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Cemented on the Rock. A Pleistocene Outer Shelf Lithobiont Community from Sicily, Italy

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Abstract: The lithobiont community encrusting an early Pleistocene palaeocliff cropping out north of Augusta (SE Sicily, Italy) was investigated based on field observations and laboratory inspection of two rocky samples. Bryozoans, serpulids, brachiopods and bivalves encrusted part of the exposed surfaces that were bored mostly by clionaid sponges. Bryozoans, with at least 25 species detected on the rocky samples, are the most diversified skeletonized lithobionts also accounting for the highest number of colonies/specimens and highest coverage. Brachiopods, with the only species *Novocrania anomala* and a few but large cemented valves, cover wide surfaces. Serpulids, with two species identified on the sampled rocks and further two on the outcrop, were intermediate. A multiphase colonization is present, including a final epilithobiont community locally formed on eroded surfaces exposing a network of pervasive borings. The co-occurrence of very sciaphilic species having circalittoral to bathyal distributions suggests that the studied community thrived on a rocky substratum located near or at the shelf break, probably belonging to the shelf break (or RL) biocoenosis, also in agreement with observations on the fossil content of neighboring marly sediments. The observed relationships among colonizers largely represent mere superimpositions, and real interactions are not enough to state species competitiveness.

Keywords: bryozoans; serpulids; brachiopods; encrusting biota; palaeobiodiversity; shelf-edge rock biocoenosis; species interactions; Quaternary

1. Introduction

In overviews on palaeoecology and the evolution of hard substrata marine communities, references [1,2] remarked how hard substrates offer a unique opportunity for examination of spatial distribution, overgrowth competitive interactions and community succession, because organisms cemented to or boring in them can be preserved in their own life position. However, all these communities are residual because, following [1], only a low percentage of the species richness (usually less than 40%) and of the total coverage (usually less than 15%) is preserved.

Among hard substrates, shells, bones and small sized lithic clasts dispersed on soft bottoms can be ephemeral and subject to displacement during taphonomic processes; whereas boulders, blocks, hardgrounds, bioconstructions and rocky outcrops offer the advantage of remaining stable for a long time being usually preserved essentially in their primary position because less prone to physical transport. This has a twofold advantage for palaeoecologists, enabling not only examination of organism interactions but also certainty about the original spatial location of their substrata, thus providing impressive information for reconstructing the extension and morphology of depositional basins at any time and hence their evolution.

Except for reefs, however, these habitats are poorly investigated in both the present-day and the fossil record. Literature mostly relates to Cenozoic (and particularly Quaternary) rocky shore (mostly intertidal) palaeocommunities, because they provide reliable information about sea level changes worldwide (e.g., [2–4]). Information about palaeocommunities colonising rocky walls and ceilings of shallow-water caves is also rising, mostly involving Quaternary caves from the Mediterranean area [5–8]. Few examples of colonization on shallow-water rounded boulders and blocks have been reported, among which the spectacular Cretaceous communities from Ivö Klack [9] and the those from the Pleistocene clinostratified conglomerates of a delta Gilbert foreset in southern Italy [10]. In contrast, examples from deeper (circalittoral to bathyal) settings are rare and virtually unreported for long intervals, except for hardgrounds, often linked to seeps [2–11]. To our knowledge, the only existing data relate to Plio-Pleistocene cliffs in Mediterranean localities where strong tectonic activity produced exposed sindepositional fault palaeoscarps with blocks detached from them and collapsed into the basins, thus providing hard surfaces suitable for organism colonization at a relevant depth [8,12–14]. Some of these encrusted surfaces provided evidence of the superimposition of palaeocommunities pointing to different bathymetric settings documenting palaeobasin history.

Encrusting bryozoans, serpulids and brachiopods are common lithobionts since their appearance in very early Palaeozoic and their competitive interactions have been documented since the Silurian [1]. Interactions have been mostly investigated on shells and cobbles, and include: 1. superimpositions produced by simple successions of colonies/specimens belonging to subsequent generations; 2. competitions leading to overgrowth of species on each other, with possible lethal consequences for the overgrown species; 3. stand offs, i.e., growth stoppage of both organisms, in contact or some distance from each other; 4. fusion of colonies within particular bryozoan species; 5. fouling of recruits on adult colonies/specimens; 6. overcrusting and bioimmuration of soft-bodied organisms [2,15–19]. However, no information is available for organism interactions on either present-day or fossil deep-water bedrocks, seemingly because sampling of present-day deep rocks is still difficult and fossil outcrops are rare.

In this context, the present paper aims at: i. describing the lithobiont community discovered on early Pleistocene hard bottoms cropping out near Augusta (SE Sicily); ii. assessing residual palaeobiodiversity; iii. reconstructing the palaeohabitat; iv. investigating the nature of interactions documented by preserved encrusters.

2. Geographical and Geological Setting

Material originates from "Scardina", a locality near the "second railway overpass" [20], about 1 km north of Augusta, a town of the Ionian coast of Sicily, south of Catania (Figure 1).

The area is situated along the northeastern side of the Hyblean Plateau (HP) that represents the foreland for the Sicilian sector of the Apennine-Maghrebian chain. HP consists of undeformed carbonate sedimentary successions with submarine to subaerial volcanic products intercalated at different heights. Sediments deposited in contiguous palaeobasins include: (1) western, Oligocene to Miocene, neritic to pelagic ramp settings and (2) eastern Upper Cretaceous to Upper Miocene shallow-water palaeoenvironments [21]. During Quaternary, the steeply sloping submerged edges of the HP isle provided settings for deposition in shallow-to-deep-waters. The succession recognized on the eastern HP side includes an early Pleistocene deepening upward sedimentation starting with basal yellow calcarenites and sands, followed by silts and silty clays, unconformably overlain by middle Pleistocene cemented biocalcarenites and conglomerates of shallow water settings (e.g., [22,23]). Active faulting produced grabens hosting small and deep palaeobasins.

Figure 1. Geographical location of Sicily in the Mediterranean Sea (**A**), of the study area in Sicily (**B**) and of Augusta zone (**C**). Geological map of the study area near Augusta (**D**) from [21]. Asterisk indicates the geographical location of the outcrop.

During Quaternary cold–warm climatic phases, local topography and the interaction between tectonics and sea-level changes controlled the sedimentation and the development of different facies in these basins (e.g., [24–26]). One of them, NW–SE trending, developed immediately north of Augusta, and was filled by calcarenites in the north and by finer sediments in the south [24]. The latter is locally represented by yellowish to whitish marls, rich in fossils and mostly in bryozoans and brachiopods, and cropping out in dm to m thick, small, discontinuous bodies. These sediments were already known in the palaeontological literature of the second half of the 19th century (e.g., [20,27,28]), and bryozoan content was studied by [29]. First reported as Pliocene in age, these sediments actually including reworked Pliocene faunas, are now currently dated to the early Pleistocene, possibly Calabrian (e.g., [24]). Deposition took place in a shelf environment not shallower than 80 m as already argued by [29]. In [20], it was first reported that these sediments locally crop out close and along sindepositional fault scarps cutting the early to middle Miocene limestone of the Monti Climiti Formation.

3. Methods

Field surveys in the "Scardina" locality, along the NE boundary of the basin hosting the bryozoan-rich marls, allowed the discovery of an exposed, few metre high, cliff in the limestone, with some blocks covered by skeletonized encrusters that were unreported to date.

Encrustations were documented by field photos (Figure 2), and a pair of prominent rocks was detached (Figures 3 and 4) and carefully cleaned to remove the locally attached slightly cemented sediment.
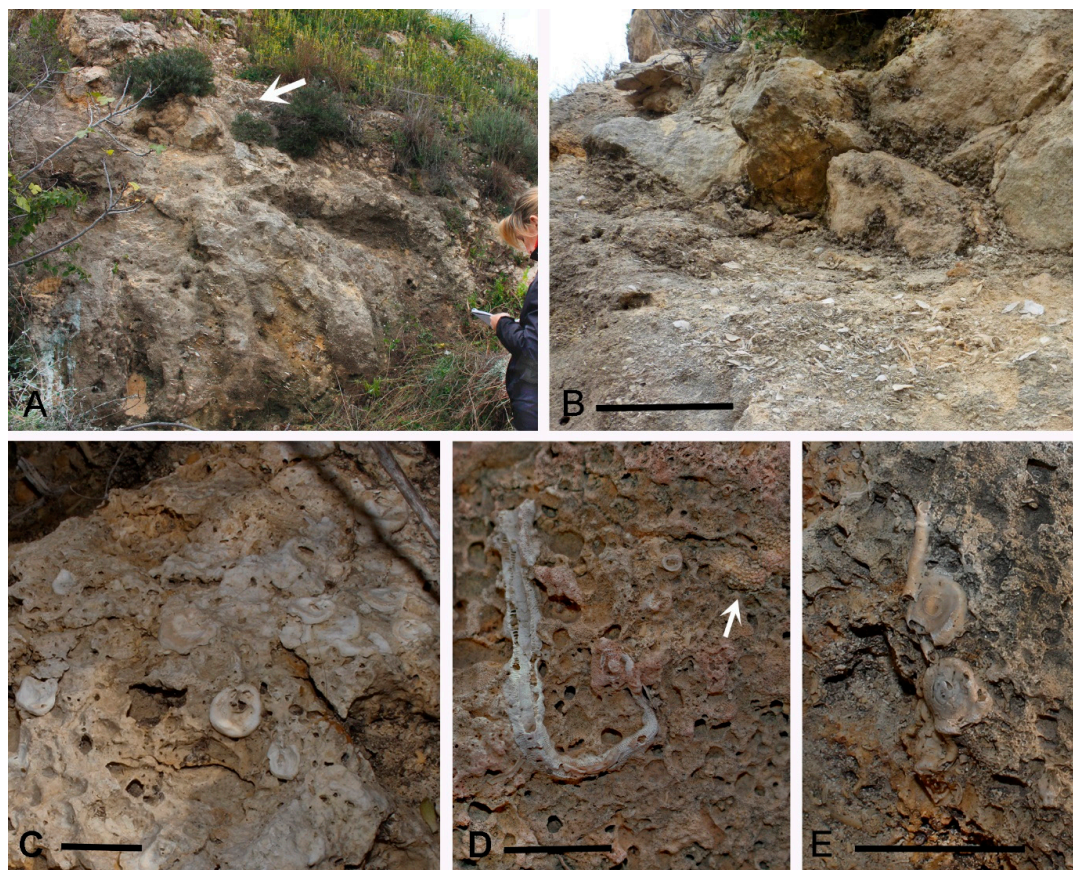
Figure 2. The studied palaeocliff exposed in the field. (**A**) Outcrop with heavily encrusted surfaces arrowed. (**B**) Some encrusted boulders engulfed in the fossiliferous marls. (**C**) Clustered valves of *Novocrania anomala*, some cemented on dead, already disarticulated specimens. (**D**) The polychaete *Serpula lobiancoi* on a bioeroded surface. An undetermined bryozoan colony arrowed. (**E**) Largely eroded tube of the polychaete *Spirobranchus lima*. Scale bars: 20 cm (**B**), 2 cm (**C–E**).

The surface of the blocks was examined for identification of preserved skeletonized lithobionts and for borers recording. Identification of bryozoan species (at the lowest possible taxonomic level) was partly hampered by the poor preservation state of some colonies and by the inability to use Scanning Electron Microscopy for colonies that were strongly attached to a very large substratum. This translates into uncertainties expressed with interrogation marks before species names indicated in Table 1, but not in the text for simplicity. Analogously, authorities are introduced only in Table 1. Individual organisms were counted. In contrast, owing to uneven and partial preservation, it was difficult to assess the real number of colonies for several bryozoans, and mostly for species developing large-sized, irregularly shaped colonies. Reported numbers of colonies are only indicative, as are coverage values. The coverage of single taxa was roughly estimated and is reported in Table 2 using three intervals: <10; 11–100 and >101 mm^2. The coverage of high taxonomic groups was roughly measured as projections on photographs (Figure 3E,F).
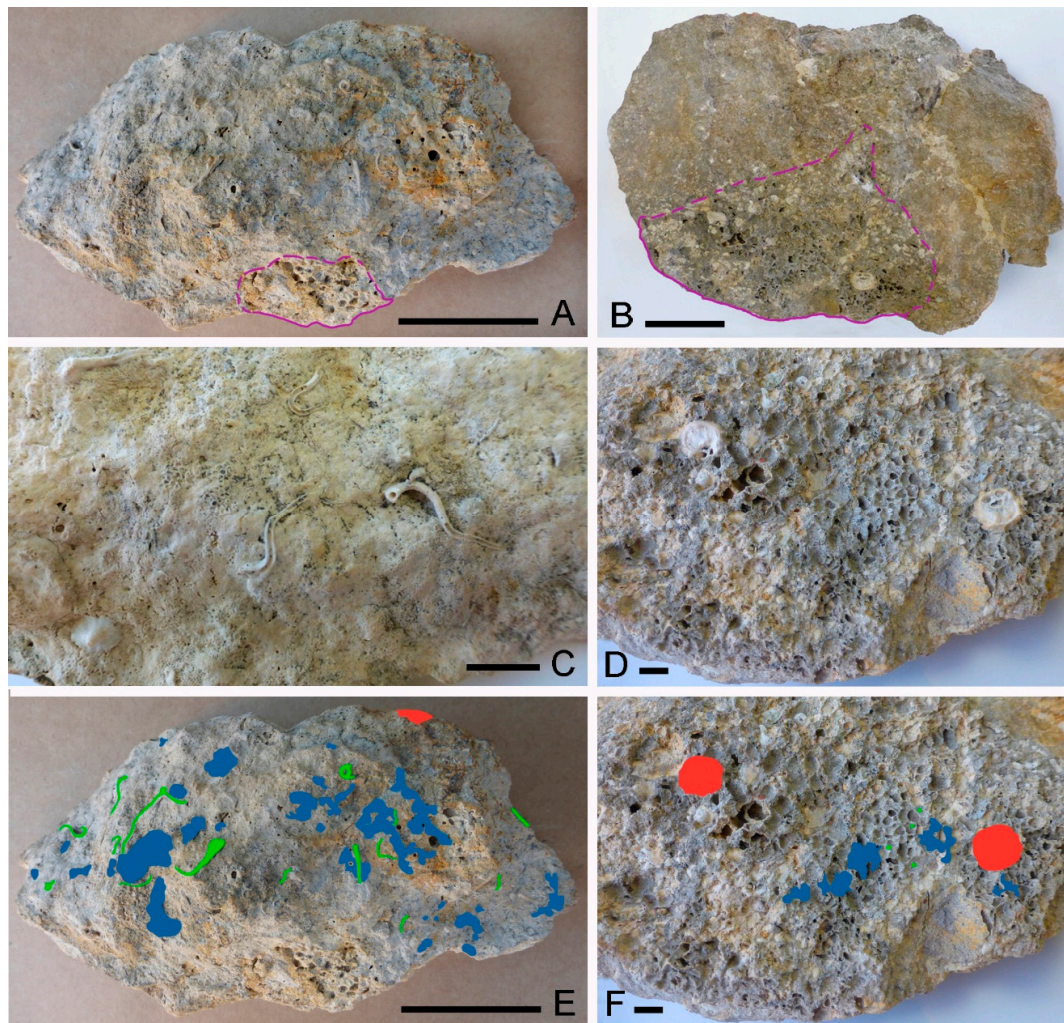
Figure 3. Lithobionts on the studied blocks. (**A**,**B**) the small block (SB) and the large block (LB). Pitted surfaces produced by heavy bioerosion are outlined in violet. (**C**) Close-up of the up-left side of SB with obvious serpulids and less evident bryozoans missing frontal surfaces. (**D**) Close-up of the exposed surface of the LB, heavily bioeroded and partly encrusted. (**E**,**F**) Epilithobiont coverage detected on the SB and LB, respectively. Blue: bryozoans; green: serpulids; red: brachiopods. Scale bars: 5 cm (**A**,**B**,**E**), 1 cm (**C**,**D**,**F**).
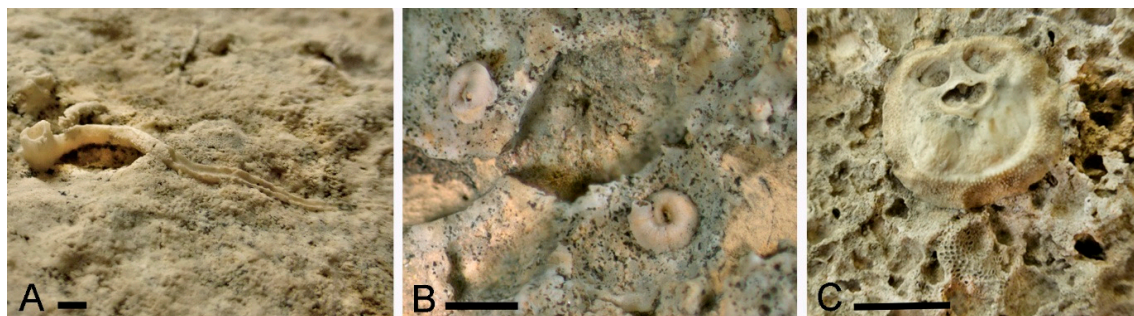

Figure 4. Serpulid and brachiopod lithobionts. (**A**) Partly eroded tube of the serpulid *Placostegus tridentatus* on the small block. (**B**) Two specimens of the spirorbid *Pileolaria militaris*, each situated inside an eroded *Entobia* pit on the large block. (**C**) A large valve of the brachiopod *Novocrania anomala* cemented on the bioeroded surface of the large block. A calloporid colony occurs in the foreground. Scale bars: 1 mm (**A**,**B**), 1 cm (**C**).

Table 1. List of skeletonized lithobiont species found on Pleistocene hard surfaces of Augusta, Sicily.

Skeletonized Epilithonionts	Small Block		Large Block		Field
Bryozoans	**N.**	**Cov.**	**N.**	**Cov.**	
? *Oncousoecia* sp.	1	*	1		
? *"Microecia suborbicularis"* sensu Harmelin 1976	4	*			
Diplosolen obelius (Johonston, 1838)	3	*	1		
? *Plagioecia platydiscus* Harmelin, 1976	1	*			
Harmelinopora indistincta (Canu and Bassler, 1929)	7	***			
? *Annectocyma major* (Johnston, 1847)	1	*			
? *Entalophoroecia deflexa* (Couch, 1842)	1	*			
Crisiid sp. encrusting stolon	1	*			
Hornera sp. base	1	*			
? *Disporella hispida* (Fleming, 1828)	6	*			
Cyclostomatid spp.			1		*
Ramphonotus minax (Busk, 1860)			1		
Callopora sp.	1	*	1	*	
? *Hincksina flustroides* (Hincks, 1877)	3	*			
? *Puellina setosa* (Waters, 1899)	3	**	1	*	
? *Cribrilaria radiata* (Moll, 1803)	1	*			
? *Cribrilaria venusta* (Canu and Bassler, 1925)	6	**			
Cribrilinid sp.	2	*			
Trypostega sp.	2	*			
Escharoides coccinea (Abildgaard, 1806)	4	**			
? *Prenantia ligulata* (Manzoni, 1870)	2	*			
Escharina dutertrei protecta Zabala, Maluquer, Harmelin, 1993	1	*	2	**	
Herentia hyndmanni (Johnston, 1847)	5	**			
Microporella appendiculata (Heller, 1867)	2	*			
Microporella gr. *ciliata* (Pallas, 1766)	1	*			
Phydoloporid sp. bases of erect species	5	*			
Cheilostomatid spp.	4	*			***
Total Number of Bryozoan Colonies	**68**		**8**		
Serpulid Polychaetes					
Serpula lobiancoi Rioja, 1917					*
Spirobranchus lima (Grube, 1862)					*
Placostegus tridentatus (Fabricius, 1779)	15	**	1	*	
Pileolaria militaris Claparede, 1870	1	*	4	*	
Total Number of Serpulid Specimens	**9**		**5**		
Brachiopods					
Novocrania anomala (O.F. Müller, 1776)	3	***	2	***	
Total Number of Brachiopod Specimens	**3**		**2**		
Molluscs					
Anomiidae sp.	1	*			
Total Number of Mollusc Specimens	**1**				

For each species, the number of colonies/specimens and the estimated coverage on each of the two analyzed blocks is reported. Cyclostomatid sp. and cheilostomatid sp. indicate taxa undeterminable owing to their bad state of preservation. N: number of colonies or specimens; Cov: coverage; Field: observed in the field; *: <10 mm^2; **: 11–100 mm^2; ***: >101 mm^2.

Table 2. Inter- and intraspecific relationships recognized between lithobiont, mainly skeletonized taxa, and presumed soft-bodied organisms, found on Pleistocene hard surfaces of Augusta, Sicily.

Interactions	? "M. suborbicularis"	D. obelius	? P. platydiscus	H. indistincta	? A. major	Cyclostomatid sp.	? P. setosa	? C. radiata	? C. venusta	Cribrilinid sp.	E. coccinea	H. hyndmanni	Trypostega sp.	Phydoloporid sp.	P. tridentatus	N. anomala	Unpr.soft organisms
?M. suborbicularis	1			1								1		2			
D. obelius				1									1		1o?		1o
H. indistincta	1	1	1	7 so	1			1	2	1					1 s	1	2, 2s
? A. major												1					
Hornera sp.												1					1o
D. hispida												1					1o
? H. flustroides	1s			1													
? P. setosa																	1s
? C. venusta					1			1									
Cribrilinid sp.												1f					
E. coccinea		1	1														
? P. ligulata	2					1						1s			1s		
H. hyndmanni				1					1	?1	1					1	
E. dut. protecta																	
Trypostega sp.		1												1			
Phydoloporid sp.				1													
P. tridentatus				1f						1							
Anomiid sp.										1							

Numbers indicate superimposition/overgrowths of species in the first column on those reported in the top line. S: standoff; 1, 2 … : superimposition/overgrowth; so: intracolonial, self-overgrowth; f: fouling. For species authorities and genus names refer to Table 1.

Where lithobionts were preserved in contact with each other, the nature of these contacts was investigated in order to detect if they represented interactions and, if so, of what kind. The terminology proposed by [2,30] subsequently adopted by [16] and recently revised by [19], was employed. Low magnification images were acquired with a Zeiss Discovery V8A stereomicroscope equipped with an Axiocam and an Axiovision acquisition system.

One additional Miocene limestone block, MEDCOR-58, collected during the homonym cruise, east of Malta, at 116 m depth, 35°55′32.73″ N, 14°33′44.91″ E, whose surface hosted living encrusters, was also examined for the occurrence of high taxonomic groups in order to make a comparison.

The two Pleistocene blocks are stored in the Palaeontological Museum of the University of Catania under the codes: PMC.I.Pl. rock 1.2015 and PMC.I.Pl. rock 2. 2015.

4. Results

Examination of exposed surfaces in the field (Figure 2A,B) allowed the recognition of several lithobionts, among which encrusting valves of the brachiopod *Novocrania anomala* were the most common, usually dispersed but locally clustered (Figure 2C). Some large-sized serpulids also occurred, i.e., *Spirobranchus lima* (Figure 2D) and *Serpula lobiancoi* (Figure 2E), together with smaller species. Bryozoan colonies were very abundant, but the identification of species was difficult on the outcrop owing to colony preservation and visibility of diagnostic characters (see Methods). Bioerosion traces were also observed, locally pervasive and particularly obvious when they became partly to deeply truncated (Figure 2C–E). Borings mostly belong to *Entobia* but possible *Gastrochanolites* also occur, together with subordinate elongated borings.

The two sampled limestone slices had surfaces of about 122 (small block: SB) and 450 cm^2 (large block: LB) which were exposed on the outcrop (Figure 3). Encrusters were distributed on all exposed surfaces on the SB (Figure 3A,C,E). In contrast, on the LB, wide sectors of the surface were clearly cut (probably by human activity in recent times) and missed evidence of colonization (Figure 3B); whereas an area of about 120 cm^2 exposed extensively eroded clionaid boring systems, which appeared as pocketed, with contiguous, encroaching pits, each 2−5 mm in diameter (Figure 3D,F). Due to the shape, size and arrangement of the chambers, these borings could tentatively be identified as *Entobia magna*. Skeletonized encrusters occurred, often widely spaced from each other, but less numerous and more spaced on the LB (Figure 3F) rather than on the SB, where they were also found to be in contact with each other, although some areas remained barren (Figure 3E). Analogously, coverage was lower on the LB where lithobionts covered less than 4% of the exposed surface, whereas it was about 10% on the SB. Bryozoans were the main encrusters on the SB (8.29 cm^2), followed by brachiopods and serpulids (1.80 and 1.08 cm^2, respectively). In contrast, brachiopods with few but large sized individuals dominated on the LB covering 2.8 cm^2, followed by bryozoans (1.7 cm^2) and serpulids, only accounting for 0.04 cm^2.

4.1. Lithobiont Diversity

On the sampled blocks, skeletonized epilithobionts were represented by obvious specimens belonging to serpulids and brachiopods, and by less evident but more abundant bryozoan colonies (Figures 3–7, Table 1).
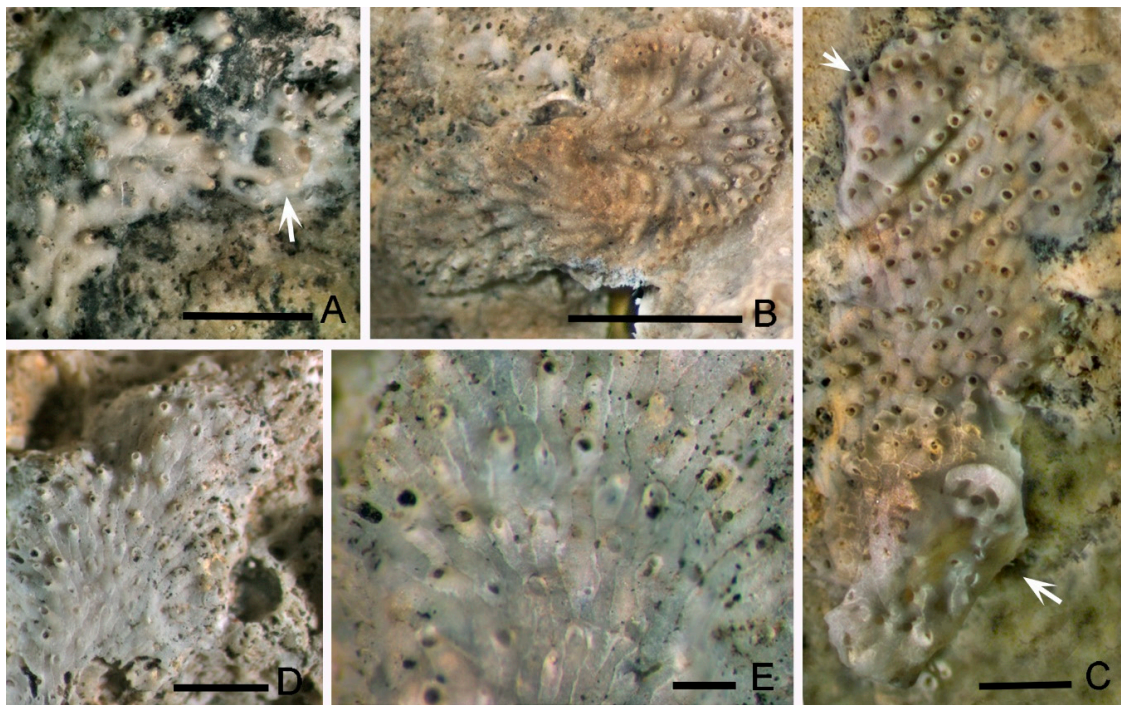
Figure 5. Cyclostome lithobionts on the small block, except for (**D**,**E**) on the large block. (**A**) *Oncousoecia* sp. Gonozooid arrowed. (**B**) "*Microecia suborbicularis*". (**C**) *Harmelinopora indistincta* (gonozooid indicated by the short arrow) and the base of a broken erect cheilostome colony (long arrow). (**D**,**E**) A *Diplosolen obelius* colony and close-up of some zooids and interspersed nanozooids. Scale bars: 1 mm (**A**–**D**) 0.2 mm (**E**).

Serpulids only consisted of one serpulin, *Placostegus tridentatus* (Figures 3C and 4A), and one spirorbin species, *Pileolaria militaris* (Figure 4B), represented by 16 and five specimens, respectively, both occurring on the two blocks but with a very different number of specimens. Brachiopods showed only few valves of the cemented species *N. anomala*, reaching up to 1.5 cm in width (Figure 3D−F and Figure 4C).

Molluscs occurred with only one fragmentary cemented valve of an undetermined anomiid. Bryozoans showed at least 76 colonies belonging to at least 25 species (Figures 3, 4C and 5, Figure 6, Figure 7; Table 1), 22 of which (nine cyclostomes and 13 cheilostomes) were identified at the species or genus level, although some tentatively. Cheilostomes prevailed in both species (58.3% vs. 41.7%) and colony (61.8% vs. 38.2%) number. Distribution of bryozoans was very different between the two blocks with all but one species found on the SB and only seven species on the LB (Table 1). Analogously, colonies were more numerous on the SB than on the LB where each taxon was represented by only one colony, except for *Escharina dutertrei protecta* (Figure 6G,H) occurring with two colonies, one being particularly wide. All species occurred with less than seven colonies and about half of them (12 species) with only one or two colonies. The most common species were *Harmelinopora indistincta* (seven colonies, Figures 5C and 7B,F–I), *Disporella hispida* (six colonies, Figure 7K), *Cribrilaria venusta* (six colonies, Figure 7C) and *Herentia hyndmanni* (five colonies, Figures 6I and 7E). A further two cyclostome species, i.e., *Diplosolen obelius* (Figure 5D,E and Figure 7B,C,J) and "*Microecia suborbicularis*" (Figure 5B) and three cheilostomes i.e., *Escharoides coccinea* (Figures 6D and 7A) *Puellina setosa* (Figure 6C) and *Hincksina flustroides*, showed three or four colonies. Coverage was mostly accounted for by bryozoans and particularly by *E. dutertrei protecta* on the LB and *H. indistincta* and cribrimorphs on the SB blocks (Figures 4 and 6).
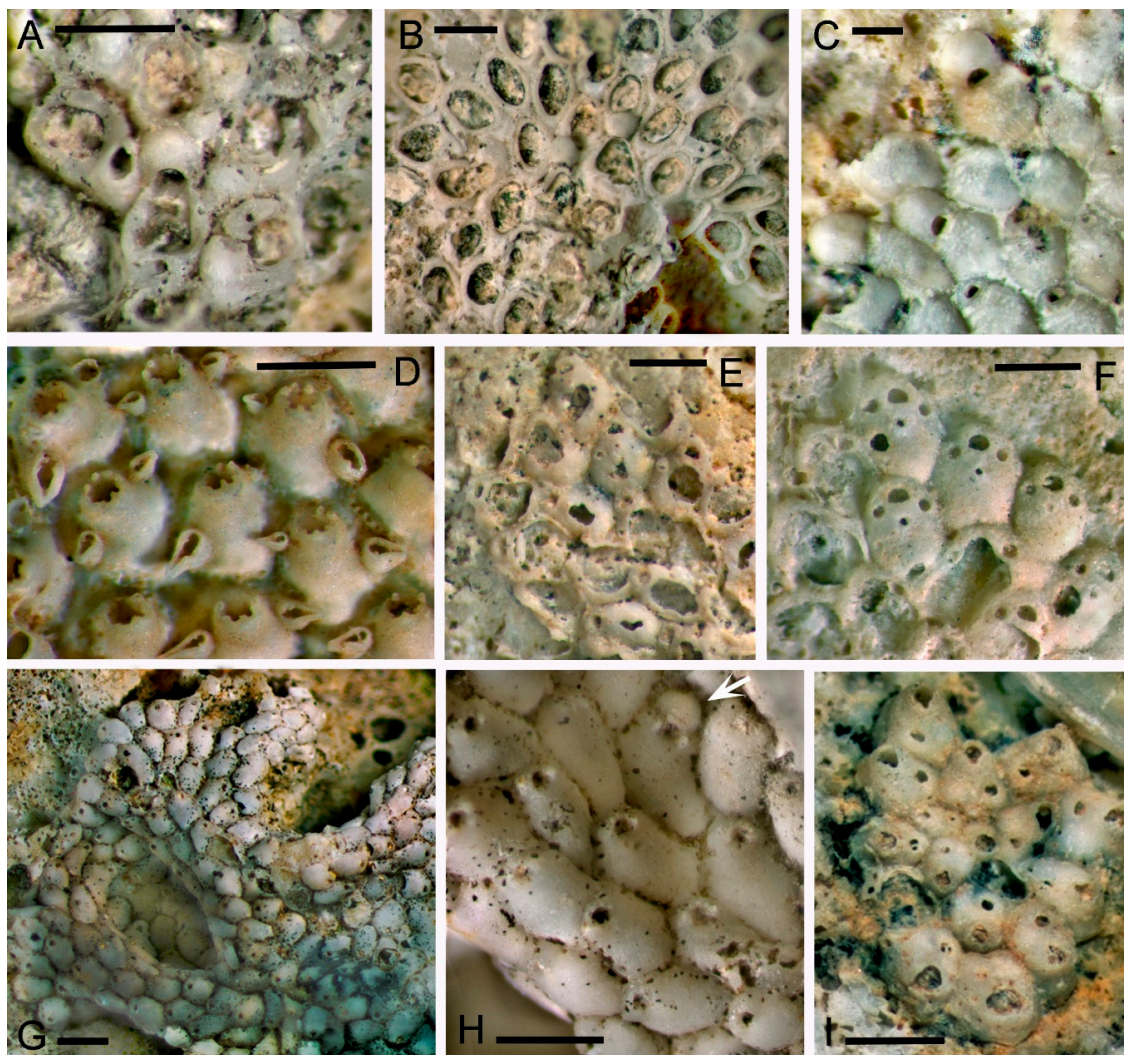
Figure 6. Cheilostome lithobionts on the small block, except for (**G**,**H**) on the large block. (**A**) *Ramphonotus minax*. (**B**) *Callopora* sp. (**C**) *Puellina setosa*. (**D**) *Escharoides coccinea*. (**E**) *Microporella ciliata*. (**F**) *Microporella appendiculata*. (**G**) Large colony of *Escharina dutertrei protecta* coating the pitted *Entobia* surface. (**H**) Close-up of some zooids, one ovicellate (arrowed), inside a pit. (**I**) A spot-like colony of *Herentia hyndmanni*. Scale bars: 0.5 mm (**A**,**B**,**E−H**), 0.2 mm (**C**), 1 mm (**D**).

Bryozoans showed encrusting, mostly unilaminar, morphotypes with few species showing small, subcircular to domiform colonies and a somewhat definite growth (such as the cyclostome *Disporella hispida* and the cheilostome *Herentia hyndmanni*). Other taxa, such as the cheilostomes *E. coccinea* and some cribrilinid species grew as irregularly shaped patches. In contrast, some cyclostomes formed pauci- to multiserial branched colonies or fan-shaped to elongated lobes, and usually reached small sizes, except for *H. indistincta*, whose sinuous ribbon-like branches repeatedly bifurcated forming a sort of network covering wide surface sectors (Figure 7F–I). Species growing as erect rigid colonies were also present, their occurrence only indicated by their encrusting bases, from which broken erect stems of less than 1 mm arose (Figures 5C and 7D). Reinforcing and attaching kenozooids indicated that most bases belonged to cheilostome phidoloporids and one to the cyclostome *Hornera* sp. Slender segmented stolon fragments also pointed to the first occurrence of at least one erect flexible colony of a crisiid cyclostome species.
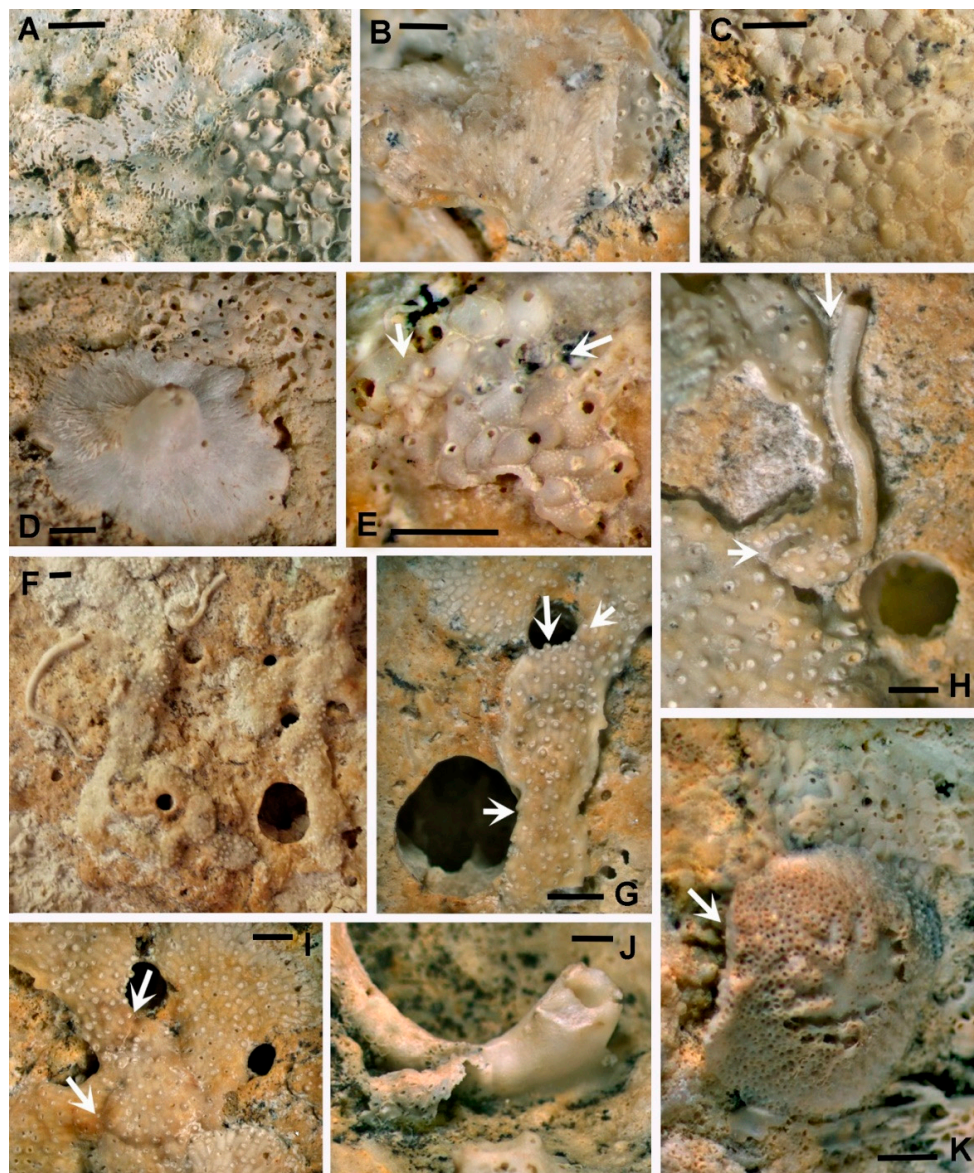
Figure 7. Lithobiont interactions on the small block. Bryozoans are involved if not specified. (**A**) *Escharoides coccinea* covering a partly abraded *Plagioecia platydiscus* colony. (**B**) *Diplosolen obelius* on *Harmelinopora indistincta*. (**C**) A *Diplosolen obelius* colony sandwiched between two subsequent *Cribrilaria* colonies. (**D**) Base of *Hornera* sp., with evidence of bioimmuration, covering *Herentia hyndmanni*. (**E**) Stand-off at the contact between *Prenantia ligulata* and *H. hyndmanni* (long arrow) further fouled by a cribrimorph (short arrow). (**F**) A large *H. indistincta* colony interacting with borers and the serpulid *Placostegus tridentatus*. (**G**) Close-up of (**F**) showing a multiserial branch halting its growth (long arrow) and lining (short arrows) borings pointing to true interactions with their producing organisms. (**H**) Close-up of (**F**) showing the serpulid *P. tridentatus* fouling a *H. indistincta* branch (short arrow), arching on some tubes and reaching the rocky substratum lining another branch of the same colony, which stops growing (long arrow). Partial breakage revealed a space below the basal lamina indicating the possible occurrence of an overcrusted soft-bodied organism. (**I**) Close-up of (**F**) showing lateral branching and self-overgrowth (arrowed) between fan-shaped *H. indistincta* branches, besides interactions with borers and soft-bodied organisms. (**J**) *Diplosolen obelius* forming a bridge possibly on an unpreserved soft-bodied organism. (**K**) *Disporella hispida* covering *Trypostega* sp. and elevating the basal lamina (arrowed) to overgrow an unpreserved, possibly soft-bodied organism. Scale bars: 1 mm (**A**,**B**,**D**−**K**), 0.5 mm (**C**,**H**).

4.2. Preservation State

The brachiopod *N. anomala* only occurred with the cemented valves, whereas serpulids showed different degrees of preservation ranging from nearly entire tubes to completely abraded/broken specimens only recognizable for the attaching portion of their sinuous progressively enlarging tubes.

Several bryozoan colonies showed a relatively good preservation state and potentially retained diagnostic characters useful for species identification, at least in more or less wide areas, or some zooids. Further colonies were completely abraded, and their first presence was indicated by basal and partly preserved lateral walls. Cemented erect taxa are uncommon, and the few recognized bryozoans always lack stems and branches. Reliable traces of organisms fixed through organic structures were not detected, probably confused in the worn surface also obliterating small-sized shallow borings only locally preserving large borings mostly produced by clionaid sponges and probably by some boring molluscs. Boring traces are often largely eroded, thus exposing their floors.

4.3. Lithobiont Interactions

Contacts and possible interactions between encrusters were observed only on the SB, because on the LB the 15 preserved skeletonized encrusters were largely apart from each other. However, all detected species on the LB encrusted on a rugged bioeroded surface.

A total of 59 interactions occurred on the SB (Table 2), involving 19 out of the bryozoan taxa detected on this block, together with the serpulid *P. tridentatus*, the brachiopod *N. anomala* and the only detected anomiid. Because encrusters cluster in particular areas, some of them remained isolated, whereas some bryozoan colonies were involved in multiple interactions. Most of these interactions pertained to only one species, i.e., *H. indistincta* (22 = 37.3%). "*M. suborbicularis*" (nine interactions = 15.3%), *D. obelius* and *E. hyndmanni* (each with seven interactions = 11.9%), and *Trypostega* sp. and the serpulid *P. tridentatus* (each showing five interactions = 8.5%) follow, whereas all other species rarely interacted. Most interactions were interspecific, but seven (=11.9%), all pertaining to *H. indistincta*, were intraspecifc.

Most interactions (39 = 66.1%) were overgrowths of one species growing on another one (Table 2; Figure 7A,B,D), with no indication of competition. In a single occasion, a colony of *D. obelius* was observed sandwiched between two subsequent colonies of *C. venusta* (Figure 7C) without any evidence of reciprocal overgrowth, thus indicating a possible superimposition of colonies of subsequent lithobiont generations. *H. indistincta* was the only species showing a relevant number (seven) of self-overgrowths (Figure 7F,I), corresponding to the 32% of the interactions involving this species. *H. indistincta* and a few other species were also involved in interactions interpreted as produced by competition. Seven of these were stand-offs (three involving *H. indistincta*) and usually consisted of a bryozoan colony halting or curving around borings (Figure 7F,G–I) in the substratum, probably hosting living specimens at the time the encruster was growing. In one case (Figure 7H), a lobe of a *H. indistincta* colony stopped its growth against the flank of the distal part of a *P. tridentatus* tube which started its growth fouling a contiguous branch of the same *H. indistincta* colony, and later slightly arching over some zooids to reach the lithic substratum. The second fouling case related to a juvenile cribrilinid colony growing on *H. hyndmanni* (Figure 7E). Finally, on four instances, colonies were detected arcing on the substratum (*D. obelius* forming a bridge between the rock and a *P. tridentatus* tube: Figure 7J) or elevating their growing edge (*D. hispida* also covering a *Trypostega* colony: Figure 7K), likely indicating the first occurrence of soft-bodied organisms which were partly overcrusted.

5. Discussion

5.1. Palaeoebiodiversity and Palaeohabitat Inferences

All species listed after sample and field observation are typical representatives of present-day Mediterranean faunas, including some taxa not identified at the species level, such as *Trypostega* sp., often reported as *T. venusta* (Norman, 1864), a presumed widely distributed taxon in need of revision.

Several species show wide distributions in middle to outer shelf, some of them also extending to deeper depths, but no species is restricted to shallow waters or includes very shallow distributions. *D. hispida* and *D. obelius* are usually considered as shelf species (e.g., [31]) with the second one distributed deeper than about 45 m [32]. A relevant number of species is particularly sciaphilic and presently restricted to very shadowed, cryptic and/or deep environments of the Mediterranean, including semi-dark and dark caves, as well as coralligenous bioconcretions in the mid circalittoral zone and deeper habitats of the outer shelf and the neighboring slope (shallow bathyal). The cyclostomes *H. indistincta, P. platydiscus* and "*M. suborbicularis*"; the cheilostomes *C. radiata, C. venusta* and *H. hyndmanni*; the spirorbin *P. militaris* and the brachiopod *N. anomala* all share dim requirements [31–33], although some of them and particularly the three cyclostomes, have been mostly found in cryptic habitats (e.g., [34]). In contrast, the other species, together with *E. dutertrei protecta* and the serpulid *P. tridentatus*, may be common in bathyal habitats usually also associated with cold-water corals [35–38]. Although the absence of taxa per se cannot drive any conclusion (e.g., [39,40]), it could be remarked that calcareous algae are missing on both the SB and LB and were not observed on the outcrop. This absence points to a possible very deep circalittoral to the shallow bathyal habitat and is consistent with inferences drawn from the preserved skeletonized encrusting community. Exposed rocks in deep settings usually host the biocoenosis of the shelf-edge rock, or "Roche du Large" (RL) of [41], and the biocoenosis of white (or cold water) corals (CWC) in the bathyal, usually at depths of more than 250−300 m. The occurrence of the bryozoans *M. appendiculata, M.* gr. *ciliata, H. flustroides* and *P. setosa,* and of the serpulids *S. lima* and *S. lobiancoi* (absent or very uncommon in the bathyal: [33,42–44] and RS, personal observations), supports an attribution of the studied assemblage to an original RL biocoenosis. This is also consistent with the abundance of *P. tridentatus* showing its small-sized morphotype typically replaced by a larger one at bathyal depths [45].

In the present-day Mediterranean, RL biocoenosis occurs at 90−250 m depth, on rocky outcrops and spotted blocks usually covered with a thin sediment veneer. Biotic composition of RL is still poorly known, but in recent years, the employment of Remotely Operated Vehicles has been documenting the dominance of large sized suspension-feeders, such as sponges and cnidarians [41,46,47] most of which lack mineralized skeletons or only have sclerites separating after death. However, the cnidarians *Dendrophyllia cornigera* (Lamarck, 1816) and *Corallium rubrum* (Linnaeus, 1758), typically found in RL assemblages although also reported from CWC habitats (e.g., [48]), possess carbonate skeletons and cement on their substratum. In the present instance, although bases were lacking on the blocks examined in the laboratory and in the field, at least some colonies thrived on the rocky palaeoscarp as indicated by the occurrence of fragments of these species in the fossiliferous marls deposited close to it (see also the list of species in [20]).

Serpulids and bryozoans have been reported as relevant in RL assemblages (e.g., [41,46]). This was also obvious from preliminary observations of a limestone boulder collected east of Malta at 116 m depth, on which serpulids dominated with several species and large-sized specimens, and bryozoans included obvious erect species mostly represented by flexible candiids and crisiids attached with chitinous rootlets. However, the diversity of these groups is unknown in RL assemblages, and data only derive from records of species associated with *D. cornigera* mostly provided by [49] based on bryozoan material from the Gulf of Genoa and from Algeria. Nearly all previous information was summarized in [38], listing a total of 10 bryozoan and eight serpulid species. Summing up, bryozoans include 12 species (*Copidozoum tenuirostre* (Hincks, 1880), *Scupocellaria incurvata* (Waters, 1896), *Glabrilaria pedunculata* (Gautier, 1956), *C. venusta, Palmiskenea gautieri* Madurell, Zabala, Domínguez-Carrió and (Gili, 2013), *Escharella ventricosa* (Hassal, 1842), *Smittina cervicornis* (Pallas, 1766), *Smittina landsborovi* (Johnston, 1847), *Schizomavella linearis* (Hassall, 1841), *E. dutertrei protecta, H. hyndmanni* and *Schizoretepora longisetae* (Canu and Bassler, 1928)), with only three species shared with the Augusta fossil assemblage. Serpulids include *Filograna* sp., *Filogranula gracilis* (Langherans, 1884), *Hyalopomatus madreporae* (Sanfilippo, 2009), *Metavermilia multicristata* (Philippi, 1844), *Protula tubularia* (Montagu, 1803), *Serpula vermicularis*

(Linnaeus, 1767), *Vermiliopsis monodiscus* (Zibrowius, 1968) and *Vermiliopsis* sp. with no species shared with the Augusta assemblage.

Cyclostomes representing about 40% in species number in the Augusta blocks are completely missing from this list, possibly as the result of the low research effort on this group [50]. Cyclostome percentage at both species and colony number, is dramatically high compared with figures for the whole Mediterranean biodiversity (14%) and individual habitats, where they invariably account for less than 20% [50]. However, this relevance somewhat parallels that shown (25–50% at the species level and 51–91% at the colony level) in particular communities of the Infralittoral Algae biocoenosis between 5 and 26 m depth in the western Ionian Sea [51].

Even omitting cyclostomes from a comparison, the low number of bryozoan and serpulid species shared between present-day and the Pleistocene deep-water lithobiont communities could seemingly result from both the extreme scantiness of knowledge about RL, and its presumed pattern of biodiversity, implying small spatial scale variability contributing to maintaining high levels of diversity at the basin spatial scale, as assessed by [46]. It must also be remarked that the list of species produced after examination of the two blocks represents only a part of the total biodiversity of the epilithobiont community. It is likely that the total number of bryozoan species will increase after close examination of further surfaces, taking into consideration the increase in the number of serpulid species that doubled when adding species detected in the field.

Examination of the Maltese limestone block showed that soft-bodied organisms occur with mm-to-cm sized, inconspicuous specimens besides the large-sized ones which can be remotely investigated [46]. Small erect cnidarians, encrusting sponges and tunicates were present, all adhering with organic tissues and consequently unpreservable as fossils on their original substratum, although all possessing mineralized skeletons in the form of more or less isolated sclerites. Specimens, of up to 5–7 mm in height, of the cemented foraminifer *Miniacina miniacea* (Pallas, 1766) were also common on this block. Traces of soft bodied organisms were also detected on the examined blocks pointed out by the bridge-like structures and edge elevations produced by encrusters (see interactions below) and borings, mostly by clionaid sponges.

With all the limits outlined above, we suggest that the examined lithobiont community could be considered as a residual community sensu [52] belonging to an original RL biocoenosis giving a first insight on the biodiversity that RL biocoenosis expressed in the early Pleistocene. Further studies are needed for improving knowledge about both fossil and present-day assemblages.

5.2. Interactions and the History of Colonization

Only a relatively small part of the surface (less than 5 cm^2 on the LB and about 12 cm^2 on the SB), is covered with lithobionts, whereas large areas remain barren. However, it cannot be assessed if this free space was first covered, at least partly, by unpreservable taxa such as sponges and ascidians. These encrusters usually are common representatives on modern hard substrata (see above) covering wide areas and often being good competitors [19].

A large majority of species but a more restricted number of colonies/specimens is involved in the observed interactions, whereas some colonies/specimens remain isolated. Mostly on wide surfaces, this is a common feature that is produced by the chance that encrusters recruit close to each other even when free space is available. Closeness enhances competition [19,53,54] for space between colonies/specimens of the same lithobiont generation, and to superimposition indicating a mere temporal succession between colonies/specimens belonging to subsequent generations. However, the distinction between superimpositions produced by live–live interactions of organisms with different competitive performances, or by live–dead organisms, also possibly indicating ecological succession, is not always possible [40].

Analysis of interactions clearly indicates that only part of the detect lithobionts actually lived contemporarily on the investigated Augusta rocky surfaces. This is the case for boring sponges, producing some of the observed *Entobia* traces, and colonies of *H. indistincta* and *Cribrilaria* spp. as well

as for the multiple fouling/standoff interactions involving a *H. indistincta* branch and a specimen of *P. tridentatus* (see above).

However, owing to the small number of intraspecific unquestionably true interactions, it is difficult to put forward hypotheses about species competitiveness in the assemblage. Encrusting soft-bodied organisms seemingly competed with, and were partly covered by, some of the preserved lithobionts. However, in all instances, we can state contemporaneity only for each pair/group of colonies/specimens interacting. In contrast, we cannot assess or discard contemporaneity between different interacting colonies/specimens and clusters of interacting colonies/specimens. Few superimpositions, however, clearly indicate that interaction happened after the death of one contractor. This is the case for colonies of *H. indistincta* and *H. hyndmanni* encrusting the inner surface of the attached valves of *N. anomala*.

Subsequent generations of *N. anomala* were also observed in the field with encrusting valves cemented to each other (Figure 2C). Furthermore, the different preservation state of bryozoan colonies and serpulid tubes also points to multiple subsequent episodes of colonization of the same surfaces over time. However, the substantial ecological consistency of identified lithobionts could indicate that they all formed in the same palaeohabitat, when blocks were exposed at or close to the shelf break. This RL colonization episode was seemingly preceded by an erosive event abrading/detaching previous lithobionts and, locally, even a thin rocky layer, producing the partial destruction of a previous *Entobia* (possibly *E. magna*) network of borings, now exposed on the LB (and on large surfaces observed in the field). The resulting pitted surface exposing bases of the empty sponge chambers locally filled by whitish marls was the substratum for several coating species including thin unilaminar cheilostome bryozoans. This succession could indicate a possible first colonization of the rocky outcrop at inner to middle shelf depths, followed by a degradation/erosion phase and a new episode of colonization at the shelf break before final burying, somewhat paralleling a similar lithobiont succession in Rhodes [8]. This observation joined with the location of the outcrop along one of the faults separating Miocene limestone and Pleistocene sediments, indicate that the studied lithobiont community formed along a palaeocliff bounding the Augusta Pleistocene paleobasin, and document its deepening during time.

6. Conclusions

The analysis of the lithobiont community preserved on two Miocene limestone blocks along a fault scarp delimiting a Pleistocene palaeobasin presently cropping out in the area located immediately north of Augusta (Hyblean plateau, eastern Sicily) allowed: 1. the description of an early Pleistocene deep-water lithobiont community referable to an original RL biocoenosis, although residual and only consisting of the preservable cemented, skeletonized component organisms, i.e., essentially bryozoans, serpulids and brachiopods; 2. a first insight about the diversity of such taxonomic groups in fossil RL habitats, largely differing from that reported to date for present-day analogous habitats, a pattern that was partly expected and seemingly produced by the putative high diversity at a wide scale joined with a high spatial heterogeneity of this assemblage at a small scale; 3. preliminary ideas about relationships between lithobionts in this habitat during the early Pleistocene; 4. a new piece of evidence for reconstructing the colonization of marginal areas of one of the small palaeobasins located along the Hyblean plateau that were shortly active during the Pleistocene and to trace its evolution.

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