

***Turbicellepora incrassata* and *Corallium rubrum*: unexpected relationships in a coralligenous habitat from NW Sardinia, Mediterranean Sea**

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ABSTRACT

The examination of a coarse bioclastic sample collected at about 80 m depth off NW Sardinia, at the base of an underwater cliff colonised by a coralligenous community allowed the opportunity to record for the first time, mutual interactions between the large erect cheilostome *Turbicellepora incrassata* (Lamarck, 1816) [= *T. avicularis* (Hincks, 1860)] and the octocoral *Corallium rubrum* (Linnaeus, 1758). An assemblage of bryozoans coexisting with these species consisted of celledorids and multilaminar encrusters belonging to 40 species. The celledorid *T. incrassata* dominated in volume in this assemblage, forming branched colonies about 15 cm high. In the examined sample, *T. incrassata* is intimately associated with *C. rubrum*: most collected bryozoan branches develop on the coral axial skeleton, but the red coral itself can also overgrow *T. incrassata*. Bryozoan colonisation happens on exposed portions of the coral skeleton sometimes when the coral was still attached to the rock. In most instances, however, the occurrence of soft tissue (coenenchyme) and sclerites of red coral below or alternating with layers of *Turbicellepora* zooids indicates that the two species can overgrow each other. Other bryozoan species also interact with red coral, colonizing

exposed parts of the coral skeleton, and, being sometimes overgrown by *C. rubrum*.

INTRODUCTION

Known as precious coral, the red coral *Corallium rubrum* (Linnaeus, 1758) is an Alcyonacean octocoral endemic to the Mediterranean Sea and Atlantic areas nearby the Gibraltar Strait. It thrives in poorly-lit or dark habitats from shallow depths in submarine caves (Laborel and Vacelet 1961) to deeper sites along rocky cliffs and overhangs in the coralligenous habitat where it plays a significant role as an engineer species (e.g. Cattaneo-Vietti and Cicogna 1993). The deepest records are from about 1000 m in the Sicily Straits (Taviani *et al.* 2010; Knittweis *et al.* 2016), where it coexists with cold-water corals [*Desmophyllum dianthus* (Esper, 1794), *Madrepora oculata* Linnaeus, 1758]. *C. rubrum* is a long-lived, slow-growing species (Garrabou and Harmelin, 2002). Following active harvesting during centuries and overexploitation (Cattaneo-Vietti *et al.* 2016, and references therein), this species is presently partly protected in Sardinia and its exploitation regulated (e.g. Cau *et al.* 2016). *C. rubrum* has white polyps with eight tentacles immersed in a coenenchyme



covering a red mineralised carbonate skeleton, which is repeatedly branched and arborescent, sculptured with longitudinal ridges, furrows and small protuberances. Small sclerites dispersed in the coenenchyme add rigidity to the latter.

Turbicellepora incrassata (Lamarck, 1816), a heavily mineralised Atlanto-Mediterranean celledorid bryozoan, is typically associated with gorgonians in the coralligenous habitat (Fig. 1) (Gautier 1959, 1962; Hayward and McKinney 2002; Chimenz Gusso *et al.* 2014). Colonies are pale orange to greenish (when colonized by micro-algae), celledoriform when young, forming mounds or nodules with small, and stout, irregularly ramified branches ('vinculariiform'), up to 20 cm in size when fully developed. Branches are cylindrical with conical ends and their surface is somewhat irregular owing to frontal budding of convex zooids.

Co-occurrence and interactions between *T. incrassata* and *C. rubrum* had never been reported. Even relationships between the red coral and bryozoans in general have so far been scarcely considered in published works, except for single minor mentions (e.g. Harmelin 1984; Giannini *et al.* 2003; Casas-Güell *et al.* 2016). However, more data may exist in the grey-literature, such as the fouling of dead *C. rubrum* colonies by 19 bryozoan species at

Monaco (rocky wall, 23-30 m depth, Harmelin 2003, unpublished report). This colonization likely occurred after mass mortality of red coral in shallow-water sites affected by abnormal warming during late summer 1999 (Garrabou *et al.* 2001).

The association between large-sized bryozoans and gorgonians is more commonly observed and reported. Bare portions of the gorgonian colonies offer a 'filiform' substratum around which colonizers can attain a 3D development. Epibiosis on erect slender substrata is an effective strategy to elevate from the bottom boundary layer, largely exploited nowadays as in the geological past (e.g. Di Martino and Taylor, 2014). In the Mediterranean, available data, refer especially to monitoring of gorgonacean populations (also including *C. rubrum*) after mortality events following long-lasting sea temperature raise, and consequently remark as bryozoans settle on exposed skeletons after decay of living tissues (Harmelin 1984; Harmelin and Marinopoulos 1994; Garrabou *et al.* 2001; Linares *et al.* 2005; Gili *et al.* 2014). Competition between bryozoans and small scleractinian corals is a natural phenomenon common in the same habitat as *C. rubrum*. Encrusting bryozoans colonise the thecal portion bounding the calice of corallites during periods of coral growth stasis, and can afterwards be covered by coral

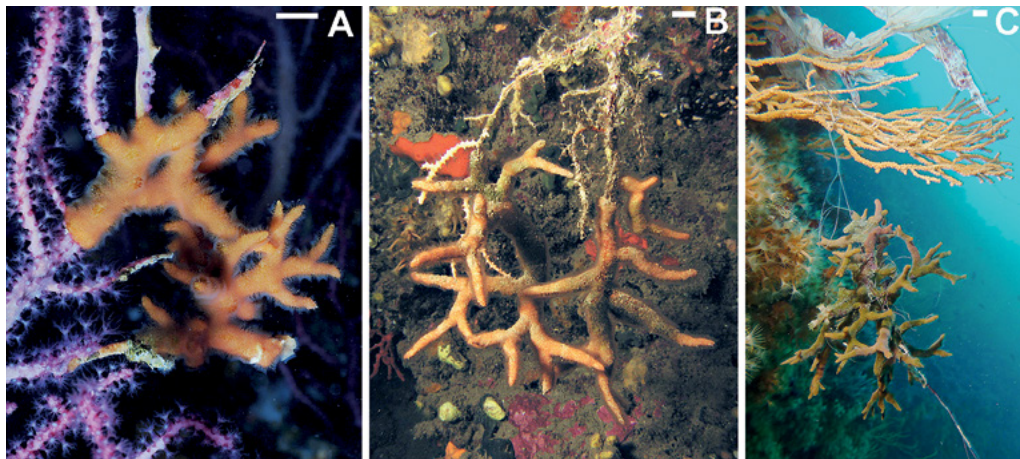


Figure 1. Underwater images of *Turbicellepora incrassata*. (A) Associated with the gorgonian *Paramuricea*. (B) A partly fouled colony on *Eunicella*. (C) Large colony on a fishing line. Largest colony branches about 1 cm in diameter in all images.

tissues and skeleton layers after polyp recovery (Harmelin 1990).

The present paper aims at describing and discussing: 1. Bryozoan assemblages associated with *C. rubrum*; 2. Relationships between *C. rubrum* and *T. incrassata*; 3. Occasional relationships between *C. rubrum* and further bryozoan species with small encrusting colonies; 4. The role of *T. incrassata* in the assemblage and 5. The taxonomic status of *T. incrassata*, a species often reported as *T. avicularis*, supporting the maintenance of the senior synonym.

MATERIAL AND METHODS

Examined material originates from a single sample of coarse bioclastic fragments (about 1.2 litres in volume), collected off Alghero, NW Sardinia (approximately 40°25'N and 8°11'E). Sampling was performed in September 2002 with the collecting devices of the ROV PLUTO 1000, at the base of a low steep underwater cliff, at 80 metres depth. Deep-water red coral populations are known in the area and ROV surveys carried out in 2007 reported colonies growing in patches on 1-5 m high boulders surrounded by detritic bottoms (Cannas *et al.* 2010; Follesa *et al.* 2013). Large-sized coral colonies having a basal diameter exceeding 1 cm and reaching 15-20 cm in height were abundant, representing more than 30% (Follesa *et al.* 2013). These authors also reported some associated taxa, including scleractinian corals, molluscs, brachiopods and a few bryozoan species, namely *Myriapora truncata* (Pallas, 1766), *Cellepora pumicosa* (Pallas, 1766), *Reteporella grimaldii* (Jullien, 1903) [as *R. septentrionalis* (Harmer, 1903)], and *Patinella radiata* (Audouin, 1826) [as *Lichenopora radiata* (Audouin and Savigny, 1816)].

The sample was washed and examined preliminarily for bryozoan species in the Palaeoecological Laboratory of the Dipartimento di Scienze Biologiche, Geologiche e Ambientali (DSBGA) of the University of Catania. In view of the abundance of red coral fragments, material was afterwards examined in order to identify the relationships between bryozoans and

the red coral. Low magnification photographs were taken with a Zeiss Discovery V8A stereomicroscope equipped with an Axiovision acquisition system. High magnification images were obtained using back-scattered electrons on selected specimens examined uncoated under a low vacuum Scanning Electron Microscope at the Microscopical Laboratory of the DSBGA. Material is housed in the Paleontological Museum of the University of Catania (PMC), under the collection code PMC.I.H.2002. Sardinia red coral Rosso Collection.

RESULTS

Collected material largely consisted of biogenic fragments (about 75%) and subordinate pieces of biogenic concretions and heavily bioeroded limestone substratum. Most fragments are large-sized (usually larger than 1 cm) and sharp-edged. A large percentage (about 40%) of biogenic pieces consisted of living bryozoan fragments showing chitinous mandibles/opercula and soft tissue inside zooids. Colony branches of *Turbicellepora incrassata*, up to 7-8 cm long and 2 cm in maximum diameter, dominated. A large proportion of these branches presented a core occupied by broken skeleton of the red coral *Corallium rubrum*. Red coral fragments were also encrusted by membraniporiform multi-layered and celleporiform bryozoans. Other taxa included solitary scleractinians (mostly *Leptosammia pruvoti* Lacaze-Duthiers, 1897), serpulids [mostly *Serpula vermicularis* Linnaeus, 1767 and *Spirobranchus lima* (Grube, 1862), and subordinate *Spirobranchus triqueter* (Linnaeus, 1758), *Hydroides* spp., *Serpula lobiancoi* Rioja, 1917], spirorbids, large-sized vermetid gastropods, sparse specimens of the brachiopod *Novocrania anomala* (O.F. Müller, 1776), boring and byssate bivalves, and the encrusting foraminifer *Miniacina miniacea* (Pallas, 1766).

Associated bryozoans

In total, 40 bryozoan species were recognised (Tab. 1) in the sample (35 cheilostomatids and 5 cyclostomatids). Among them, 30 species



Table 1. Systematic list of bryozoan species associated with *Turbicellepora incrassata* and *Corallium rubrum* from NW Sardinia. *: < 10 specimens; **: 11-30 specimens; *: > 30 specimens.**

	total number of species	Living fragments/ colonies	Dead fragments/ colonies
Bryozoa	40		
Cyclostomatida	5		
<i>Diplosolen obelius</i> (Johnston, 1838)			*
<i>Plagioecia patina</i> Lamarck, 1816			*
? <i>Annectocyma major</i> (Johnston, 1847)			*
? <i>Filifascigera</i> sp.		? *	*
Lichenoporidae sp.		? *	**
Cheilostomatida	35		
<i>Aetea</i> sp.			*
<i>Callopora dumerilii pouilleti</i> (Alder, 1857)		*	*
<i>Corbulella maderensis</i> (Waters, 1898)		**	*
<i>Crassimarginatella crassimarginata</i> (Hincks, 1880)		*	*
<i>Ellisina gautieri</i> Fernández Pulpeiro & Reverter Gil, 1993		*	
<i>Gregarinidra gregaria</i> (Heller, 1867)		*	*
<i>Beania magellanica</i> (Busk, 1852)		*	
Candidae sp. und.		*	
<i>Onychocella marioni</i> (Jullien, 1881)		*	*
<i>Cribrilaria radiata</i> (Moll, 1803)		**	*
<i>Cribrilaria venusta</i> Canu & Bassler, 1925			*
<i>Cribrilaria</i> sp.		*	*
<i>Chorizopora brongniartii</i> (Audouin, 1826)		*	
<i>Trypostega</i> cf. <i>venusta</i> (Norman, 1864)		*	*
<i>Escharoides mamillata</i> (Wood, 1844)			*
<i>Prenantia cheilostoma</i> (Manzoni, 1869)			*
<i>Prenantia ligulata</i> (Manzoni, 1870)		*	*
<i>Smittoidea reticulata</i> (MacGillivray, 1842)		*	*
<i>Schizomavella</i> (<i>Calvetomavella</i>) <i>discoidea</i> (Busk, 1859)			*
<i>Schizomavella</i> (<i>Schizomavella</i>) <i>asymetrica</i> (Calvet, 1927)		*	*
<i>Schizomavella</i> (<i>Schizomavella</i>) <i>cornuta</i> (Heller, 1867)		**	*
<i>Schizomavella</i> (<i>Schizomavella</i>) <i>linearis</i> (Hassall, 1841)		**	*
<i>Schizomavella</i> (<i>Schizomavella</i>) <i>mamillata</i> (Hincks, 1880)		*	
<i>Escharina dutertrei protecta</i> Zabala, Maluquer & Harmelin, 1993		*	
<i>Escharina vulgaris</i> (Moll, 1803)		*	*
<i>Herentia hyndmanni</i> (Johnston, 1847)		*	
<i>Fenestrulina</i> sp.		*	*
<i>Microporella appendiculata</i> (Heller, 1867)		**	*
<i>Celleporina caminata</i> (Waters, 1879)		**	**
<i>Turbicellepora avicularis</i> (Hincks, 1860)		***	**
<i>Turbicellepora coronopusoida</i> (Calvet, 1931)			*
<i>Reteporella</i> sp.			*
<i>Rhynchozoon</i> spp.		*	*
<i>Schizotheca fissa</i> (Busk, 1856)		*	*
<i>Stephanollona armata</i> (Hincks, 1861)		**	*

were present with living colonies/fragments, and the majority of them (23) also included dead representatives. By contrast, ten species exclusively occurred with dead specimens. *Turbicellepora incrassata* was the most abundant species, represented by large fragments (see below), accounting for more than 80% of the estimated volume. *Celleporina caminata* (Waters, 1879) was also common with numerous hemispherical, dome-shaped to stout and poorly branched colonies, up to 2 cm high, (often) detached from their substratum or colonising *C. rubrum* branches and limestone debris. Colonies of *Schizomavella* spp. were relatively abundant, largely represented by *S. cornuta* (Heller, 1867) and *S. linearis* (Hassall, 1841), and subordinately by *S. asymetrica* (Calvet, 1927) and *S. mamillata* (Hincks, 1880). All these species exhibited multi-laminar encrusting colonies, up to a dozen square centimetres in size. Among other, less abundant, components of the bryozoan assemblage were *Corbulella maderensis* (Waters, 1898), *Microporella appendiculata* (Heller, 1867), and *Cribrilaria radiata* (Moll, 1803), followed by *Crassimarginatella crassimarginata* (Hincks, 1880), *Onychocella marioni* (Jullien, 1882), *Smittoidea reticulata* MacGillivray, 1842, *Escharina vulgaris* (Moll, 1803) and *Stephanollona armata* (Hincks, 1862). Lichenoporidae were the only common cyclostomes.

Relationships between *Corallium rubrum* and *Turbicellepora incrassata* and other bryozoans

The collected fragments of *Turbicellepora incrassata* were parts of slender-to-stout branched colonies. Some of these fragments (up to one cm in diameter) were distal tapering branches without internal substratum, increasing in diameter through frontal budding. However, the majority of branch fragments revealed a core consisting of broken skeleton of *Corallium rubrum*, with typical longitudinal ridges (Figs 2, 3E, 4A, C, E) their red colour contrasting with the whitish bryozoan skeleton. Furthermore, several broken branches showed a central tubular cavity

roughly reproducing the morphology of *C. rubrum* axial skeleton (Fig. 2A, arrowed). In most cases, the red coral fragments were partially to heavily bioeroded and/or coated with a thin whitish-brownish layer of carbonate precipitation. However, some coral tips presented still preserved soft tissues or showed evidences of coenenchyme remains with sclerites (Figs 2B-C, G-H, 3, 4). These latter are typically 60-90 µm long, with 6-9 symmetrically arranged *c.* 20 µm long protuberances, each consisting of clumps of cone-like crystal (cf. Grillo *et al.* 1993) (Fig. 4D). In a few fragments, soft tissues are missing, but slit-like spaces occur separating the red coral skeleton from the basal wall of *T. incrassata* colonies (Fig. 2B-C). Some fragments showed *C. rubrum* basal expansions, which encrust the colony surface of *T. incrassata*, sometimes covering living zooids (Figs 2G-I, 3A-C). Finally, some fragments showed the subsequent superimposition of thin red coral layers and bryozoan colonies (Figs 2G-J, 3A-C). In a few instances, laminar expansions of *C. rubrum* outgrow other bryozoan species but leaving uncovered openings (Figs 4E-G).

DISCUSSION

Turbicellepora incrassata* vs *Turbicellepora avicularis

The most abundant bryozoan found in the examined assemblage is common in NW Mediterranean and is one of the rare bryozoans named by sport-divers ('Turbicellépore cornu', André *et al.* 2014). In the scientific literature, this species is usually reported as *Turbicellepora avicularis* (Hincks, 1860) although it is a junior synonym of *Cellepora incrassata* Lamarck (1816), as already noted by d'Hondt (1994). This synonymy has been currently questioned/unaccepted (see Rosso *et al.* 2010) in conformity with the Article 23.9 of the International Code of Zoological Nomenclature (Zoological Code; ICZN 1999) concerning the 'Reversion of Precedence'. It has been confirmed, however, by the recent digitalization of the Lamarck's types (1816) at the Muséum national d'Histoire Naturelle de Paris

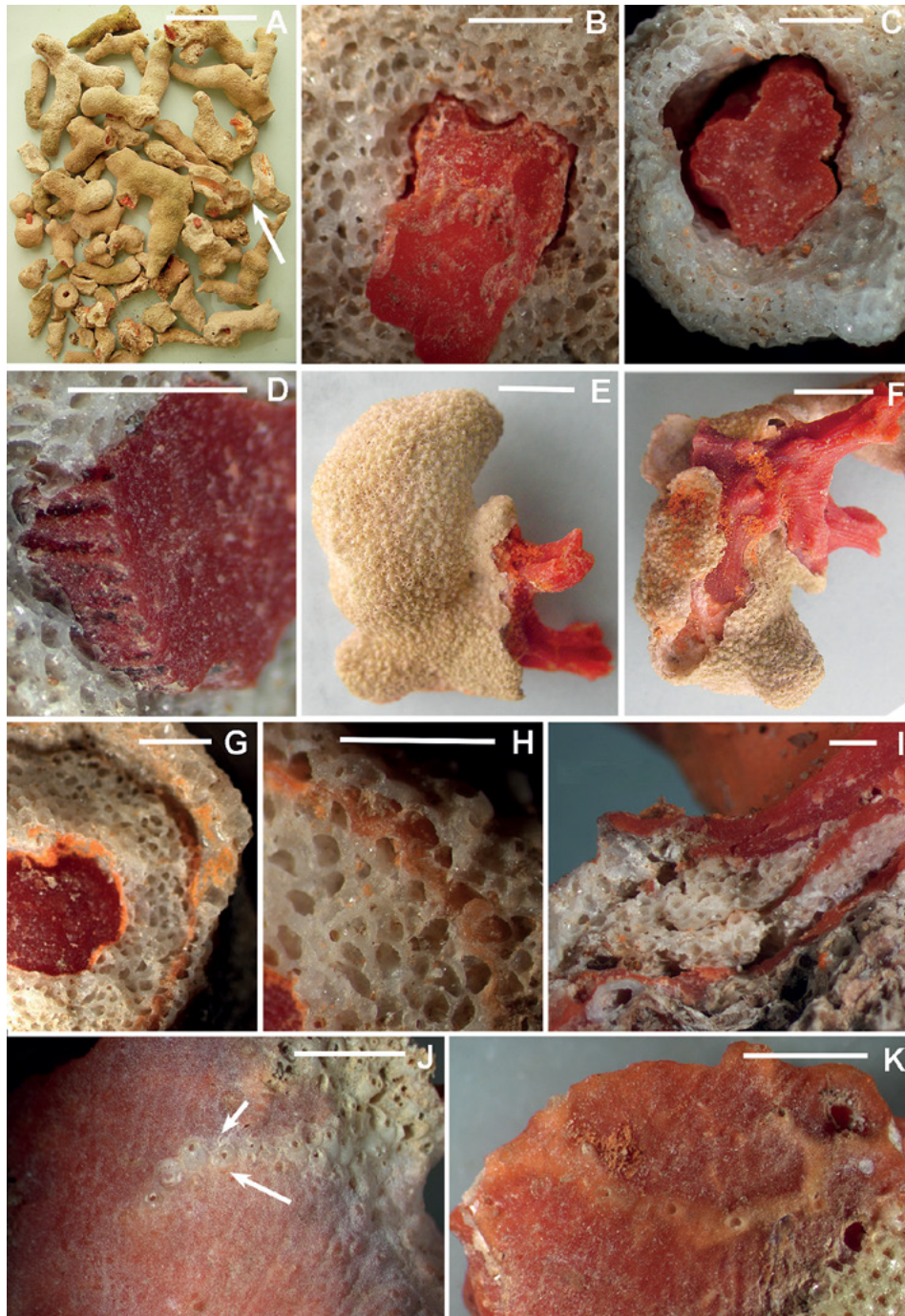


Figure 2. (A) Large colony branches of *Turbicellepora incrassata* growing on *Corallium rubrum* skeleton (red coloured). (B–C) Branch cross-sections: fissures between the coral skeleton and the bryozoan colony point to the first occurrence of coral tissues and/or soft-bodied organisms. (D) *T. incrassata* adhering to coral skeleton pointing to colonisation of exposed skeleton. (E–F) Views of *T. incrassata* encrusting a coral fragment with growing tips in the opposite direction. (G–I) Repeated superimpositions of *T. incrassata* and *C. rubrum*. (J) Intergrowth of *C. rubrum* and *Turbicellepora coronopusoida* (Calvet, 1931). Zooids left uncovered can ensure survivorship of the colony. (K) *C. rubrum* covering a tubuliporine cyclostome, leaving the tube orifices free. Scale bars: A: 5 cm; B–D, G–I: 1 mm; E–F: 5 mm; J–K: 2 mm.

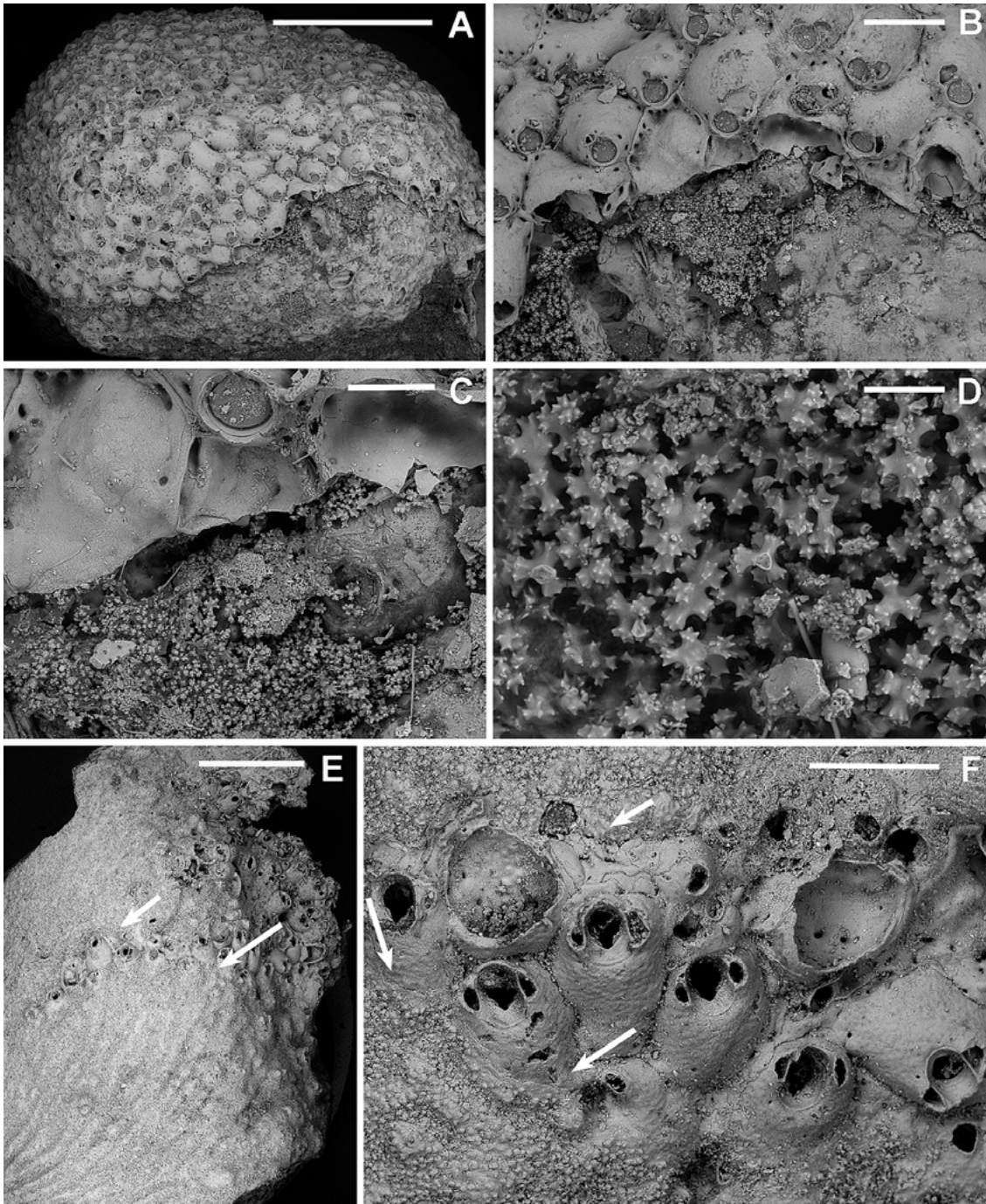


Figure 3. (A-C) General view (A) and enlargements (B and C) of the superimposition of *T. incrassata* on *C. rubrum*. The presence of coenenchyme is indicated by soft tissue still enveloping sclerites diagnostic of the species. (D) Close-up of *C. rubrum* sclerites. (E-F) SEM view and details of Figure 2J showing zooids of *T. coronopusoida* overgrowing (short arrows) and overgrown (long arrows) by the coral. Scale bars: A-B, F: 500 μ m; C 200 μ m; D: 50 μ m; E: 2 μ m.

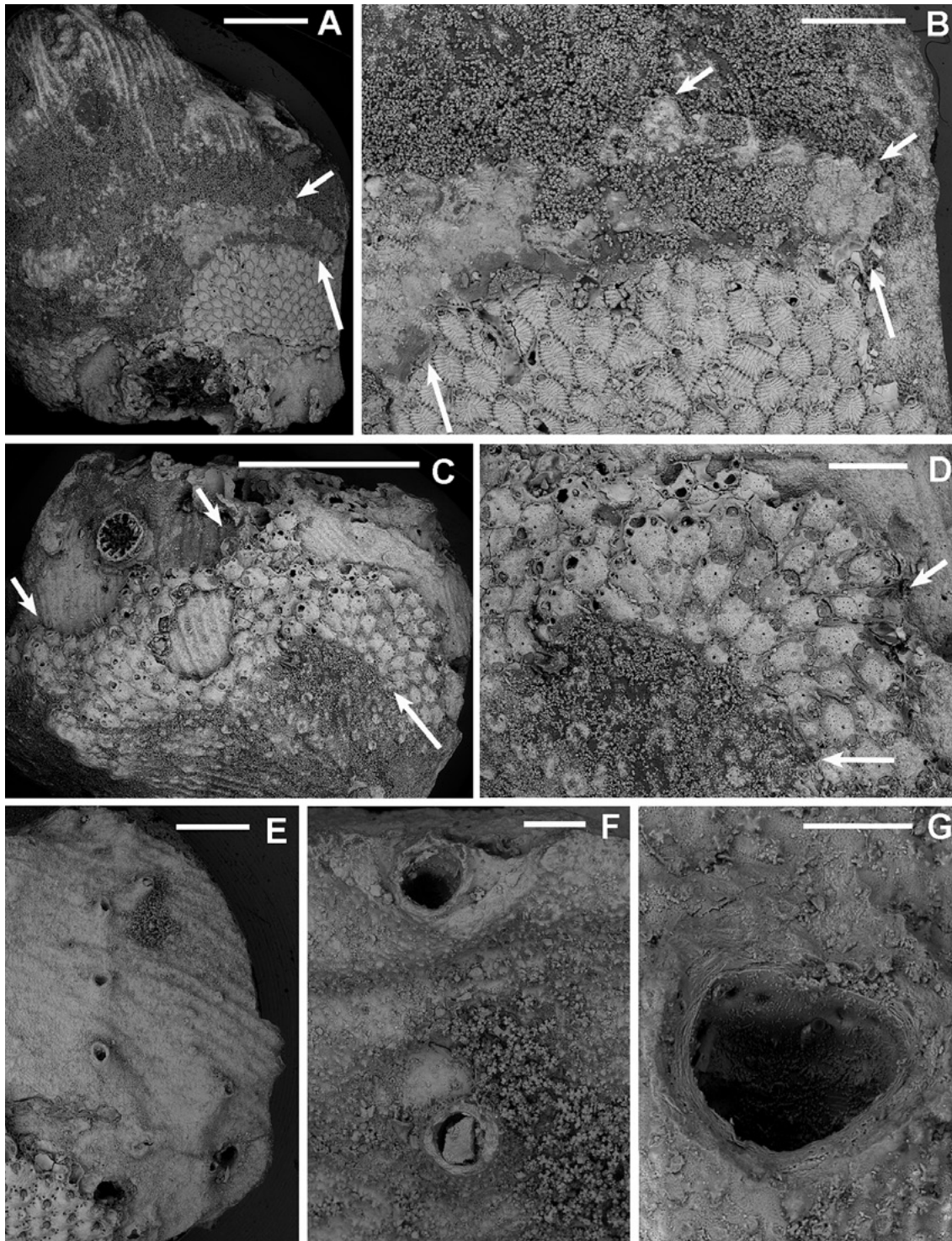


Figure 4. (A-B) General view and close-up of *Criblaria radiata* (Moll, 1803) growing on (short arrow) and overgrown by (long arrow) *C. rubrum*. (C-D) General view and close-up of *Microporella appendiculata* growing on (short arrow) and overgrown by (long arrow) *C. rubrum*. (E-G) SEM view and details of Figure 2K showing the tubuliporine tubes surrounded by the coral.

Scale bars: A, C: 5 mm; B, D, E: 1 mm; F: 200 mm; G: 100 mm.

(program RECOLNAT – ANR-11-INBS-0004 – <https://science.mnhn.fr/all/list?originalCollection=Coll.+Lamarck>) that provided pictures of the type material at high resolution. Embracing ideas by Dubois (2010), we here choose, and suggest the use of the subjective senior synonym *T. incrassata*.

Bryozoan assemblage and habitat

All species found in the sampled bryozoan assemblage are known to be widely distributed in mid-to-outer shelf environments of the Mediterranean Sea. Most of them [among which the abundant *C. maderensis*, *C. crassimarginata*, *S. (S.) linearis*, *S. (S.) mamillata*, *E. vulgaris* and *M. appendiculata*] are usually associated with coralligenous habitat (Gautier 1962; Laubier 1966; Harmelin 1976; 2017; Rosso and Sanfilippo 2009). Some species, such as *Escharina dutertrei protecta* Zabala, Maluquer and Harmelin, 1993 and *Herentia hyndmanni* (Johnston, 1847), have typically been recorded from relatively deep shelf sites and the upper slope (Zabala *et al.* 1993; Berning *et al.* 2008; Mastrototaro *et al.* 2010; Rosso *et al.* 2014). Conversely, *T. incrassata* is usually reported from water depths shallower than 60 m (Gautier 1962; Harmelin 1976; 2017; Hayward and McKinney 2002; Chimenz Gusso *et al.* 2014). This species thrives in coralligenous and precoralligenous habitats (Harmelin 1976; 2017), where it often occurs as an epibiont on axes of large-sized gorgonians (Moissette and Pouyet 1991; André *et al.* 2014; Gatti *et al.* 2015; Harmelin 2017; online underwater images on the Doris web page). Young colonies of *T. incrassata*, less than 2 cm high, were collected on erect stems of *Flabellia petiolata* (Turra) Nizamuddin from a deep coralligenous bottom (86–113 m) in the Sicily Straits (Di Geronimo *et al.* 1993). *T. incrassata* was so far never recorded as being intimately associated with *C. rubrum* (see section *Corallium rubrum-Turbicellepora incrassata relationships*). The occurrence of large-sized living colony branches of *T. incrassata* on dead or partly alive branches of *C. rubrum*, attests that the two species thrived together on deep coralligenous walls from NW Sardinia. The dimensions of branches of

T. incrassata in the studied sample allow inferring large (up to 15–20 cm) colony sizes, possibly larger than colonies of red coral from the same site. These large sizes point not only to conditions suitable for the species (including the occurrence of near-bottom currents providing oxygen and food) but also to good quality of the environment, because this species is highly sensitive to pollution (Harmelin and Capo 2002). Owing to its repeatedly branched, large-sized colonies, *T. incrassata* may play an important role in promoting habitat complexity. Indeed, *T. incrassata* branch surfaces offer colonisable space for small encrusting and erect bryozoans and other biota, especially when and where zooids become senescent.

Corallium rubrum-Turbicellepora incrassata relationships

This sample allowed us to state not only that *Corallium rubrum* and *Turbicellepora incrassata* lived together (see section *Bryozoan assemblage and habitat*) but also that they were strictly associated and established relationships with each other. *T. incrassata* (and, very subordinately, other bryozoans) could have colonised limestone clasts and some worn red coral fragments after they accumulated on the bottom surface at the base of the underwater cliff. This is indicated by: (1) *Turbicellepora* colonies that cover only one side of some coral branches and (2) complete or partial encrustation of broken surfaces of some coral fragments. Most *T. incrassata* colonies, however, possibly colonised *C. rubrum* when the coral was still attached to its substratum. This idea is supported by the branched morphology of the bryozoan colonies, which are usually sleeve-shaped around red coral branches and exhibit functional zooids on their surfaces. Close adhesion of some colonies of *T. incrassata* to the red coral skeleton indicates that colonisation occurred when the coral was dead or that at least the particular encrusted skeletal portion was exposed. Colonisation of exposed axial skeletons of Mediterranean gorgonians (mostly belonging to *Paramuricea* and *Eunicella*) and antipatarians [(*Leioopathes glaberrima* (Esper, 1788)], by large-



sized bryozoans (and by other epibionts/sclerobionts including *T. incrassata*) is a common phenomenon (e.g. Weinberg and Weinberg 1979; Linares *et al.* 2005; Garrabou *et al.* 2009; Angiolillo and Canese 2018). These papers record encrustations that are usually restricted to the stems and branches where gorgonian skeletons are naked owing to colony senescence and mostly to local damage produced in relation to environmental stress and partial or total mortality of colonies connected with exceptionally high sea temperature during summer (e.g. Linares *et al.* 2005). In particular, Garrabou *et al.* (2001) and Harmelin (2003) reported encrustations of bryozoan colonies on bare skeletons of *C. rubrum* in populations of the French Mediterranean coast and Monaco, which were affected by partial mortality in 1999. Harmelin and Marinopoulos (1994) and Gili *et al.* (2014) remarked that epibiosis of benthic organisms, including bryozoans, on gorgonians could be promoted/enhanced by the removal of soft tissues following abrasion produced by several factors, including fishing lines. Linares *et al.* (2005) also suggested that the growth extent of epibiont cover could be considered as an indicator of time elapsed from the injury event.

Literature records largely come from underwater observations. Therefore, close documentation of relationships between species is missing. Data acquired from the examination of NW Sardinia fragments, clearly indicate that *T. incrassata* is able to grow on bare portions of the red coral skeleton and also on coral tissue. Indeed, in some instances the abfrontal walls of zooids from the basal layer of *T. incrassata* colonies are separated from the enveloped red coral fragments by fissures measuring from hundreds of microns to about one millimetre. These fissures often result from the decay of the coral tissues which became “immured” following the bryozoan encrustation. This is indicated by reddish tissue remains and/or clusters of sclerites diagnostic of *C. rubrum* (cf. sclerite description in Grillo *et al.* 1993) which occur within several fissures. However, the simple occurrence of a thin layer of coenenchyme including sclerites does not

unequivocally indicate that red coral branches were healthy when overgrown, and that they possessed functional polyps that were never observed in the available material.

The occurrence of some *C. rubrum* basal colony expansions encrusting the surface of *T. incrassata* indicated that this species also served as substratum for *C. rubrum*. Some of these coral colonies reached large sizes on the cliff wall, as pointed out by the size of some broken branches (about one cm in diameter). Finally, subsequent superimpositions of thin layers of *C. rubrum* and *T. incrassata* skeletons indicate that these species can actively overgrow each other, possibly competing for space and/or to elevate from the colonised rocky wall to intercept local current flow carrying oxygen and food. However, it is sometimes difficult to ascertain if covering represents an overgrowth, i.e. an interaction between living colonies, and hence a real competition, or a mere superimposition, i.e. a colonisation after death of the encrusted specimens/colony. In the former hypothesis, it could be remarked that overgrowth, if occurring at the base of the coral colony could be relatively insignificant for the latter, whose basal expansions usually lack feeding polyps. Conversely, it seems substantially dangerous for the bryozoan, at least locally, because zooids occur on the whole exposed surface of colonies and usually become sealed and hidden beneath coral skeleton, when overgrown.

CONCLUSIONS

Accumulation of a large quantity of fragments in the sampled site, at the base of a cliff indicate that it was colonised by a possibly dense population of red coral in agreement with direct observations in the area (Cannas *et al.* 2010; Follesa *et al.* 2013). Natural breakage and downfall of detached colonies is possible, but only marginally, i.e. produced by borers or a strong physical disturbance. Indeed, the occurrence of unworn, sharp-edged small fragments could point to human impact in relation to red coral harvesting activity that has been intense in Sardinia

before the issuing of restrictive regulations in 2006 and 2008 (Cannas *et al.* 2010).

Examined fragments pointed to the co-occurrence of *C. rubrum* and *T. incrassata* in deep coralligenous habitats and allowed to describe for the first time relationships between these two species, including their competition for space. The two species seem to have the ability to overgrow each other, with final stages sometimes including the complete coating of some coral growing tips and consequently partial death of the impacted red coral branches. However, the competition with the bryozoan did not presumably prevent the red coral colonies in the area to reach large sizes. Furthermore, with colonies usually reaching two decimetres in size, *T. incrassata*, like *C. rubrum*, acts as an engineer species in deep coralligenous habitats, increasing the spatial complexity and providing colonisable elevated surfaces for further species.

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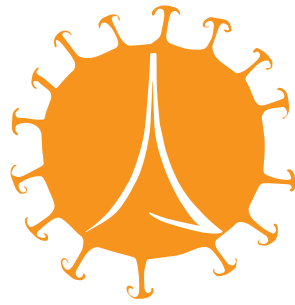
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