Bryozoans and serpuloideans in skeletobiont communities

from the Pleistocene of Sicily: spatial utilisation and competitive interactions

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Abstract

Sessile encrusters with mineralised skeletons in the fossil record generally retain their original spatial relationships to the substrate and each other. Being short living and not significantly time averaged, communities on shelly substrates represent excellent systems to study such relationships.

Bryozoan and serpuloidean skeletobionts on molluscs and rhodolites from Lower Pleistocene localities in Sicily have been studied. Species composition and specimen sizes testify to a short exposure of the shells on the sea floor. Skeletobiont community structure is characterised by the dominance of a few species (5 bryozoans out of 87 and 3 serpuloideans out of 17). Substrate coverage is usually low (<5%), rarely reaching 50-60% or more. On bivalves, skeletobiont distribution does not exhibit a clear trend for inner/outer sides or left/right valves.

Oriented growths, differential patterns in microenvironment utilisation of the substrate and spatial competition have been analysed. Several of the recorded overgrowths resulted from superimposition of specimens growing on skeletons of previous, already dead encrusters. True competitive interactions mainly involved bryozoans and only a few serpuloideans. Within bryozoans interspecific encounters usually led to overgrowth or abutment whereas intraspecific encounters commonly resulted in standoffs and growth side by side in cheilostomes, and to fusion of colonies in some cyclostome species.

Keywords: skeletobionts, bryozoans, serpuloideans, interactions, Pleistocene, Sicily.

Introduction

On soft bottoms, shells of epibenthic organisms, during life and after death, together with exhumed skeletal remains of endobenthic organisms, supply hard substrates, which, although small in size, are suitable for colonisation by organisms constituting peculiar "hard bottom" communities.

Living shells and skeletons must lie at the bottom-water interface for a time span enough to permit zoobionts and skeletobionts (*sensu* Taylor and Wilson 2002, 2003) to settle and grow.

Moreover, when the time span before final burial is not too long, it can be assumed that skeletobionts form true communities and at least some of them lived contemporaneously, interacting in ecological time (see Lescinsky 2001). It follows that, although biased by the removal of some unfossilizable organisms, these fossil assemblages closely represent the preservable portion of the original biological community, including the record of ecological successions and relationships among species, which can be inferred analysing overgrowths and other interactions (Taylor 1984;

Taylor and Wilson 2003). Besides skeleton-bearing, usually encrusting, organisms, traces of other organisms are preserved, which belong not only to the sessile component but also to mobile species, often grazers and predators, living within the community.

These generally "unstable (easily moved about or buried) and ephemeral (easily broken) substrata" (McKinney and Jackson 1989, McKinney 1995a) contain a high portion of early successional taxa with mineralised skeletons among which bryozoans and serpuloideans are common and likely to be preserved in the fossil record. Such fossil communities show a higher taphonomic fidelity than those encrusting more stable (and durable) hard substrata where later successional, usually soft-bodied encrusters dominate (Rasmussen and Brett 1985), which are lost during fossilization.

Alternatively, if exposure time on the sea-bed is long, sometimes comprising successive phases of burial and exhumation, the record may comprise multiple, often hardly detectable, generations of skeletobionts. Nevertheless, these time-averaged communities differ from soft bottom communities, as they can preserve a layered succession of co-occurring skeletobionts.

Conditions suitable for shell colonisation mainly occur on soft bottoms characterised by mixed, sandy-to-gravely sediments containing a large coarse organogenic fraction, swept by moderate-to-strong bottom currents that allow some stability of shells and lithic clasts but still prevent particle shifting, abrasion of colonisers and deposition of fine grained sediments. Such conditions occur mainly in mid shelf (circalittoral) environments swept by bottom currents, as is in the present day Mediterranean, where the "coarse Sands and fine Gravels swept by Bottom Currents" (SGCF) or rheophylic facies of the Detritic Bottoms (DC) Assemblages (*sensu* Pérès 1982) are developed. Comparable facies are recorded in Quaternary successions from southern Italy. Recent disarticulated bivalve shells studied by Lescinsky (1993) and McKinney (2000) and Pliocene shells analysed by Reguant and Mayoral (1994) come from somewhat similar palaeoenvironments. Although rare, colonised shells can also be found in deeper environments with fine-grained bottoms, localised within the deep shelf (Harmelin 1976) and also the bathyal.

Studies of fossil skeletobiont assemblages are mainly devoted to Palaeozoic and Mesozoic examples whereas those from the Neogene have been less investigated (Taylor and Wilson 2003 for a review).

The aim of the present paper is to analyse the composition of skeletobiont communities from Lower Pleistocene fossiliferous sediments cropping out in Sicily, focusing on interactions at high taxonomic level and within groups, with special emphasis on bryozoans and serpuloideans, and aiming to recognise preferences in substrate utilisation, ecological successions (if any) and spatial competition among encrusters while not considering distribution patterns on skeletal substrates and related taphonomic implications which will be deal with elsewhere (Rosso and Sanfilippo in prep.).

Materials and methods

Materials come from three different localities in Sicily: the Case Catarinicchia section (BC), cropping out along the Belice river, in W Sicily; the Megara section along the S. Marcellino river (MEG) and the Catallarga outcrop (CAT), respectively located westward and south-westward of Catania (E Sicily). Data is available in Di Geronimo et al. (1994), Di Geronimo et al. (2000), respectively for the first two localities and in Di Geronimo (1984), Rosso (1987), Di Geronimo and Sanfilippo (1992) for the Catallarga outcrop.

All fossiliferous layers are characterised by: 1) coarse-grained sediments (sands or gravelly sands extremely rich in centimetre-sized bioclasts); 2) deposition on mid-shelf current-swept soft bottoms and 3) during cold phases of the Early Pleistocene, as shown by the presence of *Arctica islandica* and other Boreal Guests. It is noteworthy that skeletobiont assemblages lived during phases of moderate-to-strong hydrodynamism, leading to the development of DC and SGCF palaeocommunities, and transitions and alternations between them. Nevertheless, the skeletobionts used as substrata not only shells of species which lived in these communities but also others, some introduced from neighbouring environments and others of mud-dwelling infauna exhumed from older assemblages that lived in low hydrodynamic conditions. The three localities share most of the colonising

	BC	CAT	MEG		BC	CAT	MEG
CYANOBACTERIA	*	*	*	BRYOZOA			
ALGAE				*Disporella hispida* (Fleming)	34		3
Thallophita	*	*	*	*Patinella radiata* (Audouin)	28	3	24
Corallinacea	***	**	*	*Plagioecia sarniensis* (Norman)	203	1	1
				Tubulipora liliacea (Pallas)	9		2
FORAMINIFERA	*		**	*Tubulipora plumosa* Harmer	21	4	3
				Sum of the above Cyclostomes	459	12	57
PORIFERA				Other Cyclostomates (9 species)	14	6	9
Clionidae	*	**	*	Undetermined Cyclostomes	38	3	7
				Total Cyclostomata	**511**	**21**	**73**
CNIDARIA							
Astroides calycularis (Pallas)		*		*Aetea* sp.	1		14
Caryophyllia sp.		*		*Callopora dumerili* (Audouin)	1		14
				Calpensia nobilis (Esper)	9	16	5
MOLLUSCA				*Calyptotheca* sp.	2		34
Ostrea sp.	*			*Celleporina globulosa* (d'Orbigny)	17	1	2
Chama sp.		*		*Chorizopora brongniarti* (Audouin)	74	7	7
Anomia sp.			*	*Fenestrulina malusii* (Audouin)	2	3	9
Gastrochaenidae	*			*Hagiosynodus latus* (Busk)	2	47	8
Vermetidae	*			*Hemicyclopora multispinata* (Busk)	12		
				Hippothoa flagellum Manzoni	15		2
ANNELIDA				*Membraniporella nitida* (Johnston)	1		20
Meandropolydora sp.	*			*Microporella ciliata* (Pallas)	50	11	9
Serpuloidea				*Microporella ciliata personata* (Hincks)	59		3
Serpula vermicularis Linnaeus	192	12	5	*Neolagenipora collaris* (Norman)	61		
Serpula concharum Langerhans	54	1		*Onychocella marioni* (Jullien)		30	
Hydroides norvegicus Gunnerus	733	71	676	*Phylactella mediterranea* Rosso	13		
Hydroides stoichadon Zibrowius	2	10		*Puellina (Cribrilaria) radiata* (Moll)	17	1	1
Vermiliopsis striaticeps (Grube)		3		*Puellina (Cribilaria) venusta* (Canu & Bassler)	12	6	
Vermiliopsis labiata (O.G. Costa)	3			*Reptadeonella violacea* (Johnston)	89	43	14
Vermiliopsis sp.	77	5		*Rosseliana rosselii* (Audouin)	14	2	
Metavermilia multicristata (Philippi)	5			*Schizomavella cornuta* (Heller)	149	55	443
Semivermilia crenata (O.G. Costa)	4			*Schizomavella* sp. A	12	12	
Semivermilia cribrata (O.G. Costa)	5			*Schizomavella* cf. *rudis* (Manzoni)	1	1	32
Filogranula calyculata (O.G. Costa)	2			*Schizomavella* cf. *teresae* R.-Gil & F.-Pulpeiro	18		
Spirobranchus polytrema (Philippi)	1			*Schizoporella dunkeri* (Reuss)	283	16	8
Pomatoceros triqueter (Linnaeus)	808	27	5	*Schizoporella magnifica* (Hincks)	49	10	
Filograna sp.	53	142	102	*Schizoporella mutabilis* Calvet	10	1	8
Protula sp.	2		5	*Turbicellepora coronopus* (Wood)	3	2	6
Serpulidae spp.	326	36	40	Su of the above Cheilostomes	976	264	639
Janua pagenstecheri (Quatrefages)	2977	14	12	Other Cheilostomes (44 species)	108	34	43
Sprirobis spirorbis (Linnaeus)			32	Undetermined Cheilostomes	61	25	2
Spirorbidae spp.	2117	4	33	**Total Cheilostomata**	**1145**	**323**	**684**
Total Serpuloidea	**7361**	**325**	**906**	**Total Bryozoa**	**1656**	**344**	**757**

Tab. 1. List of skeletobionts from BC, MEG and CAT sites. The number of specimens is reported for serpuloideans and bryozoans; for the remaining taxa stars are used: * = present, ** = common, *** abundant.

skeleobiont species.

All the analysed fossils come from bulk and picking samples collected for previous palaeoecological analyses.Most are bivalves with subordinate gastropods. Rhodoliths are also present, though restricted to the Belice outcrop.

All the skeletobionts were checked to identify the composition of this special community. Skeletobionts were analysed separately for each host to look for any specific associations or relationships; their location with respect to interior or exterior surface of bivalves, and on the outer surface or within the aperture of gastropods was noted. Areal coverage was evaluated visually. Attention was focused on interactions among skeletobionts.

Skeletobiont community

Rhodoliths, usually including encrusting skeletonised organisms as secondary constituents alternating with coralline talli, commonly show small to large bryozoan sheets and serpuloidean tubes on their surfaces. In total, 59 algal rhodoliths were examined (not exceeding 8-10 cm in size), all
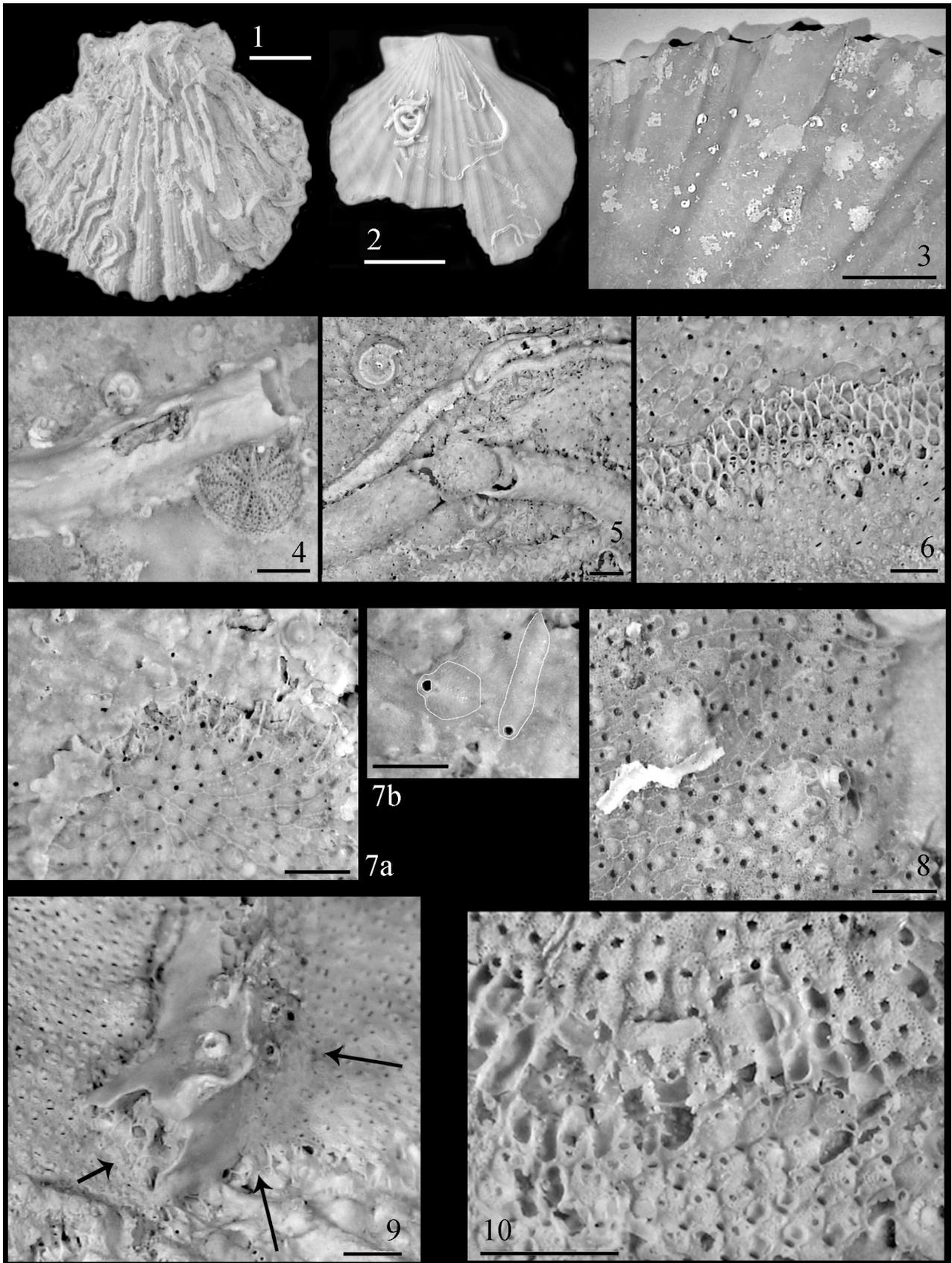
from the Belice section.

Among molluscs, only a relatively small number of species from each locality are actually colonised.

Usually, only large sized species exhibit a variable percentage of encrusted shells.

Plate 1

Fig. 1, Tubes of the serpulid *Pomatoceros triqueter* preferentially aligned between the ridges of a *Pecten* valve and mainly growing towards the posterior commissure. BC site. Scale bar: 1 cm. Fig. 2, Tubes of the serpulid *Hydroides norvegicus,* partly spirally coiled, on a *Aequipecten* valve. BC site. Scale bar: 1 cm. Fig. 3, Specimens of the spirorbid *Janua pagestecheri* selectively fouling protected areas offered by the furrows of a *Pecten jacobaeus* valve. Algal crusts, on the contrary, are randomly distributed also locating on ridges, showing no preference. BC site. Scale bar: 1 cm. Fig. 4, Spirorbids and a colony of the bryozoan *P. radiata* settled near a *Pomatoceros triqueter* tube, potential spatial refuge from overgrowth. BC site. Scale bar: 2 mm. Fig. 5, Densely colonised shell involving multi-layer encrustations belonging to, at least, two subsequent colonisation phases as testified by eroded and broken serpuloidean tubes. The discoidal *Plagioecia* colony growing inside the tube clearly settled after an erosive event. MEG site. Scale bar: 1 mm. Fig. 6, *Reptadeonella violacea* overgrowing, or more likely settling on, a colony of *Schizoporella dunkeri*. MEG site. Scale bar: 1 mm. Figs. 7, Overgrowing of a *Schizomavella* colony by an algal lamina spreading from the top side (a) and close-up of a sector (b) showing as covering is not lethal at least for some zooids, which exhibit empty, "functional" apertures. Also some *Aetea* zooids (settled on *Schizomavella* and also overgrown by the alga) show hollows corresponding to the junctions between adnate and stem parts. BC site. Scale bars: 1 mm (a), 500 μm (b). Fig. 8, A *Schizomavella* colony overgrowing two spirorbids (arrowed swellings) one of which (right side) survives raising its aperture. MEG site. Scale bar: 1 mm. Fig. 9, Mutual interaction between the bryozoan *R. violacea* and the serpulid *P. triqueter* whose tube is partly overgrown by zooids frontally budded from the underlying colony sheet (long arrows) and the serpulid aperture is invaded by peripheral zooids (short arrow). BC site. Scale bar: 1 mm. Fig. 10, *M. ciliata-S. cornuta* encounter with the latter species (upper part) overgrowing the former (lower part) despite the production of large peripheral zooids, some lacking frontal avicularia, deflecting from their previous growth direction, in *M. ciliata*. BC site. Scale bar: 1 mm.

Taking into account only the species whose shells hosted at least one skeletobiont, 359 gastropods and 999 disarticulated bivalve shells, respectively colonised by 18 and 28 species, were analysed. Taking into account only encrusting species, the percentage of colonised shells varies in the three localities from 86% (Megara) to 21% (Catallarga) with an intermediate value for the Belice section (56%). Several of these shells host one or a few skeletobionts only. Coverage is less than 5% on most shells, although some bivalves from the Belice and Megara sections show 50-60% coverage or more, being sometimes completely enveloped, mainly by algal laminae. Dense coverage is seen on some bivalves, mainly *Callista chione*, *Arctica islandica* and *Dosinia exoleta*. *Pecten jacobaeus*, *Aequipecten opercularis, Glycymeris glycymeris, Venus verrucosa, V. casina, Acanthocardia tuberculata* and *A. mucronata*, although showing a high percentage of encrusted valves, usually exhibit low coverage densities, except for single valves. The remaining 36 molluscan species (Rosso and Sanfilippo, in prep.) always show low coverage or are uncolonised.

These results agree with data on ephemeral shelly substrates presented by McKinney and Jackson (1989) and McKinney (1995a) where encrusted surface is usually less than the space actually available.

Serpuloideans

Serpuloideans are the dominant representatives within the skeletobiont communities considering the total number of encrusting tubes, among which spirorbids are particularly abundant. In total, 17 serpuloidean species make up the skeletobiont communities, with a total of 7361, 325 and 906 specimens respectively from the BC, CAT and MEG sites (Tab. 1).

Only five of the species are shared by all localities; *H. norvegicus* is the most common followed by *J. pagenstecheri* and *P. triqueter*, especially abundant in the BC site (2977 and 808 specimens respectively) where the large-sized *P. triqueter* tubes may densely cover pectinid valves and rhodoliths (Pl. 1, Fig. 1). Finally, *Filograna* sp. and *S. vermicularis* are subordinate. Among the remaining species, found in one and, more rarely, two sites, only *S. concharum* and *Vermiliopsis* sp.

are relatively common, whereas all the others are quite rare (1 to 5 specimens).

Serpuloidean communities from each locality are characterised by the high dominance of a few species (*H. norvegicus, P. triqueter, J. pagenstecheri*), which together constitute 34% (CAT), 61% (BC) and 76% (MEG) of the total assemblages, generally co-occurring on almost all of the colonised shells.

Coverage is relatively low both on internal and external surfaces, compared to the large number of skeletobionts present. Values usually do not exceed 2-5%, reaching 70% (BC site: *P. triqueter* on *A. opercularis*) and 50% (BC site: *P. triqueter* on rhodoliths) only on a few substrata. These low values are largely due to the small size of some species like the spirorbids, whose coiled tubes do not exceed 1-2 mm in diameter as well as to the growth morphology of serpulids such as *H. norvegicus* whose tubes are partially coiled upon themselves (Pl. 1, Fig. 2).

All the recognised species are known as the main representatives within present-day Mediterranean communities encrusting shells and small cobbles on soft bottoms (Zibrowius 1968; Bianchi 1979; Ben-Eliahu and Fiege 1996), at depths probably slightly deeper than those inferred for the Sicily sites, as well as in the Pleistocene Mediterranean (Di Geronimo and Sanfilippo 1992; Di Geronimo et al. 1994, 2000) and modern NE Atlantic serpuloidean assemblages, at comparable depths (Zibrowius 1968; Kupryianova and Jirkov 1997).

Studies on abundance and frequency of serpuloidean communities from shelly substrates are lacking, except for those by Lescinsky (1993) and McKinney (1996), the former mentioning *S. vermicularis* and *Spirorbis* sp. from skeletobiont communities on two *Chlamys* species in the Pacific from 20-110 m depth, the latter reporting only *Hydroides dianthus* from a sand flat 1-2 m below tide in the NW Atlantic.

Seemingly, Pleistocene records of serpuloidean skeletobionts are extremely rare, an exception being Miller and Metelman Alvis's (1986) report of *Hydroides* and *Spirorbis* encrusting inner surfaces of bivalve shells from the Middle Pleistocene of North Carolina.

Bryozoans

Bryozoans, almost entirely consisting of sheet-like colonies, with subordinate uniserial runners and a few bases of erect species, represent the second main constituent of the studied skeletobiont communities, in terms of abundance and coverage.

In total 87 species have been identified, comprising 15 cyclostomes and 72 cheilostomes. Most are rare (i.e. represented by a single or a few colonies) and infrequent (i.e. restricted to a single locality), although some (21 species, usually of high abundance) are present at all the study sites (Tab. 1). The difference between the BC community (consisting of 70 species and 1656 specimens) and the MEG and CAT communities (comprising 46 and 43 species, and 757 and 344 specimens respectively) seemingly relates to both sample size and slightly different palaeoecological conditions (Di Geronimo et al. 1994, 2000; Rosso and Sanfilippo in prep.).

Out of the recorded 2757 colonies (Tab. 1), a few of which are not identified at species level owing to bad preservation, 605 belong to cyclostomes and 2152 to cheilostomes. A high proportion of the species (53), each represented by no more than 10 specimens, accounts for less than 8% versus the 92% of the remaining 34 species. Considering only species with more than 20 specimens, a pool of 21 species (15 common to all sites) represents more than 84% of colonies present. Of these, a mere 5 species account for more than 57% of colonies. It follows that the structure of the community as a whole (and the individual communities) is marked by the strong dominance of a few species, namely the cyclostomes *A. major* and *P. sarniensis* and the cheilostomes *R. violacea, S. cornuta* and *S. dunkeri*.

Both compositionally and structurally the Pleistocene communities have a counterpart at the present day communities living on small hard substrata on soft bottoms from the north-western Mediterranean, at depths between 35 and 55m (Harmelin 1976), which is comparable to the environment inferred for the studied fossil skeletobiont communities. A good 48 species out of the 68 recorded by Harmelin (1976) are rare, being present in 1-2 stations, whereas only 11 species are abundant in almost all samples. Several among these latter, such as *C. brongniarti, R. violacea, S. cornuta* (as *S. auriculata*)*, T. plumosa, Plagioecia sarniensis,* are shared with the fossil communities from Sicily.

A somewhat comparable structure is seen in a Recent bryozoan skeletobiont community described by McKinney (2000) from lower infralittoral to upper circalittoral bottoms in the Adriatic sea where only 15 species (10 cheilostomes and 5 cyclostomes) constitute the main component, accounting for the 96% of colonies. It is also noteworthy that nearly all the species are shared by both the Recent Adriatic and the Pleistocene Sicilian skeletobiont communities, as well as the more frequent and abundant ones, i.e. *S. dunkeri, R. violacea, M. ciliata, C. brongniarti, S. magnifica, T. plumosa* and *D. hispida*. A similar community structure has been observed also for the less diverse bryozoan community encrusting living *Aequipecten opercularis* from the Isle of Man by Ward and Thorpe (1991).

The total number of species, greater in the fossil and the NW Mediterranean communities than in Adriatic Recent communities, could perhaps be explained by the slightly deeper and seemingly coarser-grained bottoms in the first two instances, and the addition to a pool of frequent species of rare species belonging to later generations and/or living in similar but not exactly equivalent environmental conditions.

Despite the large total number of colonies, coverage is relatively low, visually evaluated as not exceeding 1-2% on most shells, although reaching 50-60% in a few instances. This result matches low coverage values, usually less than 3% but rarely up to 28%, which have been reported in the Pliocene of SW Spain (Reguant and Mayoral 1994). Most colonies, in fact, are small in size and several species are present which reached sexual maturity early in development, including several cyclostomes and some cheilostomes such as *N. collaris, M. ciliata, C. dumerilii* and *P. mediterranea*. In contrast only a few species, namely *C. nobilis, R. rosselii, P. sarniensis* and especially *S. cornuta* and *R. violacea*, form large colonies reaching up to 3-4 square centimetres, with only *S. dunkeri* growing to about 8 square centimetres. Colonies of this latter species, reaching about 69 square mm, are the largest, also among the Adriatic skeletobiont bryozoans studied by McKinney (2000).

Lastly, it should be remarked that only one or a few species are normally present on each shell.

Nevertheless, up to 9 species recruited into some *A. opercularis* and *L. lutraria* valves, and a maximum of 14 species have been found on a single *G. glycymeris* valve.

	Serpulids	Spirorbids	Bryozoans	Algae	Foraminifers	Bivalves	Vermetids
Serpulids	121	2	133	33	1		
Spirorbids	30		68	485			
Bryozoans	324	70	116	37			1
Algae	445	1059	47				
Foraminifers			4				
Boring Sponges	2		1				
Bivalves		10					
Vermetids			1				

Tab. 2. Overgrowth relationships among skeletobiont taxa. Numbers indicate overgrowths of taxa in the first column on others.

Other episkeletobionts

Coralline algae, present in all the studied assemblages, are abundant, followed by calcareous and agglutinated foraminifers, mainly encrusting *Aequipecten* (Tab. 1). Molluscs are subordinate. Bivalves consist of a few encrusting *Ostrea* sp. and *Chama* sp., and also *Anomia* sp., inferred by *Centrichnus eccentricus* leaved by its attachment muscle. Among gastropods only very rare vermetids are present. Lastly, both colonial (*Astroides calycularis*) and solitary (*Caryophyllia* sp.) corals, found exclusively at the Catallarga locality, are very rare. Finally, the former presence of sclerite-bearing and/or entirely soft-bodied encrusters can be inferred in a few instances from algal talli and bryozoans that elevate their growth margins and serpulids exhibiting raised portions. These extremely rare occurrences are comparable with the fossil record elsewhere and probably partly reflect the minor coverage by soft-bodied organisms on ephemeral shell litters (Lescinsky 1997; Taylor and Wilson 2003).

Endoskeletobionts

Endoskeletobiont activity is revealed by borings (Tab. 1) mainly belonging to domichnia caused by clionid sponges (*Entobia* spp.) and gastrochaenid
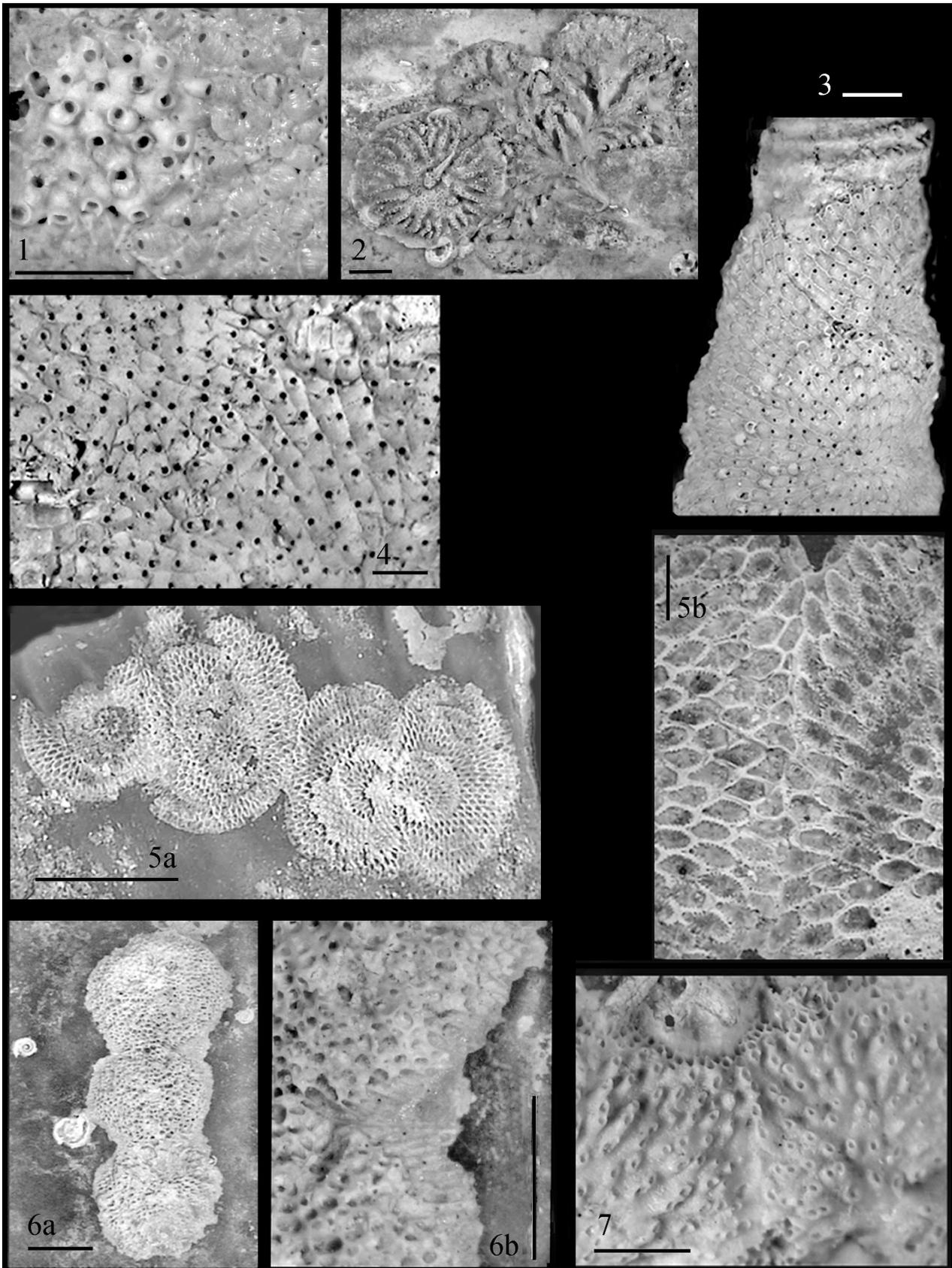
bivalves (*Gastrochaenolites*, sometimes with in-place shells). *Maeandropolydora* is subordinate whereas ctenostome borings belonging to *Spathipora comma* are extremely rare. Etching traces left by *Hippothoa flagellum* referable to the ichnogenus *Leptichnus* have also been observed. Microborings are locally abundant, mainly attributable to cyanobacterians and thallophytes.

Mobile community constituents

Predatory borings are common in all the studied assemblages, especially at Catallarga, with morphologies typical of both naticid and muricid gastropods (Sciuto 1995). Scraping traces have been observed which could be identified as *Radulichnus*, pointing to the presence of grazing gastropods and/or chitons, and *Gnathichnus* produced by echinoids (see Taylor and Wilson 2003).

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Plate 2
Fig. 1, Multiplicity of mutual interactions between colonies of *Neolagenipora collaris* and *Chorizopora brongniarti,* comprising standoff (middle) and reciprocal overgrowths along either side. BC site. Scale bar: 1 mm. Fig. 2, Colonies of the cyclostomes *Patinella radiata* and *Tubulipora liliacea* substantially stopping their growth, partly modifying normal morphology, and trying to overgrow each other by elevating their basal laminas. BC site. Scale bar: 1 mm. Fig. 3, Abutment and deflection of growth by two *Schizomavella cornuta* colonies which continue to grow side by side, although separately. MEG site. Scale bar: 1 mm. Fig. 4, Cessation of growth by two *Schizoporella dunkeri* colonies covering the entire available substratum surface between them. BC site. Scale bar: 1 mm. Figs. 5, Regulation of growth (at an early stage) and subsequent standoff of worn *Reptadeonella violacea* colonies, completely covering the available surface (a). Zooids at contact are separated by a single wall (b). BC site. Scale bars: 1 mm (a), 200 μm (b). Figs. 6, Fusion of three isodimensional colonies of *Patinella radiata*, probably originating from the same spat-fall (a) and detail of the growing edge at contact point to show the newly formed common basal lamina (b). BC site. Scale bars: 2 mm (a), 1 mm (b). Fig. 7, Fusion in *Plagioecia sarniensis*. The contact is marked by a standoff, a gentle bending of the zooids and fusion of the basal laminae without evidence of a suture. BC site. Scale bar: 1 mm.

Skeletobiont recruitment

Skeletobionts seem to be randomly localised, usually showing neither a recurrent distribution pattern across shell surfaces nor on inner/outer sides or left/right valves (Rosso and Sanfilippo in prep.). Nevertheless, recruitment preferentially occurred on rough rather than smooth surfaces and/or in sheltered parts of shells, i.e. hollows inside the hinge, bases of auricles, grooves between ridges (Pl. 1, Fig. 3), bases of spiny and tubercular projections and near other large epibionts (Pl. 1, Fig. 4), seemingly to minimise the chance of destruction. The only apparent "host specific" species are the serpulid *Filograna* sp. (CAT) and the bryozoan *H. kirchenpaueri* (MEG and CAT) which preferentially colonized pagurized gastropods, the former selectively settling within the apertural zone.

Specimens of all other species, although not showing clear preferences for any substrate, can be particularly abundant or exclusively present on a few valves of the same host. Moreover, such skeletobionts usually show similar sizes and are often located side by side on the same shell, being often equally spaced in a homogeneous distributional pattern. These clusters of individuals on a few shells lead to a patchy distribution seemingly resulting from single settlement episodes and/or related to the gregarious recruitment habit of some species (Ward and Thorpe 1989; Lescinsky 1997) and to the scattering on the bottom of shells acting as island habitats (Taylor 1984). Examples are the bryozoans *N. collaris* on *Lutraria lutraria* and *Pecten jacobaeus*, *Patinella radiata* and *P. sarniensis* on pectinids, and the spirorbid *J. pagenstecheri* on *Callista*, *Aequipecten* and *Pecten*.

Most bryozoans and serpuloideans are juveniles, thus suggesting a short exposure of the valves on the sea floor before their final burial. The presence of large-sized serpulid specimens of the pioneer species *P. triqueter,* could be related to its rapid growth rate (Relini et al. 1977). Also the bryozoans *S. dunkeri* and *R. violacea* may be fast growing species. Very large-sized and/or high ranked succession species appear to be absent.

Interactions

Interactions between organisms encrusting hard substrata mainly reflect competition to acquire and

maintain space (McKinney and Jackson 1989). From this it follows that competition is stronger and its effects more obvious on long lasting substrata than on ephemeral shell litters with a short residence time on the sea floor (Jackson 1985).

In the studied skeletobiont communities a low total coverage and a concomitant low incidence of interactions (mostly in the CAT assemblage) has been observed, as predicted. Nevertheless, several interactions do occur in the BC and MEG assemblages, usually on a few, densely encrusted, shells (Tabs. 2-4). Not all species interact (only 37 out of 87 bryozoans and 3 out of 17 serpuloideans) and interactions do not depend on the size of the skeletobionts. Small sized organisms, such as the individual spirorbids and some spot-like bryozoan colonies, are often overgrown.

Most of the observed interactions consist of overgrowths between encrusters (Tab. 2; Pl. 1, Figs. 5-10). In such instances the main interpretive problem is whether the observed superimpositions result from the growth of a skeletobiont on the skeleton of an already dead organism or if the skeletobionts were alive at the same time and consequently actually interacting (see McKinney 1995a; Taylor and Wilson 2003).

A close examination of the studied material suggests that a large proportion of the overgrowths probably resulted from settlement and growth on dead skeletons, thus actually consisting of "post mortem" superimposition of skeletobionts (see Lescinsky 1993; McKinney 1995a).

Sometimes a subsequent generation of skeletobionts can be unequivocally recognised, when abraded or bioeroded underlying skeletons are encrusted, as exemplified by a specimen of the bryozoan *P. inoedificata* growing within a broken tube of the serpulid *H. norvegicus* (Pl. 1, Fig. 5). In this instance the differential preservational state of the two skeletobionts and, above all, the position of the overgrowing encruster, indicates that the overgrowth occurred not only after death of the serpulids but after the tube was broken by a predator or after an erosive event involving the rolling and/or shifting of the shell on the bottom seemingly during an high hydrodynamic phase. Several spirorbids on algal laminae and scattered over the surfaces of some bryozoan colonies (Tab. 2) could perhaps be interpreted as possible fouling organisms produced during subsequent recruitment

events, thus pointing to an ecological succession, otherwise not easily distinguishable. Also the overgrowth of *H. norvegicus* on *P. triqueter* (Tab. 3) could be similarly interpreted, as the latter species is known among pioneer species (Relini et al. 1977). It is also worth noting that spirorbids, some spot-like bryozoan colonies and also the ancestrulae of larger sized colonies are often located along the tubes of the serpulid *P. triqueter* (Pl. 1, Fig. 4). This location could reflect active choice of protected areas and/or an adaptation for avoiding the overgrowth by other organisms, at least by the overgrown serpulids, as pointed out by Rubin (1985).

	H. norvegicus Gunnerus	*H. stoichadon* Zibrowius	*J. pagenstecheri* (Quatrefages)	*M. multicristata* (Philippi)	*P. triqueter* (Linnaeus)	*V. labiata* (O.G. Costa)	Serpulidae
Hydroides norvegicus Gunnerus	57		1		11		
Janua pagenstecheri (Quatrefages)					29		1
Pomatoceros triqueter (Linnaeus)		1	1		20	1	
Serpula vermicularis (Linnaeus)	1						

Tab. 3. Overgrowth relationships among skeletobiont serpuloidean species. Numbers indicate overgrowths of species in the first column on others.

The growth of some bryozoan colonies and serpulids onto the tubes of other serpulids (accounting for a large portion of the 121 serpulid-serpulid scored interactions and the 324 bryozoan-serpulid ones) without any apparent disadvantage to the encrusted organism (if alive) could be interpreted as colonization of a "secondary substratum" (*sensu* Dayton 1971, *fide* Lescinsky 1997). This type of overgrowth when intraspecific within the serpulids *H. norvegicus* and *P. triqueter* could be enhanced by larval gregarious behaviour (Pl. 1, Figs. 1, 2).

True biotic interactions are those involving the commissural and aperture areas of solitary organisms and modular units, and the growing edges of colonial organisms, all living contemporaneously. If skeletobionts lived together,

	Callopora dumerili (Audouin)	Calpensia nobilis (Esper)	Calyptotheca sp.	Chorizopora brongniarti (Audouin)	Copidozoum planum (Hincks)	Collarina balzaci (Audouin)	Entalophoroecia deflexa (Couch)	Escharella variolosa (Johnston)	Escharina dut. protecta Zabala et al.	Escharina vulgaris (Moll)	Fenestrulina malusii (Audouin)	Hagiosynodus latus (Busk)	Hippothoa flagellum Manzoni	Microporella appendiculata (Heller)	Microporella c. ciliata (Pallas)	Microporella c. personata (Hincks)	Neolagenipora collaris (Norman)	Patinella radiata (Audouin)	Phylactella mediterranea Rosso	Plagioecia sarniensis (Norman)	Prenantia cheilostoma (Manzoni)	Prenantia lygulata (Manzoni)	Puellina (C.) innominata (Couch)	Reptadeonella violacea (Johnston)	Rosseliana rosselii (Audouin)	Schizomavella cornuta (Heller)	Schizomavella hastata (Hincks)	Schizomavella cf. rudis (Manzoni)	Schizoporella dunkeri (Reuss)	Schizoporella magnifica (Hincks)	Schizoporella mutabilis Calvet	Tubulipora liliacea (Pallas)
Aetea sp.				1						1																2						
Annectocyma major (Johnston)																				1						1						
Callopora dumerili (Audouin)																		1														
Calpensia nobilis (Esper)								1																	1				1			
Calyptotheca sp.																									1	1						
Chorizopora brongniarti (Audouin)																4																
Escharella variolosa (Johnston)				1															2													
Fenestrulina malusii (Audouin)		1																														
Membraniporella nitida (Johnston)																										1						
Microporella appendiculata (Heller)		1																												1		
Microporella ciliata ciliata (Pallas)					1													1								(1) / *1*						
Microporella ciliata personata (Hincks)													3		1	(5)		1							1	1						
Neolagenipora collaris (Norman)				4									4	4	1								1									(1)
Patinella radiata (Audouin)																		[5]														
Phylactella mediterranea Rosso					2														(2)							1						
Plagioecia sarniensis (Norman)													1					(1)		[4]												
Prenantia cheilostoma (Manzoni)																						1										
Prenantia lygulata (Manzoni)				1				1							1																	
Puellina (Cribrilaria) radiata (Moll)	1																															
Puellina (Cribilaria) venusta (Canu & Bassler)				1	1																								1			
Reptadeonella violacea (Johnston)			1										1		1										(5)				4			
Rhynchozoon sp.																									1							
Schizomavella cornuta (Heller)	1	1							1				1													(3) / {5}			2			
Schizomavella hastata (Hincks)																												(2)				
Schizomavella cf. *rudis* (Manzoni)																													{1}			
Schizoporella dunkeri (Reuss)		2											1		1							1				3			3 / (2) / {5}	1	1	
Schizoporella magnifica (Hincks)								1																	1						1	
Tubulipora liliacea (Pallas)																										1			1			

Tab. 4. Overgrowth relationships between skeletobiont bryozoan species. Numbers indicate overgrowths of species in the first column on others. 1, simple overgrowth; {1}, intracolonial overgrowth; *1*, change of growth direction; (1), standoff; [1], fusion.

mutual overgrowth, mutual growth cessation or differential success in spatial competition can all occur (McKinney 1995a).

In the latter instance ranking of taxa in a competitive hierarchy can be undertaken. According to McKinney (1995a), when sufficient overgrowths have been scored, a statistically significant preferential overgrowth of one taxon over another can be accepted to indicate that the overgrowing species is a superior competitor.

Nevertheless, overgrowth is not necessarily lethal. This is the case for an algal lamina overgrowing the sheet-like bryozoan *Schizomavella* which exhibits at least some zooids with open "functional" apertures and on *Aetea* sp. where the erect distal parts of the zooids pass through the alga, thus escaping total overgrowths (Pl. 1, Figs. 7a, b).

The only solitary organisms involved in possible true overgrowths are serpuloideans, mainly spirorbids, which are often covered by algae and bryozoans (Tab. 2). Nevertheless, it has been

observed that when a single algal lamina or a bryozoan colony covers patches of the gregarious spirorbid *J. pagenstecheri*, a few elevate their encircled apertures to prevent occlusion (Pl. 1, Fig. 8) but the vast majority are completely covered. This could be the result of overgrowth of senescent and dead specimens rather than of presumed spirorbid low competitive ability. Spirorbids partly covered, although not killed, by bryozoans are known from present day environments (Stebbing 1973) and are also recorded back to the Cambrian (Lescinsky 1997), although the taxonomic attribution of Palaeozoic "spirorbids" is controversial (Weedon, 1994). As already suggested by Lescinsky (1997), the predicted competitive hierarchy with colonial organisms winning and small solitary organisms losing (Jackson 1977, 1983) could be better interpreted in terms of ecological succession.

Only a single recognised mutual interaction has been documented, involving a serpulid competing with the bryozoan *R. violacea* (Pl. 1, Fig. 9). In this instance the *P. triqueter* tube growing on a large *Reptadeonella* colony is, in turn, partly overgrown by zooids frontally budded from the sheet-like bryozoan while some peripheral zooids invade the tube aperture, obviously after the soft body and operculum were lost.

Regarding modular bryozoans, relationships appear to be more easily detectable and it has been often possible to ascertain when interactions were mutual. Nevertheless, data is often insufficient not only for statistical treatment but also to put forward any hypothesis of competitive hierarchy (Tab. 4). At high taxonomic rank, cheilostomes generally overgrow cyclostomes, a common feature in competitive interactions (McKinney 1995b). For interspecific overgrowths no clear hierarchy can be detected between pairs of species; nevertheless, some species appear to be better competitors than others. Taking into account McKinney's (1995a) results, in the rare instances of several interactions involving the same species, some observations are of interest. Colonies of the runner *H. flagellum*, formed by slender uniserial chains of zooids, systematically lose their encounters (as predicted by Jackson 1979), always being overgrown by *S. dunkeri* (1 instance), *M. ciliata personata* (3 times) and *N. collaris* (4 times), even though the latter always forms, in the present material, small to medium sized colonies. *M. ciliata personata* appears

to be highly competitive, winning in 7 encounters with 5 different species and being overgrown only once. A similar pattern is shown by *S. dunkeri* which wins 13 and loses 9 encounters. *S. cornuta, C. brongniati* and *M. ciliata* show an opposite trend, respectively losing 11, 7 and 5 encounters and winning 6, 4 and 2 times (Tab. 4).

Observations from the present material suggest that at least in some pairs of species, both exhibit an equivalent competitive ability. A *N. collaris-C. brongniarti* encounter (Pl. 2, Fig. 1) involves a multiplicity of mutual interactions with a stand off in the middle part, where zooids meet at a high angle, and overgrowth along the sides, each species being a winner and a loser. In this pair of species, each overgrows the other 4 times. Taking into account previous observations, their relationship may not be related to post mortem colonization of a secondary substratum but interpreted as due to similar competitive ability. Also two colonies of the cyclostomes *Patinella radiata* and *T. liliacea* partly overgrow each other slightly elevating their basal laminas (Pl. 2, Fig. 2). Reciprocal overgrowths have been already recorded from the Pliocene (Taylor and Wilson 2003) and the Recent (Lescinsky 1993). A peculiar overgrowth is exhibited by a few species belonging to *Schizomavella* and *Schizoporella*, particularly by those forming large colonies, as *S. cornuta* and *S. duncheri*. Large portions of their colonies are covered by zooids originating as frontal buds, a strategy consolidating their hold on the substratum and also perhaps elevating them within the water column for better access to food resources (Jackson 1979; McKinney and Jackson 1989).

Evidence that colonies were alive at the same time is clear for a *M. ciliata-S. cornuta* encounter (Pl. 1, Fig. 10). Near the contact point, *S. cornuta* develops its basal lamina, the zooidal rows continuing to grow with unchanged directions, whereas *Microporella* buds larger peripheral zooids which form a slight angle to the earlier zooids apparently in order to encounter the *S. cornuta* colony frontally. Moreover, these zooids are larger than their parents and some of them lack the single constant frontal avicularium, which can be interpreted as an energetic saving for faster growth to avoid overgrowth, although unsuccessfully. This result is predictable (Lidgard and Jackson 1989) taking into account the zooidal budding modes of the two species, zooidal for *S. cornuta* and intrazooidal and less competitive, for *M. ciliata*.

Nevertheless in a further instance the two species avoid contact stopping their growth and reorienting their growing margins. Similar defensive strategies, and above all raising of the basal laminas, have been recorded for other species (Harmelin 1976; McKinney and Jackson 1989; Taylor and Wilson 2003, for a review).

True life interactions are documented also for some colonies belonging to the same species (e.g. *A. major*) which seem to space themselves out across the substratum in order to avoid encounters, thus minimising intraspecific competition. A similar behaviour has been observed for solitary organisms having almost determinate growth (Stebbing 1973), such as *Spirorbis* (Knight-Jones and Moyse 1961), which space themselves on settlement. Moreover some conspecific clusters of colonies belonging to *S. cornuta* and *R. violacea* exhibit a peculiar ability for regulating their growth, at least in young stages (Pl. 2, Fig. 3 and Pl. 2, Fig. 5a, respectively), mainly in directions opposite to the ancestrulae of nearest neighbouring colonies, a strategy seemingly adopted to maximise available surface before any possible encounter. A somewhat similar strategy has been reported for Triassic encrusting bivalves which radially oriented their growth in a four-leaved clover patterns, on densely colonised surfaces (Duringer 1985; Taylor and Wilson 2003). Nevertheless, reorientation of growth usually only delays encounters. When colonies meet cessation of growth happens at some distance or at the contact (sometimes marked by a raised edge) following several main patterns in the present material:

a) Simple cessation of growth or stand off of the colonies covering the entire available surface between them, distorting normal development and budding some irregularly shaped zooids, as is the case for *M. ciliata-M. ciliata, M. ciliata personata-M. ciliata personata* and *S. dunkeri-S. dunkeri* encounters (Pl. 2, Fig. 4). A comparable standoff is known for Pliocene specimens of *Biflustra commensale* (Kidwell and Gyllenhaal 1998).

b) Abutment of growth at the point of contact and a slight to marked deflection of growth directions laterally, with colonies continuing to grow separately but side by side. This has been observed for *S. cornuta, S. hastata* and *S. dunkeri* (Pl. 2, Fig. 3). Also colonies of *R. violacea* seemingly show this pattern (Pl. 2, Figs. 5a, b). Kenozooids are often formed along the contact line marked by a double wall, each formed by the peripheral zooids of the two interacting colonies. Nevertheless, clear con-nections through adjacent zooids have jet to be observed. Thus, although colonies seemingly recognise each other, they do not fuse their tissues - "homosyndrome"- as shown in more primitive taxa such as *Membranipora* species by Stebbing (1973).

c) Fusions have been observed for two species, namely the cyclostomes *Patinella radiata* (Pl. 2, Figs. 6a, b) and *Plagioecia sarniensis* (Pl. 2, Fig. 7). In both instances interacting colonies have similar sizes and the contact between colonies is marked by a standoff at the contact point and a bending of zooids lateral to this point, such that they continue to grow side by side. At the growing margin the basal lamina, although inflected, shows no evidence of suture and the new zooids bud from a common lamina. Such fusions appear to be rare and only Harmelin (1976) has recorded them for living colonies of *Diplosolen obelium* and, in a single instance, *Microecia suborbicularis,* from the Mediterranean. The same author reported in *P. sarniensis* intraspecific encounters where old colonies overgrow juveniles whereas growth abuts when colonies of the same age meet.

All these interactions imply that the contestants lived contemporaneously and that each colony recognised the other one as conspecific. It follows that colonies which interact in such a manner usually have similar sizes as they seemingly belong to a single recruitment event during which several colonies originated from the same parental colony, thus possessing a similar genotype, or the same genotype in polyembryonic cyclostomes, as remarked by Harmelin (1976).

Conclusions

- Skeletobionts from three Pleistocene Sicily localities have been studied on disarticulated bivalves, rhodoliths and gastropods. On such ephemeral substrates skeletobiont assemblages, showing high taphonomic and ecological fidelity, are composed of early successional taxa, mainly coralline algae, serpuloideans and bryozoans, which are mostly skeleton-bearing and thus fossilisable.

- Despite the loss of soft-bodied taxa, compositional and structural patterns of the skeletobiont assemblage, as well as spatial distributions of organisms, are likely to be almost

entirely preserved.

- Coverage is relatively low, both on internal and external surfaces, usually less than 5%, rarely reaching the 50-60% or more, and only a few shells are completely enveloped.

- Skeletobionts are randomly distributed on shells, colonising indifferently the inner/outer sides and the left/right valves. Neither host specificity, nor a clear preference for any substrate has been observed, except for *H. kirchenpaueri* and *Filogranula* sp. preferring pagurised shells.

- The structure of the skeletobiont communities is characterised by strong dominance of a few species (5 bryozoans and 3 serpuloideans). Small sized species reaching sexual maturity early, such as spirorbids and spot-like bryozoans together with juveniles, prevail, testifying to the short exposure time of shells on the sea floor before burial. The presence of a few large sized serpulids and bryozoan colonies could be related to their rapid growth rate, some being pioneer species.

- Relatively few interactions have been observed. Recorded overgrowths largely result from superimposition of individual skeletobionts growing on the skeletons of older dead encrusters forming "secondary substrata" pointing to ecological succession. Although usually not easily recognisable, such successions become more obvious when separated by erosional phases.

- True competitive interactions have been proven for only a few serpuloideans, mainly spirorbids, and several bryozoan colonies. Overgrowth seems not to have been lethal for serpulids but was so for spirorbids, except for some, that elevated their apertures. Also in overgrown modular bryozoans, some zooids seemingly survived, their orifices remaining uncovered.

- Among bryozoans, overgrowth is common in interspecific encounters although no clear ranking of species competitive ability can be traced owing to the infrequency of interactions, except for the runner-like species *H. flagellum* which always loses. In intraspecific encounters standoffs prevail, either involving a simple cessation of growth at some distance or at the contact point, or deflection of newly formed zooids which continue growth side by side, as observed especially for some cheilostomes species. Finally, intraspecific encounters among some cyclostomes (*Patinella radiata* and *Plagioecia sarniensis)* involve fusion of colonies. Such behavioural patterns mean that colonies recognise themselves as conspecific or even as siblings, possessing the same or similar genotype.

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Riassunto

[Briozoi e serpuloidei in associazioni di scheleto-bionti del Pleistocene della Sicilia: sfruttamento dello spazio e interazioni competitive]

Le conchiglie degli organismi epibionti e quelle dissepolte degli endobionti rappresentano, sui fondi mobili, piccoli substrati duri disponibili per la colonizzazione da parte di numerosi organismi incrostanti. Oltre al ricoprimento dell'ospite in vita (epibiosi), la colonizzazione degli scheletri continua dopo la morte (scheletobiosi) in funzione della permanenza sul fondale. Le comunità di scheletobionti, effimere e non sensibilmente "*time averaged*", sono ottimali per lo studio delle relazioni spaziali degli incrostanti a scheletro mineralizzato fra loro e col substrato.

Vengono analizzate comunità a scheletobionti riscontrate in giacimenti fossiliferi del Pleistocene inferiore della Sicilia, con particolare riferimento a briozoi e serpuloidei, esaminandone la distribuzione sugli scheletri e le interazioni reciproche. Le comunità studiate sono caratterizzate dalla elevata dominanza di poche specie (5 briozoi e 3 serpuloidei). I ricoprimenti sono solitamente inferiori al 5%, nonostante alcuni substrati siano molto colonizzati (fino al 50-60% e oltre). La distribuzione degli scheletobionti sembra casuale, senza alcun pattern fra superfici interne ed esterne e, per i bivalvi, fra valve destre e sinistre, sebbene si noti una preferenza delle larve per settori protetti. Mancano specificità per l'ospite, ad eccezione del serpulide *Filograna* sp. e del briozoo *H. latus,* presenti solo su gasteropodi. Tutto ciò suggerisce una colonizzazione prevalentemente *post mortem*, con incrostazioni ereditate solo in minima parte. L'elevato numero di esemplari giovanili, gli spirorbidi e le numerose colonie di briozoi di piccola taglia, suggeriscono tempi di esposizione relativamente brevi al fondo, prima del definitivo seppellimento. Poche specie di taglia elevata, come il serpulide *P. triqueter,* hanno un rapido tasso di crescita.

Sono state osservate numerose crescite orientate sia dei tubi di serpulidi che delle colonie di briozoi. Inoltre, sono molto frequenti i ricoprimenti, dati dalla semplice sovrapposizione di esemplari su scheletri di organismi presumibilmente già morti. Effettive interazioni competitive sono state documentate per alcuni briozoi e pochi serpuloidei fra cui soprattutto gli spirorbidi, solitamente ricoperti da talli algali o da briozoi con esito spesso letale. Esempi di sopravvivenza sono tuttavia testimoniati dal sollevamento delle aperture sopra l'organismo ricoprente. Tra i briozoi, incontri interspecifici consistono in frequenti ricoprimenti di uno dei due contraenti o in arresti della crescita o ricoprimento reciproco su settori diversi lungo il contatto. Negli incontri intraspecifici, invece, si verifica solitamente un arresto della crescita ("*standoff*") o una crescita delle colonie fianco a fianco, come osservato per numerosi cheilostomi. Per alcuni ciclostomi, infine, incontri intraspecifici fra colonie della stessa taglia possono portare a fusione. Nel presente lavoro viene discusso il significato di queste diverse interazioni.