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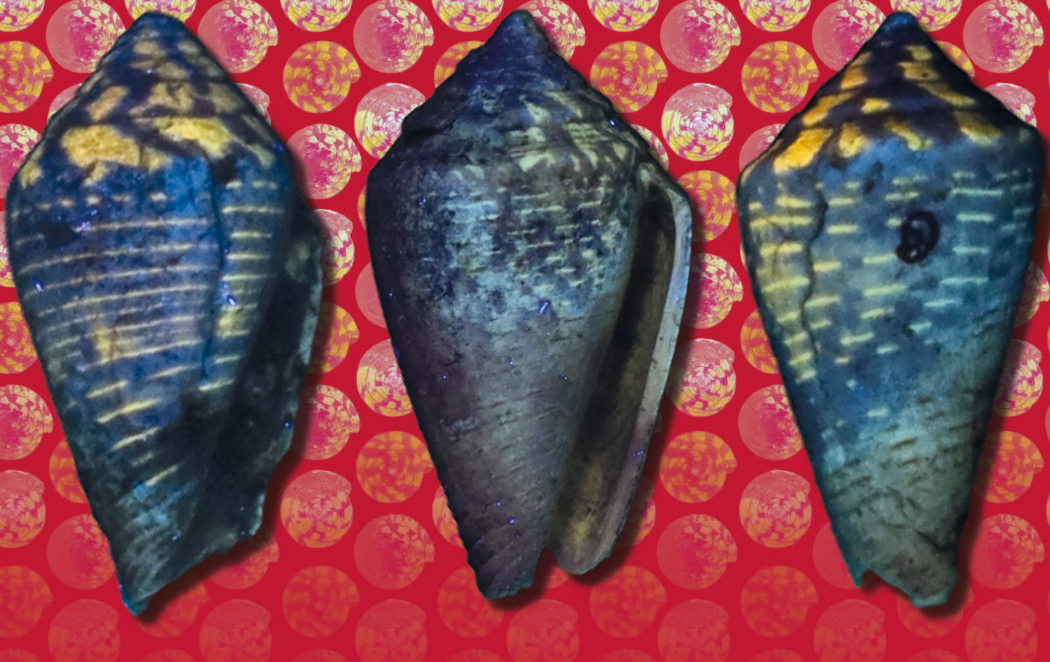

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The Pleistocene Conidae (Mollusca: Gastropoda) from the island of Rhodes (Greece) and their palaeoecological significance

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ABSTRACT

Fossil Conidae from Greece were recently studied in Late Miocene deposits and revealed a very diverse tropical fauna of 33 species, but this diversity decreased during the Pliocene (around six species). From the Pleistocene, four species were previously recorded in the island of Rhodes *Conus* (*Lautoconus*) *ventricosus* Gmelin, 1791 (synonym of *Conus* (*Lautoconus*) *mediterraneus* Hwass in Bruguière, 1792), *Chelyconus pelagicus* (*sensu* Chirli & Forli, 2011, non Brocchi, 1814), *Chelyconus striatulus* (*sensu* Chirli & Forli, 2011, non Brocchi, 1814) and *Lithoconus mercati* (*sensu* Chirli & Forli, 2011, non Brocchi, 1814). To update our knowledge on the conids from Rhodes, we studied material from the Tsampika section (265 ka - 140 ka corresponding from MIS 8 to MIS 6). We used ultraviolet light to observe intraspecific variations in the residual colour patterns. Three species are identified: *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp., *Conus* (*Lautoconus*) sp. and *Conus* (*Monteiroconus*) *tsampikaensis* n. sp. [previously assigned to *C.* (*M.*) *mercati* Brocchi, 1814]. Based on information about the habitat of the extant *Conus* (*Monteiroconus*) species, living today in West Africa and Caribbean in sea surface temperatures above 18 °C, we can hypothesise that the age of the specimens is within the interglacial period of MIS 7e to MIS 7c (241.8-212.9 (±0.4) ka). The different conid assemblages between the interglacial periods MIS 7 (*Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp., *Conus* (*Lautoconus*) sp., and *Conus* (*Monteiroconus*) *tsampikaensis* n. sp.) and MIS 5 ("*Conus* (*Lautoconus*) *ventricosus*" Gmelin, 1791, *Conus* (*Chelyconus*) *ermineus* Born, 1778 and *Conus* (*Monteiroconus*) *tabidus* Reeve, 1844) in the Mediterranean suggest a colonisation of different species during specific interglacial periods, and the subsequent disappearance of most of those during the glacial periods.

KEY WORDS
Pleistocene,
Greece,
Rhodes,
Conidae,
Conus,
palaeoecology,
climate change,
MIS 7,
new subspecies,
new species.

RÉSUMÉ

Les Conidae (Mollusca: Gastropoda) du Pléistocène de l'île de Rhodes (Grèce) et leur importance paléoécologique.
Les conidés du Miocène supérieur de Grèce ont été récemment étudiés et ont révélé une faune tropicale très diversifiée de 33 espèces, mais cette diversité a diminué au cours du Pliocène (environ six espèces). Dès le Pléistocène, quatre espèces ont déjà été recensées dans l'île de Rhodes (*Conus* (*Lautoconus*) *ventricosus* Gmelin, 1791 (synonym of *Conus* (*Lautoconus*) *mediterraneus* Hwass in Bruguière, 1792, *Chelyconus pelagicus* (*sensu* Chirli & Forli, 2011, non Brocchi, 1814), *Chelyconus striatulus* (*sensu* Chirli & Forli, 2011, non Brocchi, 1814) et *Lithoconus mercati* (*sensu* Chirli & Forli, 2011, non Brocchi, 1814). Pour compléter nos connaissances sur les conidés de Rhodes, nous avons étudié le matériel de la coupe de Tsampika (265 ka - 140 ka correspondant aux périodes MIS 8 à MIS 6). Nous avons utilisé la lumière ultraviolette pour observer les variations intraspécifiques des motifs résiduels de couleur et déterminer chaque espèce. Trois espèces sont identifiées : *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp., *Conus* (*Lautoconus*) sp. et *Conus* (*Monteiroconus*) *tsampikaensis* n. sp. [précédemment attribué à *C.* (*M.*) *mercati* Brocchi, 1814]. Se fondant sur les informations sur l'habitat actuel des espèces existantes de *Conus* (*Monteiroconus*), qui vivent en Afrique de l'Ouest et dans les Caraïbes dans des eaux de surface supérieures à 18 °C, on peut supposer que l'âge des espèces rencontrées se situe dans la période interglaciaire chaude de MIS 7e à MIS 7c (241,8-212,9 (±0,4) ka). Les différents assemblages de Conidae entre les périodes interglaciaires MIS 7 (*Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp., *Conus* (*Lautoconus*) sp. et *Conus* (*Monteiroconus*) *tsampikaensis* n. sp.) et MIS 5 ("*Conus* (*Lautoconus*) *ventricosus*" Gmelin, 1791, *Conus* (*Chelyconus*) *ermineus* Born, 1778 et *Conus* (*Monteiroconus*) *tabidus* Reeve, 1844) en Méditerranée suggèrent une colonisation par des espèces différentes, puis la disparition de la plupart d'entre elles pendant les périodes glaciaires.

MOTS CLÉS
Pléistocène,
Grèce,
Rhodes,
Conidae,
Conus,
paléoécologie,
changement climatique,
MIS 7,
sous-espèces nouvelles,
espèces nouvelles.

INTRODUCTION

Conidae are venomous predatory gastropods (Olivera *et al.* 2015; Safavi-Hemami *et al.* 2015) that live mainly in the tropics. They have a rich evolutionary history from the Early Eocene (Duda & Kohn 2005) to the Holocene, diversifying during several radiation events (Kohn 1990).

Conidae from the Late Miocene of Greece have recently been revised, revealing a diversified fauna of 33 species (Psarras *et al.* 2021, 2022, 2023). Conidae from the Pliocene of Greece have been sporadically researched and the exact number of species is unknown and many might be misidentifications, both in collections and published in the literature. The species found so far are reported from the Pliocene localities of the Peloponnese. Two species were recorded by Melentis (1970) (*C. mercati* Brocchi, 1814 and *C. ponderosus* Brocchi, 1814), two were identified by Koskeridou (2006) (*C. ventricosus* Gmelin, 1791 and *C. mediterraneus* Hwass in Bruguière, 1792) and one identified by Koskeridou *et al.* (2017) (C. *striatulus* Brocchi, 1814). Dermitzakis & Georgiades-Dikeoulia (1987) also mention *C. pelagicus* Brocchi, 1814 in one of their tables.

Six Conidae species have been identified in the fossil record from the Mediterranean region during the Pleistocene.

1) *Conus* (*Lautoconus*) *ventricosus* Gmelin, 1791 (junior synonym: *Conus mediterraneus* Hwass in Bruguière, 1792). The name *Conus mediterraneus* is given to almost all specimens found in the Pleistocene that are medium to high spired (e.g., Malatesta 1960; Cuerda 1987). *Conus* (*Lautoconus*) *vayssieri* Pallary, 1906 (Central Mediterranean, deep waters; Monnier *et al.* 2018b) was identified by Cuerda (1987) from the island of Mallorca (MIS 5e), but later Juárez & Matamales-Andreu (2016) rejected this assumption and synonymised it with *Conus* (*Lautoconus*) *ventricosus*. This extant species has been found in many shallow marine Pleistocene faunas around Greece during the MIS 5e (e.g., Mitzopoulos 1933; Psarianos 1961; Anapliotis (1961, 1963a, b, 1966; Anapliotis & Georgiadou-Dikeoulia 1967; Angelier *et al.* 1977). In Rhodes, it has been found by Chirli & Linse (2011) in Kritika (Kritika Formation > 2 Ma according to Moissette *et al.* 2016)), Ladiko (Ladiko-Tsampika Formation, MIS 8-6 according to Cornée *et al.* 2018)) and Malona. Despite the name of the locality, the specimens studied are not from Malona Synthem, deposited during MIS 3-2 (Cornée *et al.* 2018), but are found in the Arkhangelos Fm (from the middle Calabrian (calcareous nannofossil biozone CNPL9, 1.24 Ma; Moissette *et al.* 2010) to Chibanian (calcareous nannofossil biozone CNPL10, between 560 ka and 458 ka; Cornée *et al.* 2018).

2) *Conus* (*Chelyconus*) *ermineus* Born, 1778 is a low-angle-spired cone that was first identified in Tyrrhenian deposits of the Mediterranean as *Conus guinaicus* Hwass, 1792 from Tunisia (de Lamothe 1905) and later identified as *Conus testudinarius* Hwass, 1792 (Dautzenberg 1906) based on its morphology and colour pattern. *Conus testudinarius* is now considered as a junior synonym of *Conus* (*Chelyconus*) *ermineus* Born, 1778 (Vink 1984; Tucker 2010) (distribution in West Africa: Senegal and Cape Verde to Angola; Monnier *et al.* 2018b). *Conus* (*Chelyconus*) *ermineus* Born, 1778, mainly together with *Thetystrombus latus* (Gmelin, 1791) (formerly known in the literature as *Strombus bubonius* Lamarck, 1822), is used as an identifier of the so called 'Senegalese fauna' of the Tyrrhenian MIS 5e, during the last interglacial warm period 128-116 ka (where present is 1950 CE) (e.g., Anapliotis 1966; Muhs

et al. 2015; Repetto *et al.* 2020). It has been found in various localities of Greece (Desio 1931; Mitzopoulos 1933; Anapliotis 1963a, b, 1966; Anapliotis & Georgiadou-Dikeoulia 1967; Keraudren *et al.* 2000).

3) *Conus* (*Monteiroconus*) *tabidus* Reeve, 1844 (Senegal and Cape Verde to Angola, see Fig. 5) was identified from Tyrrhenian deposits (MIS 5e) of Mallorca Island, Spain (Juárez & Matamales-Andreu 2016). This species has not been found in Greece.

In addition, Chirli & Linse (2011), along with *Conus* (*Lautoconus*) *ventricosus* Gmelin, 1791, cited three further species from the Pleistocene of the island of Rhodes (Greece) but did not provide more precise stratigraphic data.

4) *Chelyconus pelagicus* (Brocchi, 1814) (now accepted as *Conus* (*Lautoconus*) *pelagicus* Brocchi, 1814) and recorded from the early Miocene (Burdigalian) to late Pliocene of Europe; Landau *et al.* 2013; Harzhauser & Landau 2016). It was also found in the Pleistocene of Malona (Chirli & Linse 2011) (CNPL9-CNPL10; Moissette *et al.* 2010; Cornée *et al.* 2018), with well-preserved specimens displaying patterns of irregularly arranged yellow to orange spire lines.

5) *Chelyconus striatulus* (Brocchi, 1814) (now accepted as *Conilithes striatulus* (Brocchi, 1814)) is recorded in the Miocene and the Pliocene of Europe (Psarras *et al.* 2021) and was found in the sections of Lardos (Lindos Bay and Cape Arkhangelos formations = 2 Ma to 458 ka; E.K. personal observations), Tsampika (MIS 7, 265-140 ka; Cornée *et al.* 2018), Faliraki (MIS 3, 38-18 ka; Cornée *et al.* 2018) and Malona (CNPL9-CNPL10; Moissette *et al.* 2010; Cornée *et al.* 2018). It displays some light spiral brown lines.

And 6) *Lithoconus mercati* (Brocchi, 1814) (now accepted as *Conus* (*Monteiroconus*) *mercati* Brocchi, 1814). This species was recorded in Malona (CNPL9-CNPL10; Moissette *et al.* 2010; Cornée *et al.* 2018). As most Miocene references to this species were misidentifications, the age of the species has been restricted to the Pliocene of the Mediterranean, see Psarras *et al.* 2021, 2022, 2023).

Today, three extant species are hinted to occur in the Mediterranean, excluding Lessepsian species: *Conus* (*Lautoconus*) *ventricosus* Gmelin, 1791, *Conus* (*Lautoconus*) *vayssierei* Pallary, 1906, and *Conus* (*Lautoconus*) *desidiosus* A. Adams, 1854 (see WoRMS – World Register of Marine Species [2022]), although other authors consider only *Conus* (*Lautoconus*) *ventricosus* as a valid species (Filmer 2011). Recently, it has been suggested that *Conus* (*Lautoconus*) *ventricosus* is a name that includes at least three cryptic species (Abalde *et al.* 2023), but more studies are needed to validate this proposal.

Considering that conids display wide morphological variations (e.g., Malatesta 1960; Chirli & Linse 2011; Monnier *et al.* 2018a, b), and that most of the Pleistocene species have been identified solely based on their shell morphology, we propose a study of Pleistocene material adding the residual colour pattern revealed under UV light. The diversity of colour patterns is helpful to distinguish many living species and is an important tool for the identification of fossil conids (e.g., Hendricks 2015; Psarras *et al.* 2021, 2022, 2023 for the Miocene of Crete). In this paper, we study a Middle Pleistocene site (Tsampika) on the island of Rhodes, Greece, to clarify which species existed during a specific period (MIS 8-MIS 6 = 265-140 ka; Cornée *et al.* 2018) before the invasion of the Tyrrhenian 'Senegalese fauna' into the Mediterranean (MIS 5e = 128-116 ka).

GEOLOGICAL BACKGROUND

Rhodes is located in the eastern part of the Hellenic forearc (Jolivet *et al.* 2013) (Fig. 1A). Due to the increased curvature of the forearc, the eastern part has been subjected to stretching accommodated along the NE-SW trending strike-slip faults parallel to the plate boundary with Africa (e.g., ten Veen 2004; Tur *et al.* 2015; Kaymakcı *et al.* 2018). As a result of this movement, the Rhodes Basin, located east of the homonymous island, began to open during the Messinian, before 6 Ma (Aksu *et al.* 2018; Cornée *et al.* 2018). This process involved considerable subsidence and uplift of the island, which was responsible for the deposition of Pleistocene marine sediments that are now mainly found on the east coast of the island (Cornée *et al.* 2018; Quillévéré *et al.* 2019) (Fig. 1B). The Pleistocene marine sediments and their faunas have been extensively studied in recent years. These works discussed fish associations (Moissette *et al.* 2013; Agiadi *et al.* 2018, 2019, 2022, 2023), seagrass associations (Moissette *et al.* 2007; Koskeridou *et al.* 2019), pollen and marine faunal oscillations (Joannin *et al.* 2007), chiton findings (Koskeridou *et al.* 2009), bivalve faunas (Thomsen *et al.* 2009; Porz *et al.* 2024), bryozoans (Moissette *et al.* 2010), as well as isotope and climatic analyses (Lécuyer *et al.* 2012).

The studied locality of Tsampika belongs to the Ladiko-Tsampika Formation, whose age has recently been constrained from 265 ka (Middle Pleistocene = Chibanian) to 140 ka (Upper Pleistocene) (Cornée *et al.* 2018), deposited from MIS 8 to MIS 6. The Formation was unconformably deposited over the eroded Cape Arkhangelos Formation, the basement or the Kritika Formation in palaeovalleys (Cornée *et al.* 2006, 2018). The Ladiko-Tsampika Formation contains siliciclastic deposits of mostly marine shallow-water sediments. There are eight depositional sequences, with a ninth sequence only slightly exposed in the upper part of the series, being probably eroded during an interglacial stage (MIS 6) (Cornée *et al.* 2006). Those sequences have been attributed to glacial and interglacial stages (Cornée *et al.* 2006).

The material was collected mainly from a new road west of Tsampika beach in a small section about 13 m thick (Figs 1F; 2), located in front of a palaeo-cliff of Jurassic limestone (basement, Fig. 1E), perforated by lithophagids (Fig. 2B, C). The base of the section consists of greyish sandy marls 2 m thick (bed TSS a of Fig. 1), with cerithids and a diversified fauna (Fig. 2B-F). The second unit (bed TSS b of Fig. 1) consists of greyish marls 2 m thick with abundant coral branches of *Cladocora caespitosa* (Linnaeus, 1767) (Fig. 2D). The third unit (bed TSS c) consists of silty to sandy grey marls 3 m thick with a few macrofossils (Fig. 2). Two more units have

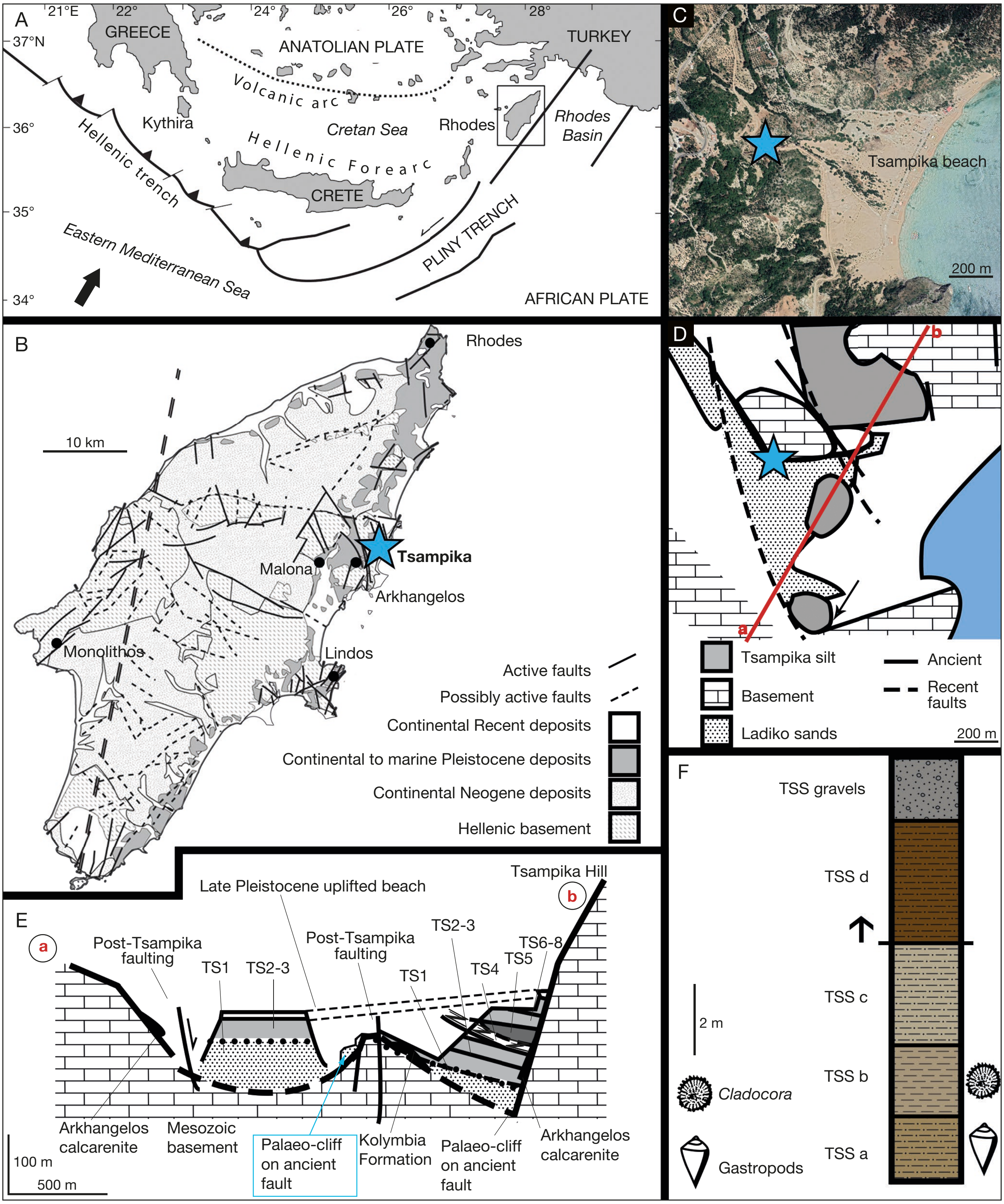

Fig. 1. — Information about the studied section of Tsampika in Rhodes, Greece: **A**, general tectonic setting of the southern Aegean. **B**, geological map of Rhodes with the site of Tsampika as a blue star (✶); **C**, satellite position of the studied section; **D**, geological map of Tsampika area, displaying the section (✶), the cross section of Cornée *et al.* (2006) (**red line a-b**) and the location of the section of Cornée *et al.* (2018) (**black arrow**); **E**, cross section of the Ladiko-Tsampika Formation in Tsampika that was studied by Cornée *et al.* (2006), highlighting the area of study with a **blue arrow**; **F**, synthetic stratigraphic column of the section with the Conidae specimens recovered from TSS a. Notice that TSS d and TSS gravels (**above arrow**) were not visible on the figured section (Fig. 2), but were identified in nearby smaller sections. Maps A and B were modified from Cornée *et al.* 2018; D-E from Cornée *et al.* 2006. TSS beds belong to the TSS1 sequence of Cornée *et al.* (2006, 2018).

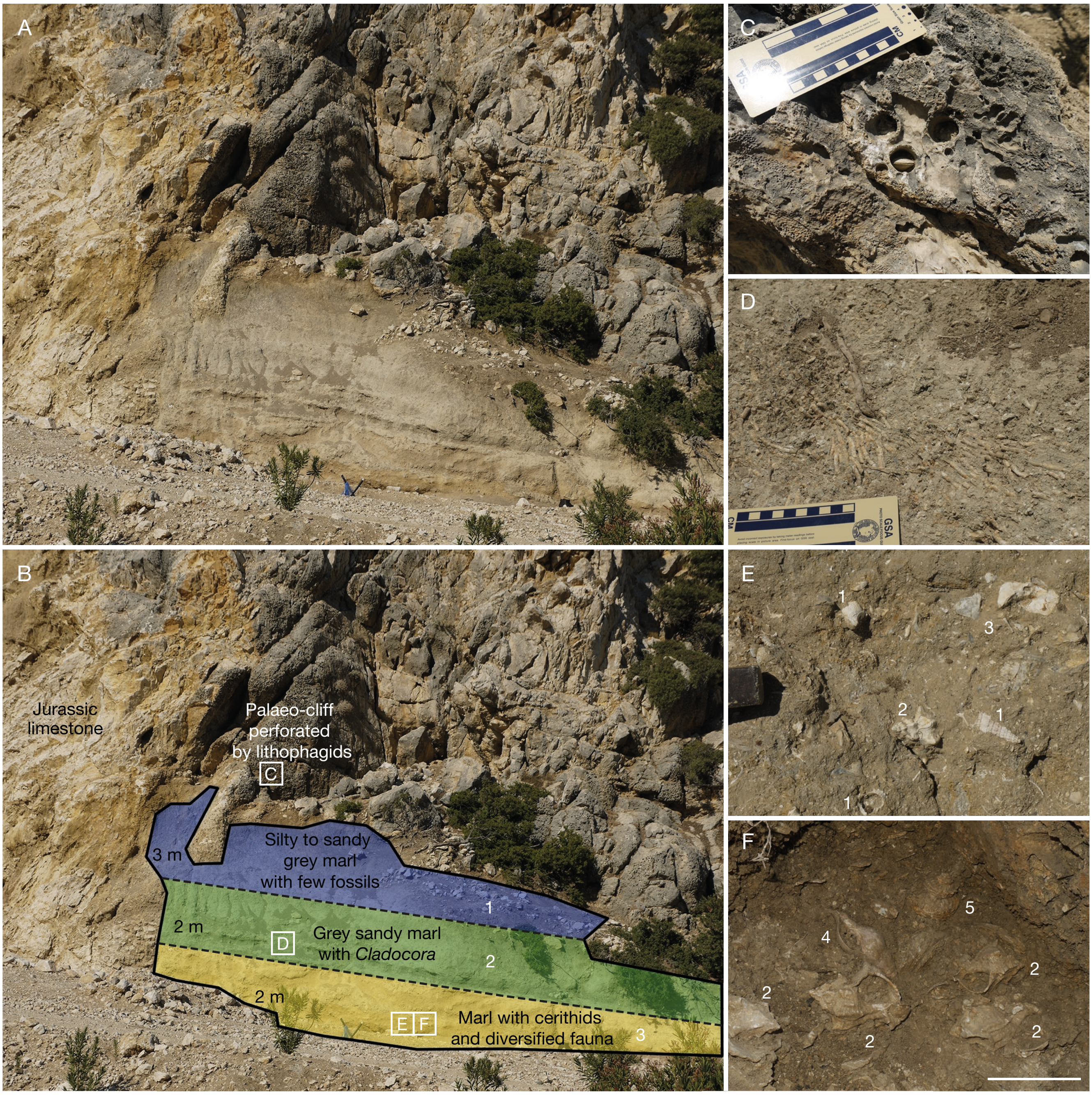

FIG. 2. — Small section of Tsampika along the new road on the south of Tsampika beach: **A**, the section is located in front of a palaeo-cliff of Jurassic limestones and has a small inclination; **B**, the section is divided into three units, from the base to the top: **1**, sandy marl with cerithids and a rich malacofauna (= TSS a bed of Fig. 1F); **2**, grey marl unit rich in *Cladocora* (= TSS b bed of Fig. 1F); **3**, silty to sandy grey marl bed (= TSS c bed of Fig. 1F); numbers indicate the position of the associated faunas; **C**, detailed view of the palaeo-cliff perforated by the bivalve *Lithophaga*; **D**, *in situ* coral branches of *Cladocora caespitosa*; **E**, assemblage with *Hexaplex* (*Truncularíopsis*) *trunculus* (Linnaeus, 1758) (**2**), *Cerithium vulgatum* Bruguière, 1792 (**1**) and *Ostrea edulis* Linnaeus, 1758 (**3**) (hammer for scale); **F**, Assemblage with *Hexaplex* (*Truncularíopsis*) *trunculus* (Linnaeus, 1758) (**2**), *Euthria cornea* (Linnaeus, 1758) (**4**), and *Bolma rugosa* (Linnaeus, 1767) (**5**). Scale bar: F, *c.* 4 cm.

been identified North-East of the section: a 3.5 m thick unit (TSS d) of brown sandy marls with lignite and a 2 m thick unit containing gravelly sands (Fig. 1F). The section has been attributed to the TSS1 unit of Cornée *et al.* (2006, 2018) (Fig. 1E).

Cornée *et al.* (2006) thoroughly studied TS1 unit (= TSS1 according to Cornée *et al.* 2018), concluding that it acted as infill of the deepest part of the Ladiko-Tsampika palaeovalley resting on bioeroded palaeo-cliffs. On top of fluvial deposits (not present in this section), they recorded *Cladocora caespitosa* and the genera *Anadara* J. E. Gray, 1847, *Calliostoma* Swainson, 1840, *Conus* Linnaeus, 1758, *Triphora* Blainville, 1828, *Hexaplex* (*Truncularíopsis*) Cossmann, 1921, and rare planktonic foraminifers (Cornée *et al.* 2006), acting as representatives of a nearshore environment of waters reaching depths of up to 40 metres. Cornée *et al.* (2018) found this fauna on the southern part of Tsampika beach inside blackish clay deposits (Fig. 1D, see arrow). Both their results coincide with our TSS a and TSS b, where we also spotted *Cladocora caespitosa*, and a very diversified molluscan fauna of around 120 species indicating shallow marine palaeoenvironments (see Fig. 2C-F). Furthermore, they have also identified horizons of rare marine input (Cornée *et al.* 2006, fig. 9) coinciding with our findings on TSS c. Finally on the upper parts of TSS1, they found lagoonal and lacustrine deposits, covered by fluvial conglomerates of calcareous pebbles, very similar to those identified herein (Fig. 1F). Therefore, the correlation of those sections can be made. We conclude that the studied section here is part of TS1 of Cornée *et al.* (2006), as well as TSS1 of Cornée *et al.* (2018).

MATERIAL AND METHODS

Material

The studied Conidae were collected throughout the last decade from various parts of the Tsampika beach. All of them come from the lower horizons of Tsampika, namely TSS1, TSS2 and TSS3 (according to Cornée *et al.* 2018), found in shoreface deposits. Most of the material studied was collected during a field trip in September 2012 by Didier Merle, Efterpi Koskeridou, Pierre Moissette, Bruno Caze, Christina Giamali, and Konstantina Agiadi. The material is kept at the Muséum national d'Histoire naturelle, Paris, and at the Museum of Geology and Paleontology of the National and Kapodistrian University of Athens.

Methods

The Tortonian Conidae of Crete, Greece, have recently been re-evaluated using UV light (Psarras *et al.* 2021, 2022, 2023). Here we follow the same approach to identify the species. The material was photographed under natural and UV light to describe the species (e.g., in older papers, Olsson 1967; Vokes & Vokes 1968; Krueger 1974; Hoerle 1976; in more recent papers, Merle *et al.* 2008; Caze 2010; Caze *et al.* 2011b, 2011a; Landau *et al.* 2013; Caze *et al.* 2015; Hendricks 2015; Harzhauser & Landau 2016; Hendricks 2018).

As in previous studies of fossil conids (Psarras *et al.* 2021, 2022, 2023), species description is based on a combination of morphological characters and residual colour patterns under UV light (Olsson 1967; Vokes & Vokes 1968; Krueger 1974; Hoerle 1976; Merle *et al.* 2008; Caze 2010; Caze *et al.* 2011a, 2011b; Landau *et al.* 2013; Caze *et al.* 2015; Hendricks 2015; Harzhauser & Landau 2016; Hendricks 2018; Crippa & Masini 2022). Most specimens were not bleached in sodium hypochlorite, as the patterns were clearly visible under UV light. The holotype of *Conus* (*Monteiroconus*) *tsampikaensis* n. sp. was bleached in dilute bleach for 15 hours, then washed and soaked in water for another day to remove all the bleach. It was then left to dry. Unfortunately, this experiment did not result in any change in the patterns already shown on the anterior part of the shell and the spire, before bleaching.

In order to assess the current species occurrences, we got georeferenced occurrence data of *Conus* (*Monteiroconus*) *ambiguus* Reeve, 1844, *Conus* (*Monteiroconus*) *tabidus* Reeve, 1844, *Conus* (*Monteiroconus*) *bellocqae* van Rossum, 1996, and *Conus* (*Chelyconus*) *ermineus* Born, 1778 of their native ranges from the Global Biodiversity Information Facility database (GBIF, https://www.gbif.org). Those were verified from other sources such as the SeaLifeBase (www.sealifebase.org; Palomares & Pauly 2023), International Union for Conservation of Nature's Red List of Threatened Species (IUCN Red List, https://www.iucnredlist.org/) databases and other references such as the works of Tenorio *et al.* (2020) and Monnier *et al.* (2018a). The occurrences were plotted on the map of West Africa. Current temperature estimates of the shallow waters of West Africa were taken from Sessa *et al.* (2013) temperature estimations for each region surrounding Africa (average of data from 0-50m depths).

Photographs: the figures from the MNHN, Paris were taken with two ATLAS MMT GmbH Fluotest Forte UV lamps placed diagonally on either side of the figured specimen. For the preparation of the figures, we follow Psarras *et al.* (2023).

Shell terminology and measurements: we follow the terminology of Smith (1930), Röckel *et al.* (1995) and Hendricks (2009) for the shell descriptions. For the measurements of the subsutural flexure, we follow Harzhauser & Landau (2016). Measurements were made on individual shells using Photoshop and are therefore considered not entirely accurate, but sufficient for this type of study. SL = shell length (shell lengths are distinguished as follows: large (> 80 mm), moderately large (55-80 mm), medium-sized (35-55 mm), moderately small (25-35 mm), small (15-25 mm) and very small [< 15 mm]). For the systematic classification, we follow Puillandre *et al.* (2014, 2015) and refer to *Lautoconus* Monterosato, 1923 and *Monteiroconus* da Motta, 1991 as subgenera, as Psarras *et al.* (2021, 2022, 2023) have done. For the descriptions of the colour pattern, we use the phrase 'levels of pigmentation' from Meinhardt (1998) for the patterns that show two to four different colours.

Abbreviations

Institutional abbreviations

AMPG (IV)	National and Kapodistrian University of Athens, Museum of Geology and Paleontology, Invertebrate Collection;
MNCN	Museo Nacional de Ciencias Naturales, Madrid;
MNHN	Muséum national d'Histoire naturelle, Paris;
MNHN.F	MNHN, collection de paléontologie, Paris.

Collection abbreviations

SC	Specimen from Sicily, stored in MNCN;
CR	Specimen from Crete, stored in MNCN;
BAU	Malacological collection of the Department of Biology and Biotechnologies 'Charles Darwin' (BBCD), Sapienza University, Rome, Italy.

Other abbreviations

MIS	Marine isotope stages;
CNPL	Calcareous nannofossil biozones in the Pliocene-Pleistocene-Recent interval;
TSS	Tsampika section.

SYSTEMATIC PALAEONTOLOGY

Class GASTROPODA Cuvier, 1795
Subclass CAENOGASTROPODA Cox, 1960
Order NEOGASTROPODA Wenz, 1938
Superfamily Conoidea Fleming, 1822
Family Conidae Fleming, 1822

Genus *Conus* Linnaeus, 1758

Type species. — *Conus marmoreus* Linnaeus, 1758 by subsequent designation by Children (1823: 107). Recent, Indo-Pacific.

Subgenus *Lautoconus* Monterosato, 1923

Type species. — *Conus mediterraneus* Hwass in Bruguière, 1792 (synonym of *Conus ventricosus* Gmelin, 1791) by original designation. Recent, Mediterranean Sea and adjacent Atlantic Ocean region.

Remarks

The Tortonian species of this subgenus were recently discussed in Psarras *et al.* (2022). They differ from the species of *Conus* (*Monteiroconus*) da Motta, 1991 by the convex spire and the straight to convex sutural ramps, as well as the relatively small size.

Conus* (*Lautoconus*) *ventricosus rhodesensis n. subsp.
(Figs 3-5)

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Chelyconus pelagicus – Chirli & Linse 2011: 165, pl. 56, figs 1a-d, 6 (non Brocchi, 1814).

Chelyconus striatulus – Chirli & Linse 2011: 165, pl. 56, figs 2a-d (non Brocchi, 1814).

Lautoconus mediterraneus – Chirli & Linse 2011: 166, pl. 56, figs 3a-d. (non Hwass, 1792).

Etymology. — From the island of Rhodes, where the species has been found.

Type locality. — Tsampika, Tsampika section, Rhodes, Greece.

Type horizon. — Ladiko-Tsampika Fm, Pleistocene, Rhodes, Greece.

Type material. — **Greece** • 9 specimens; Rhodes; Ladiko-Tsampika Fm, Tsampika section, TSS block; Lower Pleistocene (Gelasian) to Upper Pleistocene; holotype: MNHN.F.A88160; paratypes: MNHN.F.A88161-A88168 • 1 specimen; Ladiko-Tsampika Fm, Tsampika section, TSS 2; Lower Pleistocene (Gelasian) to Upper Pleistocene; paratype: AMPG (IV) 4048 • 5 specimens; Ladiko-Tsampika Fm, Tsampika section, TSS south; Lower Pleistocene (Gelasian) to Upper Pleistocene; paratypes: AMPG (IV) 4049-4053.

Other material examined. — **Greece** • 14 specimens; Rhodes; Ladiko-Tsampika Fm, Tsampika section, TSS 2; AMPG (IV) 4034-4047 • 2 specimens; Rhodes; Ladiko-Tsampika Fm, Tsampika section, TSS 3; Lower Pleistocene (Gelasian) to Upper Pleistocene; AMPG (IV) 4054, 4055 • 2 specimens; Rhodes; Ladiko-Tsampika Fm, Tsampika section, TSS 1; Lower Pleistocene (Gelasian) to Upper Pleistocene; AMPG (IV) 4056, 4057 • 1 specimen; Rhodes; Kritika Fm, Kritika Hospital; Lower Pleistocene (Gelasian) to Upper Pleistocene; MNHN.F.A90344 • 104 specimens; Rhodes; Ladiko-Tsampika Fm, Tsampika section; Lower Pleistocene (Gelasian) to Upper Pleistocene MNHN.F.A90343 (lot) • 1 specimen; Rhodes; Archangelos Fm, Malona; Lower Pleistocene (Gelasian) to Upper Pleistocene; AMPG (IV) 4060.

Stratigraphic range. — Gelasian (Lower Pleistocene) to Upper Pleistocene of Rhodes, Greece (Chirli & Linse 2011; this work).

Description

Shell

Small to moderately-sized shells (maximum length of about 25.7 mm), with conical spire of variable height. Spire whorl outline slightly concave to slightly convex. Early spire whorls conical with spiral grooves on sutural ramps. Later spire whorls conical, straight to slightly convex, with occasional spiral grooves on sutural ramp, sometimes slightly striated to elevated. Shoulder angulated to smooth, with maximum diameter on shoulder to just below shoulder. Subsutural flexure shallow, moderately curved, nearly symmetrical. Spiral grooves and cords along the last whorl, intense at anterior third of last whorl.

Colour pattern

Colour pattern of the spire whorls consists of one level of pigmentation of broad axial to thin flammulae. The pattern on the shoulder consists of a non-fluorescent band at carina. The axial flammulae levels of pigmentation of the spire whorls rarely overlap the non-fluorescent band (E3). The colour pattern on the last whorl consists of spiral rows of dashes, of variable length (Fig. 4), alternating with non-fluorescent dots. Fluorescent bands exist in different heights and widths. Usually there is one band in the middle whorl and one in the anterior part of the last whorl, separated by a non-fluorescent band. In this fluorescent band, the spiral rows of dashes are less long and dense.

Remarks

We have examined 140 specimens. This group shows a great morphological diversity, as there are both shells with elevated spires and low spired ones and the spiral whorls can be striated or smooth (Fig. 3). Nevertheless, the residual colour patterns are similar in all specimens studied. There are some specimens (Fig. 4) with aberrant colour patterns, but we provisionally consider them as intraspecific variations.

Recently, Abalde *et al.* (2023) found evidence of at least three mitochondrial '*Conus ventricosus*' clades corresponding to three cryptic species. They (Abalde *et al.* 2023) provisionally named those clades based on the colours used on their analyses (with the main clades being green, violet, cyan), with the 'green' and 'cyan' clades being present today in Greece, while the 'violet' clade is present in central and western Mediterranean (Abalde *et al.* 2023) (see colours in Fig. 5). The likelihood of many cryptic species in the Mediterranean specimens (Tenorio *et al.* 2020; Abalde *et al.* 2023) is evidenced by mitochondrial studies, but the morphology and colour pattern characteristics of those clades remain

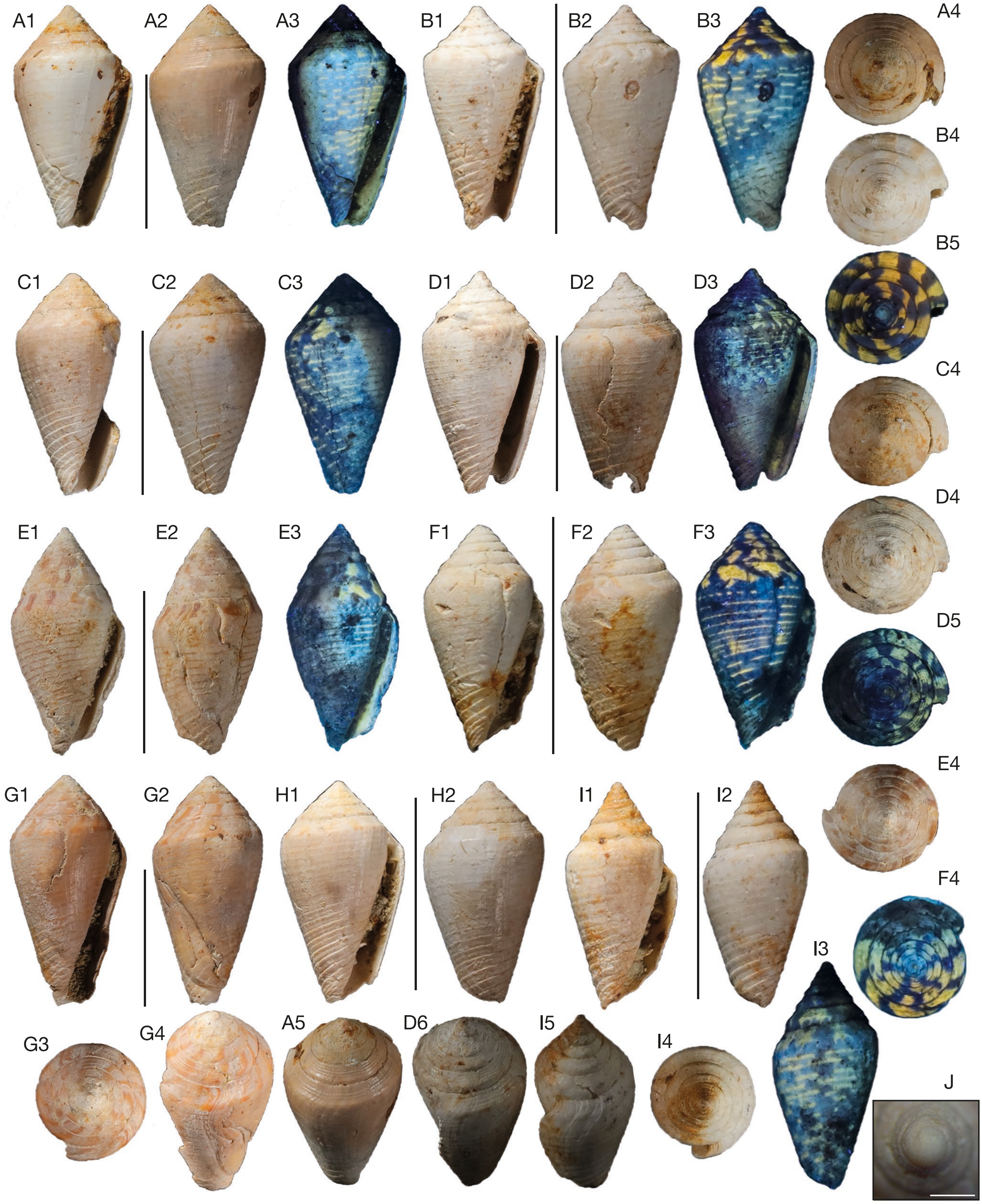

Fig. 3. — *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp. from the Pleistocene of Tsampika, Rhodes (Greece) under natural (**A1**, **A2**, **A4**, **A5**, **B1**, **B2**, **B4**, **C1**, **C2**, **C4**, **D1**, **D2**, **D4**, **D6**, **E1**, **E2**, **E4**, **F1**, **F2**, **F4**, **G1-G4**, **H1**, **H2**, **I1**, **I2**, **I4**, **J**) and UV (**A3**, **B3**, **B5**, **C3**, **D3**, **D5**, **E3**, **F3**, **F4**, **I3**) light: **A**, holotype MNHN.F.A88160; **B-J**, paratypes; **B**, MNHN.F.A88161; **C**, MNHN.F.A88162; **D**, MNHN.F.A88163; **E**, MNHN.F.A88164; **F**, MNHN.F.A88165; **G**, MNHN.F.A88166; **H**, MNHN.F.A88167; **I**, MNHN.F.A88168; **J**, AMPG (IV) 4048, protoconch of juvenile shell. Scale bars: A-I, 1 cm; J; 500 µm.

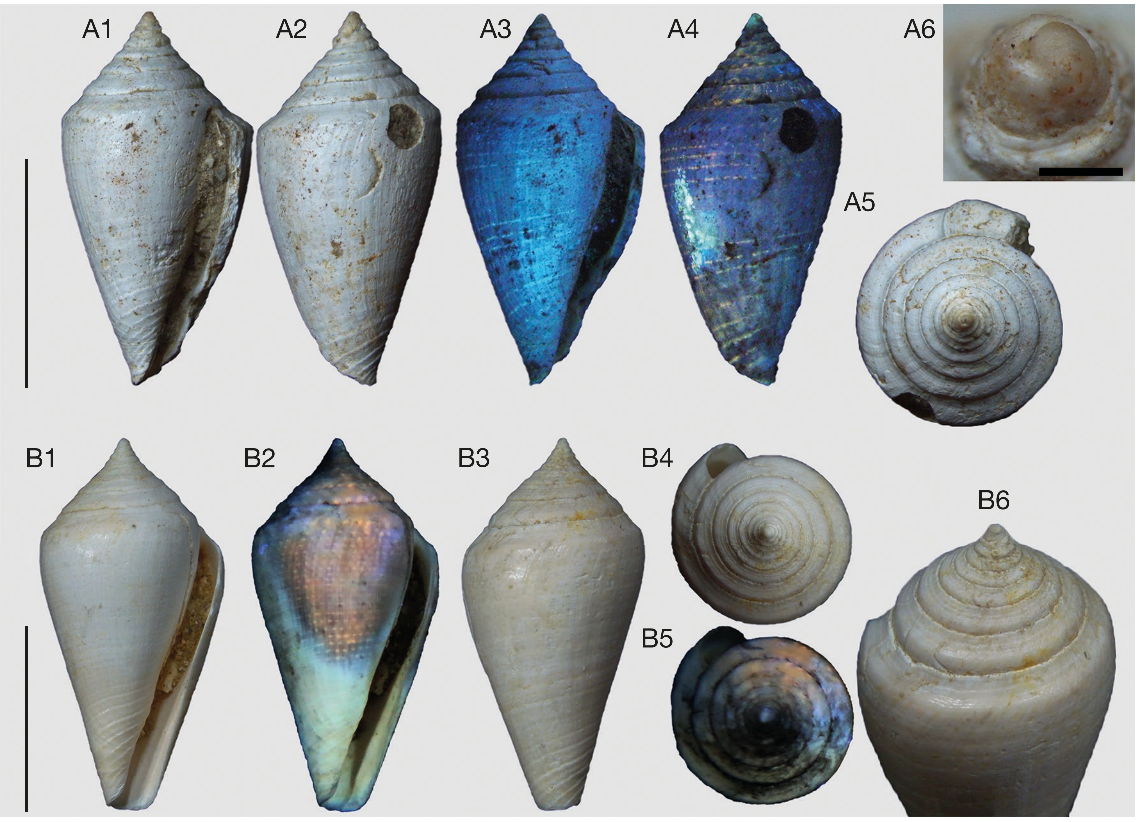

Fig. 4. — Specimens of *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp. from the Pleistocene of Rhodes (Greece), displaying aberrant patterns under natural (**A1**, **A2**, **A5**, **A6**, **B1**, **B3**, **B4**, **B6**) and UV (**A3**, **A4**, **B2**, **B5**) light: **A**, paratype AMPG (IV) 4053, Tsampika: a pattern of almost continuous spiral lines; **B**, specimen AMPG (IV) 4060, Malona: a pattern of very dense and small spiral dashes. Scale bars: A1-A5, B1-B5, 1 cm; A6, 500 µm; B6, close up view of B1, not to scale.

unclarified, since specimens of the same lineage present greatly diversified morphology and pattern variations (Fig. 5C4-C5) (Abalde *et al.* 2023).

The Pleistocene juvenile forms (Fig. 5A) are rather similar to the extant C. (*Lautoconus*) *ventricosus* Gmelin, 1791 *sensu lato*. However, comparing the Pleistocene adult specimens with extant adult of "*C. ventricosus*", there are some differences in the colour patterns. The spiral rows of extant adult "*Conus* (*Lautoconus*) *ventricosus*" are more numerous and the flakes, as well as the blotches, are axially coordinated, sometimes in a zigzag pattern. Given the supposed great morphological and colour pattern variability of "*Conus* (*Lautoconus*) *ventricosus*", the studied specimens could be attributed to this species, but the molecular phylogeny results of Abalde *et al.* (2023) are troubling from a palaeontological perspective, because the unnamed cryptic species cannot be distinguished using shells characters (Abalde *et al.* 2023). On the other hand, we prefer to avoid erecting a new species, as the Pleistocene specimens are geologically young (2 Ma (Kritika) to 140 ka (Tsampika); Moissette *et al.* 2016; Cornée *et al.* 2018) and could belong to one of the extant cryptic species mentioned in Abalde *et al.* (2023). Therefore, taking account of the differences of colour patterns observed in the Pleistocene specimens, we erect a new chronostratigraphic subspecies *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp. as an ancestral subspecies of one of the '*C.* (*Lautoconus*) *ventricosus*' clades. The concept of chronosubspecies is related to the phyletic gradualism model of evolution, and it also relies on an extensive fossil record since morphological changes accumulate over time. It is widely used by the palaeontologists (e.g., Ward & Kennedy 1993 for the ammonites; Fordinál 1997 for the bivalves; Merle *et al.* 2011 for the gastropods Muricidae); Saupe & Becker 2022 for the conodonts).

The pattern of *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp. could also be compared with other species considered as *Conilithes* Swainson, 1840, such as *Conilithes* sp. and *Conilithes striatulus* (Brocchi, 1814) from the Tortonian of Crete (Psarras *et al.* 2021), both of which display patterns of dashes along the last whorl. The outline of the juvenile *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp. also resembles that of several extinct *Conilithes* Swainson, 1840, the main difference being that the sutural ramps are smooth in *Conilithes*, whereas *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp. has spiral grooves on the sutural band. *Conilithes striatulus* (Brocchi, 1814) from the Pliocene of Italy has a similar pattern (Pavia *et al.* 2022: fig. 26g), but has an angulated shoulder and a coeloconoid suture, all features that diverge from the subgenus *Conus* (*Lautoconus*). The two species identified by Chirli & Linse (2011) as *Chelyconus striatulus* (Brocchi, 1814) and *Chelyconus pelagicus* (Brocchi, 1814) are both morphologically similar

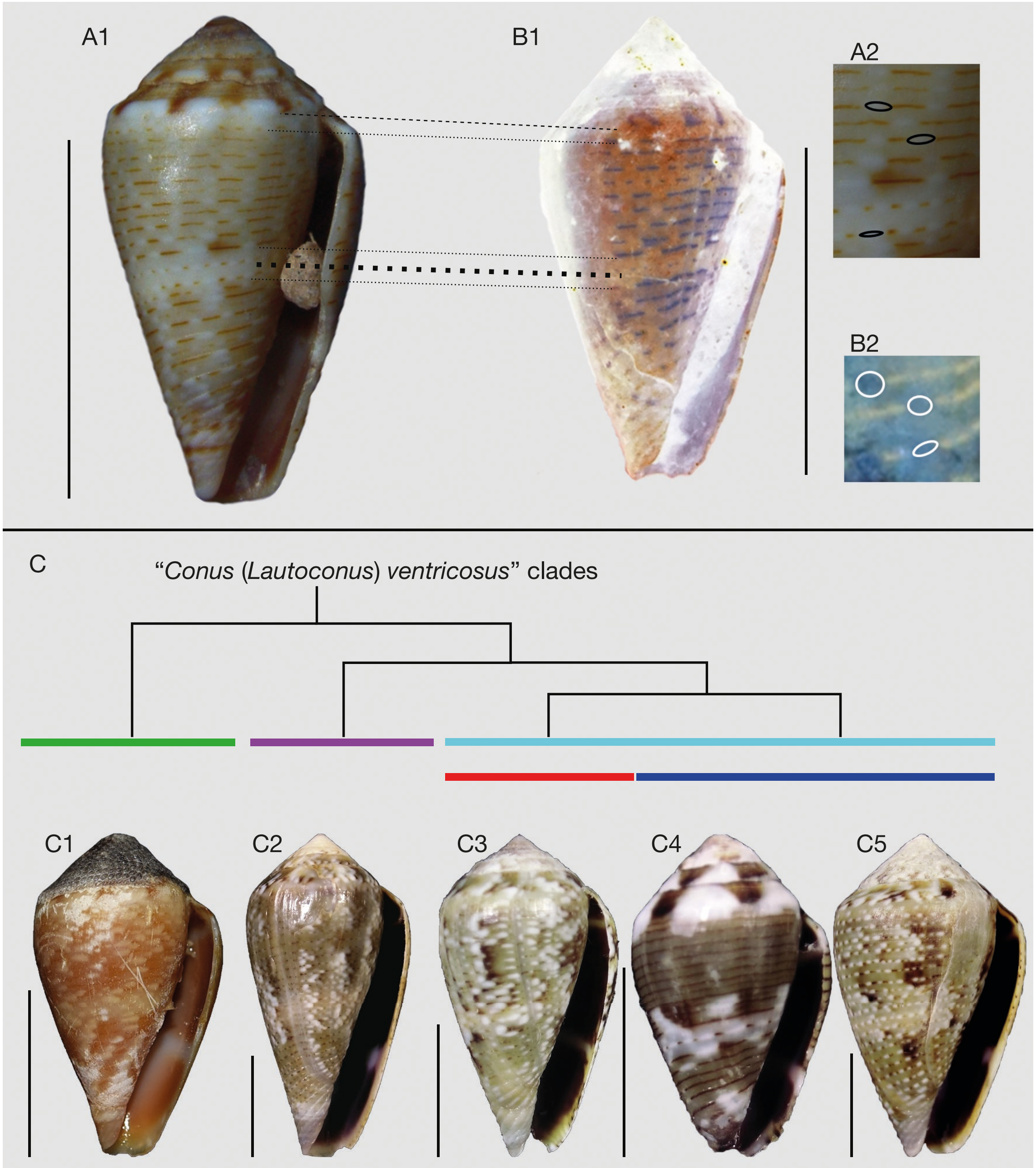

Fig. 5. — Colour pattern comparison between the extant *Conus* (*Lautoconus*) *ventricosus* complex species (natural light) clades (**A**, **C1**-**C4**) and *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp. from the Pleistocene of Tsampika, Rhodes (Greece) (UV light, inverted colours) (**B**). Thin dashed lines (**A1**, **B1**) include non-fluorescent bands, thick dashed line indicates the included spiral row of dashes. Encircled areas (**A2**, **B2**) are non-fluorescent spiral snowflakes in between the spirally arranged dashes. Depiction of five specimens of "*Conus ventricosus*" mitochondrial clades (green, violet and cyan, the latter divided into red and blue) of Abalde *et al.* 2023 (**C**). Note that specimens of the same clade have very different morphological and colour pattern characteristics (**C3**-**C5**). **A**, AMPG (IV) 4033, Artemis, east Attica, Recent, Greece; **B**, holotype MNHN.F.A88160, Tsampika, Rhodes; **C1**, BAU_1550.1, Koutsomiti island, Astypalaia, Greece; **C2**, SC002, Punta Regilione-Marina di Modica, Sicily, Italy; **C3**, CR18, Kakkos Bay, south-east Crete, Greece; **C4**, CR23, Kakkos Bay, south-east Crete, Greece; **C5**, CR009, Plaka, north-west Crete, Greece. Specimen figures **C1**-**C5** from Manuel J. Tenorio and Samuel Abalde. Scale bars: 1 cm.

to *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp. and have similar patterns of spiral rows of dashes.

Conus (*Lautoconus*) *ventricosus rhodesensis* n. subsp. has been observed in several areas on Rhodes, namely Kritika (Gelasian), Faliraki, Malona, Lardos, and Ladiko (Chirli & Linse 2011; personal observations). It seems that this subspecies was present on Rhodes throughout the early and late Pleistocene.

Conus (*Lautoconus*) sp.
(Fig. 6)

Locality. — TSS1 (TSS1 of Cornée *et al.* 2006, 2018), Rhodes, Greece, Ladiko-Tsampika Fm, Tsampika section (Fig. 1).

Horizon. — Tsampika section, Chibanian (Middle Pleistocene) of Ladiko-Tsampika Fm,

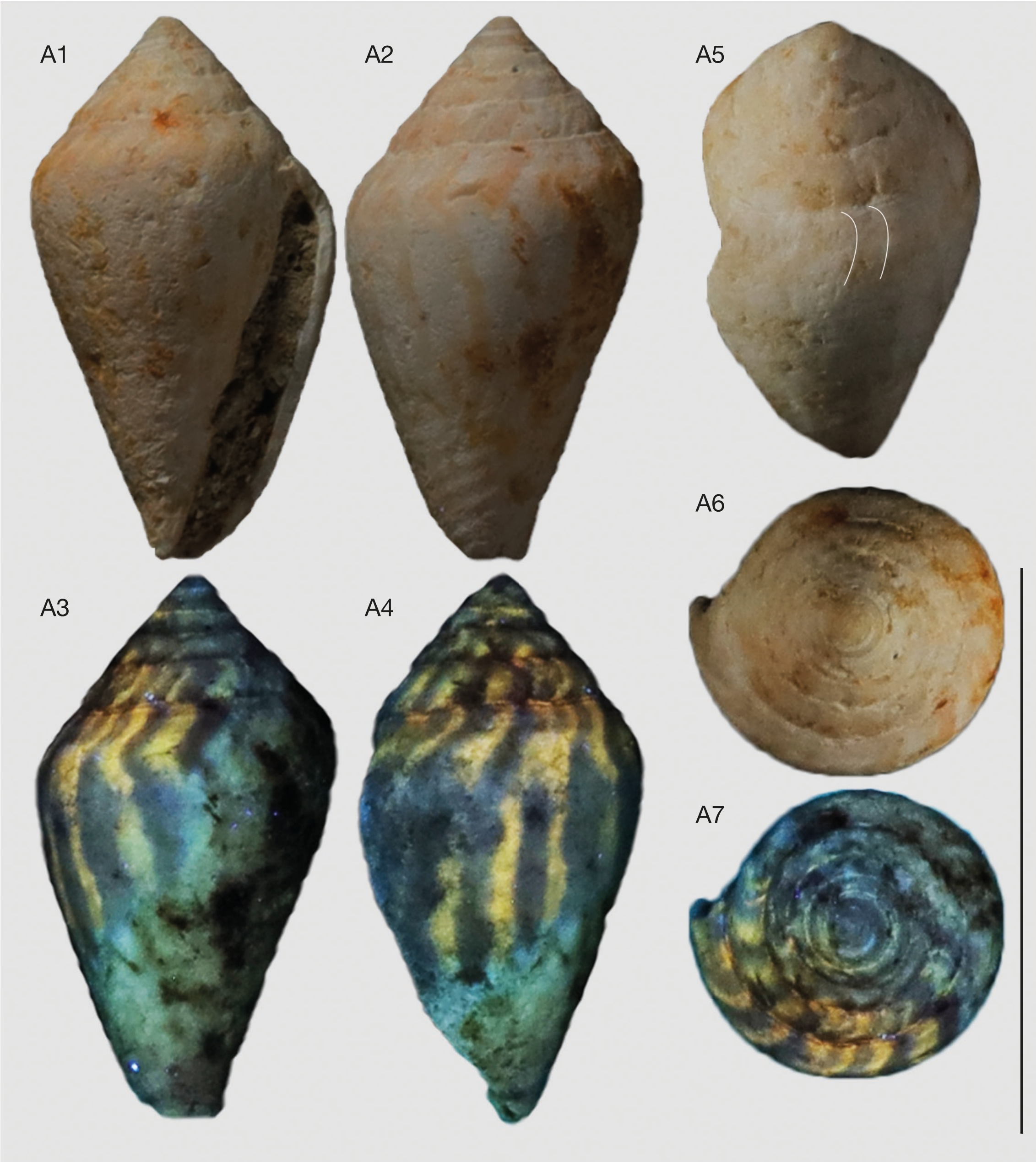

Fig. 6. — *Conus* (*Lautoconus*) sp. from the Pleistocene of Tsampika, Rhodes (Greece) under natural (**A1**, **A2**, **A5**, **A6**) and UV (**A3**, **A4**, **A7**) light: **A**, MNHN.F. A88169. Lines on **A5** indicate the subsutural flexure. Scale bar: 1 cm.

Material examined. — **Greece** • 1 specimen; Rhodes; Ladiko-Tsampika Fm, Tsampika section, TSS1; Chibanian (Middle Pleistocene); MNHN.F.A88169.

Stratigraphic range. — Chibanian (Middle Pleistocene) of Ladiko-Tsampika Fm, Rhodes, Greece.

Description

Shell

Small-sized shell (max length of about 9.6 mm), with nearly straight spire. Spire whorl outline straight to slightly convex, with faint spiral groove on sutural ramp. Shoulder smooth, with maximum diameter below shoulder. Suture impressed. Subsutural flexure very shallow, moderately curved, moderately asymmetrical.

Colour pattern

The colour pattern consists of one level of pigmentation of broad axial flammulae beginning at the sutural ramp and continuing axially along the last whorl.

Remarks

This specimen (Fig. 6) is morphologically very similar to *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp., but has a completely different colour pattern. We consider it to be

FIG. 7. — *Conus* (*Monteiroconus*) *tsampikaensis* n. sp., holotype from the Pleistocene of Tsampika section, Rhodes (Greece), AMPG (IV) 4058, seen under natural (**A1**, **A3**-**A5**, **A7**) and UV (**A2**, **A6**, **A8**) light. Scale bars: 1 cm.

a *Conus* (*Lautoconus*) species due to its spiral groove and the straight to convex spire, characteristics of this subgenus, but more specimens need to be found to describe this species. The pattern with axial flammulae is similar to other *Conus* (*Lautoconus*) species (see for example in Monnier *et al.* 2018b, *Conus zebroides* Kiener, 1848, *Conus bulbus* Reeve, 1843 and *Conus guinaicus* Hwass in Bruguière, 1792).

Subgenus *Conus* (*Monteiroconus*) da Motta, 1991

TYPE SPECIES. — *Conus ambiguus* Reeve, 1844 by original designation. Recent, West Africa.

REMARKS

Tortonian species of *Conus* (*Monteiroconus*) from Crete (Greece) were recently discussed by Psarras *et al.* (2023). Members of this subgenus do not occur in the Mediterranean today, but it seems that they were present at least during the Pleistocene (Juárez & Matamales-Andreu 2016), as specimens identified as *Conus* (*Monteiroconus*) *tabidus* Reeve, 1844 were recovered from Tyrrhenian deposits (MIS 5e, 128-116 ka) from Mallorca. Furthermore, the discovery of another species (*Conus* (*Monteiroconus*) *tsampikaensis* n. sp.) confirms that species of *Conus* (*Monteiroconus*) were present in the Mediterranean during warm Pleistocene interglacial periods.

***Conus* (*Monteiroconus*) *tsampikaensis* n. sp.**
(Figs 7-9)

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Lithoconus mercati – Chirli & Linse 2011: 166, pl. 57, figs 1a-d (non Brocchi, 1814).

ETYMOLOGY. — Named after the type locality of Tsampika section where it was found.

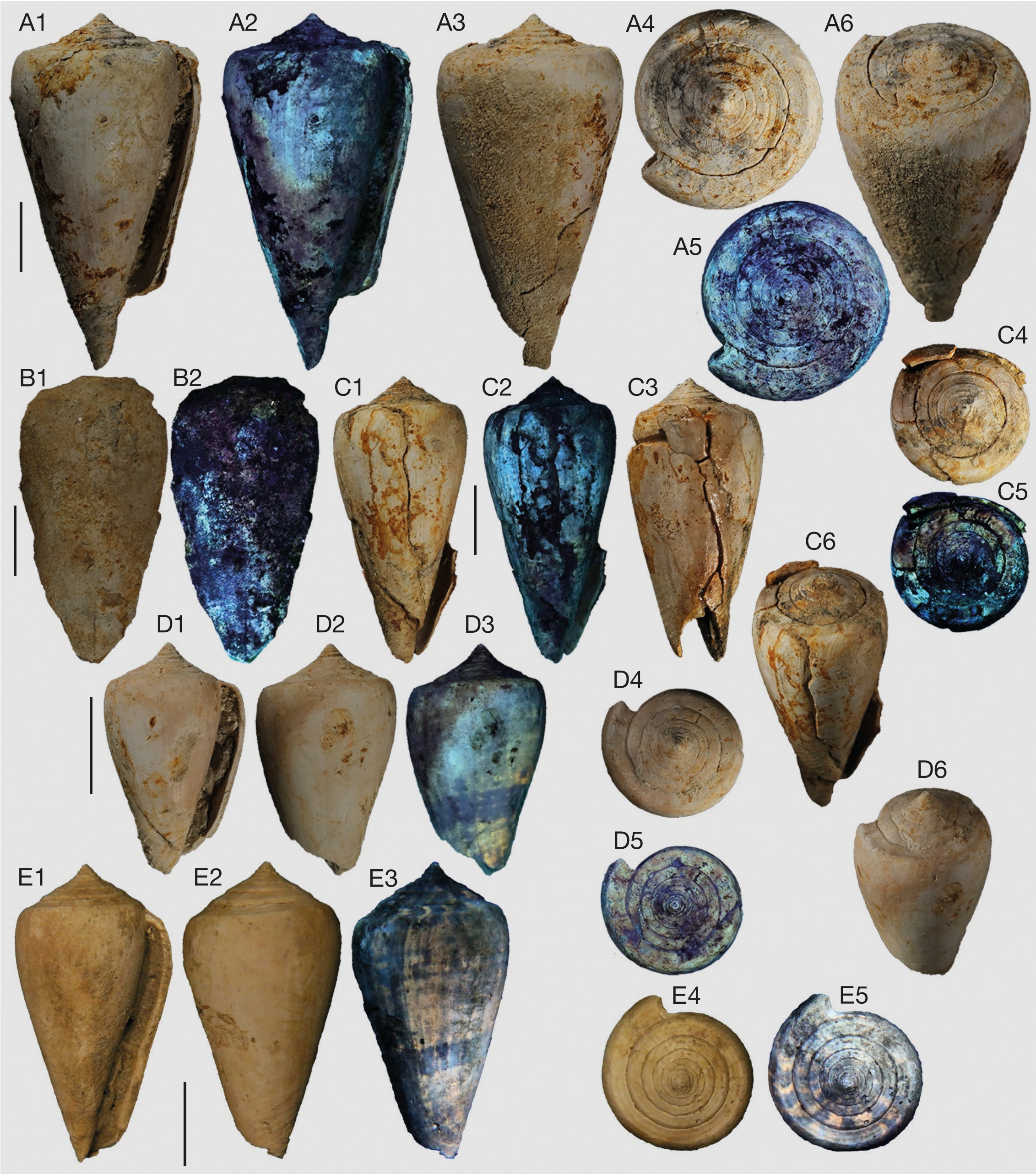


Fig. 8. — *Conus* (*Monteiroconus*) *tsampikaensis* n. sp. from the Pleistocene of Rhodes (Greece) seen under natural (**A1**, **A3**, **A4**, **A6**, **B1**, **C1**, **C3**, **C4**, **C6**, **D1**, **D2**, **D4**, **D6**, **E1**, **E2**, **E4**) and UV (**A2**, **A5**, **B2**, **C2**, **C5**, **D3**, **D5**, **E3**, **E5**) light: **A**, paratype MNHN.F.A88170, Tsampika section; **B**, paratype MNHN.F.A88171, Tsampika section; **C**, paratype MNHN.F.A88172, Tsampika section; **D**, specimen MNHN.F.A88173; **E**, specimen AMPG (IV) 4059, Malona. Scale bars: 1 cm.

Type locality. — Tsampika, Tsampika section, Rhodes, Greece (Fig. 1).

Type horizon. — Ladiko-Tsampika Fm, Pleistocene, Rhodes, Greece (Fig. 2).

Type material. — **Greece** • 1 specimen; Rhodes, Tsampika; Ladiko-Tsampika Fm, Tsampika section; Middle Pleistocene (Chibanian) to Upper Pleistocene; holotype: AMPG(IV) 4058 • 3 specimens; Rhodes, Tsampika; Ladiko-Tsampika Fm, Tsampika section, small Tsampika section herein; Pleistocene; paratypes: MNHN.F.A88170-A88172.

Other material examined. — **Greece** • one specimen (not complete specimen, shell shard); Rhodes; Tsampika section, TSS; Middle Pleistocene (Chibanian) to Upper Pleistocene; MNHN.F.A88173 • 8 specimens; Rhodes, Tsampika; Ladiko-Tsampika Fm, Tsampika section; Middle to Upper Pleistocene; MNHN.F.A90345.

Stratigraphic range. — Chibanian (Middle Pleistocene) to Upper (?) Pleistocene of Rhodes, Greece (this work).

Description

Shell

Medium-sized shell (max length of about 52.3 mm), with low angled coeloconoid spire. Early spire whorls coeloconoid, slightly elevated with three to four spiral grooves on sutural ramp. Later spire whorls flatten with coeloconoid sutural ramps.

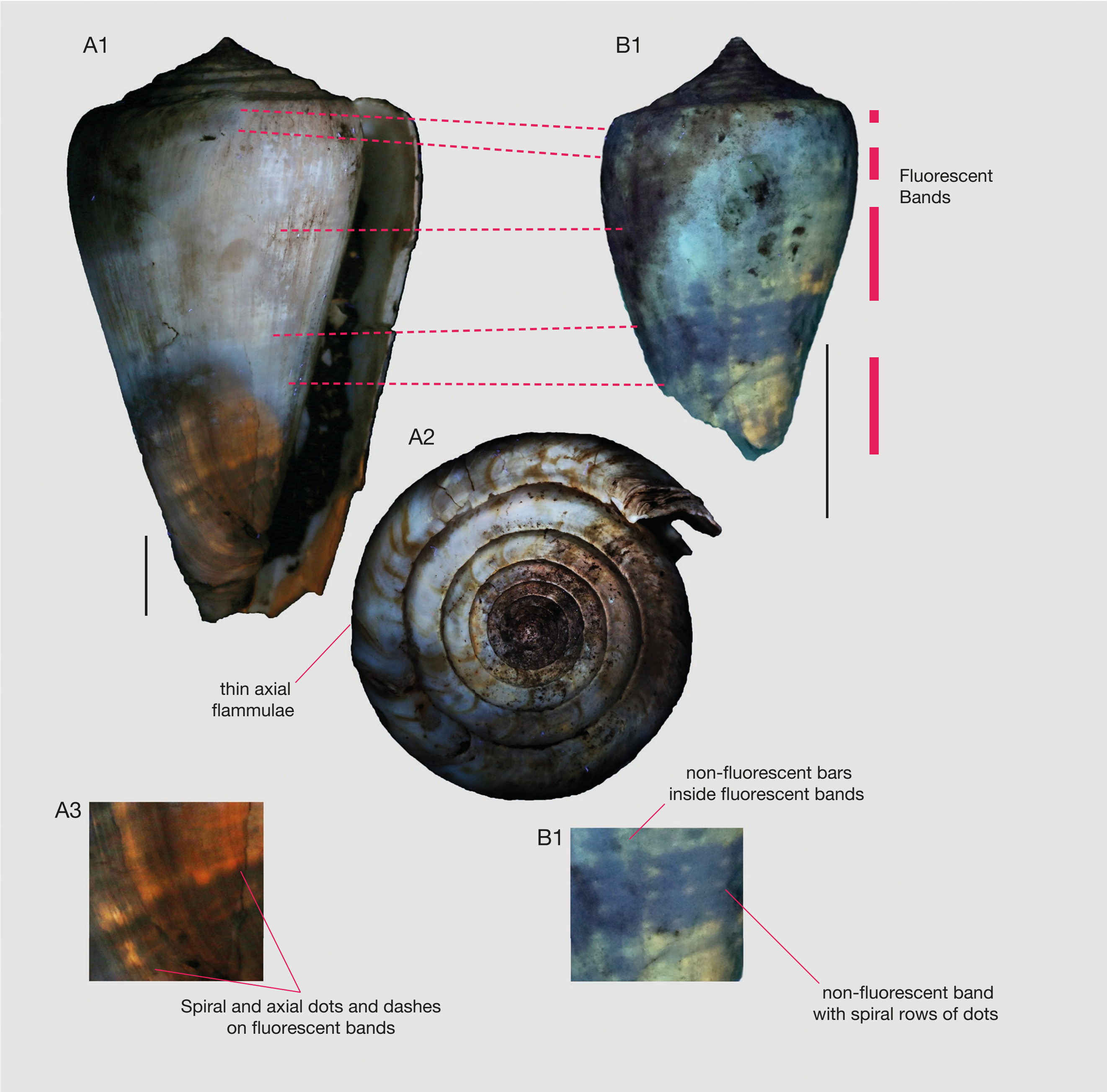


Fig. 9. — Detailed figures of *Conus* (*Monteiroconus*) *tsampikaensis* n. sp. and colour pattern comparison, whenever possible: **A**, holotype, AMPG (IV) 4058; **B**, paratype MNHN.F.A88172. Scale bars: 1 cm.

Shoulder angulated, with maximum diameter below shoulder. Subsutural flexure moderately deep to shallow, strongly curved, moderately asymmetrical. Last whorl elongated, conical.

Colour pattern

The colour pattern on the spire whorls consists of thin axial flammulae. The pattern on the last whorl consists of two levels of pigmentation. The first one consists of two broad spiral bands, separated by a wide non-fluorescent band along the anterior part of the last whorl. The second level of pigmentation consists of spirally and axially arranged fluorescent dots, dashes and small flakes interrupted by non-fluorescent bars or small blotches. The second level of pigmentation persists on the fluorescent bands and the non-fluorescent areas.

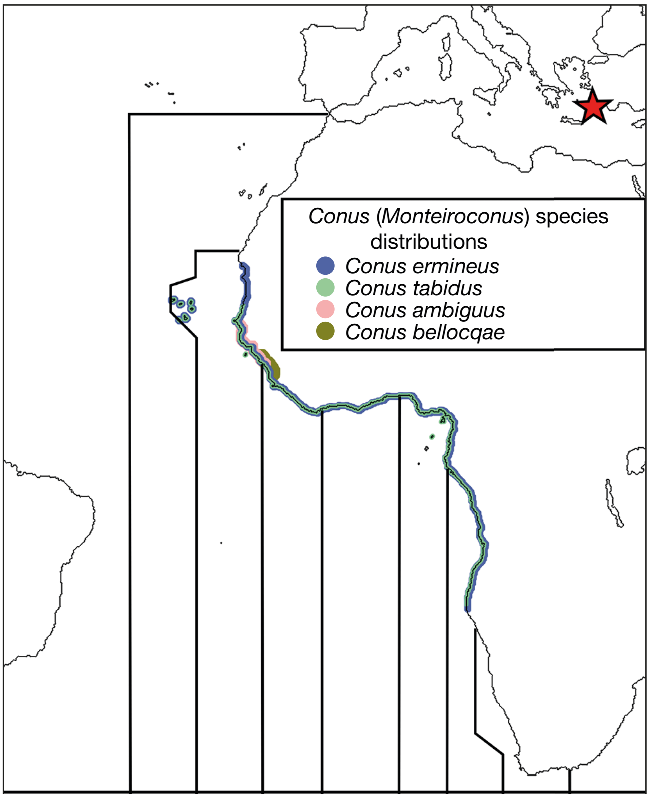
Remarks

The specimens from Tsampika (Figs 7-8) are considered to be of the subgenus *Conus* (*Monteiroconus*) due to their coeloconoid and spirally grooved sutural ramp, and the relatively low spire outline. They resemble the morphology of *Conus* (*Monteiroconus*) *ambiguus* Reeve, 1844 in terms of the angulated shoulder, the low, angled spire, and the size of this species reaches 75 mm, while the largest specimen found in Tsampika is 70 mm. However, the spire of *Conus* (*Monteiroconus*) *ambiguus* Reeve, 1844 does not have spiral cords (Monteiro *et al.* 2004) or has three deeply incised spire grooves (Petuch 1975) and thus differs from the specimens from Tsampika. In addition, the pattern of the last whorl of *Conus* (*Monteiroconus*) *ambiguus* is usually pale and consists of a purple-cream ground colour (Monnier *et al.* 2018a), although it has rarely been observed to have evenly distributed spiral rows and two slightly darker spiral bands in the middle and anterior part of the last whorl (Reeve 1844: pl. 54, fig. 244; see also Monnier *et al.* 2018a: fig. 2). The colour patterns of *Conus* (*Monteiroconus*) *ambiguus* and *Conus* (*Monteiroconus*) *tsampikaensis* n. sp. differ in the density of the axial flammulae on the spire (which are denser in *Conus* (*Monteiroconus*) *ambiguus*) and in the presence of spiral dashes, dots, flakes and non-fluorescent bars on the spiral pattern of the Tsampika population (Fig. 9).

Conus (*Monteiroconus*) *tsampikaensis* n. sp. (Figs 7; 8) resembles other *Conus* (*Monteiroconus*) species from the Pliocene, such as *Conus* (*Monteiroconus*) *antiquus* Lamarck, 1810, *Conus* (*Monteiroconus*) *villalvernensis* Pavia & Dulai & Festa & Gennari & Pavia & Carnevale, 2022, and *Conus* (*Monteiroconus*) *virginalis* (Brocchi, 1814) recently discussed from Italy (Pavia *et al.* 2022). However, *Conus* (*Monteiroconus*) *antiquus* has a different colour pattern variation (see Psarras *et al.* 2023), while the two species discussed in Pavia *et al.* (2022) have a higher spire and elevated spire whorls, so we do not consider them conspecific to the Rhodes material. Juárez & Matamales-Andreu (2016) identified *Conus* (*Monteiroconus*) *tabidus* Reeve, 1844, a species originally described from West Africa, from the Tyrrhenian (MIS 5e) of Mallorca. This species usually lacks a colour pattern or displays fine and irregular spiral stripes, or occasionally some subquadrate blotches on an overall white background. This pattern is very different from that observed on the Rhodes specimens. Juárez & Matamales-Andreu (2016) did not describe a residual colour pattern on the Mallorcan material.

Several elongate and low spired specimens have been identified as *Conus testudinarius* Hwass in Bruguière, 1792 (synonym of *Conus* (*Chelyconus*) *ermineus* Born, 1778), an extant West African species (e.g., Cuerda 1957; Anapliotis 1961, 1963a, b, 1966; Charrier 1961; Vazzana 1988; Ruggeri & Buccheri 1968; Callapez & Soares 2000; Vicens *et al.* 2012; Zazo *et al.* 2013). The occurrence of *Conus* (*Chelyconus*) *ermineus* Born, 1778 in the Mediterranean during the Tyrrhenian (e.g., Muhs *et al.* 2015) is also questionable, as no one has yet shown any of the fossils under UV light. *Conus* (*Monteiroconus*) *tsampikaensis* n. sp. differs strongly from *Conus* (*Chelyconus*) *ermineus* in the colour pattern and in the morphology of the coeloconoid spire.

Chirli & Linse (2011) found specimens resembling *Conus* (*Monteiroconus*) *tsampikaensis* n. sp. at Malona. The figured specimens are very similar to those found at Tsampika. One specimen from Malona, stored at the AMPG, confirms *Conus* (*Monteiroconus*) *tsampikaensis* n. sp being present



Warmest	26-28	27-29	28	26-27	28.5	27.5	18-20	25-27
Coldest	16-18	18-19	26	22-24	25	19.5	10-12	20-22
Conus ambiguus		●	●					
Conus tabidus		●	●	●	●	●		
Conus ermineus		●	●	●		●		
Conus bellocqae			●					

Fig. 10. — Current distribution of the subgenus *Monteiroconus* on African coast, after Monnier *et al.* 2018a, b and Tenorio *et al.* 2020. Temperature ranges (in Celsius degrees) of the four species. Map and temperatures modified from Sessa *et al.* 2013. Star indicates Rhodes.

in that locality (Fig. 8E). The presence of this species in Arkhangelos Fm, which is certainly older than Tsampika (Cornée *et al.* 2018), indicate that the species was present in the Mediterranean during the Middle Pleistocene in at least two interglacial periods.

PALAEOZOOGEOGRAPHY

Inferences about the species found in a particular place can give us clues about the past climate and palaeotemperatures of that region. This can be done by examining the modern zoogeography of the species found in the fossil assemblages. In particular, for species whose modern ranges lie in specific sea surface temperatures (SSTs) with specific range endpoints, they can be used to inform extralimital northern or southern species that are colder or warmer than modern

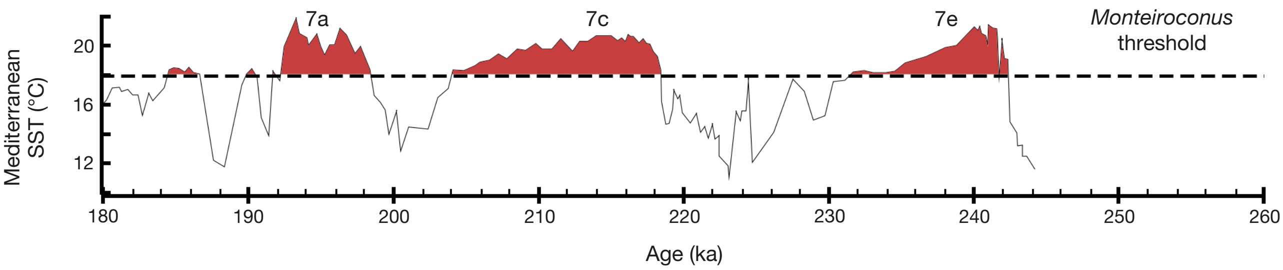


FIG. 11. — Graph of Mediterranean Sea surface temperatures during the penultimate interglacial MIS 7. The dashed line indicates the threshold of 18°C that the sea temperature must exceed for *Monteiroconus* species to flock into the Mediterranean (shown in red). Graph modified after Dutton *et al.* (2009) and Wendt *et al.* (2021).

SSTs, respectively (Muhs *et al.* 2015). This is especially true for ectotherms like Conidae, whose life is very dependent, among other parameters, on temperature variations (Bennett *et al.* 2021; Martinez *et al.* 2022). While some efforts have been made to assess the upper temperature limits of Conidae (Lugo *et al.* 2016), no studies exist on the preferred temperature (Crickenberger *et al.* 2020). Nevertheless, the geographic distribution of some Indo-Pacific species has been recently discussed (Siqueira-Silva & Martinez 2023) and evidence of those shifts have been recorded during the Pleistocene (e.g., Sessa *et al.* 2013; Muhs *et al.* 2015).

In the West African region, the average temperatures of shallow waters have been calculated (Sessa *et al.* 2013) and the distribution of Conidae species seem to be directly linked to water temperatures (Fig. 10). *Conus* (*Monteiroconus*) species today appear to require water temperatures above 18 °C to thrive (Fig. 10), as their distribution in West Africa today does not extend beyond that of the Senegal and Cape Verde Islands (GBIF; IUCN Red List; Monnier *et al.* 2018a; Tenorio *et al.* 2020; Palomares & Pauly 2023), which are part of the so-called 'Guinean' or 'Senegalese' Province.

Since Tsampika was deposited from MIS 8 to MIS 6 (Cornée *et al.* 2018), with MIS 8 and MIS 6 considered glacial periods, it can be inferred that the *Conus* (*Monteiroconus*) species present in the Ladiko-Tsampika Fm could only survive during the warm period of the interglacial MIS 7. Several other localities in the Mediterranean have been attribute to MIS 7 (e.g., Hearty *et al.* 1986; Goy & Zazo 1986, 1988; Mauz & Hassler 2000; Garilli 2011; Chakroun & Zaghbib-Turki 2017). During this time, there were three major temperature increases, MIS 7e (241.8-236.0 [± 0.3] ka), MIS 7c (215.7-212.9 [± 0.4] ka) and MIS 7a (201.8-197.1 [± 0.5] ka) (Martrat *et al.* 2004, 2007; Dutton *et al.* 2009; Wendt *et al.* 2021) when sea surface temperatures exceeded the threshold of 18 °C at which *Conus* (*Monteiroconus*) can thrive. Therefore, we assume that species of *Conus* (*Monteiroconus*) entered the Mediterranean Sea during at least one of these MIS 7 warm events. Interestingly, the tropical gastropod species *Thetystrombus latus* (Gmelin, 1791) first appears in the Mediterranean during the MIS 7a (Zazo 1999). On the other hand, the tropical *Conus* (*Monteiroconus*) species in Tsampika (MIS 7) coincides with the presence of warm faunas in the Canary Islands and the Mediterranean Iberia that happened during MIS 7 (Zazo 1999). The absence of *Thetystrombus latus* from Tsampika section implies it was deposited before MIS 7a. Therefore, we conclude that the stratigraphic age of the Tsampika deposits is constrained to MIS 7e-MIS 7c, 241.8-212.9 (± 0.4) ka (Fig. 11).

The occurrence of *Conus* (*Monteiroconus*) *tsampikaensis* n. sp. in the Mediterranean before MIS 11 (Arkhangelos Fm the uppermost part been deposited between 560 and 458 ka; this work) suggests that the Mediterranean has been colonised several times by Conidae in each interglacial event. Their presence so far in the stratigraphic record from the Mediterranean (older than MIS 11, MIS 7 and MIS 5e) suggests that either *Conus* (*Monteiroconus*) found shelter in the warmer waters of the south-eastern Mediterranean during the glacial phases and sporadically appeared during the interglacial phases (Raffi & Marasti 1982; Chirli & Linse 2011), or that they completely disappeared from the Mediterranean during the glacial phases, retracting their distribution only to West Africa, similar to what we see today.

CONCLUSION

Four species: *Conus* (*Lautoconus*) *ventricosus* Gmelin, 1791, *Chelyconus pelagicus* (Brocchi, 1814), *Chelyconus striatulus* (Brocchi, 1814) and *Lithoconus mercati* (Brocchi, 1814) have been identified so far in Rhodes, but, excluding *Conus* (*Lautoconus*) *ventricosus* Gmelin, 1791, all were misidentified. After their revision, three species were found in the Pleistocene of Rhodes: *Conus* (*Lautoconus*) *ventricosus rhodesensis* n. subsp., *Conus* (*Lautoconus*) sp. and *Conus* (*Monteiroconus*) *tsampikaensis* n. sp. The hidden diversity of the Conidae in nearly recent strata is exciting because it shows the complex variability of this family. We suggest that the observation of *Conus* (*Monteiroconus*) species indicates sea-surface temperatures above 18°C during their deposition, so the age of the Tsampika section is 241.8-212.9 (±0.4) ka. It is problematic that, except for the Conidae, there are no other strictly thermophilic species. For example, the muricid genera *Favartia* Jousseaume, 1880 and *Exquisitor* Merle, Garrigues & Pointier, 2022, which occur today in West Africa and were present in the Mediterranean during the Late Miocene (*Exquisitor, Homalocantha* and *Favartia*) and the Pliocene (*Favartia* and *Homalocantha*), are missing in the Pleistocene (Merle *et al.* 2022). One explanation for this could be that the water was sufficiently warm for several Conidae species, but not for other thermophilic forms such as *Favartia* or *Exquisitor*. A geochemical study of

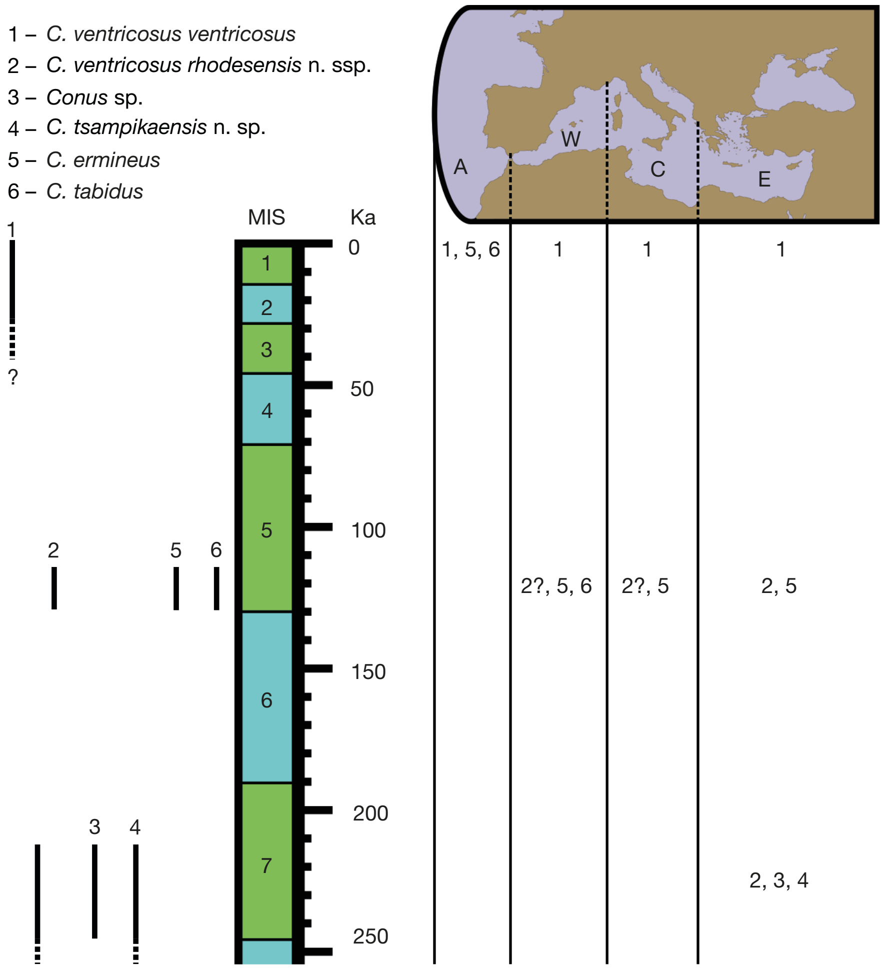


FIG. 12. — Distribution of the various species of Conidae found in the Mediterranean regions, during the late Pleistocene and their current distribution: **A**, Atlantic Ocean; **W**, western Mediterranean; **C**, central Mediterranean; **E**, eastern Mediterranean.

the palaeotemperature seems necessary to clarify the SST in the western and eastern Mediterranean during the MIS 7. If our assumptions are true, the stratigraphic position of these shells in the interglacial MIS 7 is valuable as it indicates that not only *Conus* (*Chelyconus*) *ermineus*, which is thought to have entered the Mediterranean during the Tyrrhenian (MIS 5e), but several other species arrived in the Mediterranean through the Strait of Gibraltar and diversified during different interglacial periods, while they possibly disappeared during the interglacial periods as the waters became colder. Furthermore, the presence of different *Conus* species that have colonised the Mediterranean during several time periods could drastically affect the stratigraphic significance of this family, as these conids could possibly serve as index fossils for the different interglacial periods of the Mediterranean (Fig. 12). As such, a thorough revision of conids of the Mediterranean Pleistocene is necessary.

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