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Symbiont-Bearing Colonial Corals and Gastropods: An Odd Couple of the Shallow Seas

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Abstract: In order to investigate the serendipitous find of a gastropod encrusted by the symbiont-bearing colonial coral *Oculina patagonica*, we examined several specimens of cnidarian-encrusted gastropods, ranging in age from the Pliocene to the Recent, and characterized in detail their sclerobiont cover. The results of our analysis suggest that gastropod shells can be encrusted by symbiont-bearing colonial corals at various times: (1) when the gastropod is alive; (2) when the shell is being used by a secondary inhabitant (e.g., hermit crabs or sipunculid worms); (3) when the shell is discarded but yet to be buried. The relationship between the symbiont-bearing coral and the inhabitant(s) of the encrusted shell is an example of facultative mutualism, i.e., it is non-obligate yet beneficial for both ends as the former obtains the capability to move, and the latter improves the resistance and resilience of its armor, thus obtaining extra protection from predators. Being able to move could prove particularly useful for a symbiont-bearing coral because, in addition to removing the risk of being smothered by sediment, it would also favor the photosynthetic activity of its algal endosymbionts by allowing the coral to be always clean of sedimentary particles. Although the resulting epibiotic association would be limited in size by the ability of either the gastropod or the secondary inhabitant of the shell to move at the seafloor, these small and easy-to-miss benthic islands might become the seeds that allow sessile carbonate producers such as hermatypic colonial corals to colonize unconsolidated substrates.

Keywords: *Cladocora caespitosa*; *Oculina patagonica*; Muricidae; *Crepidula*; Pliocene; symbiosis; epibiosis; taphonomy



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1. Introduction

Symbiont-bearing, stony, colonial corals are among the most charismatic and iconic organisms of the shallow-water realm [1]. Modern tropical reefs are essentially built by the combined activity of corals (which form the main frame of the bioconstruction) and coralline algae (which bind and stabilize the whole structure). Such reefs represent some of the most biodiverse ecosystems of the shallow seas and comprise some of the most prolific extant carbonate factories. Nowadays, in oligotrophic euphotic waters, healthy hermatypic colonial corals can grow at a fast pace to keep up with eustatic oscillations [2]. Symbiont-bearing colonial corals are not limited to the tropics but also occur in temperate environments. In the Mediterranean Sea, the endemic species *Cladocora caespitosa* builds large bioconstructions in the shallow waters of coastal bays and other protected marine environments [3–8]. Symbiont-bearing colonial corals have been prominent carbonate-producing organisms since the Paleozoic, building extensive reefs in the Devonian, Late Triassic, Middle and Late Jurassic, and from the Oligocene onward [9–11].

Even though symbiont-bearing colonial corals are a common feature of the shallow seas at tropical and temperate latitudes, compared to other carbonate producers, they are limited by the availability of stable substrates and can be easily smothered by sediments. Coralline algae can easily colonize unstable substrates [12], while large benthic foraminifera can cope better than corals with sediment burial since they can self-extract from the sediment [13,14]. In order to overcome the limitations associated with a sessile lifestyle, some symbiont-bearing colonial corals have developed a simple solution: colonizing a “moving” substrate. The effectiveness of such an approach is evidenced by the many invertebrate lineages that have convergently adopted similar life habits: for instance, acorn barnacles of the superfamily Coronuloidea have become able to “ride” different motile substrates—whales, turtles, and crabs, to name just a few [15–17]. Choosing the right kind of living substrate can provide a sessile organism with most of the beneficial traits of a motile lifestyle, including the capability to escape unfavorable conditions, avoid predation, and survive burial. In the case of colonial corals, the potential benefits also include the capability to colonize fine-grained, mobile seafloors.

During their long and successful evolutionary history, corals repeatedly tried to “hitch a ride” on gastropod shells. The earliest evidence for such an epibiotic interaction dates back to the Silurian: the fossiliferous beds of the Yokokurama Formation (Japan) include a mudstone horizon that is rich in shells of the gastropod *Semitubina sakoi* encrusted by the tabulate coral *Favosites* [18]. Other coral-gastropod interactions have been reported from the Devonian, Pliocene, and Pleistocene [19–25] (Table 1). Except for the aforementioned *Semitubina sakoi*-*Favosites* interaction, which is regarded as a case of symbiosis between a living gastropod and the coral [18], the other relevant occurrences of colonial corals encrusting gastropods are thought to reflect symbiosis between the coral and a secondary inhabitant of the shells, either a hermit crab or a sipunculid worm (Table 1). This is consistent with neontological observations revealing that corals usually encrust gastropod shells that have been occupied by some other invertebrate [26–33].

Table 1. General overview of relevant occurrences of gastropod shells encrusted by stony corals through geological time.

Occurrence	Time	Coral	Substrate	References
Yokokurama Formation (Japan)	Silurian	<i>Favosites</i> (tabulate coral)	Shells of the gastropod <i>Semitubina sakoi</i>	[18]
Hamilton Group (New York, USA)	Devonian	<i>Pleurodictyum americanum</i> (tabulate coral)	Mainly shells of gastropod <i>Palaeozygopleura hamiltoniae</i> occupied by a secondary inhabitant, but also other molluscs and brachiopods	[20]
Bohemia (Czech Republic)	Devonian	<i>Hyostragulum</i> (tabulate coral)	Mainly hyolithids but also nautiloids and gastropods	[19]
Tropical to sub-tropical shallow water	Early Cretaceous—Recent	<i>Heterocyanthus</i> , <i>Heteropsammia</i> (symbiont-bearing solitary scleractinian corals)	Gastropod shells inhabited by sipunculid worms and, more rarely, by hermit crabs	[26,28–32]
Buckingham, Duplin, Tamiami and Yorktown formations (East Coast, USA)	Pliocene	<i>Septastrea marylandica</i> (colonial scleractinian coral)	Various gastropod shells occupied by secondary inhabitants	[21–25]
Yorktown Formation (Virginia, USA)	Pliocene	<i>Astrangia lineata</i> (colonial scleractinian coral)	Shells of the gastropod <i>Crepidula</i>	This work
La Serra, Valdelsa Basin (Tuscany, Italy)	Piacenzian	<i>Cladocora caespitosa</i> (symbiont-bearing colonial scleractinian coral)	Shells of muricid gastropods, both living and occupied by secondary inhabitants	This work
Port Marrant Formation (Southeastern Jamaica)	Upper Pleistocene	<i>Siderastrea radians</i> (symbiont-bearing colonial scleractinian coral)	A large shell of the gastropod <i>Aliger gigas</i>	[25]

Table 1. Cont.

Occurrence	Time	Coral	Substrate	References
Intertidal shelfal sand patches (Great Britain)	Recent	<i>Caryophyllia smithii</i> (non-symbiont-bearing solitary scleractinian coral)	Mainly tubes of the polychaete <i>Ditrupa arietina</i> , but also gastropod shells inhabited by sipunculid worms	[27]
Lagoon of the Dongsha Atoll (South China Sea)	Recent	<i>Porites</i> (symbiont-bearing colonial scleractinian coral)	Shells of gastropods inhabited by hermit crabs	[32]
Shallow sub-tidal of Glyfada (Athens, Greece)	Recent	<i>Oculina patagonica</i> (symbiont-bearing colonial scleractinian coral)	Shells of a living muricid gastropod of the genus <i>Hexaplex</i>	This work

Similar to corals, hydractinians (including calcified forms) are also known to associate with shells occupied by hermit crabs in both the Recent and the fossil records [23,29]. These relationships represent examples of mutualism: in fact, the encrusting coral acquires the capability of inhabiting otherwise inhospitable substrates (e.g., muddy seafloors) and is kept above the sediment-water interface (which is crucial for light-dependent species), while the secondary inhabitant of the gastropod shell obtains a growing and self-repairing armor [20,23,29–31,33].

Although this kind of ecological interaction is clearly beneficial for both partners, it represents an overall rare occurrence, with just a few taxa of solitary corals being known as obligate symbionts [31]. Symbiosis is thought to represent a major evolutionary driver [34], and the fossil record provides an incredibly broad array of largely overlooked case histories that could help in shedding light on the deep past of symbiotic relationships (e.g., [35]), especially for common carbonate producers such as colonial corals [36]. This contribution aims at providing new data on the symbiotic interactions between symbiont-bearing colonial corals and gastropods by (i) describing the first known occurrence of an extant symbiont-bearing colonial coral as an epibiont on a living, non-sessile gastropod and (ii) comparing it with various fossil examples of gastropod shells encrusted by cnidarians.

2. Materials and Methods

Five groups of specimens have been examined and compared: (i) a Recent, coral-encrusted muricid specimen; (ii) a Recent muricid shell displaying evidence of hermit crab inhabitation; (iii) nine coral-encrusted muricid specimens from the Late Pliocene of Northern Italy; (iv) three coral-encrusted specimens of *Crepidula* from the Pliocene Yorktown Formation of Virginia; (v) two hydractinian-encrusted gastropod specimens from the Pliocene of Tuscany (Figure 1).

The Recent coral-encrusted muricid was collected by one author (GC) in the summer of 2018 at Glyfada beach (37°52'25.9" N 23°43'54.3" E, Athens, Greece), at less than 1 m water depth, on a seabed dominated by cobbles and boulders. The available hard substrate in the area was inhabited by barnacles, coralline algae, bryozoans, and the encrusting, symbiont-bearing colonial coral *Oculina patagonica*. Both the muricid gastropod and the coral were alive at the time of capture. This specimen is stored at the Dipartimento di Scienze dell'Ambiente e della Terra, Università di Milano-Bicocca (Italy). The Recent hermitted muricid shell was examined to better understand the different taphonomic features of hermitted and non-hermitted gastropod shells. This specimen is stored at the Dipartimento di Scienze della Terra, Università di Pisa (Italy).



Figure 1. Map with the location of the studied specimens. Upper left inset panel indicates the position of the samples across the globe. The main panel provides the position of the samples from the Tuscan Pliocene in the framework of a simplified regional geological map.

Upper Pliocene coral-encrusted muricids were collected from the La Serra quarry (N 43°39'28", E 10°48'57"; Tuscany, Italy) (Figure 1). This quarry is located in the northwestern sector of the Valdelsa Basin, an extensional basin filled by Upper Miocene to Pleistocene continental and marine deposits [37]. The La Serra succession consists of paralic and shallow-marine strata consisting of, from bottom to top, estuarine/deltaic, barrier island, coastal-lagoonal, and shoreface/offshore transition deposits of Pliocene (likely Piacenzian) age [37–41]. The latter deposits consist of highly fossiliferous clayey sands featuring abundant remains of both vertebrates and macroinvertebrates, including abundant molluscs as well as an exceptionally rich decapod assemblage [39,42,43]. This stratal package was interpreted by Garassino et al. [39] as a shallowing-upward deposit that formed in a low-energy, shallow-marine palaeoenvironment across the offshore transition and lower shoreface settings. The studied specimens from La Serra are currently stored at the Museo Geopaleontologico GAMPS (Gruppo Avis Mineralogia e Paleontologia Scandicci) (Italy) (catalog numbers GAMPS 676, GAMPS 836, and GAMPS 1055 to GAMPS 1061).

The analyzed coral-encrusted Pliocene specimens of *Crepidula* were collected from a quarry outcrop of the Yorktown Formation near Newport News (37°04'50" N 76°25'59" W, Virginia, USA). Stretching along the Atlantic Coastal Plain from Virginia to North Carolina, the Yorktown strata consist of fine-grained sandy clays and shell marls that deposited in an open shelf setting over several transgressive and regressive cycles [44,45]. There is some indication in the literature [46] that the upper (i.e., Late Pliocene) part of the Yorktown Formation may be the source of our *Crepidula* shells. The latter is now part of the collections of the Museo di Storia Naturale, Università di Pisa (=MSNUP, Italy) with accession numbers MSNUP I-16955 to MSNUP I-16957.

The studied hydractinian-encrusted gastropods were collected from the strata exposed in the vicinities of Pietrafitta (43°27'25" N 11°04'37" E; Tuscany, Italy; not to be confused with the homonymous vertebrate-bearing locality of Umbria) (Figure 1). Here, the shallow-marine Pliocene sands and clayey sands have long been studied for their remarkable malacological content [47–51]. Our material from Pietrafitta is currently stored at the GAMPS with catalog numbers GAMPS 840 and GAMPS 841.

The encrusting sclerobiont suite of each specimen was analyzed, and, following the guidelines for recognizing hermitted shells proposed by Walker [23], special attention was given to the aperture of the shell.

3. Results

The Recent specimen from Glyfada is a 3-cm-long muricid shell that most likely belongs to the genus *Hexaplex* (possibly *Hexaplex trunculus*). Most of the diagnostic shell characters are hidden by the encrusting coral, thus frustrating any attempt of species-level determination (Figure 2A–C). The encrusting coral colony displays a laminar plocoid morphology formed by small corallites, each of which is characterized by ca. 24 septa (Figure 2D). These characters allow for identifying the colony as belonging to *Oculina patagonica*, a common member of the benthos at Glyfada. Even though the coral encloses the whole exterior of the shell but a small portion on the left of the aperture, the overall shape of the underlying shell can still be discerned, suggesting a thin coating. The only other sclerobiont observed on the shell is a small serpulid tube that occurs close to the apertural end of the siphonal canal (Figure 2C). The aperture itself is completely free of sclerobionts and does not display any evidence of boring (Figure 2C). As a comparison, the Recent hermitted muricid (*Bolinus* sp.) shell displays a conspicuous, irregular cover that comprises various sclerobionts, including oysters, bryozoans, and calcareous and agglutinated tube-worms (Figure 2E,F). The shell aperture is also completely encrusted, and calcareous tubes extend well into the body chamber (Figure 2F). Evidence of infestation by shell-perforating organisms can be observed in the form of boreholes in various regions of the shell (Figure 2F).

Nine coral-encrusted gastropod shells from the Pliocene of La Serra were examined. These specimens range in length from 3 to 10 cm and most likely belong to the muricid genera *Hexaplex*, *Bolinus*, *Purpurellus*, and *Ocenebra* (Figure 3). They were divided into well-preserved (Figure 3A–D) and poorly preserved (Figure 3F–H) based on their degrees of encrustation and bioerosion. In all the shells, the encrusting coral colonies displayed a phaceloid morphology, with corallites being slightly less than 0.5 cm in diameter and characterized by ca. 40 septa each (Figure 3E). Their characters suggest placement within the genus *Cladocora*, most likely as members of *C. caespitosa*. In some specimens, the coral cover is restricted to part of the abapertural surface (Figure 3A,B), which represents the most elevated point when the shell is lying on its apertural side. In other specimens, the phaceloid colony extends over the whole abapertural shell surface, thus largely obliterating the original shape of the shell (Figure 3C,D). The apertural shell side is generally free from corals or displays minimal encrustations (Figure 3A–D). In well-preserved specimens, the aperture is devoid of sclerobiont encrustations and preserves fine shell details (Figure 3B,D). In poorly preserved specimens, the aperture is partially encrusted by sclerobionts whose skeletons extend into the body chamber (Figure 3G,H). The sclerobiont assemblage of all nine specimens is largely dominated by *C. caespitosa*, but some display a higher diversity of encrusting organisms, including oysters, serpulids, and barnacles (Figure 3H,I). The latter include both opportunistic epibionts, such as balanids, and specialized ones, such as pyrgomatids (Figure 3I). Poorly preserved specimens display a more conspicuous cover, a wider variety of sclerobionts, and encrustations that extend into or even partially occlude the body chamber (Figure 3F–H). Pervasive boring was not observed, but a higher number of perforations was noted in severely encrusted specimens concerning both the gastropods and the sclerobionts (Figure 3G).

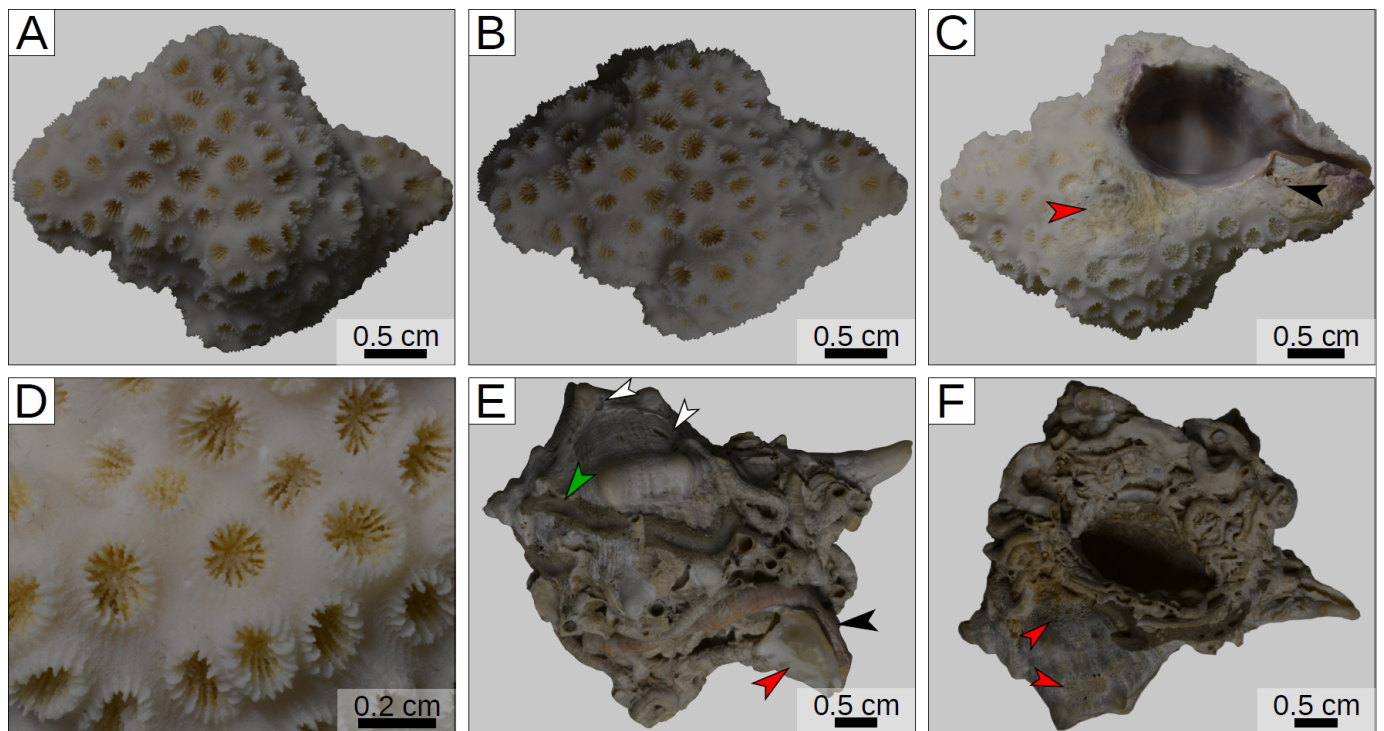


Figure 2. Recent specimens. (A,B) Abapertural views of the Recent muricid from Glyfada (Greece), encrusted by *Oculina patagonica*, taken under different light conditions to better highlight the shape of the shell. (C) Apertural view of the Recent muricid from Glyfada; red arrowhead indicates the only portion of the shell that is not encrusted by the coral, black arrowhead indicates the serpulid worm tube that occurs close to the apertural end of the siphonal canal. (D) Detail of the *O. patagonica* corallites. (E) Abapertural view of the Recent muricid displaying evidence of having been used by a hermit crab; white arrowheads indicate boreholes; green arrowhead indicates an agglutinating worm tube; black arrowhead indicates a calcareous worm tube; red arrowhead indicates an oyster. (F) Apertural view of the Recent hermitted muricid displaying sclerobiont encrustations extending into the body chamber; red arrowheads indicate bryozoan encrustations.

All the Pliocene *Crepidula* specimens from the Yorktown Formation are encrusted by *Astrangia lineata* (Figure 4A–G). These coral colonies have a phaceloid morphology and feature short corallites with a diameter of ca. 0.5 cm each (Figure 4G). In all the specimens, corals occupy a crescentic area on the abapertural surface of the shell (Figure 4A–C). In life position, the area covered by *A. lineata* would have been located at the opposite of the attachment substrate of *Crepidula*. Corals never encrust the juvenile portion of the shell. The examined shells exhibit varying degrees of preservation. The best-preserved features very few boreholes on the abapertural shell surface, both in the coral-free area and on the colony itself, but not in the body chamber (Figure 4A,D). A less well-preserved shell displays extensive boring on its abapertural surface and moderate boring on the corals and within the body chamber (Figure 4B,E). The poorly preserved shell displays extensive boring on both the abapertural side and the body chamber (Figure 4C,F). Limited perforations were also observed on the corals themselves (Figure 4C). Differing from the other *Crepidula*, the coral encrustation also extends into the body (Figure 4F).

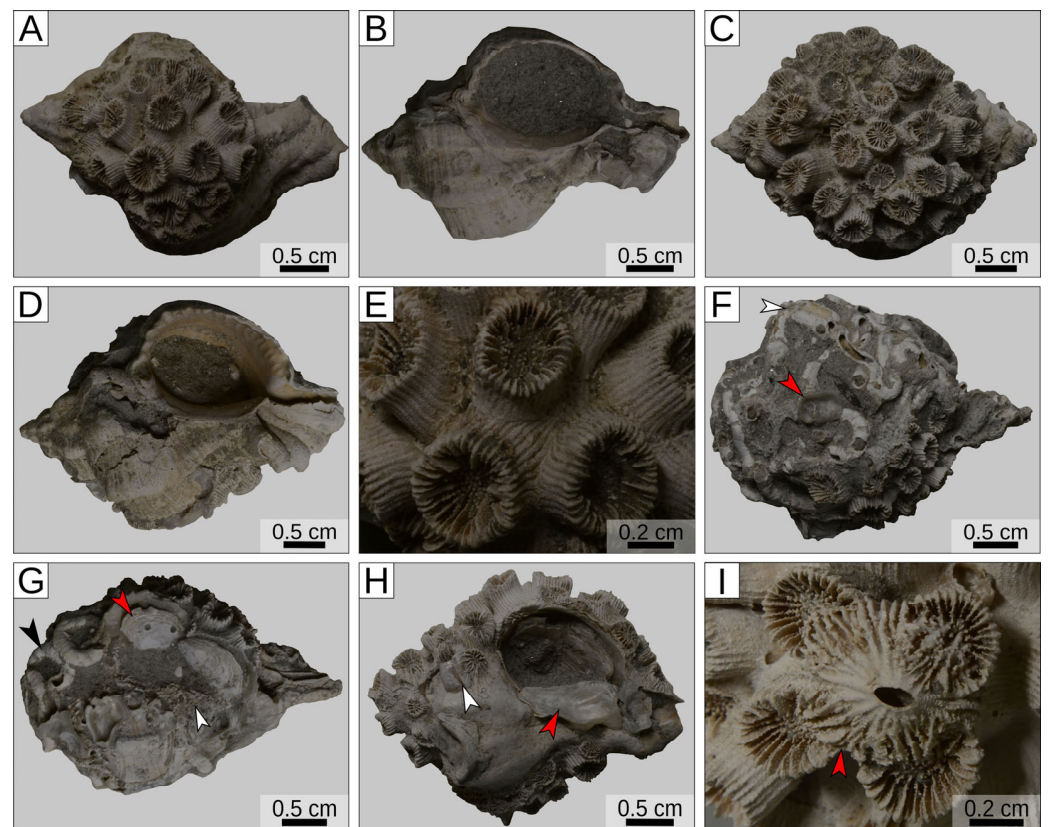


Figure 3. Pliocene coral-encrusted muricids from La Serra. (A) Abapertural view of a well-preserved specimen (GAMPS 1055a, b). (B) Apertural view of the same specimen as in panel (A). (C) Abapertural view of another well-preserved specimen (GAMPS 1056a, b) exhibiting a large coral cover and some limited damage on the apertural side. (D) Apertural view of the same specimen as in panel (C); note the well-preserved aspect of the shell material in the body chamber as well as the lack of sclerobionts therein. (E) Detail of the *Cladocora caespitosa* corallites from the specimen depicted in panels (A,B). (F) Abapertural view of a poorly preserved specimen (GAMPS 1057a, b); white arrowhead indicates serpulid worm tubes; red arrowhead indicates an oyster. (G) Apertural view of the same specimen as in panel (F); note the almost completely occluded aperture; red arrowhead indicates a borehole in an oyster located within the aperture; black arrowhead indicates a serpulid worm tube. (H) Apertural view of another poorly preserved specimen (GAMPS 1058a, b, c); red arrowhead indicates an oyster growing within the aperture; white arrowhead indicates an acorn barnacle that encrusts the shell and is partially overgrown by a corallite. (I) Close-up of a pyrgomatid barnacle growing over the *C. caespitosa* corallites that encrust the muricid specimen of panel (H); red arrowhead indicates where the external ridges of the barnacle merge with the septa of the coral.

The two gastropod shells from the Pliocene of Pietrafitta are completely enveloped by a hydractiniid encrustation (Figure 4H–L). Due to the ubiquitous encrustation of the shell's exterior, a precise taxonomic identification of the Pietrafitta gastropods was not possible. The encrusting hydrozoan developed characteristic horn-like processes, most of which broke down and are currently preserved as stubs (Figure 4H,I). In the best-preserved shell, the hydractiniid encrustation extends deeply into the body chamber (Figure 4J). In the other shell, the aperture and body chamber are partially encrusted by oysters, and borings occur within the inner surface of the latter (Figure 4K,L). In both cases, serpulids and barnacles are also present (Figure 4).

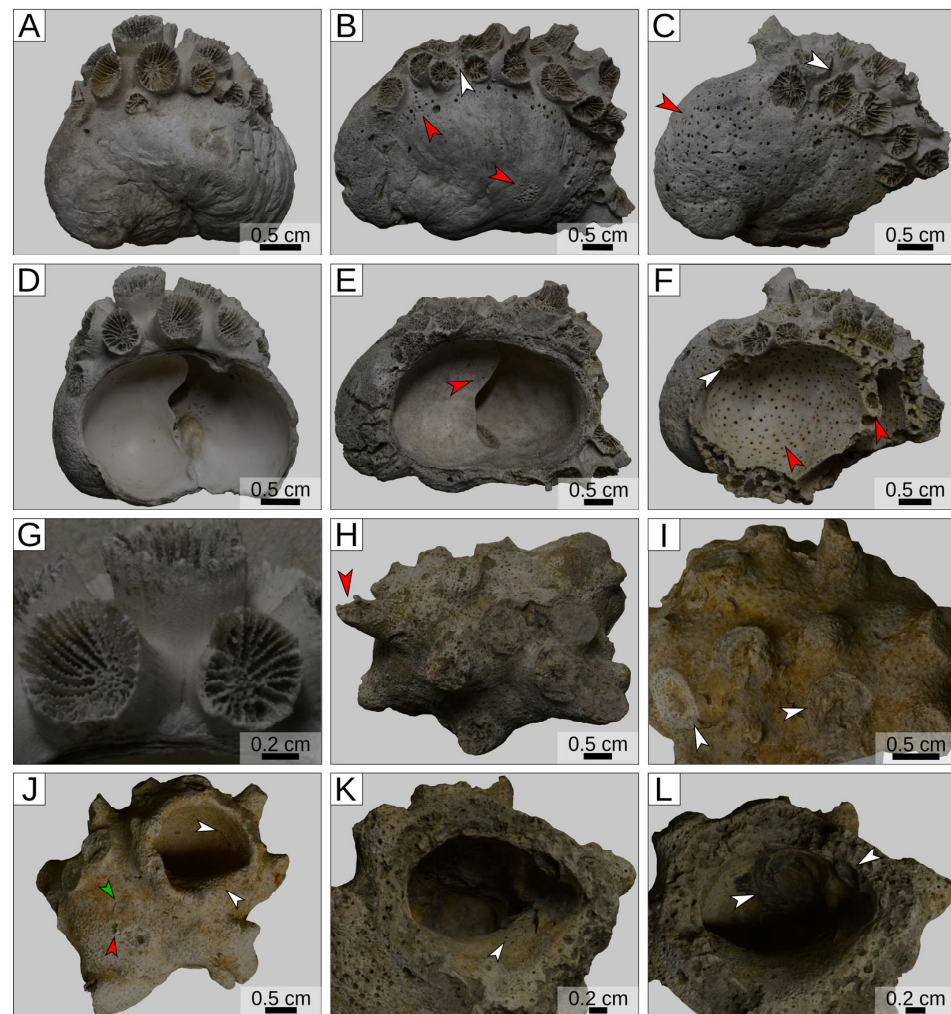


Figure 4. Pliocene specimens of *Crepidula* from the Yorktown Formation and hydractinian-encrusted gastropods from the Pliocene Pietrafitta outcrop. (A) Abapertural view of the best-preserved *Crepidula* specimen (MSNUP I-16955); (B) Abapertural view of the moderately preserved *Crepidula* specimen (MSNUP I-16956); white arrowhead indicates boreholes on the colony of *Astrangia lineata*; red arrowheads indicate boreholes on the shell itself. (C) Abapertural view of the poorly preserved *Crepidula* specimen (MSNUP I-16957); white arrowhead indicates boreholes on the coral; red arrowhead indicates boreholes on the shell. (D) Apertural view of the best-preserved *Crepidula* specimen. (E) Apertural view of the moderately preserved *Crepidula* specimen; red arrowhead indicates boreholes in the wall of the body chamber. (F) Apertural view of the poorly preserved *Crepidula* specimen; red arrowheads indicate boreholes on the shell; white arrowhead indicates *A. lineata* encrusting the inner surface of the body chamber. (G) Detail of corallites of *A. lineata* from the specimen depicted in panel (A). (H) Abapertural view of the least preserved hydractinian-encrusted gastropod from Pietrafitta (GAMPS 841); red arrowhead indicates one of the broken horn-like processes of the encrusting calcareous hydrozoan. (I) Broken horn-like processes (white arrowheads) on the abapertural surface of the best-preserved specimen of hydractinian-encrusted gastropod from Pietrafitta (GAMPS 840). (J) Apertural view of the specimen depicted in panel (J); white arrowheads indicate the hydrozoan encrustation extending deep into the body chamber; red arrowhead indicates the calcareous tube of a serpulid; green arrowhead indicates the basal plate of an acorn barnacle. (K) Apertural view of the same specimen as in panel (H); white arrowhead indicates boreholes on the inner surface of the body chamber, close to the aperture. (L) Apertural view of the same specimen as in panels (H,K) under different light conditions; white arrowhead indicates an oyster growing within the body chamber.

4. Discussion and Conclusions

Whenever precise taxonomic identifications could be performed, both the analyzed gastropods and their encrusting corals were revealed to be coherently related to shallow-water settings (e.g., [52–54]).

The examined specimens indicate that colonial coral encrustation can occur at different times during the existence of a gastropod shell, as detailed below.

(1) Colonization can occur when the gastropod is still alive (in vivo colonization). This is clearly testified by the Recent muricid shell encrusted by *Oculina patagonica*, as both taxa were alive when the specimen was collected (Figure 2). The well-preserved Pliocene *Crepidula* shell encrusted by *Astrangia lineata* may also represent an example of in vivo colonization. In fact, its aperture is pristine (Figure 4D); furthermore, the coral occupies an area of the shell that, when the encrusted *Crepidula* was alive, would have been the most hydrodynamically favorable for any organism feeding on suspended nutrient particles (Figure 4A–C). In vivo colonization seems to be the most logical hypothesis as *Crepidula* shells are usually not used by hermit crabs [55], and they are known to represent a suitable basibiont for colonial cnidarians (e.g., [56]). Thus, it is reasonable to hypothesize that the corals attached onto living gastropods (and, possibly, on mature individuals, based on the position of the colonies on the abapertural side of the shells). The well-preserved Pliocene muricid from La Serra, characterized by a pristine aperture without sclerobiont overgrowths and no evidence of boring or encrustation in the body chamber (Figure 3A–E), are also likely to represent examples of in vivo colonization. *Cladocora caespitosa* is very common in the sedimentary fill of the late Neogene and Quaternary basins of central Italy [8,57–60] and was also probably common in the La Serra area, as suggested by the presence of pyrgomatid barnacles that only grow onto corals (Figure 3I).

(2) Colonization can occur after the death of the gastropod when the shell is occupied by a secondary inhabitant, such as a hermit crab. This is testified by the poorly preserved muricid shells from La Serra, which display borings and sclerobiont encrustations on the aperture and in the body chamber (Figure 3F–H). This feature is also clear in the Recent hermitted muricid (Figure 3E,F) as well as in the Pliocene hydractiniid-encrusted shells (Figure 4J–L). The close relationship between cnidarians (both solitary and colonial forms) and the secondary inhabitants of the gastropod shells (essentially hermit crabs and sipunculid worms) is well-known from the extant seas and includes several cases of obligate or nearly obligate symbiosis [61] (Table 1). Among the latter, those with hydractiniids (e.g., *Hydractinia echinata* and *Stylactaria inabai*) and the ahermatypic coral *Epizoanthus* are the most well-known and ecologically relevant [61].

(3) Colonization can occur when the shell is no longer inhabited but not yet buried (*post-mortem* colonization). This may be the case for the two worst preserved specimens of *Crepidula* from the Yorktown Formation (Figure 4B,C,E,F). Both shells display perforations in the body chamber (Figure 4E,F), and, in the least complete, coral encrustation also extends into the body chamber (Figure 4F). Since the shells of *Crepidula* are unlikely to have been occupied by a secondary inhabitant, such as a hermit crab, the colonization may have occurred when the gastropod shell was empty before its final burial. This might also be the case for the most encrusted and poorly preserved muricid shell from La Serra, whose aperture is entirely filled by sclerobionts. Even without an organism moving the shell, the latter still represents an available hard substrate, which would prove especially important on muddy seafloors where shell debris constitutes the few “benthic islands” suitable for colonization by hard-substrate dwellers [62–65]. It is also important to underline that colonization can start as a form of epibiosis (e.g., while the shell is inhabited by a hermit crab) and continue after the shell inhabitant’s death (e.g., as the shell is discarded on the seafloor). This was most likely the case for the worst preserved shells from the Yorktown Formation and La Serra.

The symbiosis between colonial corals and gastropods/secondary shell inhabitants is an example of facultative mutualism. The coral colony gains the capability to move on different substrates and avoid burial, plus a constant flow of seawater (and consequently of

nutrients) provided by the shell movements [18,20,30–33,61]. These benefits are especially remarkable for symbiont-bearing corals as keeping them clean from sediment particles improves the photosynthetic activity of their algal symbionts. The shell movements could also benefit the coral during reproduction by increasing the chance of cross-fertilization [61]. These benefits occur regardless of the nature of the shell's "driver". Secondary inhabitants of the shell gain a self-repairing and self-growing armor, thus greatly reducing the need for new shells [18,20,33,61]. Further benefits could be related to the extra protection from predators provided by the production of noxious chemicals, as well as by the camouflage delivered by the coral skeleton [61]. The increased protection provided by the coral would also represent a net benefit for a gastropod. Such an extra cover can actually hinder the settlement of boring parasites, thus contributing to keeping the shell intact [61,66]. Although these features are more relevant for secondary inhabitants that cannot repair their shells, they may prove useful for gastropods as well.

The present study and existing body of literature (Table 1) highlight that both solitary and colonial, hermatypic and ahermatypic, and branching and massive corals can "hitch a ride" on gastropod shells. Furthermore, this kind of symbiotic relationship is clearly overall beneficial to both ends. Therefore, why is it so rare to find colonial corals encrusted on gastropod shells, especially as far as living gastropods are concerned? Most coral-encrusted shells are likely hermitted, as their secondary inhabitants are less able than gastropods to prevent the settlement of marine propagules on their shells. Hermitted shells are also generally used for long time-spans [67], thus increasing the chance of settlement of corals or other sclerobionts [68,69]. It is actually unsurprising that, among the investigated specimens, those with a higher diversity of sclerobionts, a higher sclerobiont cover, and a higher frequency of boreholes are the same for which occupation by a secondary shell inhabitant is hypothesized. There is no clear answer regarding the overall rarity of this relationship. Certainly, most of these shells reside in shallow-water, high-energy environments, as well as in the taphonomically active zone, for a long time, increasing the chance of damage, bioerosion, and other processes that can reduce their fossilization potential. However, it is possible that the need of the gastropod/secondary shell inhabitant to move significantly limits the maximum size achievable by the coral colony, resulting in this relationship being only able to produce small "benthic islands" that can easily go unnoticed. Although these moving communities are small and frail compared to the large bioconstructions that symbiont-bearing corals can develop, their existence might have been relevant in influencing the spread of corals and the development of reefs. In fact, these motile benthic islands might have allowed corals to disperse on unconsolidated seafloors, thus providing a first foothold for the settlement of other carbonate producers, which in turn might have been able to trigger reef development in an otherwise unsuitable environment. Carbonates are born, not made [70], and as such, their seeds are crucial for their survival.

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