and red = max temperature tolerance), with the green shade indicating the temperature range at which most species found can survive. (B) Depth ranges for the species studied (blue = min depth range and red = max depth range; dotted lines indicate that species depth exceeds those of the presented graph), with the green shade indicating the depth range at which most species found can thrive. [Color figure can be viewed at wileyonlinelibrary.com]

misidentifications (e.g., Khalili and Vinn, 2023, fig.3; Gaaloul et al., 2025, fig. 8(A),(B)). Furthermore, Ávila et al. (2015) explicitly reported the absence of *Hyotissa* in the Azores, but according to the data set of Melo et al. (2023), species of *Hyotissa* are recorded from the Canarian Islands and Cabo Verde ecoregions (Cabero del Río, 2009 and references therein). Today, *Hyotissa hyotis* is considered an Indo-Pacific species, with a range from the Red Sea to the West coast of Mexico. According to Bieler et al. (2004), *Hyotissa hyotis* is restricted to the Indo-Pacific, with the exception of Florida (Kirkendale et al., 2004), where the species has been introduced by ship ballast waters. The *Hyotissa* species found in the tropical waters of the eastern and western Atlantic is *Hyotissa mcgintyi* (Harry, 1985) (Guo et al., 2018; Melo et al., 2022a). Since *Hyotissa hyotis* appears to have been recently introduced to the Atlantic through the Panama Canal, its presence in the Mediterranean during MIS 5e is unlikely. However, its Atlantic counterpart, *Hyotissa mcgintyi* (Harry, 1985), could expand its range into the eastern Atlantic and the Mediterranean Sea. Muhs et al. (2015) mentioned the name *Parahyotissa rosea* (Gmelin, 1791), a synonym of *Hyotissa mcgintyi* (Harry, 1985), while recently, La Perna et al. (2025) mentioned *Hyotissa mcgintyi* in their list of species. Therefore, we consider the *Hyotissa* specimens described herein, as well as those figured in Santagati et al. (2024), to represent *Hyotissa mcgintyi* (Harry, 1985) (Fig. 3(G)).

Sea surface temperatures during the LIG

Today, the fossil molluscs of the "Senegalese fauna" inhabit regions with higher SSTs than the Mediterranean and are considered inhabitants of the West African Transition Province, though some parts of the current Mediterranean show SSTs able to sustain such inhabitants due to climate change (Albano et al., 2024). For example, *Thetystrombus latus* (Gmelin, 1791) is found today in waters with usual temperatures of 18°C to 29°C, when the mean winter SSTs are at least 19°C (Garilli, 2011; Ávila et al., 2016) and the coldest month being at least 16°C (Harzhauser and Kronenberg, 2013; Chakroun and Zaghbib-Turki, 2017), thriving at a mean annual SST of 23.5°C (Santagati et al., 2024). Given its temperature preferences, this species has been consistently used as an indicator of the LIG.

Furthermore, according to Duprat-Bertazzi and García-Domínguez (2005), *Hyotissa hyotis* requires temperatures above 20.5°C to spawn. Comparable thresholds are reported for *Hyotissa numisma* (~19.5°C; JTMD, 2025), suggesting that species of *Hyotissa* generally thrive in conditions above 19.5°C. Although no direct data exist for *Hyotissa mcgintyi* (Harry, 1985), it is reasonable to assume a similar requirement. However, as noted in the methodology, such estimates must be treated with caution, due to the possibility of long-term adaptations of the species to slightly different thermal regimes (Monegatti and Raffi, 2001; Meco et al., 2002; Meco, 2008; Garilli, 2011; Ávila et al., 2015, 2016; Psarras et al., 2024; Santagati et al., 2024).

Polinices lacteus (Guilding, 1834) has long been considered part of the "Senegalese fauna." However, the current range of this planktotrophic mollusc covers both sides of the Atlantic (amphi-Atlantic). According to Ávila (2025), *Polinices lacteus* occurs today from the Warm Temperate Northwest Atlantic Province (including the Carolinian Ecoregion and the Northern Gulf of Mexico Ecoregion), from the Tropical Northwestern Atlantic Province (with confirmed reports from the Bermuda, Bahamian, Eastern Caribbean, Greater Antilles, Southern Caribbean, Southwestern Caribbean and Western Caribbean Ecoregions) and from the Tropical Southwestern Atlantic Province (it is recorded from the Trinidade and Martim Vaz Islands Ecoregions), all located in the Western Atlantic. It is also reported from the eastern Atlantic, with occurrences found in the Lusitanian Province (from the Madeira and Canaries Archipelagos of the Webbnesia Ecoregion); the Cabo Verde subprovince and the Sahelian Upwelling Ecoregion (reported in Senegal), both in the West African Transition Province; and finally, it is reported from the Gulf of Guinea Province (from São Tomé and Príncipe Archipelago, in the Gulf of Guinea Islands Ecoregion; from Gabon in the Gulf of Guinea South Ecoregion; and from the Angolan Ecoregion). In the eastern Atlantic, the species inhabits waters with sea surface temperatures ranging between 16°C and 28°C. While this species lives mainly in the tropics, its presence in the Mediterranean during the LIG was not unexpected, as it occurs today in the Lusitanian Province (Cabero et al., 2013).

The studied fauna from Bed 5 at Kastellos shows a clear preference for temperatures of around 20°C (Figs. 5 and 6). Most species are characteristic of the Lusitanian Province (62/65 species, 97%) (Fig. 6), with a significantly higher proportion characteristic of the warmer waters of the West African Transition Province (27.6%) (Fig. 6) and very few species found in the Northern European Seas Province (Fig. 6) (Freitas et al., 2019). These results suggest that SSTs were approximately 20°C during deposition of Bed 5, which aligns with the estimates for the LIG. Such temperatures have been achieved in basins adjacent to Karpathos (Core LC21, Marino et al., 2007) and in the Mediterranean (Muhs et al., 2015). Mean annual SSTs in the Mediterranean during the LIG were around 20.8°C ± 0.9°C (Santagati et al., 2024), supporting the hypothesis that Karpathos also experienced similar conditions.

Our results differ from those of Santagati et al. (2024; fig. 5), who reported 25% of West African Transition and 28% of Northern European taxa in eastern Italy. Such a discrepancy with Karpathos fauna may result from local factors (Santagati et al., 2024) or from the latitudinal and longitudinal differences between regions (e.g., Keppel et al., 2012). Colder waters from the Adriatic Sea may have influenced the Gulf of Taranto, which may have acted as a refugium for cold-water species in the North Ionian Sea, contributing to the differences in the assemblages.

The importance of updated lists of Greece

Melo et al. (2023) recently pointed out the importance of datasets in the accumulation of information and identification of specific environmental conditions. The addition of the Aegean Ecoregion to this data set adds important information regarding the faunas of the Mediterranean.

First, previous species lists (Mitzopoulos, 1933; Anapliotis, 1963a; Angelier et al., 1977) indicate that, in addition to the well-documented "Senegalese fauna" of the LIG in the Mediterranean, additional species from that Province have been identified in LIG deposits of Greece. This highlights the enduring taxonomic interest in LIG faunas (Ávila, Landau, et al., 2025) and suggests that existing lists of "Senegalese fauna" reported from the Mediterranean LIG may be incomplete, with the potential for additional tropical species to be discovered in Mediterranean LIG deposits, as recently shown by La Perna et al. (2025).

Second, there are differences between the faunas of the Mediterranean Ecoregions from East to West, if one excludes Tunisia (Fig. 4). Indeed, the Tunisian Plateau Ecoregion shows fewer reported species compared to the rest of the well-studied Ecoregions (see Supplementary Material). The problematic data of the Tunisian Ecoregion point out the need for more detailed and taxonomically updated species lists in the Mediterranean, to figure out the actual similarities or

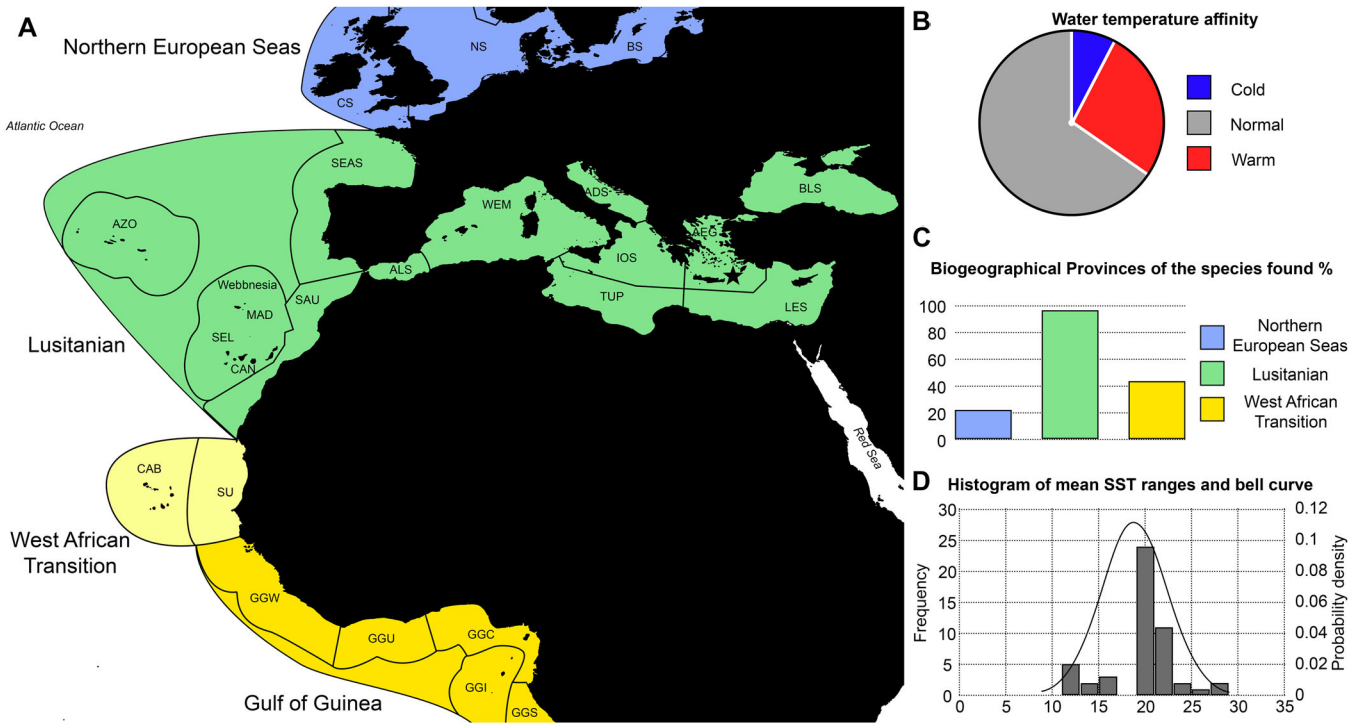


Figure 6. Map of the ranges of the Provinces of East Atlantic (A), according to Spalding et al. (2007) and updated by Freitas et al. (2019), the water temperature affinity of the species found in Karpathos (B), the biogeographical Provinces where the species of the fauna are found (C) and the overall ranges of mean temperature for each species (D), indicating that there is a clear species preference towards a water temperature of about 20°C in Karpathos. Notice that the bell curve is negatively skewed (skewness = −0.7). Ecoregions of the Northern European Seas Province displayed: CS, Celtic Sea; NS, North Sea; and BS, Baltic Sea. Ecoregions of the Lusitanian Province: AZO, Azores Archipelago, Webbnesia Ecoregion, which includes the archipelagos of Madeira (MAD), Selvagens (SEL) and Canary Islands (CAN) (Freitas et al., 2019); SAU, Saharan Upwelling; SEAS, South European Atlantic Shelf; ALS, Alboran Sea; WEM, Western Mediterranean; ADS, Adriatic Sea; IOS, Ionian Sea; TUP, Tunisian Plateau/Gulf of Sindra; AEG, Aegean Sea; LES, Levantine Sea and BLS, Black Sea. Ecoregions of the West African Transition Province: CAB, Cabo Verde, SU, Sahelian Upwelling. Ecoregions of the Gulf of Guinea Province: GGW, Gulf of Guinea West; GGU, Gulf of Guinea Upwelling; GGC, Gulf of Guinea Central, GGS, Gulf of Guinea South and GGI, Gulf of Guinea Islands. The black star on the map indicates the location of Karpathos Island. [Color figure can be viewed at wileyonlinelibrary.com]

differences between Ecoregions during the LIG. Some differences in the faunas have been found (Fig. 4(D)–(F)), but they seem to be artefacts of either low sampling effort or different environmental settings in each locality. With the exception of *Alvania colossophilus* Oberling, 1970—an endemic eastern Mediterranean species—the unique occurrences reported here are likely artefacts of an incomplete fossil record, reflecting sampling biases and the limited preservation of certain palaeohabitats. Consequently, the observed differences in taxonomic richness across Mediterranean Ecoregions are probably due to this insufficient sampling rather than true palaeobiogeographic patterns, and the faunas are expected to have been relatively homogeneous.

According to our results, the Aegean Ecoregion now acts as a link between the Levantine Sea Ecoregion, which displays eastern Mediterranean species [e.g., *Tritia louisi* (Pallary, 1912)], and the Ionian Sea Ecoregion, which yielded Atlantic and Mediterranean species that are also common in the Northern European Seas Province [e.g., *Nucula nucleus* (Linnaeus, 1758)]. The taxa-rich ecoregions are the Western Mediterranean and the Ionian Sea, a pattern consistent with modern faunas (Coll et al., 2010, 2012). Today, the Northwestern Mediterranean hosts the highest diversity, likely linked to primary productivity, depth and temperature, whereas the Southeast supports comparatively poorer faunas, aside from the influx of Lessepsian species through the Suez Canal.

During the LIG, species with colder affinity appear more abundant in Italy (Santagati et al., 2024) than in Greece (this work), likely due to cooler surface waters in the Ionian and Western Mediterranean ecoregions and the greater availability of refugia in these areas (Keppel et al., 2012), reinforced by their relative proximity to the Atlantic. However, more work needs to be done on the species richness of the LIG localities in the Mediterranean, as it can act as a critical example to possible future invasions of tropical species from the Atlantic (Albano et al., 2024).

Ecoregion groupings and dispersal routes in the LIG

Our updated cluster analysis of LIG faunas (Fig. 7(C),(D)) shows clear differences with the ecoregion groupings reported by Melo et al. (2023) (their figs. 2–3, reproduced here as Fig. 7(A),(B)). For bivalves, these authors identified six groups across the Macaronesian archipelagos and NE Atlantic + MED ecoregions: CAB + LES, MAD + SEL, Azores (distinct), CAN, WEM and IOS, with SAU as an outlier. In their gastropod cluster, LES was the outlier, and interestingly, the SAU was clearly in close relation to the Mediterranean ecoregions. With the new updated data from the Mediterranean, the awkward groupings of Cabo Verde and Levantine Sea are clearly distinguished and the Levantine Sea Ecoregion is now in the same group as the rest of the Mediterranean ecoregions (Fig. 7(C),(D)).

A key result is the position of the Saharan Upwelling (SAU) as an outlier within the Mediterranean cluster. This contrasts with Melo et al. (2023), who found SAU to be an outlier to both the Macaronesian archipelagos and the NE Atlantic + MED ecoregions in their bivalve clusters. From our results, it is clear that, as to today, the Mediterranean ecoregions had a clear connection with the Saharan Upwelling Ecoregion (Fig. 7(E)). Furthermore, Melo et al. (2023) indicated that the term "Macaronesia" should only be used with a strict geographic meaning. Since our data set hardly affected the

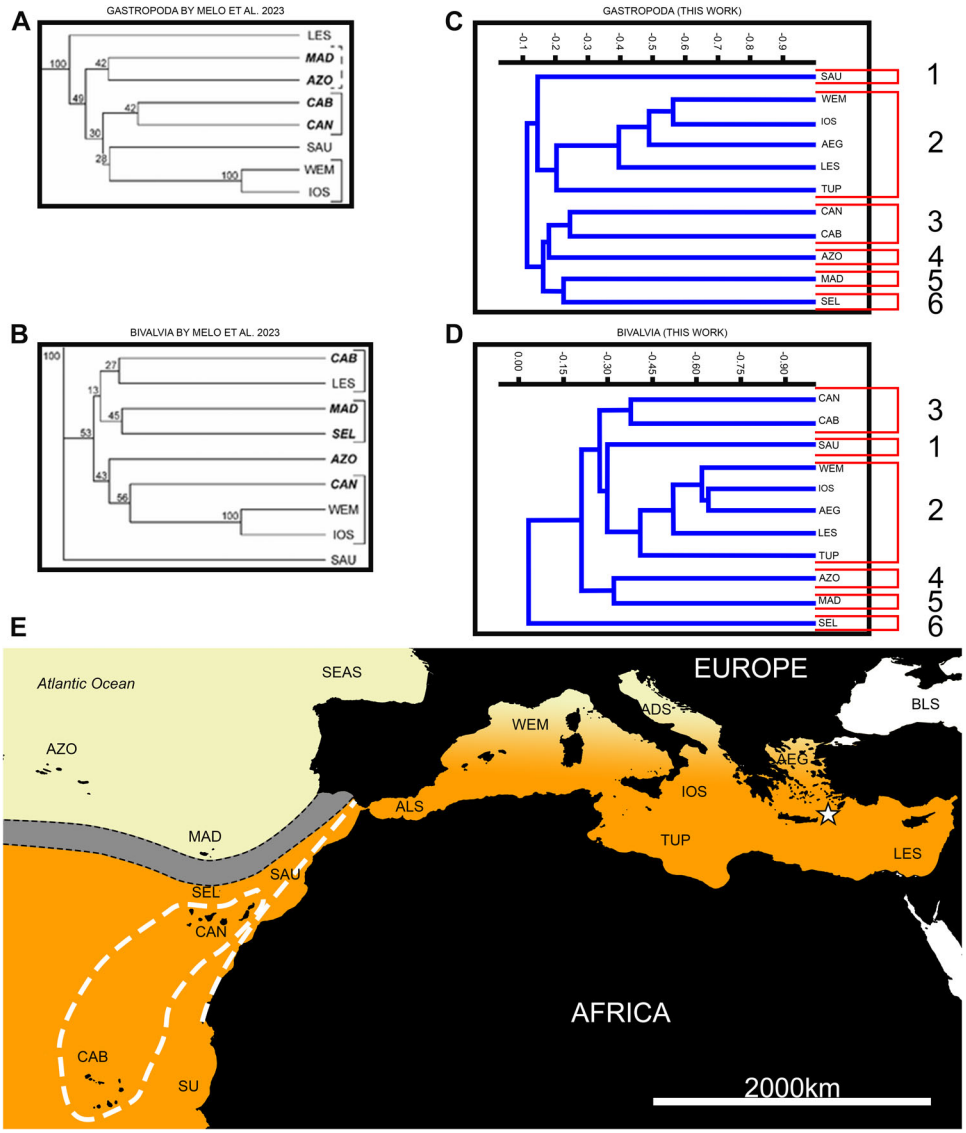


Figure 7. Comparison of graphs of Melo et al. (A–B) and the ones in this work (C–D). Notice the numbers in C and D, indicating 6 distinct regional groupings. (E) Map of the ranges of the Provinces of East Atlantic during the MIS 5e according to Melo et al. (2023), with updated insights on SAU, in comparison to the rest of the ecoregions. Sea colours indicate the sea surface water temperature category: Cream: Temperate waters, Orange: Tropical waters, Grey: Transitional zone. AZO, Azores Archipelago, (MAD), Selvagens (SEL) and Canary Islands (CAN); SAU, Saharan Upwelling; SEAS, South European Atlantic Shelf; ALS, Alboran Sea; WEM, Western Mediterranean; ADS, Adriatic Sea; IOS, Ionian Sea; TUP, Tunisian Plateau/Gulf of Sindra; AEG, Aegean Sea; LES, Levantine Sea; and BLS, Black Sea. CAB, Cabo Verde, SU, Sahelian Upwelling. The white star on the map indicates the location of Karpathos Island. [Color figure can be viewed at wileyonlinelibrary.com]

species lists in the Macaronesian archipelagos that Melo et al. (2023) created, we agree that the ecoregions are not consistent in terms of marine molluscan faunas, with a slight exception of Canary and Cabo Verde archipelagos, where the data on bivalves and gastropods cluster together (Fig. 7(C),(D)), as discussed in Melo et al. (2022a, 2023).

The clusters and the faunal assemblages in the Mediterranean show that, while the Ionian and Western Mediterranean ecoregions had more Atlantic species as discussed above, they were still closely connected to the rest of the Mediterranean and to the Saharan Upwelling. In contrast to Melo et al. (2023), who interpreted the Saharan upwelling system during the LIG as a barrier preventing the northward dispersal of warm-water faunas along the NW African coast, our results indicate that the Saharan Upwelling Ecoregion shares stronger faunal affinities with the Mediterranean basin. This suggests that, at least during certain intervals of the LIG, the Saharan upwelling zone may not have represented a strict biogeographic barrier, but rather a transitional area facilitating connections between the Atlantic and Mediterranean provinces. It is important to note that in our analysis, while the Saharan Upwelling is an outlier within the broader Mediterranean cluster, it shows closer faunal affinity with the Mediterranean than to the Atlantic provinces. It also maintains a connection, particularly in the bivalve clusters, with the Macaronesian archipelagos like the Canaries and Cabo Verde (Fig. 4(D)–(F)).

Recent studies further point that the Saharan upwelling region is not a static barrier, but one whose effectiveness changes with climate forcing. Albano et al. (2024) showed that while the NW African coast is largely unsuitable today for tropical West African taxa, fossil evidence and climate modelling indicate that during the LIG, upwelling was significantly curtailed, allowing range expansions into the Mediterranean. Their simulations predict a similar weakening of this barrier under future warming, with the Canaries and Madeira acting as key stepping stones, consistent with the role that these archipelagos may also have played in past interglacials (Melo et al., 2022a). Our results, showing faunal affinities between the Saharan Upwelling Ecoregion and the Mediterranean during the LIG, are consistent with this pattern:

they support the interpretation that upwelling intensity in NW Africa fluctuated with climate and that these fluctuations periodically allowed connectivity across what is often considered a major ecological divide.

Our results also indicate a strengthened Mediterranean–SAU connection and suggest that the SAU may have served as a viable route for the dispersal of tropical species into the Mediterranean. However, they do not allow us to fully distinguish between the two main hypothesised routes of dispersal that enabled a limited number of tropical species to extend their ranges northward during the LIG (Ávila, 2005; Ávila et al., 2009, 2015, 2019; Muhs et al., 2014; Meco et al., 2022; Melo et al., 2023). Still, case studies of individual species provide critical insights. One particularly significant example is the bivalve *Hyotissa mcgintyi* (Harry, 1985). This species, previously regarded as part of the "Senegalese fauna," may be more important than previously expected for our understanding of LIG biogeography. The distinctive morphology of this species makes it easily identifiable, and its presence in Cabo Verde and the Canary Islands (Melo et al., 2023 and references therein) suggests that its dispersal likely followed the archipelagic route, extending from Macaronesia to the Mediterranean. This is consistent with its absence from the Azores Ecoregion (Ávila et al., 2015) and with palaeobiogeographic reconstructions that showed that suitable tropical and subtropical waters were restricted to more southerly latitudes during the LIG (Melo et al., 2023, fig.6(B),(E)). However, this hypothesis is not without caveats. The alternative pathway—northward dispersal along the West African coast under conditions of reduced upwelling—remains plausible, and the possibility that *Hyotissa* also occupied African coastal environments before or during the LIG cannot be excluded. Future discoveries of *Hyotissa* fossils along the northwest African coast may therefore prove key to clarifying these dispersal routes.

This archipelagic route hypothesis finds support in other species with similar dispersal strategies. *Polinices lacteus* (Guilding, 1834), a widespread amphi-Atlantic species with a planktotrophic larval stage, shows a Pleistocene range expansion that may also indicate this pathway. Similarly, if the presence of *Conus (Chelyconus) ermineus* Born, 1778 in the Mediterranean LIG is confirmed, its planktotrophic larvae (Monnier et al., 2018) would suggest a similar mechanism for its spread into the Mediterranean, as proposed for *Polinices* and *Hyotissa*.

Conclusions

In the Kastellos Bay area, only the topmost bed 5 of the marine so-called "Tyrrhenian" has deposited during MIS 5e. The underlying beds found in the previously identified "Tyrrhenian" terraces have deposited earlier during MIS 6. The updated molluscan assemblage from MIS 5e in Karpathos, integrated with Greek data sets into the global Pleistocene map, provides key insights into faunal composition and climatic conditions during the Last Interglacial. The identification of 64 species, including representatives of the "Senegalese fauna," suggests a mean annual SST of ~20°C in the region, consistent with other Mediterranean data. Several species highlighted in this study and previous Greek literature reveal gaps in the taxonomic knowledge of the Mediterranean LIG. Greek data sets now connect Mediterranean ecoregions, showing similarities across most ecoregions, except the Tunisian one. These findings highlight the importance of refining age calibrations and expanding comprehensive species inventories across Mediterranean LIG localities to strengthen the chronostratigraphic and palaeobiogeographic framework and better understand faunal distributions and climatic changes during this critical period.

Supporting information

Additional supporting information can be found in the online version of this article.

Supplementary file Psarras *et al.* 2025.

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Data Availability Statement

The data that support the findings of this study are available in the supplementary material of this article.

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