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TWO WEST AFRICAN MOLLUSCAN SPECIES (GASTROPODA, ACTEONIDAE) FROM MIS 5.5 IN THE TARANTO AREA (SOUTHERN ITALY)

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Keywords: *Acteon senegalensis*; *Acteon maltzani*; Last Interglacial; Senegalese Guests; Apulia.

Abstract: Two gastropods of the family Acteonidae, *Acteon senegalensis* (Petit de la Saussaye, 1851) and *Acteon maltzani* Dautzenberg, 1910, are reported for the first time from shallow-water deposits of the Last Interglacial (MIS 5.5) cropping out in the Taranto area (Southern Italy). Both species inhabit the coast of West Africa, and their presence in the MIS 5.5 deposits is attributable to the northward flow of tropical species, referred to in the literature as Senegalese Guests. The two species exhibit non-planktotrophic larval development, confirming that species without a long planktonic life stage can spread effectively in response to climate change.

INTRODUCTION

The Marine Isotope Stage 5.5 (MIS 5.5), i.e. the Last Interglacial (LIG), ranging about from 132 to 116 ky according to different authors (Stirling et al. 1998; Shackleton et al. 2003; Kopp et al. 2009; Murray-Wallace & Woodroffe 2014; Antonioli et al. 2018), is mainly known in the past literature on the Mediterranean area as Tyrrhenian (Issel 1914; Cita et al. 2005; Cita 2008), while Eemian has been used in North Sea stratigraphy (Cleveringa et al. 2000; Shackleton et al. 2003).

During the climatic optimum of MIS 5.5 global mean surface temperature was about 1.5 °C warmer than today (Turney & Jones 2010; Lunt et al. 2013). Polar regions in both hemispheres experienced even greater warming, with temperatures 3–5 °C above present values (Otto-Bliesner et al. 2006, 2013). Correspondingly, eustatic sea level stood roughly 6–9 m higher than the modern mean.

Still, there are some different interpretations of the factors that drove sea level changes during

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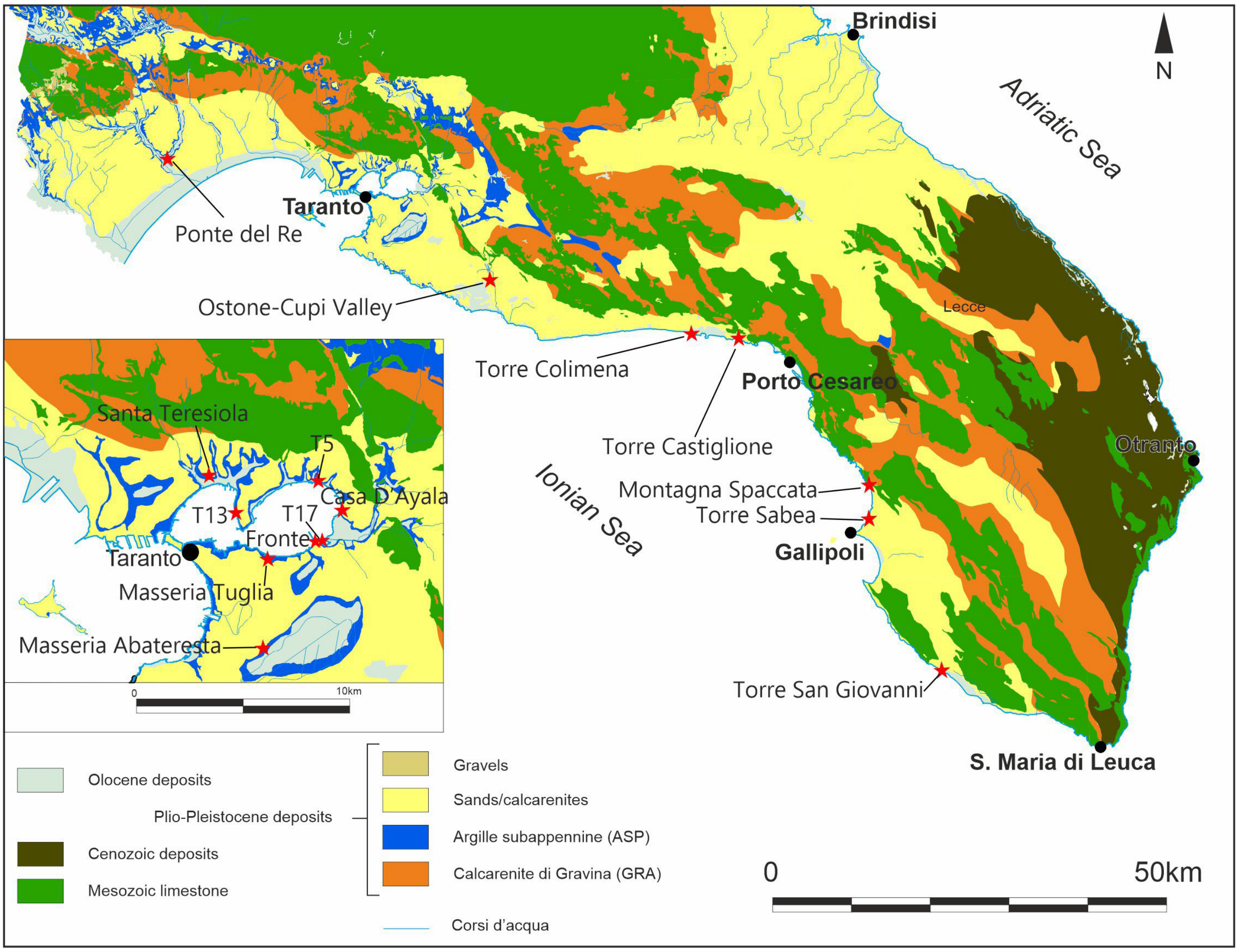

Fig. 1 - Schematic geological map of southern Apulia with localities mentioned in the text.

the LIG, mostly related to disagreements about the timing and contribution of melting from the Greenland and Antarctic ice sheets (Dutton & Lambeck 2012; O'Leary et al. 2013; Dutton et al. 2015a, b; Rohling et al. 2019). Recently, in the central Mediterranean area, different authors (Bini et al. 2020; De Santis et al. 2023, 2024; Giaccio et al. 2024; Isola et al. 2024) highlighted a trend with an early highstand followed by a rapid drop and, finally, a sea level roughly stable or slightly oscillating until the end of MIS 5.5.

Bini et al. (2020) and Isola et al. (2024), based on U/Th dating, tephra fingerprinting and *Lithophaga* boreholes (as sea level indicators) from the Cilento area (Tyrrhenian coast of southern Italy), inferred a sea-level drop of at least 6 m between 125 and 120 ky, and a relative sea level lower than +2 m before 120 ky.

Using similar methods, Giaccio et al. (2024) found that in the Circeo area (Tyrrhenian Sea coast of central Italy), after stabilizing at approximately +9 m, MIS 5.5 sea level dropped to around +3 m by 123 ky and never rose above this elevation during later phases of the LIG or thereafter.

In particular, for the Ionian coast of the Salento peninsula, in the Cupi stream valley (near Lizzano) (Fig. 1), De Santis et al. (2024) identified two paleoshorelines (PS2 and PS3) at +30 ± 2 m and +19 ± 2 m, respectively, along with their associated Terraced Deposits 2 and 3 (TD2 and TD3), both dating back to MIS 5.5. The higher PS2/TD2 and the lower PS3/TD3 indicate two sea-level stillstands during MIS 5.5 (separated by a sea-level drop), with the earlier stillstand being higher than the second (De Santis et al. 2024).

Further south along the Ionian coast of the Salento peninsula, De Santis et al. (2023) modelled paleoshorelines and associated terraced deposits in the Gallipoli area (Fig. 1), recognizing the presence of traces of two sea-level stillstands dating back to

MIS 5.5, modelled respectively at 127 and 120 ky.

The Tyrrhenian deposits, frequently represented by marine terraced deposits and mostly cropping out near the coast (e.g. Ferranti et al. 2006; Rovere et al. 2016; Antonioli et al. 2018), have attracted the attention of scholars for a long time due to the presence of faunal elements currently absent from the Mediterranean, coming from the coasts of West Africa, often cited as "Senegalese fauna" or "Senegalese Guests" in the past literature (*espèces sénégaliennes* after Gignoux 1913; Ferranti et al. 2006; Garilli 2011; Hearty & Dai Pra 1992; Amorosi et al. 2014). These species are considered paleoclimatic indicators of generalized tropicalized conditions (Amorosi et al. 2014; Negri et al. 2015).

Several Senegalese Guests, all belonging to the Mollusca, have been reported in the literature, such as *Thetystrombus latus* (Gmelin, 1791) (= *Strombus bubonius* Lamarck, 1822; *Persististrombus latus* (Gmelin, 1791)), *Polinices lacteus* (Guilding, 1834) (= *Natica lactea* Guilding, 1834), *Gemophos viverratus* (Kiener, 1834) (= *Tritonidea viverrata* Kiener, 1834), *Conus ermineus* Born, 1778 (= *Conus testudinarius* Hwass, 1792), *Monoplex trigonus* (Gmelin, 1791) (= *Cymatium trigonum* (Gmelin,1791), *Tritonium ficoides* Reeve, 1844), *Acteocina knockeri* (E.A. Smith, 1872), *Anadara geissei* (Kobelt, 1891), *Brachidontes puniceus* (Gmelin, 1791), *Cardita rufescens* Lamarck, 1819 (= *Cardita calyculata senegalensis* (Reeve, 1843), *Hyotissa mcgintyi* (Harry, 1985) (= *Hyotissa hyotis*, Linnaeus, 1758). Of them, *T. latus* is the best known and most frequently cited, serving as almost the official representative of the Senegalese fauna in the Mediterranean during the LIG. As indicated by the modern distribution of *Thetystrombus latu*s (WoRMS Editorial Board, 2025), the Senegalese Guests originated from a wide latitudinal range, spanning from the southern border of Angola (approximately 17°S) to Senegal and Cape Verde (approximately 14°N).

Regarding the distribution of *Tethystrombus latus* in the Italian deposits, it has been observed (Ferranti et al. 2006) that its occurrence is restricted to the coasts of the Tyrrhenian and Ionian Seas. In contrast, the species is absent from the Adriatic Sea, probably due to different paleoceanographic conditions between the Adriatic and Tyrrhenian-Ionian Seas during MIS 5.5.

After the substage MIS 5.5, two other sea-level highstands followed, MIS 5.3 and 5.1, respectively, at approximately 100 ky and 80 ky (Waelbroeck et al. 2002; Spratt & Lisieki 2016). Both of them were characterized by sea levels and temperatures lower than those recorded for MIS 5.5 (Siddal et al. 2003; Grant et al. 2014; Rohling et al. 2014). Up to now, specimens of Senegalese fauna from MIS 5.3 and 5.1 deposits are scarcely documented.

Some species reported in the past literature as Senegalese Guests would need a critical revision, both systematically and biogeographically. For example, the tiny actaeonid gastropod, *Acteocina knockeri* was categorized by De Castro-Coppa (1970) as one of the Senegalese Guests. Still, more recent evidence suggests that this species existed in the Mediterranean basin during the Pliocene (Ragaini & Bernieri, 2007). Hoenselaar & Gulden (1991) reported an empty shell from the Kerkennah Islands in Gulf of Gabès; however, despite more than three decades of focused malacological surveys, no additional specimens have been found. Some researchers (Antit et al. 2011) have even proposed that the Tunisian shell might belong to the morphologically similar Indo-Pacific species *Acteocina mucronata* (Philippi, 1849), which is already established in the Levant Sea. This possibility further diminishes the reliability of the Mediterranean record of *A. knockeri*. Therefore, until new and unequivocal material is discovered, *A. knockeri* should be regarded as a "Senegalese Guest" from West Africa rather than a confirmed member of the contemporary Mediterranean fauna.

In addition, the Senegalese Guests reported so far are all large or medium-sized species, which are easy to detect. Still, it is expected that the list will be longer if more careful studies are conducted on the Tyrrhenian associations, including smaller species.

In the present work, two small gastropods of West African origin are reported from deposits of the MIS 5.5 in the area of Taranto.

GEOLOGICAL FRAMEWORK

The Apulian Foreland was subjected to two major geodynamic phases during the Pliocene and Pleistocene (Ricchetti et al. 1992). The first phase led to the strong subsidence of the westernmost sectors due to subduction beneath the Apennine Chain, resulting in the creation of the Bradanic Trough foredeep (Doglioni et al. 1994, 1996). The sedimentary cycle associated with the Bradanic

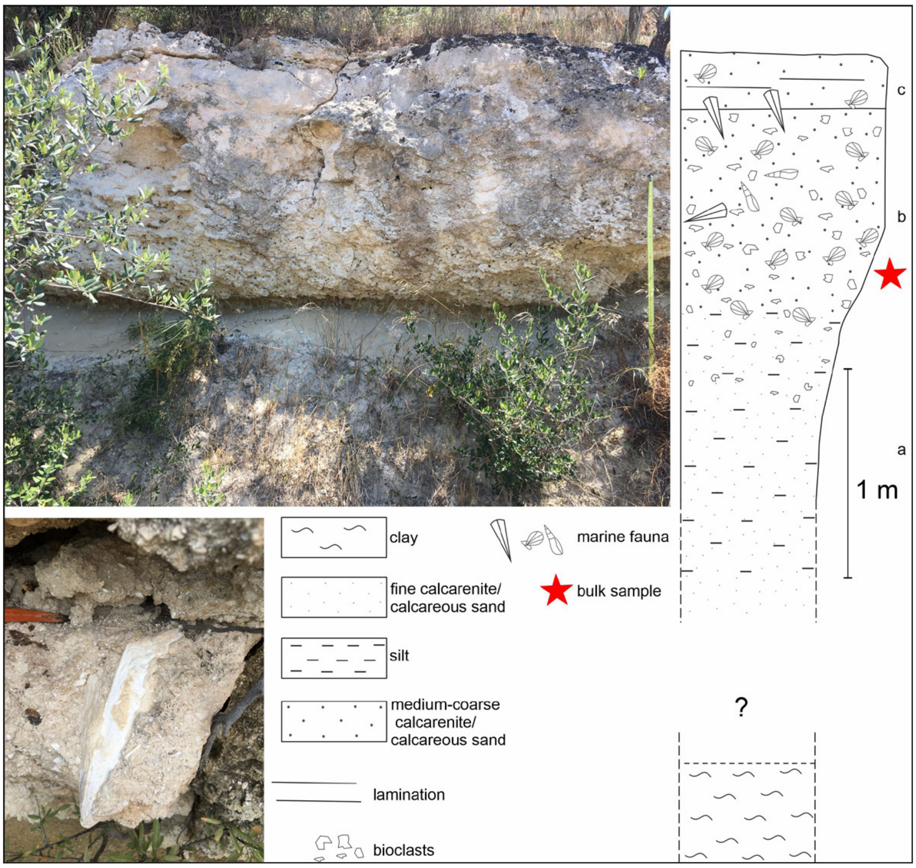

Fig. 2 - Photos and stratigraphic section of T5 outcrop. Below-left: a specimen of *Pinna nobilis* in life position within the upper calcarenite layer.

Trough (Ricchetti et al. 1992; Tropeano et al. 2002) resulted in the accumulation of coastal deposits belonging to the Calcarenite di Gravina Formation (Azzaroli et al. 1968), culminating in hemipelagic silty clay deposits belonging to the Argille Subappennine Formation (Azzaroli et al. 1968) (Fig. 1). In the Middle-Late Pleistocene, the entire Apulian Foreland experienced a regional uplift, which led to the closure of the Bradanic Trough and the widespread formation of marine terraces/palaeoshorelines along the coastal sectors (Ciaranfi et al. 1992; Ricchetti et al. 1992; Mastronuzzi et al. 2007).

Several studies have recognized, along the Apulian coasts, the occurrence of terraced deposits and palaeoshorelines related to MIS 5 and, in particular, to the LIG (Dai Pra & Sterns 1977; Boenzi et al. 1986; Hearty & Dai Pra 1992; Belluomini et al. 2002; De Santis et al. 2021, 2023, 2024).

PREVIOUS STUDIES ON THE SENEGALESE FAUNA FROM THE IONIAN APULIA

In the Taranto area, the presence of a calcarenite bed characterized by *Thetystrombus latus* ("*couches a Strombes*" by Gignoux 1913), cropping out with good continuity along the coast of Mar Piccolo, transgressive on the sub-Apennine clays, has since the 19th century attracted scholars of macrofauna (Philippi 1836, 1844; Kobelt 1874). However, detailed indications about the localities described by these early authors are lacking.

The first record of West African species from the Tyrrhenian deposits in the area of Taranto was provided by Philippi (1836, 1844), who mentioned *Strombus coronatus* Defrance, 1827. However, this identification is most likely a misidentification of *Tethystrombus latus*, as *Strombus coronatus* is a Miocene to Early Pliocene species (Harzhauser & Kronenberg 2008). The two strombids are notably similar to each other. Still, *Tethystrombus coronatus* differs mainly by having a lower, sharper spire and strong, prominent spines on the last whorl that produce a "coronate" pattern. In contrast, *T. latus* has a higher, stouter spire and shorter spines on the last whorl (Meco 1977; Harzhauser & Kronenberg 2008).

Kobelt (1874), again from the area of Taranto, reported a long list of species, including *Strombus coronatus* (i.e., *Tethystrombus latus,* as discussed above) from Punta della Penna (Mar Piccolo). The citation of *Dentalium elephantinum* Linnaeus, 1758, a scaphopod living in the Red Sea and Indian Ocean and mentioned as a fossil in the Italian Neogene and Quaternary, should be referred to the extinct *Fissidentalium rectum* (Gmelin, 1791) (Caprotti 1979).

Gignoux (1913) provided a more comprehensive list of proper Senegalese species referred, in general, to the "*couches a Strombes*," but without specifying the sites of discovery. In addition to *Thetystrombus latus*, he listed *Monoplex trigonus*, *Polinices lacteus*, *Gemophos viverratus*, *Conus ermineus* and *Anadara geissei* (according to the updated nomenclature). Recent geologic-stratigraphic work has been carried out in the Taranto area. The Ionian coast of Apulia has reported the presence of a fauna with Senegalese affinity. However, only *Thetystrombus latus* has been cited (Fig. 1). Dai Pra & Stearn (1977) recognized this species at Fronte, Casa d'Ayala, Santa Teresiola and in the Cupi stream valley (near Lizzano). Dai Pra & Hearty (1992) found it in the Salento peninsula at Torre Castiglione and Torre Sabea. Dai Pra (1982) found it at Torre Castiglione, while Hearty & Dai Pra (1992) reported the species from east of Santa Teresiola, at Fronte and from the Salento peninsula at Torre Colimena, Torre Sabea, Torre San Giovanni and Torre Castiglione.

More detailed reports on the Senegalese fauna in the Gulf of Taranto deposits are from Ponte del Re (Boenzi et al. 1986; Caldara 1987) (Fig. 1), from which the following species were listed: *Cardita rufescens*, *Hyotissa mcgintyi*, *Thetystrombus latus*, *Conus ermineus, Monoplex trigonus, Acteocina knockeri* and *Corbula revoluta* (Brocchi, 1814), which should be excluded from the Senegalese Guests, being a Pliocene-Pleistocene species closely related to a living West African species (Garilli 2011; Cosel & Gofas 2019).

Amorosi et al. (2014) recognized *Thetystrombus latus* at Masseria Tuglia, Masseria Abateresta and Casa Ayala, while at the Fronte section they found it with *Polinices lacteus*, *Conus ermineus*, *Gemophos viverratus* and *Acteocina knockeri* (Fig. 1).

De Santis et al. (2021, 2023) reported *Thetystrombus latus* from Montagna Spaccata, and De Santis et al. (2024) found it again near Lizzano, along the Ostone stream valley (Fig. 1).

Santagati et al. (2023, 2024) studied the rich fauna from three localities around Mar Piccolo (T5, T13, and T17) (Fig. 1), which were sampled by researchers from the University of Bari (D'Alessandro and colleagues) at the end of the 1970s. They compiled a long list of species, among which those of Senegalese origin are *Thetystrombus latus*, *Conus ermineus*, *Hyotissa mcgintyi* and *Cardita rufescens*.

Material and methods

The studied material was collected in the 1970s during campaigns on the Tyrrhenian deposits of the Taranto area by researchers from the Dipartimento di Scienze della Terra e Geoambientali dell'Università di Bari. The two specimens in the present work were obtained from a bulk sample of approximately 12 kg, consisting of sands rich in bioclasts and fossils. The sample was wet-sieved through 2 mm, 1 mm and 0.5 mm screens. All fractions greater than 1 mm were examined under a stereomicroscope. In addition to mollusks, material related to other systematic groups occurring in the sample (cirripedes, decapods, echinoderms, bryozoans, coralline algae and scleractinians) was also sorted. All the molluscan fauna was identified to species or genus level.

Photographs were taken using a Nikon SMZ 745T microscope, equipped with a Digital Sight DS-Fi1c camera, and managed by the NIS-Elements program. The focus stacking technique was performed using the Affinity Photo program.

Acronyms and abbreviations: sh – shell, MSTB – Museo di Scienze della Terra dell'Università di Bari Aldo Moro.

Data and results

Study section

The two gastropods of the present study come from a locality near the eastern part of Mar Piccolo. This locality, known in the literature as T5 (Santagati et al. 2023, 2024) (Fig. 1), was attributed to MIS 5.5 based on the presence of Senegalese fauna and stratigraphic correlations with the Fronte section (Amorosi et al. 2014).

The outcrop (Fig. 2) is located south of Masseria San Pietro (now Relais Histò San Pietro), to the left of a modest river incision (40°30'8.52"N 17°18'45.74"E). Here, the "*couches a Strombes*" (Gignoux 1913) crop out for several hundred meters in length and about 1.5 m in height.

The following Senegalese species were recognized: *Brachidontes puniceus*, *Hyotissa mcgintyi* and *Polinices lacteus*. The base (Fig. 2a) consists of fine calcareous sands and yellowish-white silt. The macrofaunal content is represented by species typical of sandy bottoms of the infralittoral stage (biocoenosis of fine well-sorted sands, SFBC *sensu* Pérès 1967), such as *Spisula subtruncata* (da Costa, 1778), *Acanthocardia tuberculata* (Linnaeus, 1758), *Peronidia albicans* (Gmelin, 1791), *Chamelea gallina* Linnaeus, 1758 and *Tritia mutabilis* (Linnaeus, 1758).

Toward the top, with an abrupt transition, the deposit passes to a poorly to moderately cemented layer ("panchina") (Fig. 2b), consisting of medium to coarse (bio)calcarenite/(bio)calcirudite with bioclasts. The faunal content is particularly rich, again with species typical of infralittoral sandy bottoms. In addition to the species occurring in the lower part, the following ones were recognized: *Glycymeris nummaria* (Linnaeus, 1758) and *Mactra stultorum* (Linnaeus, 1758), with the addition of many small gastropods (rissoids, trochids and cerithiids) related to vegetated bottoms (biocoenosis of the photophilic algae, AP, or biocoenosis of the *Posidonia* meadows, HP, Pérès 1967). Subordinately, species indicative of sedimentary instability (*sensu* Di Geronimo, 1984) *Moerella distorta* (Poli, 1791), *Lembulus pella* (Poli, 1791), *Nucula nitidosa* Winckworth, 1930, together with species more typical of muddy bottoms, such as *Acanthocardia paucicostata* (G.B. Sowerby II, 1834) and *Dosinia lupinus* (Linnaeus, 1758) are also present. The bulk sample studied is from the less cemented part of this layer.

Toward the top (Fig. 2c), the (bio)calcarenite/(bio)calcirudite "panchina" is interrupted by a surface that marks the transition to a laminated (bio) calcarenite devoid of large fossil fragments and with rare macrofauna. On this surface, specimens of *Pinna nobilis* (Linnaeus, 1758) are present in their natural position. In this upper part, the faunal content is represented by species typical of low-energy environments: *Loripes orbiculatus* Poli, 1791, *Cerastoderma glaucum* (Bruguière, 1789), *Lucinella divaricata* (Linnaeus, 1758), *Mytilaster* sp., with many small gastropods (rissoids and trochids) related to the HP and/or AP bottoms. Few specimens of pulmonate gastropods were also detected, such as *Chondrula tridens* (O.F. Müller, 1774) and Hygromiidae spp.

Although a detailed study of Section T5 will be presented in a subsequent article, we can anticipate here that, overall, the section exhibits a regressive trend, transitioning from a lower to a middle-upper shoreface environment.

Systematics

Family Acteonidae d'Orbigny, 1842
Genus *Acteon* Montfort, 1810

Acteon senegalensis (Petit de la Saussaye, 1851)
Fig. 3

1851 *Tornatella senegalensis* Petit de la Saussaye, p. 262, pl. 8, fig. 5.
1865 *Tornatella senegalensis* – Reeve, pl. 3, figs. 14a, b.
1893 *Actaeon senegalensis* – Thrion & Pilsbry, p. 152, pl. 18, figs. 90, 91.
1910 *Actaeon senegalensis* – Dautzenberg, p. 56.

Material: 1 sh (MSTB 2025/1A).

Description. The shell is 17.6 mm high and 6.4 mm in width, with seven whorls, including the protoconch, of which the last one is about two-thirds of the total height. Whorls are convex with deep, slightly canaliculate sutures. The paucispiral protoconch consists of one whorl. The aperture is pyriform, narrow, about 75% of the last whorl height, with a thin, medially inflexed outer lip and a narrow parietal callus. A blunt, tooth-like callus is present on the columella. Sculpture occurs throughout the shell surface and consists of evenly spaced, punctate grooves with larger interspaces. In the last whorls punctuations are conspicuous, somewhat rectangular in shape and axially elongate, very close to each other within each groove. At the same time, they are more oval or roundish on the preceding whorls. Towards the shell base, the spiral sculpture is coarser. Growth striae are present all through the shell surface.

Remarks. There are some discrepancies between the fossil shell and the original description of *Tornatella senegalensis* (Petit de la Saussaye 1851: 262, pl. 8, fig. 5), which was described as cylindrical in shape, delicate and almost transparent ("*Testa elongata, cylidracea, tenui, subpellucida...*"), while the fossil shell is neither particularly cylindric nor delicate, being instead somewhat turriculate and moderately robust. In addition, the shell was illustrated as somewhat cyrtoconoid in outline. Shell dimensions were reported as 17 mm (height) and 6 mm (width), in agreement with the present fossil shell.

Description and illustration of *Tornatella senegalensis* given by Reeve (1865: pl. 3, figs 14a, b) ("somewhat pyramidal... narrowly ovate... spire rather sharply exerted") match the fossil shell, except for the higher aperture, about 90% of last whorl height. He also remarked that it is "A very distinct species

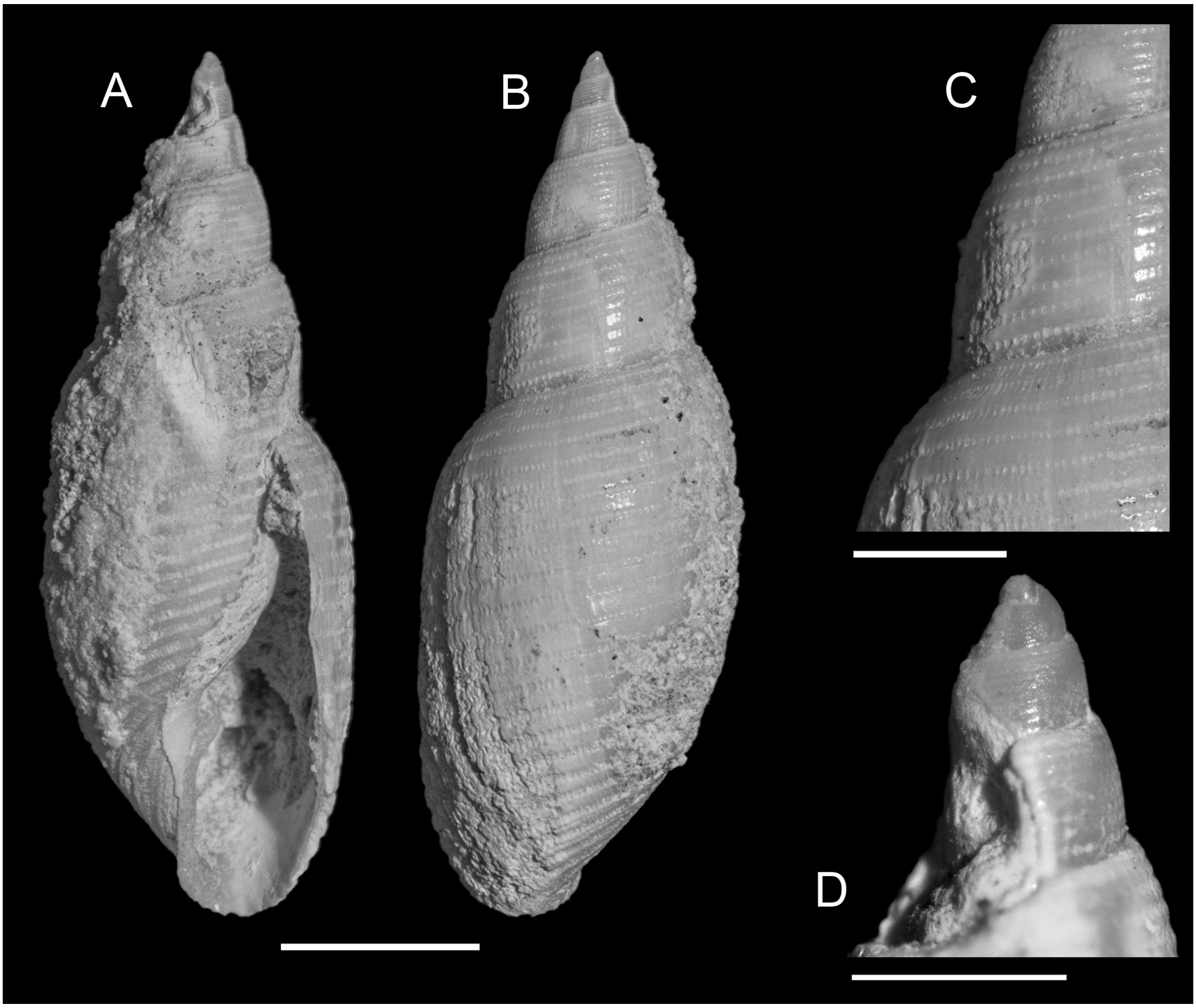

Fig. 3 - *Acteon senegalensis* (Petit de la Saussaye, 1851) (MSTB 2025/1A). A, B: Shell (scale bar 4 mm); C: Sculpture detail (scale bar 2 mm); D. Apical whorls (scale bar 1 mm).

of light structure, linearly grooved throughout with great regularity". The description by Thrion & Pilsbry (1893: 152, pl. 19, figs. 90. 91) remarks the thinness of shell ("The elongated form, thinness of the shell, and the obliquity of the columellar fold are the distinguishing features of this form"), whereas its illustration appears notably similar in outline to the fossil shell, including the slight inflexion of the outer lip (except for a higher aperture, about 90% of last whorl height). All the past illustrations reported above appear to depict the same species, and the differences in shape may be due to inaccuracies in the drawings. The fossil shell under study is referred to as the same species, despite its apparent moderate robustness, which could be due to heavy sediment encrustation.

Distribution. *Acteon senegalensis* is currently known from Angola (Rolán & Ryall 1999), Gambia, Senegal and Mauritania (Petit de la Saussaye 1851; Reeve 1865; Thrion & Pilsbry 1893; Dautzenberg 1910). The northernmost record is from the Ras Nouadhibou peninsula (Cap Blanc) (northern Mauritania, latitude 21°N).

Acteon maltzani Dautzenberg, 1910

Fig. 4

Actaeon (Amathis) senegalensis Maltzan, 1885: p. 29 - non *Acteon senegalensis* (Petit de la Saussaye, 1851).
Acteon maltzani Dautzenberg, 1910: p. 56, pl. 1, figs. 1, 2 (*nomen novum*)
Acteon maltzani - Valdés & Héros, 1998: p. 698, fig. 1B (syntype).

Material: 1 sh (MSTB 2025/1B).

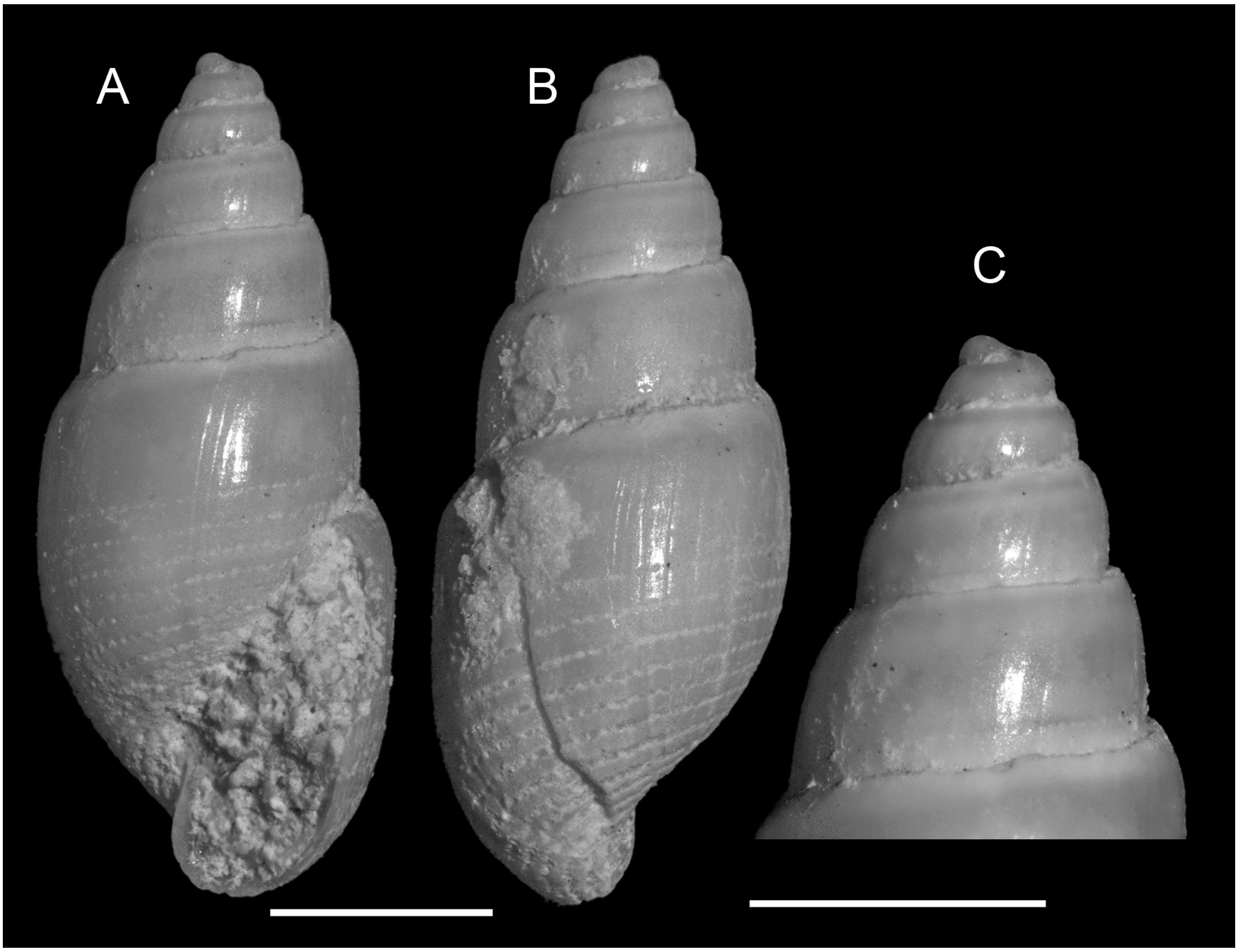

Fig. 4 - *Acteon maltzani* Dautzenberg, 1910 (MSTB 2025/1B). A, B: Shell (scale bar 2 mm); C: Apical whorls (scale bar 1 mm).

Description. The shell is 3.9 mm high and 1.7 mm in width, with six whorls, including a protoconch, of which the last one is approximately two-thirds of the total height. Whorls are convex with slightly canaliculate sutures. The paucispiral protoconch consists of 1.5 whorls. The aperture is narrow, oval-elongate and oblique, measuring approximately 75% of the last whorl height. The inner characters of the aperture cannot be seen because of the cemented infilling. The sculpture consists of thin, punctuate, spaced grooves on the last whorl, leaving the subsutural area smooth, and becoming coarser on the shell base. On the penultimate whorl, one suprasutural punctate groove is present. Interspaces are much broader than grooves. A faint punctuate groove can be seen in the preceding whorl. Punctuations are oval, conspicuous, separated from each other within each groove but tending to become fused to each other towards the shell base. Delicate growth striae are present all through the shell surface.

Remarks. Maltzan (1885: 29) described *Actaeon (Amathis) senegalensis* from the Island of Gorée (off Cape Verde, Senegal). Being the name preoccupied by *Tornatella senegalensis* Petit de la Saussaye, 1851, Dautzenberg (1910: 56, pl. 1, figs. 1, 2) replaced it with *Actaeon maltzani* and illustrated the species (reported from off Rufisque, Senegal) for the first time. This nomenclatural history was reported by Valdés & Héros (1998: 698, fig. 1B), who also illustrated a syntype of *A. maltzani*.

More recently, Rolán (2005) and Ortea & Moro (2018) reported *A. maltzani* from the Cape Verde Islands, providing illustrations and observations on the soft parts.

Amathis A. Adams, 1861, to which the species was initially assigned in subgeneric rank, is now considered a synonym of *Agatha* A. Adams, 1860, and belongs to the Pyramidellidae (Schander et al. 1999).

The fossil shell differs from the illustrated specimens only by being slightly more slender, due to a higher spire. In the syntype illustrated by Valdés & Héros (1998), there are two subsutural punctuate grooves on the penultimate whorl, instead of one as in the fossil shell.

Due to the cemented sediment infilling, the apertural characters are not visible. However, the species has a small tooth-like columellar callus, as in the original description ("*parete aperturali callo tenui obtecta*" (Maltzan 1885).

Distribution. *Acteon maltzani* has been reported from Angola (Rolán & Ryall 1999), Senegal (Dakar region) and Cape Verde (Dautzenberg 1910; Rolán 2005; Ortea & Moro 2008). It is also known from the São Tomé and Príncipe Archipelago (Ávila 2024, pers. comm.).

DISCUSSION AND CONCLUSIONS

Acteon senegalensis and *A. maltzani* are the first acteonids recorded as Senegalese Guests in the Mediterranean LIG. The Acteonidae include about 110 living species (Göbbleler & Klussmann-Kolb 2010), with a wide distribution, both geographically and bathymetrically (OBIS), and generally feeding on polychaetes (Yonow 1989).

Despite the "Senegalese" attribute for the tropical species that colonized the Mediterranean during the LIG, there is growing evidence of the importance of the Macaronesian islands in the dispersal route of these species (Meco et al. 2002; Ávila et al. 2009; Ávila et al. 2015; Melo et al. 2022, 2023). Macaronesia comprises several volcanic archipelagos (Cape Verde, Canary Islands, Selvagens Islands, Madeira, and Azores) in the North Atlantic, located between approximately 14° N and 33° N. Among them, Cape Verde is the southernmost archipelago (600-850 km off Cap-Vert). The presence of tropical species is documented in the MIS 5.5 deposits of Macaronesia, spanning from Cape Verde to the Azores (Muhs et al. 2014; Ávila et al. 2015; Melo et al. 2022). The Mediterranean, therefore, represented the northernmost position in the dispersal route of this climatically driven faunistic flow. Instead of, or in addition to a long-shore diffusion along West Africa, a "stepping stone" model has been hypothesized (Melo et al. 2022), in which the Macaronesia islands acted as springboards for northward dispersal. This hypothesis opens the possibility that some of the Senegalese Guests originated from Macaronesian populations, rather than from West Africa. This could be the case for *Acteon maltzani*, which is known to thrive at Cape Verde and in the Gulf of Guinea (São Tomé and Príncipe archipelagos).

As discussed by Albano et al. (2024), the modern interglacial conditions (MIS 1) and anthropogenic global warming would allow some tropical species to spread into the Mediterranean, as is happening with several Indo-Pacific species through the Suez Canal (Lessepsian species) (e.g., Khalil et al. 2025). The northward diffusion of tropical species would be inhibited by the presence of the NW African Upwelling System, extending from Cap Blanc to Morocco (Pelegrí & Benazzouz 2015), which acts as a thermal barrier for tropical species and is hypothesized to have been weaker during the LIG (Melo et al. 2022; Albano et al. 2024). The biogeographic model proposed for the MIS 5.5 by Melo et al. (2033: fig. 6) is actually more similar to that of the Early Pliocene than to the modern one, with the tropical Mediterranean West African Province extending north up to the Canaries and Selvagens, including the northernmost part of the Ibero-Moroccan Gulf and the Mediterranean. Conversely, in the present day, the Moroccan coasts and the Mediterranean host the subtropical Mediterranean-Moroccan Province.

It has been suggested (Melo et al. 2022, 2023; Ávila et al. 2009, 2015) that the northward diffusion of tropical species occurred during the last phase of glacial Termination II, specifically at the glacial-interglacial transition between MIS 6 and MIS 5.5 (140-130 ky), when oceanographic barriers such as the Canary Current were weakened, thus generating temporary windows for the northward dispersal of marine species.

The role of larval development in range expansion processes during the climatic phases of the Quaternary has been poorly investigated (e.g., Raffi 1986; Urra et al. 2023). The bivalve *Arctica islandica* (Linnaeus, 1767), the best known of the Northern Guests during the glacial phases in the Mediterranean Pleistocene (Malatesta & Zarlenga 1986; Raffi 1986), has planktotrophic larval development (Cargnelli et al. 1999), as does *Tethystrombus* *latus* (Carpenter & De Angelis 2016), typical representative of the Senegalese Guests. As is known, the planktotrophic larval development offers the greatest possibilities of diffusion (Scheltema 1977; Jablonski & Lutz 1983). However, both cold and warm faunistic flows in the Mediterranean Pleistocene include species with non-planktotrophic larval development, as is the case with the two species herein discussed, whose short protoconchs (1-1.5 whorls) are indicative of this type of development. Interestingly, Ávila et al. (2009) found a similar proportion of planktotrophic and non-planktotrophic species among the thermophilic prosobranchs that locally disappeared at Santa Maria Island (Azores) during the Last Glacial, in contrast to the figures for the Recent malacofauna, where planktotrophic species strongly prevail. The authors assume that these species must have arrived in the Azores during or shortly before MIS 5.5, due to the presence of temporary sea-surface currents (no longer in existence) that allowed the northward dispersal of warm-water species, either via planktotrophic larvae or by rafting. A similar model could thus explain the occurrence of non-planktotrophic species among the Senegalese Guests in the Mediterranean Sea.

Data Availability Statement

The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding Author to obtain access.

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REFERENCES

Albano P.G., Schultz L., Wessely J., Taviani M., Dullinger S. & Danise S. (2024) - The dawn of the tropical Atlantic invasion into the Mediterranean Sea. *PNAS*, 121(15): e2320687121.

Amorosi A., Antonioli F., Bertini A., Marabini S., Mastronuzzi G., Montagna P., Negri A., Rossi V., Scarponi D., Taviani M., Angeletti L., Piva A. & Vai G.B. (2014) - The Middle-Upper Pleistocene Fronte Section (Taranto, Italy): An exceptionally preserved marine record of the Last Interglacial. *Global and Planetary Change*, 119: 23-38.

Antit M., Gofas S., Salas C. & Azzouna A. (2011) - One hundred years after *Pinctada*: an update on alien Mollusca in Tunisia. *Mediterranean Marine Science,* 12: 53-74.

Antonioli F., Ferranti L., Stocchi P., Deiana G., Lo Presti V., Furlani S., Marino C., Orru P., Scicchitano G., Trainito E., Anzidei M., Bonamini M., Sansò P. & Mastronuzzi G. (2018) - Morphometry and elevation of the last interglacial tidal notches in tectonically stable coasts of the Mediterranean Sea. *Earth Science Reviews,* 185: 600-623.

Ávila S.P. (2024) - Atlantic and Mediterranean Gastropoda: geographical distribution and functional traits database. Version 1.0 https://www.researchgate.net/publication/385907293_Atlantic_and_Mediterranean_Gastropoda_geographical_distribution_and_functional_traits_database_Version_1_0

Ávila S.P., Melo C., Silva L., Ramalho R.S., Quartau R., Hipolito A., Cordeiro R., Rebelo A.C., Madeira P., Rovere A., Hearty P.J., Henriques D., da Silva C.M., de Frias Martins A.M. & Zazo C. (2015) - A review of the MIS 5e highstand deposits from Santa Maria Island (Azores, NE Atlantic): palaeobiodiversity, palaeoecology and palaeobiogeography. *Quaternary Science Reviews*, 114: 126-148.

Ávila S.P., Silva C.M. da, Schiebel R., Cecca F., Backeljau T. & Martins A.M.F. (2009) - How did they get here? Palaeobiogeography of the Pleistocene marine molluscs of the Azores. *Bulletin of the Geological Society of France,* 180: 201-213.

Azzaroli A., Perno U. & Radina B. (1968) - Note illustrative del Foglio 188 "Gravina di Puglia" della Carta Geologica d'Italia alla scala 1:100.000. Servizio Geologico d'Italia, Roma.

Belluomini G., Caldara M., Casini C., Cerasoli M., Manfra L., Mastronuzzi G., Palmentola G., Sansò P., Tuccimei P. & Vesica P.L. (2002) - The age of late Pleistocene shorelines and tectonic activity of Taranto area, Southern Italy. *Quaternary Science Reviews*, 21: 525-547.

Bini M., Zanchetta G., Drysdale R.N., Giaccio B., Stocchi P. Vacchi, M., Hellstrom J.C., Couchoud I., Monaco L., Ratti A., Martini F. & Sarti L. (2020) - An end to the last interglacial highstand before 120 ka: relative sea-level evidence from Infreschi Cave (southern Italy). *Quaternary Science Reviews*, 250: 106658.

Boenzi F., Caldara M. & Pennetta L. (1986) - La trasgressione tirreniana nei dintorni di Castellaneta (Taranto). *Geologia Applicata e Idrogeologia*, 20: 163-175.

Caldara M. (1987) - La sezione tirreniana di Ponte del Re (Castellaneta Marina, Taranto): analisi paleoecologica. *Atti della Società Toscana di Scienze Naturali, Memorie, Serie A,* 93: 129-163.

Caprotti E. (1979) - Scafopodi neogenici e recenti del bacino mediterraneo. Iconografia ed epitome. *Bollettino Malacologico*, 15: 213-288.

Cargnelli L.M, Griesbach S.J., David B., Packer D.B. & Weissberger E. (1999) - Ocean Quahog, *Arctica islandica*, Life History and Habitat Characteristics. *NOAA Technical Memorandum NMFS-NE* Series, 148: 1-12.

Carpenter K.E. & De Angelis N. (Eds.) (2016) - The living marine resources of the Eastern Central Atlantic. Volume 2: Bivalves, gastropods, hagfishes, sharks, batoid fishes, and chimaeras. FAO Species Identification Guide for Fishery Purposes, Rome, FAO: 665-1509.

Ciaranfi N., Pieri P. & Ricchetti G. (1992) - Note alla carta geologica delle Murge e del Salento (Puglia centromeridionale). *Memorie della Società Geologica Italiana,* 41: 449-460.

Cita M.B. (2008) - Summary of Italian marine stages. *Episodes*, 31: 251-254.

Cita Sironi M.B., Capotondi L. & Asioli A. (2005) - The Tyrrhenian stage in the Mediterranean: definition, usage and recognition in the deep-sea record. A proposal. *Rendiconti Lincei. Scienze Fisiche e Naturali*, s.9, 16: 297-310.

Cleveringa P., Meijer T., van Leeuwen R.J.W., de Wolf H., Pouwer R., Lissenberg T. & Burger A.W. (2000) - The Eemian stratotype locality at Amersfoort in the central Netherlands: a re-evaluation of old and new data. *Geologie en Mijnbouw/Netherlands Journal of Geosciences*, 79: 197-216.

Cosel R. von & Gofas S. (2019) - Marine Bivalves of Tropical West Africa. Faune et Flore tropicales, 48. Muséum national d'Histoire naturelle, Paris; IRD, Marseille, 1104 pp.

Dai Pra G. (1982) - The Late Pleistocene marine deposits of Torre Castiglione (Southern Italy). *Geografia Fisica e Dinamica Quaternaria*, 5: 115-119.

Dai Pra G. & Hearthy P.J. (1992) - I livelli marini pleistocenici del Golfo di Taranto. Sintesi geocronostratigrafica e tettonica. *Memorie della Società Geologica Italiana*, 41: 637-644.

Dai Pra G. & Stearns C.E. (1977) - Sul Tirreniano di Taranto. Datazione su coralli con il metodo Th^{230}/U^{234}. *Geologica Romana,* 16: 231-242.

Dautzenberg P. (1910) - Contribution à la faune malacologique de l'Afrique occidentale. *Actes de la Société Linéenne de Bordeaux*, 64: 47-228.

De Castro-Coppa M.G. (1970) - Segnalazione ed osservazioni su *Acteocina knockeri* (Smith) e *Parastrophia garganica* Moncharmont-Zei nel Tirreniano di Taranto. *Bollettino della Società dei Naturalisti in Napoli*, 79: 227-252.

De Santis V., Montagna P., Scicchitano G., Mastronuzzi G., Pons-Brancu E., Scardino G., Ortiz J.E., Sanchez-Palencia Y., Torres T. & Caldara M. (2024) - Two main highstands during the Last Interglacial: insights from palaeoshorelines and marine terraced deposits along the Ionian coast of the Apulia region, Southern Italy. *Earth Surface Processes and Landforms*. DOI:10.1002/esp.5912.

De Santis V., Scardino G., Meschis M., Ortiz J.E., Sánchez-Palencia Y. & Caldara M. (2021) - Refining the middle-late Pleistocene chronology of marine terraces and uplift history in a sector of the Apulian foreland (southern Italy) by applying a synchronous correlation technique and amino acid racemization to *Patella* spp. and *Thetystrombus latus*. *Italian Journal of Geosciences*, 140: 438-463.

De Santis V., Scardino G., Scicchitano G., Meschis M., Montagna P., Pons-Branchu E., Ortiz J.E., Sanchez-Palencia Y. & Caldara M. (2023) - Middle-late Pleistocene chronology of palaeoshorelines and uplift history in the low-rising to stable Apulian foreland: overprinting and reoccupation. *Geomorphology*, 421: 108530.

Di Geronimo I. (1984) - Stabilité des peuplements benthique et stabilité des bassins sédimentaires. *Geobios*, *Mem.* 8: 145-150.

Doglioni C., Mongelli F. & Pieri P. (1994) - The Puglia uplift (SE Italy): an anomaly in the foreland of the Apenninic subduction due to buckling of a thick continental lithosphere. *Tectonics,* 13: 1309-1321.

Doglioni C., Tropeano M., Mongelli F. & Pieri P. (1996) - Middle-late Pleistocene uplift of Puglia: an anomaly in the Apenninic foreland. *Memorie della Società Geologica Italiana*, 51: 101-117.

Dutton A. & Lambeck K. (2012) - Ice volume and sea level during the last interglacial. *Science,* 337: 216-219.

Dutton A., Carlson A.E., Long A.J., Milne G.A., Clark P.U., DeConto R., Horton B.P., Rahmstorf S. & Raymo M.E. (2015) - Sea-level rise due to polar ice-sheet mass loss during past warm periods. *Science*, 349: 6244.

Dutton A., Webster J.M., Zwartz D., Lambeck K. & Wohlfarth B. (2015) - Tropical tales of polar ice: Evidence of last interglacial polar ice sheet retreat recorded by fossil reefs of the granitic Seychelles islands. *Quaternary Science Review*, 107: 182–196.

Ferranti L., Antonioli F., Mauz B., Amorosi A., Dai Pra G., Mastronuzzi G., Monaco C., Orru P., Pappalardo M., Radtke U., Renda P., Romano P., Sansò P. & Verrubb V. (2006) - Markers of the last interglacial sea-level high stand along the coast of Italy: tectonic implications. *Quaternary International*, 145-146: 30-54.

Garilli V. (2011) - Mediterranean Quaternary interglacial molluscan assemblages: Palaeobiogeographical and palaeoceanographical responses to climate change. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 312: 98-114.

Giaccio B., Bini M., Isola I., Hu H., Rolfo M.F., Shen C., Ferracci A., Monaco L., Pasquetti F. & Zanchetta G. (2024) - Constraining the end of the Last Interglacial (MIS 5e) relative sea level highstand in central Mediterranean: New data from Grotta delle Capre, central Italy. *Global and Planetary Change*, 232: 104321.

Gignoux M. (1913) - Les formations marines pliocenes et quaternaires de l'Italie du sud et de la Sicile. *Annales de l'Université de Lyon. Nouvelle série,* 36: 1-693.

Göbbeler K. & Klussmann-Kolb A. (2010) - The phylogeny of the Actenoidea (Gastropoda): molecular systematics and first detailed morphological study of *Ricataxis punctocaelatus* (Carpenter, 1864*). Journal of Molluscan Studies*, 76: 303-316.

Grant K.M., Rohling E.J., Ramsey C.B., Cheng H., Edwards R.L., Florindo F., Heslop D., Marra F., Roberts, A.P., Tamisiea M.E. & Williams F. (2014) - Sea-level variability over five glacial cycles. *Nature Communications*, 5: 5076.

Harzhauser M. & Kronenberg G.C. (2008) - A Note on *Strombus coronatus* Defrance, 1827 and *Strombus coronatus* Röding, 1798 (Mollusca: Gastropoda). *The Veliger*, 50: 120-128.

Hearty P.J. & Dai Pra G. (1992) - The age and stratigraphy of Middle Pleistocene and younger deposits along the Gulf of Taranto (Southeast Italy). *Journal of Coastal Research,* 8: 82-105.

Hoenselaar H.J. & Gulden G.J. (1991) - First record of *Utriculastra knockeri* (E.A. Smith, 1872) in the Mediterranean Sea (Gastropoda: Scaphandridae). *Bollettino Malacologico*, 27: 56-58.

Hoffman J.S., Clark P.U., Parnell A.C. & He F. (2017) - Regional and global sea-surface temperatures during the last interglaciation. *Science*, 355(6322): 276-279.

Isola I., Bini M., Columbu A., Di Vito M.A., Giaccio B., Hu H., Martini F., Pasquetti F., Sarti L., Mule F., Mazzoleni A., Shen C. & Zanchetta G. (2024) - Last Interglacial and MIS 9e relative sea-level highstands in the Central Mediterranean: a reappraisal from coastal cave deposits in the Cilento area, Southern Italy. *Quaternary Science Advances*, 15: 100212.

Issel A. (1914) - Lembi fossiliferi quaternari e recenti osservati nella Sardegna meridionale dal prof. D. Lovisato. *Rendiconti Lincei. Scienze fisiche e naturali,* 5, 23: 759-770.

Jablonski D. & Lutz R.A. (1983) - Larval ecology of marine benthic invertebrates: paleobiological implications. *Bio-*

logical Reviews, 58: 21-89.

Khalil M.T., Mostafa A.B. & El-Naggar M.M. (2025) - Climate Change and Lessepsian Migration to the Mediterranean Sea. In: Khalil M.T., Emam W.W.M. & Negm A. (Eds.) - Climate Changes Impacts on Aquatic Environment. Earth and Environmental Sciences Library. Springer, Cham: 85-118.

Kobelt W. (1874) - Verzeichniss der von mir nach Tarent gesammelten fossilen Conchylien. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, 1: 65-77.

Kopp R.E., Simons F.J., Mitrovica J.X., Maloof A.C. & Oppenheimer M. (2009) - Probabilistic assessment of sea-level during the last interglacial stage. *Nature*, 462: 863-867.

Lunt D.J., Abe-Ouchi A., Bakke P., Berge, A., Braconnot P., Charbit S., Fischer N., Herold N., Jungclaus J.H., Khon V.C., Krebs-Kanzow U., Langebroek P.M., Lohmann G., Nisancioglu K.H., Otto-Bliesner B.L., Park W., Pfeiffer M., PhippsS. J., Prange M., Rachmayani R., Renssen H., Rosenbloom N., Schneider B., Stone E.J., Takahashi E., Wei W., Yin Q. & Zang Z.S. (2013) - A multimodel assessment of last interglacial temperatures. *Climate of the Past,* 9: 699-717.

Malatesta A. & Zarlenga F. (1986) - Northern Guests in the Pleistocene Mediterranean Sea. *Geologica Romana*, 25: 91-154.

Maltzan H. von. (1885) - Neue Gastropoden von Senegal. *Nachrichtsblatt der deutschen malakozoologischen Gesellschaft*: 17: 25-30.

Mastronuzzi G., Quinif Y., Sansò P. & Selleri G. (2007) - Middle-Late Pleistocene polycyclic evolution of a stable coastal area (southern Apulia, Italy). *Geomorphology*, 86: 393-408.

Meco J. (1977) - Los Strombus Neogenos y Cuaternarios del Atlantico Eurafricano. (Taxonomia, Biostratigrafia y Palaeoecologia). *Palaeontologia de Canaria*s, 1: 1-142.

Meco J., Guillou H., Carracedo J.-C., Lomoschitz A., Ramos A.-J. G. & Rodríguguez-Yánez J.-J. (2002) - The maximum warmings of the Pleistocene world climate recorded in the Canary Islands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 185: 197-210.

Melo C.S., da Silva C.M., Scarponi D., González E., Rolán E., Rojas A., Martinez S., Silva L., Johnson M., Rebelo A.C., Baptista L., Voelker A., Ramalho R. & Ávila S.P. (2023) - Palaeobiogeography of NE Atlantic archipelagos during the Last Interglacial (MIS 5e): A molluscan approach to the conundrum of Macaronesia as a marine biogeographic unit. *Quaternary Science Reviews*, 319: 108313.

Melo C.S., Martín-Gonzalez E., da Silva C.M., Galindo I., Gonzalez-Rodríguez A. Baptista L., Rebelo A.C., Madeira P., Voelker A.H.L, Johnson M.E., Arruda S.A. & Ávila S.P. (2022) - Range expansion of tropical shallow-water marine molluscs in the NE Atlantic during the last interglacial (MIS 5e): Causes, consequences and utility of ecostratigraphic indicators for the Macaronesian archipelagos. *Quaternary Science Reviews*, 278: 1-17.

Muhs D.R., Meco J. & Simmons K.R. (2014) - Uranium-series ages of corals, sea level history, and palaeozoogeography, Canary Islands, Spain: an exploratory study for two Quaternary interglacial periods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 394: 99-118.

Murray-Wallace C.V. & Woodroffe C.D. (2014) - Quaternary Sea-Level Changes: A Global Perspective. Cambridge University Press, Cambridge, United Kingdom, 504 pp.

Negri A., Amorosi A., Antonioli F., Bertini A., Florindo F., Lurcock P.C., Marabini S., Mastronuzzi G.S., Regattieri E., Rossi V., Scarponi D., Taviani M., Zanchetta G. & Vai G.B. (2015) - A potential global boundary stratotype section and point (GSSP) for the Tarentian Stage, Upper Pleistocene, from the Taranto area (Italy): Results and future perspectives. *Quaternary International*, 383: 145-157.

O'Leary M.J., Hearty P.J., Thompson W.G., Raymo M.E., Mitrovica J.X. & Webster J.M. (2013) - Ice sheet collapse following a prolonged period of stable sea level during the last interglacial. *Nature Geoscience*, 6: 796-800.

OBIS (Ocean Biodiversity Information System) - Acteonidae A. d'Orbigny, 1842. https://obis.org/taxon/155.

Ortea J. & Moro L. (2018) - Nuevas citas y nuevos datos sobre las lesmas do mar (Mollusca: Gastropoda) de las islas de Cabo Verde (II). *Avicennia*, 22: 49-58

Otto-Bliesner B.L., Marshall S.J., Overpeck J.T., Miller G.H. & Hu A. (2006) - Simulating Arctic climate warmth and icefield retreat in the last interglaciation. *Science,* 311: 1751-1753.

Otto-Bliesner B.L., Rosenbloom N., Stone E.J., McKay N.P., Lunt D.J., Brady E.C. & Overpeck J.T. (2013) - How warm was the last interglacial? New model–data comparisons. *Philosophical Transactions of the Royal Society a Mathematical, Physical and Engineering Sciences*, 371: 20130097.

Pelegrí J.L. & Benazzouz A. (2015) - Coastal upwelling off North-West Africa. In: Valdés L. & Déniz-González I. (Eds.) - Oceanographic and biological features in the Canary Current Large Marine Ecosystem. IOC-UNESCO, Paris. IOC Technical Series, 115: 93-103.

Pérès J.M. (1967) - The Mediterranean benthos. *Oceanography Marine Biology Annual Review*, 5: 449-553.

Petit de la Saussaye S. (1851) - Description de coquilles nouvelles. *Journal de Conchyliologie*, 2: 259-269.

Philippi R.A. (1836) - Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium quae in itinere suo observavit. Vol. 1. xiv + 267 p., pls. 1-12. Sumptibus Simonis Schroppii et Sociorum. Berolini [Berlin].

Philippi R.A. (1844) - Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium, quae in itinere suo observavit. Vol. 2.. Halle [Halis Saxorum]: Eduard Anton. iv + 303 pp., pls 13-28.

Raffi S. (1986) - The significance of marine boreal molluscs in the Early Pleistocene faunas of the Mediterranean area. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 52: 267-289.

Ragaini L. & Fabio Bernieri F. (2007) - Prima segnalazione di *Odostomia lukisii* Jeffreys, 1859, *Acteocina knockeri* (Smith E.A., 1872) e *Cylichnina crebrisculpta* Monterosato, 1884 nel Pliocene mediterraneo. *Bollettino Malacologico*, 43: 147-155.

Reeve LA. (1865) - Monograph of the genus *Tornatella*. In: Conchologia Iconica, or, illustrations of the shells of molluscous animals, vol. 15, pls 1-4 and unpaginated text. L. Reeve & Co., London.

Ricchetti G., Ciaranfi N., Luperto Sinni E., Mongelli F. & Pieri P. (1992) - Geodinamica ed evoluzione sedimentaria e tettonica dell'avampaese apulo. *Memorie Società Geologica Italiana*, 41: 57-82.

Rohling E.J., Foster G.L., Grant K.M., Marino G., Roberts A.P., Tamisiea M.E. & Williams F. (2014) - Sea-level and deep-sea-temperature variability over the past 5.3 million years. *Nature,* 508 (7497): 477-482.

Rolán E. (2005) - Malacological Fauna From The Cape Verde Archipelago. Part 1, Polyplacophora and Gastropoda. ConchBooks. Hackenheim. ISBN 3-325319-73-2, 455 pp.

Rolán E. & Ryall P. (1999) - Checklist of the Angolan marine molluscs. Lista de los moluscos marinos de Angola. *Reseñas Malacológicas,* X: 132 pp.

Rovere A., Raymo M., Vacchi M., Lorscheid T., Stocchi P., Gomez-Pujol L., Harris D., Casella E., O'Leary J. & Hearty P. (2016) - The analysis of last interglacial (MIS 5e) relative sea-level indicators: Reconstructing Sea-level in a warmer world. *Earth Science Reviews*, 159: 404-427.

Santagati P., Borrelli M., Bernasconi M.P. & Perri E. (2023) - Fossil fauna in MIS 5e deposits of Mar Piccolo basin (Taranto, Southern Italy) suggests new palaeoclimatic constraints. *Rendiconti Online Società Geologica Italiana*, 59: 16-20.

Santagati P., Perri E., Bernasconi M.P., Borrelli M., Guerrieri S. & Critelli S. (2024) - MIS 5e sea surface temperature estimation; a multi-proxy approach using a marine macrofossil assemblage (Mar Piccolo, Gulf of Taranto, Southern Italy). *Journal of Palaeogeography*, 13: 327-350.

Schander C., van Aartsen J.J. & Corgan J.X. (1999) - Families and genera of the Pyramidelloidea (Mollusca: Gastropoda). *Bollettino Malacologico*, 34: 145-166.

Scheltema R.S. (1977) - Dispersal of marine invertebrate organisms: paleobiogeographic and biostratigraphic implications. In: Kauffmann R.G. & Hazel J.E. (Eds.) - Concepts and Methods of Biostratigraphy: 73, xiii+ 658-108. Dowden, Hutchinson and Ross, Stroudsburg.

Shackleton N.J., Sanchez-Gon M.F., Pailler D. & Lancelot Y. (2003) - Marine Isotope Substage 5e and the Eemian Interglacial. *Global and Planetary Chan*ge, 36: 151-155.

Siddall M., Rohling E., Almogi-Labin A., Hemleben C., Meischner D., Schmelzer I. & Smeed D.A. (2003) - Sea-level fluctuations during the last glacial cycle. *Nature*, 423: 853-858.

Sprat R.M. & Lisiecki L.E. (2016) - A Late Pleistocene Sea level stack. *Climate of the Past*, 12: 1079-1092.

Stirling C.H., Esat T.M., Lambeck K. & McCulloch M.T. (1998) - Timing and duration of the last interglacial: evidence for a restricted interval of widespread coral reef growth. *Earth and Planetary Science Letters*, 160: 745-762.

Thrion G.W. & Pilsbry H.A. (1893) - Manual of conchology, structural and systematic: with illustrations of the species. Vol XV Polyplacophora. Academy of Natural Science of Philadelphia.

Tropeano M., Sabato L. & Pieri P. (2002) - Filling and cannibalization of a foredeep: the Bradanic Trough, Southern Italy. *Geological Society, London, Special Publications*, 191: 55-79.

Turney C.S.M. & Jones R.T. (2010) - Does the Agulhas current amplify global temperatures during super-interglacials? *Journal of Quaternary Science*, 25: 839-843.

Urra J., O. Utrilla O., Gofas S., Valencia V.A., Farias C., Gonzalez-García E., Lopez Gonzalez N., Fernandez-Salas L.M. & Rueda J.L. (2023) - Late Pleistocene boreal molluscs in the Gulf of Cadiz: Past and current oceanographic implications. *Quaternary Science Reviews*, 313: 108196.

Valdés A. & Héros V. (1998) - The types of Recent and certain fossil opisthobranch molluscs in the Muséum nalional d'Histoire naturelle, Paris. *Zoosystema*, 20: 695-742.

Waelbroeck C., Labeyrie L., Michel E., Duplessy J.C., McManus J.F., Lambeck K., Balbon E. & Labracherie M. (2002) - Sea-level and deep water temperature changes derived from benthic foraminifera isotopic records. *Quaternary Science Reviews*, 21: 295-305.

WoRMS Editorial Board (2025) - World Register of Marine Species. Available from https://www.marinespecies.org at VLIZ. Accessed 2025-06-17. doi:10.14284/170

Yonow N. (1989) - Feeding observations on *Acteon tornatilis* (Linnaeus) (Opisthobranchia: Acteonidae). *Journal of Molluscan Studies*, 55: 97-102.