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Chitons from Deep-Water Mollusk-Rich Deposits in the Southwestern Adriatic Sea (Mollusca, Polyplacophora) †

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Abstract: Sea-bottom sampling at bathyal depths off the Apulian margin (southwestern Adriatic Sea) recovered shelly biogenic sediments rich in mollusk remains. Noteworthy is the occurrence in such taphocoenoses of loose chiton valves, rarely reported in these environments. We identified four species of Polyplacophora, *Leptochiton asellus* (Gmelin, 1791), *Belknapchiton alveolus* (M. Sars MS, Lovén, 1846), *Hanleya hanleyi* (Bean in Thorpe, 1844), and the new species *Leptochiton antondohrni*. *L. asellus* (Gmelin, 1791) and *B. alveolus* are primarily of North Atlantic (boreo-celtic) affinity and thus considered to belong to last Pleistocene glacial assemblages, whose presence in the study area has long been ascertained. The same could be true for the valves of *H. hanleyi* and, possibly, *Leptochiton antondohrni* n. sp. Finally, we updated the list of mollusks found thus far in the deep-sea taphocoenoses of this area, including new records of North Atlantic-type taxa considered at present extinct in the Mediterranean basin.

Keywords: Mediterranean basin; Adriatic Sea; Bari Canyon; Mollusca; Polyplacophora; taxonomy; biogeography; Pleistocene; new species

Citation: Taviani, M.; Sosso, M.; Dell'Angelo, B. Chitons from Deep-Water Mollusk-Rich Deposits in the Southwestern Adriatic Sea (Mollusca, Polyplacophora). *Diversity* **2023**, *15*, 359. https://doi.org/10.3390/d15030359

Academic Editors: Michael Wink, Luc Legal, Ben-Erik Van Wyk and Michel Baguette

Received: 20 December 2022
Revised: 22 February 2023
Accepted: 24 February 2023
Published: 2 March 2023

1. Introduction

The deep-water environments of the southwestern Adriatic Sea (Mediterranean basin) have been the focus of intense investigation for decades. The crucial area is the Canyon Bari System, where a dramatic incision indents the Apulian margin down to the plain, cutting through terranes of different ages. In the past, part of this research was mostly devoted to collecting valuable geological and sedimentological information through sea-bottom sampling by using grab, corer and dredge gear [1,2]. With time, a less invasive approach prevailed, and priority was given to detailed geomorphological mapping and, occasionally, remotely operated vehicle observation (e.g., [3–5]). This area is also known to host lush charismatic cold water coral life [4–8] and their late Pleistocene legacy [9].

The earlier studies were pivotal in the discovery of diverse benthic faunas that encompassed both recent and pre-modern elements [10]. Besides some classic North Atlantic boreo-celtic 'cold guests' such as *Buccinum humphreysianum*, *B. undatum*, and *Pseudamussium peslutrae* [2,10,11], the occurrence of deep-water last glacial Pleistocene (ca. 115,000–11,700 years BP; defined at the time as 'würmian') mollusks in the submerged taphocoenoses (e.g., *Puncturella noachina*, *Iothia fulva*) was recorded for the first time, based upon the fraction residue of some dredge samples [12,13]. A significant contribution included taxonomic lists for particular submerged taphocoenoses [10,13], as extended by others to adjacent analog deposits [14].

In 2007, an additional survey was carried out in the area during cruise SETE-06 onboard RV *Urania*. A limited number of sea-bottom samples was taken, including also dredging the flanks of the Bari Canyon. Biogenic-rich fractions were noteworthy for their

inclusion of mollusk shells representing new records for the area; these included plates from polyplacophorans (chitons) whose presence in this habitat is of ecological interest, and also included a species described here as new. This paper updates the taxonomic knowledge on the chitons and associated mollusks of this key-sector of the Mediterranean basin and discusses the paleoclimatic implications of these findings.

2. Material and Methods

Cruise SETE-06 took place in the southwestern Adriatic Sea in spring of 2006 on-board RV *Urania* [15]. The sampling stations (code SE06) providing the material discussed in this paper are reported in Figure 1; their precise geographic position, depth, and type of gear are provided in Table 1. A share of the collected sediments was firstly washed onboard over 1 mm mesh, rinsed in freshwater, and dried in the oven at 30 °C. The resulting fraction was later analyzed in the laboratory under a binocular microscope and individual taxa were picked up and classified at the lowest taxonomic level whenever possible. Scanning Electron Microscopy (S.E.M.) was performed on chiton plates using the facility at the IMM-CNR, Bologna and at the BiGeA, University of Bologna. Type material and figured specimens are currently held in the malacological collection of the Museum of Evolution (formerly Zoology) of the University of Bologna (code MZUB), and voucher specimens in the Ismar-CNR, Bologna repository.

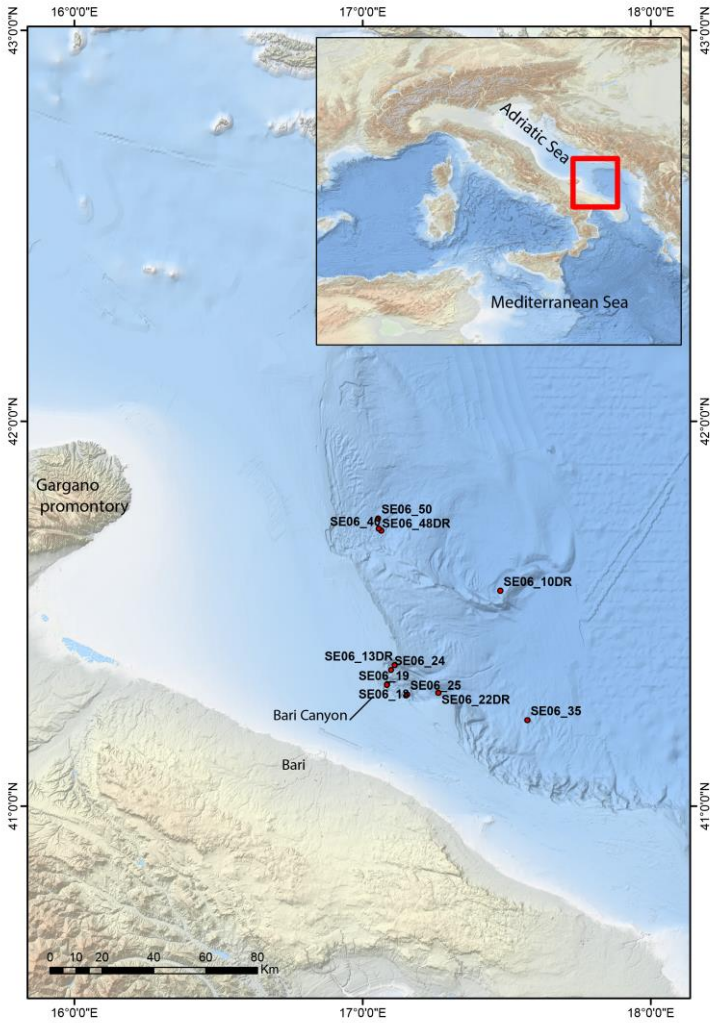

Figure 1. Bathymetric map of the southwestern Adriatic Sea showing the location of each station discussed in the article (courtesy of F. Foglini).

Table 1. Location and characteristics of the cruise SETE-06 stations discussed in the text.

Station	Depth (m)	Gear	Latitude N	Longitude E
10	335	rock dredge	4133.67	1728.70
13	423	rock dredge	4122.03	1706.72
18	341	box-corer	4119.07	1705.16
19	308	grab	4118.97	1705.10
22	722	rock dredge	4117.73	1715.83
24	199	box-corer	4121.31	1705.98
25	376	grab	4117.47	1709.29
35	878	grab	4113.46	1734.35
40	764	grab	4143.03	1703.95
48	728	epibenthic dredge	4143.31	1703.39
50	755	grab	4144.91	1703.31

The following abbreviations are used:

AA—antemucronal area, tail valve; CA—central area, intermediate valve; H—height of the valve (mm); HV—head valve; L—length of the valve (mm); LA—lateral areas, intermediate valve; PA—postmucronal area, tail valve; W—width of the valve (mm).

3. Systematics

Class Polyplacophora Gray, 1821

Order Lepidopleurida Thiele, 1909

Family Leptochitonidae Dall, 1889

Genus *Leptochiton* Gray, 1847

Type species. *Chiton cinereus* Montagu, 1803 (misapplication of name), by subsequent designation [16], *non* Linnaeus, 1767 (=*Chiton asellus* Gmelin, 1791).

Distribution. *Leptochiton* is known to have existed from the Triassic to the present-day, with a living worldwide distribution, most species being from the northeastern Atlantic and the Mediterranean Sea. Fossils determined as *Leptochiton* have been found worldwide, and *Leptochiton* is one of the most ancient genera of "modern" polyplacophorans, dating back to the Triassic [17], to the Jurassic of France, Germany, Poland, Russia and Siberia [18], and possibly even to the Lower Carboniferous [18].

***Leptochiton asellus* (Gmelin, 1791)**

Figure 2

Chiton asellus Gmelin, 1791: n. 3206, no. 21 [19]; Kaas and Knudsen, 1992: 83, figure 26, 26c [20].

Lepidopleurus (*Leptochiton*) *asellus*; Malatesta, 1962: 150, figures 5 and 6 [21]; Dell'Angelo and Palazzi, 1989: 56, plate 5 [22]; Dell'Angelo and Smriglio, 1999; 43, pls 8–9, figures 16 and 17 [23]; Dell'Angelo and Giusti, 2000: 53, figures 1–4 [24].

Leptochiton asellus; Kaas, 1981: 217, figures 1–3 [25]; Strack, 2010: 61, figures 46–49 [26].

Leptochiton (*L.*) *asellus*; Kaas and Van Belle, 1985: 39, figure 15 [27]; Sturrock and Baxter, 1993: 49, plates 1–6 [28].

Type material. Holotype at the Zoological Museum of the University of Copenhagen, a specimen attached to a shell of *Modiolus* [20] (figure 26).

Type locality. Norway, Telemark, Kragerö.

Material examined.

SE06-10: 1 intermediate valve; SE06-13: 1 head valve.; SE06-18: 2 intermediate valves; SE06-19: 1 intermediate valve; SE06-22: 1 intermediate valve; SE06-24: 1 tail valve, Figure 2J–L; SE06-25: 2 intermediate valves; SE06-35: 5 valves (2 head, 2 intermediate, 1 tail); SE06-40: 1 head valve, Figure 2C,D; SE06-48: 1 intermediate valve; SE06-50:

25 valves (4 head, 20 intermediate, 1 tail), Figure 2A,B,E–I). Maximum width of the valves (head/intermediate/tail): 3.6/5.2/4.3 mm.

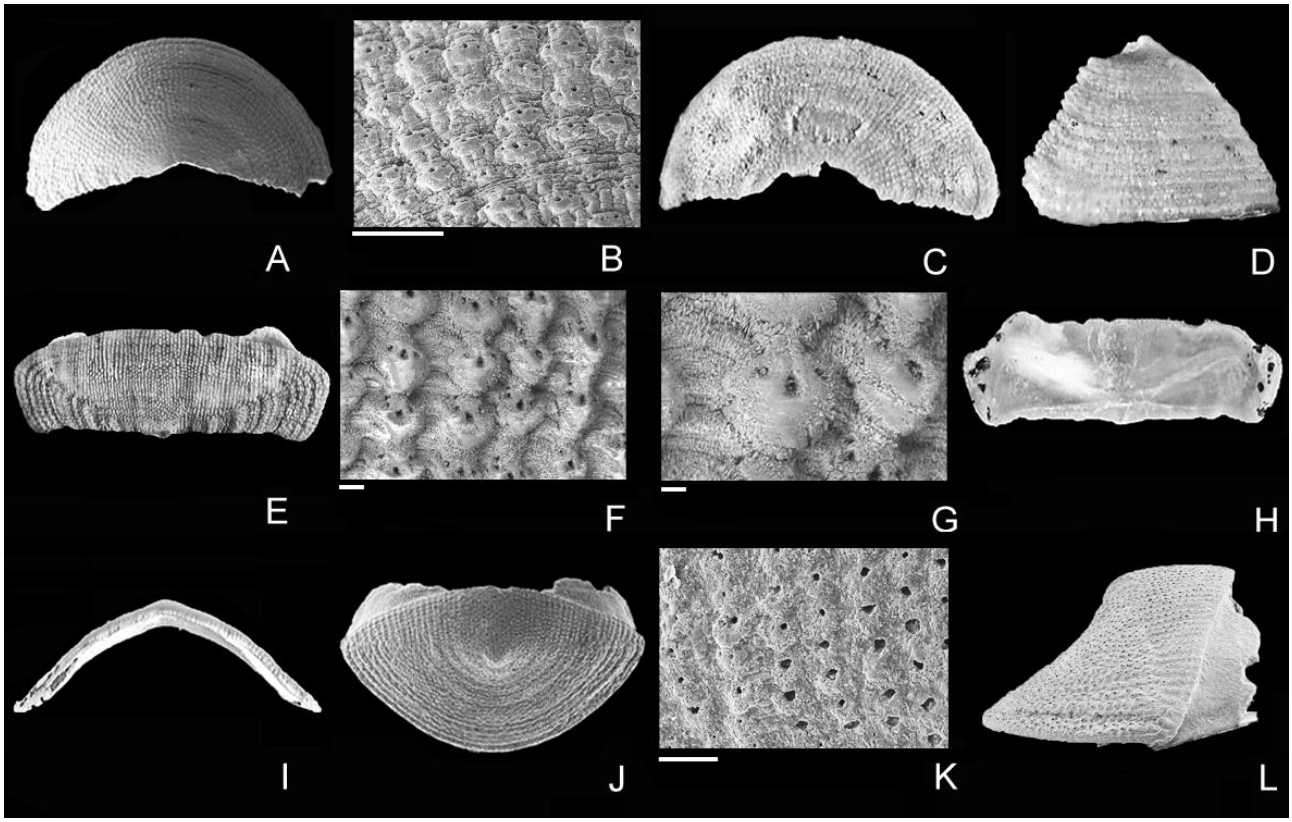

Figure 2. *Leptochiton asellus* (Gmelin, 1791); Apulian margin, offshore Bari, submerged deposits, possibly late Pleistocene (last glacial). (**A**,**B**) SE06-50, MZUB 60427, head valve, width 3 mm, dorsal view (**A**) and close-up of surface ornamentation (**B**). (**C**,**D**) SE06-40, MZUB 60428, head valve, width 3.1 mm, dorsal (**C**) and lateral (**D**) views. (**E**–**I**) SE06-50, MZUB 60429, intermediate valve, width 5.2 mm, dorsal view (**E**), close-up of surface ornamentation of central area (**F**,**G**), ventral (**H**) and frontal (**I**) views. (**J**–**L**) SE06-24, MZUB 60430, tail valve, width 2.5 mm, dorsal view (**J**), close-up of surface ornamentation of antemucronal area (**K**) and lateral view (**L**). Scale bars = 100 μm (**B**); 80 μm (**K**); 20 μm (**F**); 10 μm (**G**).

Remarks: *Chiton asellus* was originally described, although inadequately illustrated, by Chemnitz, 1785 [29] on the basis of a Norwegian specimen attached to a shell of *Modiolus*, "ex Museo Spengleriano". This description is not valid, Chemnitz's work not being strictly binomial. The taxon was validated by Gmelin [19], who added nothing new to the description, and was later better defined by Spengler [30]. This species has a complicated taxonomic history, and a thorough discussion of the interpretations given by various authors was provided by [20,25].

Leptochiton asellus (Gmelin, 1791) is characterized by the tegmentum sculpted with small granules arranged in radiating series on HV (70–80), LA (15–20), and PA, and in longitudinal series on CA (70–80) and AA, where a regular quincuncial pattern is displayed by granules of neighboring rows. Growth lines are often present in variable numbers. Aesthetes have pores of roughly the same size, one central and two to four irregularly arranged. Detailed descriptions of this species are given by [23,25,27].

The finding of *Leptochiton asellus* in the study area is quite significant. *L. asellus* was considered a 'cold guest' by [3,21]. This species was not considered living in the Mediterranean basin until a few years ago; if some older reports from this area have been recorded (i.e., [31,32]), there are no precise indications of locality. Lucas [33] reports: "*Distribution principalement arctique mais l'espèce descend jusqu'à Gibraltar et pénètre en Méditerranée*

jusqu'aux Baléares et au nord de la côte espagnole". A recent report [34] confirms the presence of *L. asellus* in the Mediterranean Sea (from Limnos, Greece, inside an amphora trawled from a depth of 600 m).

Fossil records for this species are scarce; historical records are doubtful and require confirmation. *Leptochiton asellus* is reported from the Pliocene of the U.K. [35–37] and Belgium [38,39] and the Pleistocene of the N. Atlantic [40–42], the Netherlands [26], Italy [43], and the Mediterranean Sea (off Capraia/Capo Corso [24]).

Distribution. Lower Pliocene: northeastern Atlantic: U.K. [35–37]; North Sea Basin, Belgium: Kallo [38,39]. **Pleistocene:** North Atlantic: Sweden and Norway [40–42], Netherlands [26]; central Mediterranean, Italy: Pezzo [43] and Capraia/Capo Corso-350/500 m [21,24]. **Pleistocene,** presumably last glacial: Italy: off Bari (this study). **Recent:** NE Atlantic Ocean: from Spitsbergen and the Barents Sea South along the Scandinavian coasts [44,45]; North Sea; all around the British Isles and Ireland, coasts of France [46], south to Spain [47] and Portugal [48]. Mediterranean Sea: Greece: Limnos Island [34].

***Leptochiton antondohrni* new species**

Figure 3

Type material. Holotype: MZUB 60,418, intermediate valve, width 3.4 mm, Figure 3A–E. Paratypes: MZUB 60,419 intermediate valve, width 2.9 mm, Figure 3F–J; MZUB 60,420, tail valve, width 3.1 mm, Figure 3K–O.

Type locality. Southwestern Adriatic Sea, Apulian margin, off Bari, SE06-50.

Type stage. Late Pleistocene submerged deposits, probably late glacial epoch.

Etymology. We dedicate this new species from the Mediterranean Sea to the 'Stazione Zoologica Anton Dohrn' Naples, to honour the 150th of the foundation of the first marine station ever.

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Material examined. Type material, plus: SE06-10: 1 intermediate valve; SE06-35: 4 intermediate valves; SE06-40: 3 valves (1 intermediate, 2 tail); SE06-48: 2 valves (1 intermediate, 1 tail)**;** SE06-50: 55 valves (54 intermediate, 1 tail), Figure 3P. Maximum width of the valves: –/3.4/3.1 mm.

Description. Head valve unknown. Intermediate valves broadly rectangular (W/L = 1.45–2.03), rounded in anterior profile, elevated (H/W = 0.54–0.66), anterior margin straight, side margins rounded, posterior margin straight, apex inconspicuous, lateral areas hardly or not raised. Tail valve semicircular (W/L = 1.48–1.61), anterior margin almost straight or slightly convex, mucro not prominent, in slightly anterior position, antemucronal slope slightly convex, postmucronal slope almost straight.

Tegmentum sculpture. CA and AA with well raised, rather thick but distinctly separated roundish to oval granules, extended with two or three small longitudinal varices, forming 50–55 longitudinal series with a regular quincuncial pattern displayed by granules of neighboring rows; granules with a maximum width up to 70 µm and the presence of one subcentral aesthete and up to six aesthetes irregularly disposed, with pores of the same width. LA and PA with more rectangular granules, randomly disposed along concentric lines; granules with a maximum width up to 60 µm, and the presence of 3-4 aesthetes more or less aligned, with pores of the same width. Numerous and well-marked growth lines.

Articulamentum without insertion laminae, with small, sharply triangular, widely separated apophyses.

Remarks. "*Leptochiton antondohrni* n. sp. is characterized by a tegmentum sculptured with small granules randomly arranged on HV, LA, and PA and in longitudinal series on CA and PA. Three living Mediterranean species are known with this type of sculpture: *L. cimicoides* (Monterosato, 1879), *L. sarsi* Kaas, 1981 and *L. geronensis* Kaas & Van Belle, 1985".

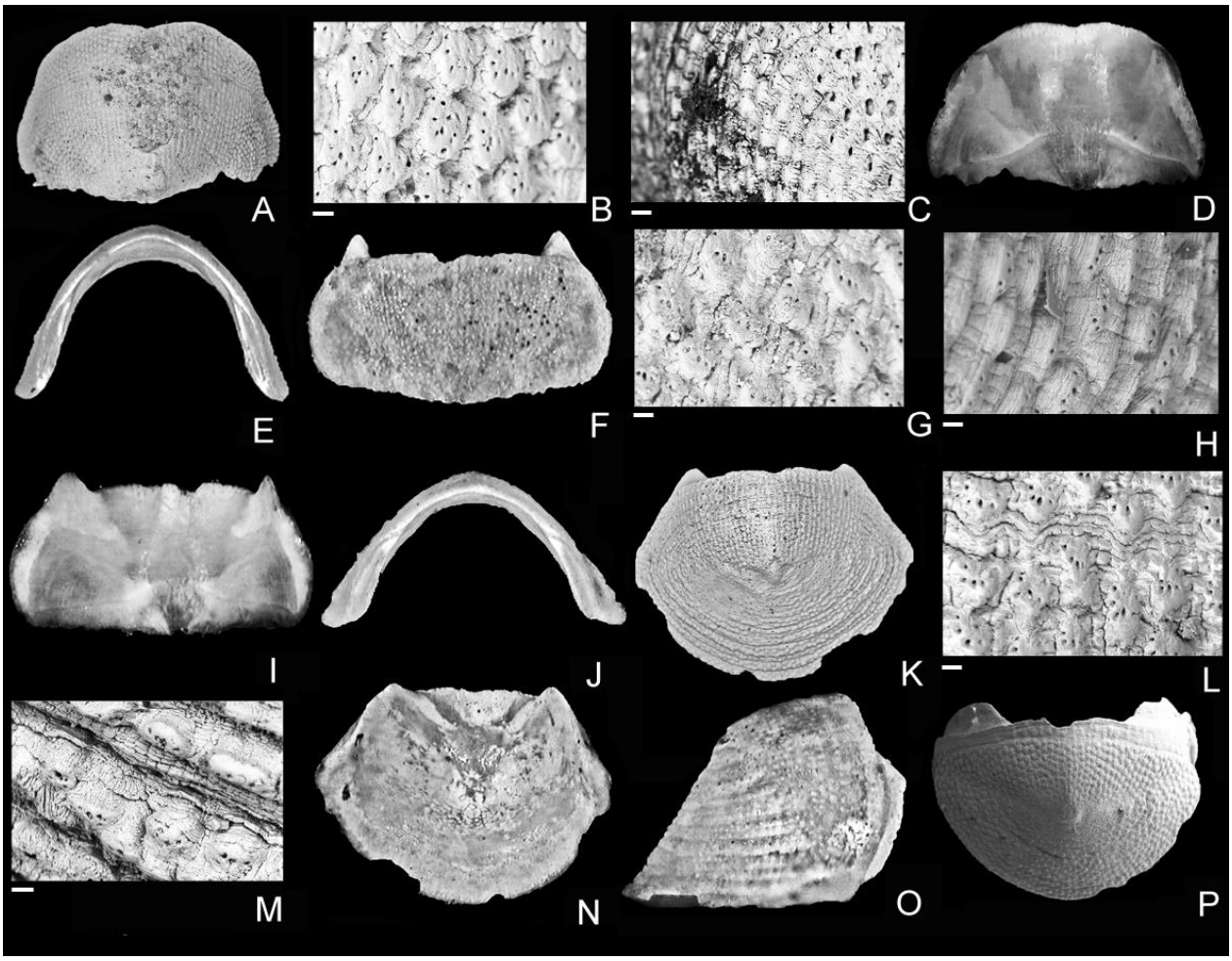

Figure 3. *Leptochiton antondohrni* new species; Apulian margin, offshore Bari (SE06-19), submerged deposits, possibly late Pleistocene (last glacial). (**A**–**E**) SE06-50, Holotype MZUB 60,418, intermediate valve, width 3.4 mm, dorsal view (**A**), close-up of surface ornamentation of central (**B**) and lateral (**C**) areas, ventral (**D**) and frontal (**E**) views. (**F**–**J**) SE06-50, Paratype MZUB 60,419, intermediate valve, width 2.9 mm, dorsal view (**F**), close-up of surface ornamentation of central (**G**) and lateral (**H**) areas, ventral (**I**) and frontal (**J**) views. (**K**–**O**) SE06-50, Paratype MZUB 60,420, tail valve, width 3.1 mm, dorsal view (**K**), close-up of surface ornamentation of antemucronal (**L**) and postmucronal (**M**) areas, ventral (**N**) and frontal (**O**) views. (**P**) SE06-50, MZUB 60,425, tail valve, width 2.6 mm, dorsal view. Scale bars = 40 μm (**C**); 20 μm (**B**,**G**,**H**,**L**,**M**).

The more similar species is *Leptochiton cimicoides* (Monterosato, 1879), from which *Leptochiton antondohrni* n. sp. differs by a tegmentum sculpture with a greater number of longitudinal striae of granules in CA, AA (50–55 vs. 30 in *L. cimicoides*), and differently shaped intermediate valves (W/L = 1.45–2.03 vs. 2.73 in *L. cimicoides*). *Leptochiton cimicoides* is a recent species, known from the Mediterranean Sea and the western Sahara [23], while some fossil records attributed to this species from the Plio-Pleistocene of Italy [22,49] and Greece [50,51] need more in-depth study to confirm the specific validity of *L. cimicoides* in the fossil state.

Leptochiton sarsi differs from *Leptochiton antondohrni* n. sp. by the rougher aspect of its tegmentum and of the granules, with stems in the apical part more evident, and other small differences in the shape of the valves (e.g., the postmucronal slope of the tail valve, almost straight in *Leptochiton antondohrni* n. sp. versus well concave in *L. sarsi*).

Leptochiton geronensis differs from *Leptochiton antondohrni* n. sp. by the shape of the intermediate valves (less elevate and with a subcarinate anterior profile) and with fewer longitudinal series of granules in CA (40 vs. 50–55 in *L. antondohrni* n. sp.).

The material studied is quite well preserved, and the intermediate valves show some variability. Two types of intermediate valves are detectable, some higher [Figure 3A–E, H/W = 0.66] and slightly larger (W = 3.4 mm, W/L = 1.45–1.60), others a little less high [Figure 3F–J, H/W = 0.54–0.55] and a little smaller (W = 2.9–3 mm, W/L = 1.91–2.03). The structure of the granules also shows slight differences; the granules in CA are more oval and up to 70 μm in size in the higher valves, and more rounded and slightly smaller (up to 60 μm) in the lower valves. We provisionally consider the intermediate valves within the limits of intraspecific variation of this species, although part of the difference could likely be due to age-related variability.

Distribution. Pleistocene, presumably last glacial: Adriatic Sea, offshore Bari (this study).

Genus *Belknapchiton* Sirenko, Saito & Schwabe, 2022

Type species. *Leptochiton belknapi* Dall, 1878 by original designation.

Distribution. *Belknapchiton* is known to have existed from the Pliocene to the present day. There are 22 recent species known to date, most inhabiting the deep waters of the Pacific Ocean, only *B. alveolus* (M. Sars MS, Lovén, 1846) being known in the Atlantic Ocean. Its fossil record includes the Pliocene to Pleistocene of Italy [52,53].

***Belknapchiton alveolus* (M. Sars MS, Lovén, 1846)**

Figure 4

Chiton alveolus M. Sars MS, Lovén, 1846, p. 159 [54].

Leptochiton alveolus; Ferreira, 1979, p. 152, figures 9–16,37,38 [55]; Kaas, 1981, p. 223, figures 8 and 10A–B [25]; Wu and Okutani, 1984, p. 6, pl. 1, figures 3 and 4, pl. 3, figures 9–14, pl. 4, Figure 1, pl. 5, figures 1–4 [56]; Dell'Angelo and Bonfitto, 2005, p. 5, figures 13–16 [57]; Dell'Angelo et al., 2013, p. 71, plate 2, figures A–D [52]; Dell'Angelo et al., 2021b, p. 410, figures 30–37 [53].

?*Leptochiton* (*Leptochiton*) *alveolus*; Squires and Goedert, 1995, p. 49, figures 3–6 [58]; Dell'Angelo et al., 2011, p. 936 [59]; Schwabe and Sellanes, 2010, table 3 [60]; Bertolaso et al., 2015, p. 9 [61].

Belknapchiton alveolus Sirenko, Saito and Schwabe, 2022, p.103–104, 115 [62].

Type material. Naturhistoriska Riksmuseet, Stockholm, type collection n. 104, one specimen in alcohol, deprived of valves (lectotype, designated by [25]).

Type locality. Bohuslän (Sweden).

Material examined. SE06-35: 1 intermediate valve; SE06-40: 18 valves (1 head, 14 intermediate, 3 tail); SE06-50: 56 valves (10 head, 40 intermediate, 6 tail), Figure 4A–L. Maximum width of the valves: 4.3/5.7/3.5 mm.

Remarks. The species is characterized by a tegmentum covered with well pronounced, neatly separated, rounded to oval granules, more or less distinctly quincuncially or randomly arranged on all the valves' surfaces, the lateral areas indiscernible from the central areas, the intermediate valves arched, the tail valve with the anterior margin almost straight and the mucro at posterior 1/3 from the posterior margin. Detailed descriptions of this species are given [25–56]. The taxonomic position of *B. alveolus* has been recently reviewed [62] and the new genus *Belknapchiton* established to accommodate this taxon. This deep-water species has a very complicated synonymy, and was initially considered to be cosmopolite, but a recent study [56] demonstrated that *B. belknapi* Dall, 1878, considered by [55] and other authors a junior synonym of *B. alveolus*, shows several differential characteristics which warrant its specific separation. *Belknapchiton alveolus* seems to be restricted to the Atlantic Ocean, while *L. belknapi* is confined to the Pacific and Indian Oceans [56].

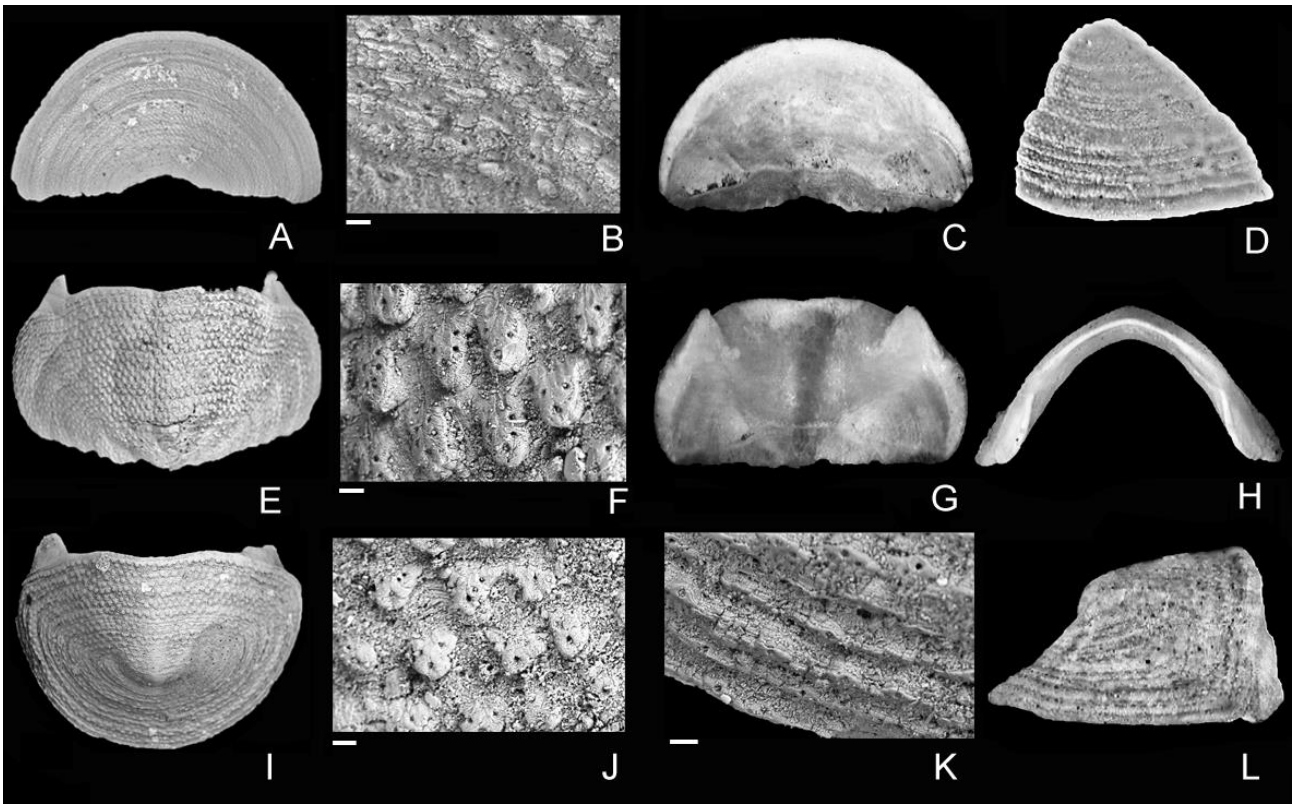

Figure 4. *Belknapchiton alveolus* (M. Sars MS, Lovén, 1846); Apulian margin, offshore Bari (SE06-50), submerged late Pleistocene (last glacial) deposits. (**A**–**D**) MZUB 60421, head valve, width 4.3 mm, dorsal view (**A**), close-up of surface ornamentation (**B**), ventral (**C**) and lateral (**D**) views. (**E**–**H**) MZUB 60422, intermediate valve, width 3.5 mm, dorsal view (**E**), close-up of surface ornamentation of central area (**F**), ventral (**G**) and frontal (**H**) views. (**I**–**L**) MZUB 60423, tail valve, width 3.5 mm, dorsal view (**I**), close-up of surface ornamentation of antemucronal (**J**) and postmucronal (**K**) areas, and lateral (**L**) view. Scale bars = 20 μm (**B**,**F**,**J**); 10 μm (**K**).

Our material fully agrees with the description of *Belknapchiton alveolus*, and compares well with a single intermediate valve from Sula Ridge, Norway, dredged at 215 m [57] (figures 13–16). The latter figure 16 is, to our knowledge, the only published figure of the granule structure, and the granules' shape and dimension agree with our material (maximum diameter of oval granules in the central area of intermediate valves ca. 77 μm vs. 73 in our material, and the same structure of one posterior megaesthete and 4–5 microaesthetes upward).

The finding of *Belknapchiton alveolus* in the study area is quite significant. This taxon is now extinct in the Mediterranean basin, although some older reports from this area were erroneously recorded, i.e., ([63] p. 32 «Napoli, Palermo, Dalmatia», probably on the basis of records from previous authors) and [64], two specimens collected by fishers at 200–250 m off Gerona, Spain, but the identification was proven wrong, and they have been reclassified as *Leptochiton geronensis* Kaas & Van Belle, 1985, by the same authors.

Belknapchiton alveolus was recorded from the Ligurian Pliocene [52,53]. Specimens reported as "*Leptochiton alveolus*" from Eocene–Oligocene cold-seep limestones in the Olympic Peninsula, Washington [58,60] have not been considered in the distribution of *B. alveolus*, because their specific assignment remains an open problem [60].

Belknapchiton alveolus is similar to *L. belknapi* Dall, 1878, from which it differs by a few morphological and anatomical characteristics [56,62], as well as by its geographic distribution and bathymetric range (270/540 m for *B. alveolus*, 100/3724 m for *B. belknapi*). Other species with the same kind of tegmentum sculpture, fully covered in randomly or

quincuncially arranged granules, are known for the fossil Neogene of the Mediterranean area: *L. tavianii* Dell'Angelo, Landau & Marquet, 2004 from the Pliocene of Estepona (Spain) (where, however, the granules are characterized by a fungiform section and are arranged in a beehive structure), *L. salicensis* Dell'Angelo & Bonfitto, 2005 from the Pleistocene of Salice (South Italy) (with more solid and dissimilar intermediate valves, and more polygonal and differently shaped granules), and *L. lignatilis* Dell'Angelo, Bertolaso & Sosso in Bertolaso et al., 2015 (the differences are reported in [61] (Table 1).

Distribution. Lower Pliocene: Italy, Liguria: Zinola [52], Borzoli [53]. **Pleistocene,** presumably last glacial: Adriatic Sea, offshore Bari (this study). **Recent:** North Atlantic: all along the Norwegian and Swedish west coast [25,45], Bay of Biscay [46], Spain, Galicia [47], NW Portugal [48], Gulf of Maine and Gulf of St. Lawrence [56].

Family Hanleyidae Bergenhayn, 1955

Genus *Hanleya* Gray, 1857

Type species. *Hanleya debilis* Gray, 1857 (=*Chiton hanleyi* Bean in Thorpe, 1844), by monotypy.

Distribution. *Hanleya* is known to have existed from the lower Oligocene to the present day. Currently, all known recent species of *Hanleya* occur only in the Atlantic Ocean and adjacent seas, from off Brazil (25.44° S) to the Barents Sea (74.27° N) [65]. Its fossil record includes the Oligocene of Germany [66], the middle Miocene of Paratethys [67,68], and the upper Miocene to the Pleistocene of Europe [38,39,69,70].

***Hanleya hanleyi* (Bean in Thorpe, 1844)**

Figure 5

Chiton hanleyi Bean in Thorpe, 1844, p. 263, figure 57 [71].

Hanleya hanleyi; Malatesta, 1962, p. 153, figures 9 and 10 [21]; Sabelli, 1972, p. 97, figures 1–6 [72]; Sabelli, 1974, figures 1–13 [73]; Kaas and Van Belle, 1985, p. 193, figure 91, map 18 [27]; Dell'Angelo and Smriglio, 1999, p. 85, plate 25 figures C–D, G, pl. 26 figures I–J [23]; Sirenko et al., 2016, p. 58, figures 1–10 [65]; Dell'Angelo et al., 2018, p. 20, figure 10 [70]; Dell'Angelo et al., 2020b, p. 52, table 9 [74]; Dell'Angelo et al., 2021a, p. 125, figure 1 [75]; Dell'Angelo et al., 2022, p. 6, figure 4 [76].

Type material. Syntype, Scarborough Museums Trust, Woodend, Scarborough, U.K. (Sirenko et al. 2016).

Type locality. Scarborough (Yorkshire, England).

Material examined. SE06-19: 1 intermediate valve, width 3.3 mm, Figure 5A–D.

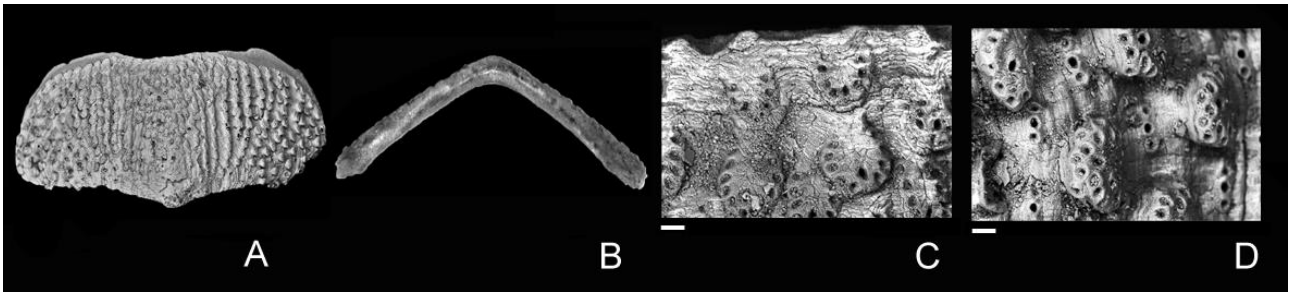

Figure 5. *Hanleya hanleyi* (Bean in Thorpe, 1844); Apulian margin, offshore Bari (SE06-19), probably submerged late Pleistocene (last glacial) deposits. (**A**–**D**) intermediate valve, width 3.3 mm, dorsal (**A**) and frontal (**B**) views, and close-up of surface ornamentation of pleural (**C**) and lateral (**D**) areas. Scale bar = 10 μm (**C**,**D**).

Remarks. The genus *Hanleya* Gray, 1857 is represented in the Mediterranean Sea by at least two living species: *H. hanleyi* (Bean in Thorpe, 1844) and *H. mediterranea* Sirenko, 2014, whose geographical distribution has been recently revised [75]. The only intermediate valve present in our material fully agrees with the description of *H. hanleyi*, characterized by the sculpture of the pleural areas of the intermediate valves and the antemucronal area of the tail valve consisting of longitudinal series of small, roundish to oval granules (length

75–100 µm) with narrow interstices, fine and close set on the jugum, growing larger and posteriorly converging towards the side margins. Each granule contains one subcentral aesthete surrounded by eight to twelve aesthetes with pores of practically equal width (Sirenko et al., 2016). Detailed descriptions of this species are given by [65].

Distribution. Upper Miocene: northeastern Atlantic (Tortonian): France [70]; Proto–Mediterranean Sea (Tortonian): N. Italy, Po Basin [69]. **Lower Pliocene:** northeastern Atlantic: U.K. [35–37]; Belgium: Kallo [38,39]; central Mediterranean, Italy: Liguria [52]. **Lower to upper Pliocene:** northeastern Atlantic: Mondego Basin, Portugal [76]. **Upper Pliocene to lower Pleistocene:** northeastern Atlantic: Anjou, France [70]. **Pleistocene:** central Mediterranean, Italy: questionable (many reports, in need of revision). **Recent:** North and Central Atlantic Ocean, near southern Greenland, North America, Europe [48], Canary Islands [77] and northern Africa, Madeira Arch. [78]; Mediterranean Sea: Italy [75], Aegean Sea, Turkey [65,75].

4. Discussion

Polyplacophora collected during cruise SETE-06 are represented by loose valves only, with two taxa, *Leptochiton asellus* and *Belknapchiton alveolus*, of North Atlantic (boreo-celtic) geographic origin. They belong probably to Pleistocene last glacial assemblages whose presence in this area was certified in the past [6] and which are known to host many other benthic mollusks of North Atlantic affinity, such as *Puncturella noachina* and *Iothia fulva*, at present considered extinct in the Mediterranean basin. As in the case of the many boreo-celtic index-markers [79], these polyplacophorans expanded their geographic range at the peak of the last glacial to include the Mediterranean basin but could not keep pace with the postglacial oceanographic conditions when the present homothermal 'warm' situation was established. In principle, these species previously entered the Mediterranean at glacial times; however, we have no confirmed records to date. The record of *Belknapchiton alveolus* for the Italian Pliocene is consistent with the lower than present temperatures at bathyal depths at that time. Interestingly, faunal lists from the Pleistocene to modern taphocoenoses in the southwestern Adriatic and adjacent Ionian margin do not record the presence of any Polyplacophora [14,80–84]. The only exception is provided by [6], which recorded *Lepidochitona cinereus*, but this taxonomic assignment cannot be confirmed at present. Our study of the accompanying mollusk fauna (Table 2) upgrades the list for this area, confirming the presence of some taxa already reported before [6,14], but also adding new records. For instance, we have identified from the study site another North Atlantic element, *Torellia delicata* (Philippi, 1844), previously cited as a glacial subfossil (as *T. vestita* Jeffreys, 1867) in the western Mediterranean [85].

As discussed by [2,6], the assemblages dredged from the area consist of mixed elements sourced from a variety of environments and of different ages. The deep-sea pre-modern component includes just a part of the entire taphocoenoses, but their paleoclimatic and biogeographic importance is noticeable. With respect to this component, the integration of the lists by [6,81] and our own research ascertains as putative last glacial mollusks in the southwestern Adriatic Sea the following taxa: *Iothia fulva* (O. F. Müller, 1776), *Puncturella noachina* (Linnaeus, 1771), *Fissurisepta granulosa* Jeffreys, 1883, *Cantrainea peloritana* (Cantraine, 1835), *Pilus conicus* (Verrill, 1884), *Torellia delicata* (Philippi, 1844), *Cerithiella metula* (Lovén, 1846), *Pleuromoides packardii* A. E. Verrill, 1872, *Typhlomangelia nivalis* (Lovén, 1846), *Belknapchiton alveolus* (M. Sars MS, Lovén, 1846), and *Cadulus ovulum* (Philippi, 1844). This is, however, a conservative figure since it is likely that other species (including *H. hanleyi*, *Leptochiton asellus*, and the new *Leptochiton antondohrni* species) only represented in these southwestern Adriatic Sea taphocoenoses as empty shells could be glacial subfossils.

Table 2. Taxonomic list of mollusks from SETE-06 stations discussed in the present study. The census includes both benthic and holoplanktonic shells, as well as reworked terrestrial shells of pulmonate gastropods. Regarding marine taxa, the systematic arrangement conforms to WoRMS [86].

Family	Genus	Species	Author	10	13	18	19	22	24	25	35	40	48	50
Lepetidae	*Propilidium*	*exiguum*	(Thompson, 1844)							X	X		X	X
Lepetidae	*Iothia*	*fulva*	(Mueller, 1776)							X			X	X
Fissurellidae	*Puncturella*	*noachina*	(Linnaeus, 1771)	X				X		X		X	X	X
Fissurellidae	*Emarginula*	*adriatica*	O.G.Costa, 1829											X
Fissurellidae	*Emarginula*	*fissura*	(Linnaeus, 1758)				X							
Fissurellidae	*Emarginula*	*rosea*	Bell, 1824				X							
Fissurellidae	*Emarginula*	*punctulum*	Piani, 1980											X
Fissurellidae	*Fissurisepta*	*granulosa*	Jeffreys, 1883											X
Scissurellidae	*Anatoma*	*crispata*	Fleming, 1828	X			X	X		X		X	X	X
Scissurellidae	*Anatoma*	*umbilicata*	(Jeffreys, 1883)				X							
Lepetellidae	*Bogia*	*labronica*	(Bogi, 1984)											
Trochidae	*Clelandella*	*miliaris*	(Brocchi, 1814)				X							
Chilodontaidae	*Putzeysia*	*wiseri*	(Calcara, 1842)										X	X
Chilodontaidae	*Danilia*	*tinei*	(Calcara, 1839)			X	X	X		X		X		
Skeneidae	*Cirsonella*	*romettensis*	(Granata Grillo, 1877)					X		X	X		X	X
Skeneidae	gen.	sp.												X
Bathysciadiidae	*Pilus*	*conicus*	(Verrill, 1884)	X										X
Rissoidae	*Alvania*	*cimicoides*	(Forbes, 1844)			X	X	X	X	X			X	X
Rissoidae	*Alvania*	*testae*	(Aradas e Maggiore, 1844)				X	X	X	X	X		X	X
Rissoidae	*Alvania*	*zetlandica*	(Montagu, 1815)				X	X		X				X
Rissoidae	*Benthonella*	*tenella*	(Jeffreys, 1869)	X			X				X		X	X
Capulidae	*Capulis*	*ungaricus*	(Linnaeus, 1758)			X	X							X
Capulidae	*Torellia*	*delicata*	(Philippi, 1844)	X										
Ovulidae	*Simnia*	*nicaeensis*	Risso, 1826		X									
Naticidae	*Euspira*	cf. *fusca*	(Blainville, 1825)											X
Cerithiidae	*Cerithidium*	*submammillatum*	(De Rayneval & Ponzi,1854)			X	X				X			
Turritellidae	*Turriterinella*	*tricarinata*	(Brocchi, 1814)					X						
Triphoridae	*Marshallora*	*adversa*	(Montagu, 1893)						X					
Triphoridae	*gen.*	sp.						X						
Cerithiopsidae	*Cerithiopsis*	*atalaya*	R. B. Watson, 1885			X				X				
Cerithiopsidae	*Cerithiopsis*	sp.			X									
Newtonielliidae	*Cerithiella*	*metula*	(Loven, 1846)							X			X	X
Epitoniidae	*Epitonium*	*algerianum*	(Weinkauff, 1866)							X	X			
Epitoniidae	*Epitonium*	cf. *algerianum*	(Weinkauff, 1866)										X	
Eulimidae	*Aclis*	*attenuans*	Jeffreys, 1883							X	X		X	
Eulimidae	*Haliella*	*stenostoma*	(Jeffreys, 1858)								X		X	X
Eulimidae	*Melanella*	*compactilis*	(Locard, 1891)	X										X
Eulimidae	*Melanella*	*petitiana*	(Brusina, 1879)				X							X
Eulimidae	*Melanella*	sp.												X
Atlantidae	*Atlanta*	*peroni*	Lesueur, 1817										X	
Atlantidae	*Atlanta*	sp.		X									X	
Muricidae	*Ocinebrina*	*helleri*	(Brusina, 1865)				X							
Muricidae	*Trophon*	*muricatus*	(Montagu, 1803)		X	X	X	X	X	X			X	X
Muricidae	*Pagodula*	*echinata*	(Kiener, 1839)	X	X	X	X	X		X		X	X	X

Table 2. *Cont.*

Family	*Genus*	*Species*	Author	10	13	18	19	22	24	25	35	40	48	50
Nassariidae	*Tyitia*	*lima*	(Dillwyn, 1817)		X		X	X						
Columbellidae	*Mitrella*	*minor*	(Scacchi, 1836)			X								
Columbellidae	*Amphissa*	*acutecostata*	(Philippi, 1844)	X								X		X
Fasciolaridae	*Pseudofusus*	*rostratus*	(Olivi, 1792)			X	X			X				
Fasciolaridae	*Pseudofusus*	sp.			X									
Raphitomidae	*Cyrillia*	*aequalis*	(Jeffreys, 1867)				X							
Raphitomidae	*Cyrillia*	*linearis*	(Montagu, 1803)				X							
Raphitomidae	*Leufroya*	sp.1				X								
Raphitomidae	*Leufroya*	sp.2						X						
Raphitomidae	*Leufroya*	*concinna*	(Scacchi, 1836)				X							
Raphitomidae	*Leufroyia*	*erronea*	Monterosato		X									
Raphitomidae	*Teretia*	*teres*	(Reeve, 1844)				X	X		X	X		X	
Borsoniidae	*Typhlomangelia*	*nivalis*	(Lovén, 1846)	X										
Borsoniidae	*Drilliola*	*emendata*	(Monterosato, 1872)				X	X						
Borsoniidae	*Drilliola*	*loprestiana*	(Calcara, 1841)			X	X	X						
Mangeliidae	*Mangelia*	*costata*	(Pennat, 1777)		X									
Mangeliidae	*Mangelia*	sp.				X								
Mangeliidae	*Mangelia*	*costulata*	Risso, 1826				X							
Architectonicidae	*Heliacus*	*fallaciosus*	(Tiberi, 1872)								X			
Mathildidae	*Mathilda*	*cochlaeformis*	Brugnone, 1873				X							
Mathildidae	*Mathilda*	*coronata*	Monterosato, 1875					X						
Mathildidae	*Mathilda*	*retusa*	Brugnone, 1873				X							
Pyramidellidae	*Turbonilla*	*micans*	(Monterosato, 1865)										X	
Pyramidellidae	*Tibersyrnola*	*unifasciata*	(Forbes, 1844)					X						
Pyramidellidae	*Parthenina*	*flexuosa*	(Monterosato, 1874)								X		X	
Pyramidellidae	*Tragula*	*fenestrata*	(Jeffreys, 1848)							X				
Pyramidellidae	*Eulimella*	*scillae*	(Scacchi, 1835)			X		X					X	
Pyramidellidae	*Eulimella*	*unifasciata*	(Forbes, 1844)				X							
Pyramidellidae	*Megastomia*	*conoidea*	(Brocchi, 1814)					X						
Pyramidellidae	*Odostomia*	*acuta*	Jeffreys, 1848											X
Pyramidellidae	*Odostomia*	*carrozzai*	Van Aartsen, 1987				X							
Pyramidellidae	*Ondina*	cf. *crystallina*	Locard, 1891							X				X
Pyramidellidae	*Ondina*	sp.									X			
Acteonidae	*Crenilabium*	*exile*	(Jeffreys, 1870)							X				
Retusidae	*Retusa*	*nitidula*	(Lovén, 1846)						X	X				
Retusidae	*Retusa*	*umbilicata*	*(Montagu, 1803)*					X						
Retusidae	*Retusa*	sp.									X		X	X
Ringiculidae	*Ringicula*	*gianninii*	F. Nordsieck, 1974							X				
Ringiculidae	*Ringicula*	cf. *gianninii*	F. Nordsieck, 1974										X	
Philinidae	*Hermania*	*scabra*	(O. F. Muller, 1784)								X			
Philinidae	*Philine*	*striatula*	Monterosato, 1874						X		X			
Laonidae	*Laona*	*quadrata*	S.V. Wood, 1839)							X				X
Laonidae	*Laona*	sp.			X									
Cylichnidae	*Scaphander*	*clavus*	Dall, 1889											X
Alacuppidae	*Roxania*	sp.									X			

Table 2. *Cont.*

Family	*Genus*	*Species*	Author	10	13	18	19	22	24	25	35	40	48	50
Cavoliniidae	*Cavolinia*	*gibbosa*	(d'Orbigny, 1835)	X										
Cavoliniidae	*Cavolinia*	*inflexa*	(Lesueur, 1813)	X				X					X	X
Cavoliniidae	*Diacria*	*trispinosa*	(Blainville, 1821)		X							X		
Cliidae	*Clio*	*pyramidata*	Linnaeus, 1767	X	X			X		X	X	X	X	X
Hyalocylidae	*Hyalocylis*	*striata*	(Rang, 1828)							X			X	
Creseidae	*Styliola*	*subula*	(Quoy & Gaimard, 1827)							X	X		X	X
Creseidae	*Creseis*	*acicula*	(Rang, 1828)								X		X	
Limacinidae	*Limacina*	*bulimoides*	(d'Orbigny, 1836)	X				X				X	X	X
Limacinidae	*Limacina*	*retroversa*	(J. Fleming, 1823)					X					X	X
Heliconoididae	*Heliconoides*	*inflatus*	(d'Orbigny, 1835)							X				X
Tylodinidae	*Tylodina*	*perversa*	(Gmelin, 1791)							X				
Nuculidae	*Ennucula*	*aegeensis*	(Forbes, 1844)	X	X			X			X	X	X	X
Nuculanidae	*Saccella*	*commutata*	(Philippi, 1844)		X				X					
Yoldiidae	*Yoldiella*	*lucida*	(Loven, 1846)	X				X		X	X	X	X	X
Yoldiidae	*Yoldiella*	*messanensis*	(Jeffreys, 1870)	X	X							X	X	X
Yoldiidae	*Yoldiella*	*philippiana*	(Nyst, 1845)		X					X	X		X	X
Yoldiidae	*Yoldiella*	*striolata*	(Brugnone, 1876)	X				X						X
Yoldiidae	*Yoldiella*	*wareni*	La Perna, 2004					X					X	
Arcidae	*Asperarca*	*nodulosa*	(O.F. Muller, 1776)	X	X	X		X		X		X	X	X
Arcidae	*Bathyarca*	*pectunculoides*	(Scacchi, 1835)		X	X	X	X		X	X	X	X	X
Arcidae	*Bathyarca*	*philippiana*	(Nyst, 1848)		X		X	X		X		X	X	
Propeamussiidae	*Cyclopecten*	*hoskynsi*	(Forbes, 1844)											X
Pectinidae	*Pseudamussium*	*clavatum*	(Poli, 1795)							X				X
Pectinidae	*Pseudamussium*	*peslutrae*	(Linnaeus, 1771)		X					X		X	X	
Pectinidae	*Deletopecten*	*vitreus*	(Gmelin, 1791)		X	X		X					X	X
Propeamussiidae	*Similipecten*	*similis*	(Laskey, 1811)				X						X	X
Propeamussiidae	*Mesopeplum*	*fenestratum*	(Forbes, 1844)	X	X	X	X	X		X			X	X
Mytiliidae	*Modiolula*	*phaseolina*	(Philippi, 1844)		X	X	X	X		X		X	X	X
Anomiidae	*Heteranomia*	*squamula*	(Linnaeus, 1758)	X				X		X	X	X	X	X
Anomiidae	*Pododesmus*	*patelliformis*	(Linnaeus, 1761)			X		X					X	
Limidae	*Limaea*	*crassa*	(Forbes, 1844)			X	X	X		X	X		X	X
Limidae	*Limatula*	*gwyni*	(Sikes, 1903)		X		X	X	X	X	X		X	X
Thyasiridae	*Leptaxinus*	*incrassatus*	(Jeffreys, 1876)									X		X
Ungulinidae	*Microstagon*	*trigonum*	(Scacchi, 1835)											X
Carditidae	*Centrocardita*	*aculeata*	(Poli, 1795)			X	X	X		X				
Astartidae	*Goodallia*	*triangularis*	(Montagu, 1803)			X	X	X						
Astartidae	*Astarte*	*sulcata*	(da Costa, 1778)		X	X		X		X			X	X
Carditidae	*Centrocardita*	*aculeata*	(Poli, 1795)		X								X	X
Cardiidae	*Papillicardium*	*minimum*	(Philippi, 1836)		X	X		X		X		X	X	X
Semelidae	*Abra*	*longicallus*	(Scacchi, 1835)		X					X	X	X		X
Kellielliidae	*Kelliella*	*miliaris*	(Philippi, 1844)					X		X	X	X	X	X
Trapezidae	*Coralliophaga*	*lithophagella*	(Lamarck, 1819)		X									X
Veneridae	*Timoclea*	*ovata*	(Pennant, 1777)		X	X	X	X		X			X	
Corbulidae	*Corbula*	sp.										X		
Hiatellidae	*Hiatella*	*arctica*	(Linnaeus, 1767)		X	X	X	X			X		X	X

Table 2. *Cont.*

Family	*Genus*	*Species*	Author	10	13	18	19	22	24	25	35	40	48	50
Xylophagaidae	*Xylophaga*	*dorsalis*	(W. Turton, 1819)	X										
Cuspidariidae	*Cuspidaria*	*jugosa*	(S. V. Wood, 1857											X
Dentaliidae	*Antalis*	*agilis*	(M. Sars, 1872)	X	X					X	X		X	X
Dentaliidae	*Antalis*	*dentalis*	(Linnaeus, 1758)											X
Fustariidae	*Fustiaria*	*rubescens*	(Deshayes, 1826)											X
Entalinidae	*Entalina*	*tetragona*	(Brocchi, 1814)				X	X		X	X		X	X
Pulselliidae	*Pulsellum*	*lofotense*	(M. Sars, 1865)											X
Gadilidae	*Cadulus*	*jeffreysi*	Monterosato, 1875			X	X		X	X			X	X
Gadilidae	*Cadulus*	*ovulum*	(Philippi, 1844)	X										
Gadilidae	*Cadulus*	cf. *subfusiformia*	(M. Sars, 1865)					X					X	
Valloniidae	*Vallonia*	*pulchella*	(O. F. Muller, 1774)											X
Lauriidae	*Lauria*	sp.											X	
Leptochitonidae	***Leptochiton***	***asellus***	**(Gmelin, 1791)**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Leptochitonidae	***Leptochiton***	***antondohrni***	**new species**	**X**							**X**	**X**	**X**	**X**
Leptochitonidae	***Belknapchiton***	***alveolus***	**(M. Sars MS, Lovén, 1846)**								**X**	**X**		**X**
Hanleyidae	***Hanleya***	***hanleyi***	**(Bean in Thorpe, 1844)**				**X**							

5. Conclusions

The analysis of mollusk-rich biogenic taphocoenoses dredged from the Apulian margin in the southwestern Adriatic Sea provided four species of polyplacophorans not recorded hitherto from this sector of the Mediterranean basin, one of which (*Leptochiton antondohrni*) appears to be new to science. Our finding updates the number of North Atlantic-type Pleistocene (sub)fossil taxa recorded from the southwestern Adriatic Sea and the Mediterranean basin as a whole. Furthermore, our study increases the number of species previously recorded from such submerged Pleistocene taphocoenoses.

Author Contributions: Conceptualization, M.T., B.D. and M.S.; Methodology, B.D., M.S. and M.T.; Investigation, M.T.; Resources, M.T.; Writing—Original Draft Preparation, M.T. Writing—Review & Editing, B.D. and M.T.; Funding Acquisition, M.T. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Data sharing is not applicable to this article.

Acknowledgments: Cruise SETE-06 (Chief Scientists Fabio Trincardi and Domenico Ridente) onboard RV *Urania* was organized in the frame of the E.U program Hermes; Captain, Crew and Scientific Staff are acknowledged for the naval support and sampling assistance. We thank Franco Corticelli (IMM-CNR Bologna) and Antonio Bonfitto (BIgEA, University of Bologna) for S.E.M. images, Federica Foglini (Ismar-CNR, Bologna) for the bathymetric map, and Giorgio Castellan for editorial help. Enrico Bonatti and Michael Marani kindly reviewed the English text. Thanks are due to three reviewers for their comments that helped to improve the clarity of the article. This is Ismar-CNR, Bologna scientific contribution n. 2073.

Conflicts of Interest: The authors declare no conflict of interest.

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