How did the carrier shell *Xenophora crispa* (König, 1825) build its shell? Evidence from the Recent and fossil record

Short title: *X. crispa* shell microstructure and agglutination

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The genus *Xenophora* comprises species of marine gastropods (Cretaceous-Recent) able to add fragments of various origins to their shells surface. Agglutination potentials vary, from species lacking attachments to species completely covered by agglutinated materials, as in the Mediterranean species *Xenophora crispa*. Here, we analyse Recent and fossil specimens of *Xenophora crispa* from the Mediterranean area using SEM and XRD, to better understand their biomineralization patterns and the mechanisms leading to the agglutination of shells, bioclasts and lithoclasts, and their evolution in time. We also provide new data on poorly studied gastropod shell microstructures. We conclude that: a) most of the *Xenophora crispa* shell consists of an aragonitic crossed lamellar fabric, but fibrous to spherulitic prismatic fabrics, seemingly of calcite, have been found in the columella and peripheral edge (the thickest parts of the shell); b) the objects attachment is mediated by a prismatic microstructure, indicating that this may be the most functional fabric in attachment areas in molluscs; c) the functional purpose of the agglutination in *Xenophora crispa* may be related to a snowshoe strategy to successfully colonize muddy substrates, coupled with tactile and olfactory camouflage. Indeed, this species secretes in the columella and peripheral edge a less dense and a more organic rich calcitic fabric, possibly to lighten the shell thickest parts in order not to sink in soft sediments and to facilitate the shell raising from the substrate to create a protected feeding area. This behaviour seems to have been maintained by *X. crispa* over 2 My time span.

Key-words: Gastropod, Scanning Electron Microscope, X-Ray Powder Diffraction, Biomineralization

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The animal kingdom offers several examples of organisms forming their exoskeletons by selecting and agglutinating objects from the surrounding environment (Linsley & Yochelson 1973). Among molluscs, the microgastropod genus *Scaliola* Adams, 1860 attaches sand grains to its shell (Bandel & El-Nakhal 1993; Al Shuaibi & Mahmoud 2018) and the bivalves *Granicorium indutum* Hedley, 1906 and *Samarangia quadrangularis* (Adams & Reeve, 1850) have a shell coated by siliciclastic and bioclastic particles taken from adjacent sediments (Taylor *et al.* 1999; Braithwaite *et al.* 2000). On a micrometrical scale, agglutinated foraminifera have their tests formed by foreign particles glued together with a variety of cements (e.g. Hemleben & Kaminski in Hemleben *et al.* 1990). Also, agglutination occurs in unrelated groups such as insects: several aquatic larvae of taxa belonging to the order Trichoptera possess cases made of silk and hardened with gravel, sand, twigs or other debris found in the surrounding environment (e.g. Wiggins 2004).

Among the most spectacular of these agglutinating organisms is the carrier shell *Xenophora* Fischer von Waldheim, 1807, a genus of marine gastropods. This taxon comprises species, known from the Cretaceous to the Recent, which have the ability to form their shells cementing various kinds of objects with different origins: coral skeletons and bivalve, gastropod, brachiopod and foraminifera shells, bioclasts and, in some species, also siliciclastic sand grains and rock fragments (e.g. Ponder 1983; Lebrun *et al.* 2016). As observed by Braithwaite *et al.* (2000) for *G. indutum* and *S. quadrangularis*, this is not a secondary incrustation, but it is a primary constructional feature of the shell.

The process of agglutination by *Xenophora* is not well understood, and has only rarely been directly observed and described (Morton 1958; Shank 1969; Zhu 1984). Morton (1958) and Shank (1969) illustrated the process in *Xenophora neozelanica* Suter, 1908 and *Xenophora conchyliophora* (Born, 1780) respectively, observing that both species are very active when looking for objects to attach, but during agglutination they experience a long period of inactivity that can last up to 10 hours, exposing the organism to predators. Although it is still an unresolved issue, two main groups of theories have emerged regarding the functional purpose of agglutination (Feinstein & Cairns 1998 and reference therein): A) a defensive strategy provided either by visual, tactile and olfactory camouflage coupled with discontinuous or slow movements (this is especially valid for species living above the photic zone) or by an increase in size and thickening of the shell cementing objects to form an armour against predators; B) a functional support strategy provided by increasing the weight and the stability against wave and current action, or by enlarging the area of the shell base, raising the aperture from the substrate and avoiding sinking and suffocation in fine-grained sediments (snowshoe strategy; see Copper 1992).

Species of *Xenophora* show different agglutination potentials, from species lacking object agglutination to species completely covered by agglutinated materials, as is the case for *Xenophora crispa* (König, 1825), the only species of the genus *Xenophora* currently living in the Mediterranean Sea. This taxon is widely distributed over the entire central and western Mediterranean Sea and in the western Atlantic Ocean, from France to Angola (Poppe & Goto 1991). As a fossil, the species has been extensively recorded from the Pliocene and Pleistocene of the Mediterranean area, especially from Italian outcrops (Caprotti 1967; Ponder 1983; Manganelli *et al.* 2004). Despite this, the (palaeo)ecology and life habits of *Xenophora crispa* are still poorly known (Manganelli *et al.* 2004). According to some authors (Ponder 1983; Kreipl & Alf 1999; Nappo & Nappo 2014), the species lives on muddy or sandy substrates in waters, from 20-30 m up to 1400 m, whereas others (e.g. Adam & Knudsen 1955; Poppe & Goto 1991) reported a maximum depth of only 300 m. Also, the shell microstructure is poorly described and only Bøggild (1930) briefly referred to the shell fabric of the family Xenophoridae. This lack of information can be extended also to gastropod shell microstructures, where knowledge is generally limited to a relatively small number of specific taxonomic groups (e.g. Bøggild 1930; MacClintock 1967; Taylor & Reid 1990; Fuchigami & Sasaki 2005; Füllenbach *et al.* 2014). In addition, there have been few observations of the cement used by the *Xenophora* organism to agglutinate bioclasts and lithoclasts to its shell. According to Zhu (1984) the object is initially glued with mucus secreted by the mantle; the growth of new mineralised shell and the definitive cementation of the object then proceed simultaneously. But there is no information in the literature about the microstructure of the biomineral cementing the object.

Here, we analysed shell sections of Recent (Mediterranean Sea, Spain) and fossil specimens (~1.8 to 1.2 Ma, lower Pleistocene, Arda and Stirone River sections, Italy) of *X. crispa* using the Scanning Electron Microscope (SEM) and powder samples from different parts of the shell by means of X-Ray Powder Diffraction (XRD). These allow us to better understand the biomineralization and the mechanisms leading to the agglutination of shells, bioclasts and lithoclasts in *X. crispa*, comparing the function and behaviour of the agglutination in the same species through time, in this case over about 2 millions of years; besides this, we provide new data on gastropod shell microstructures in general terms.

Geological setting

The Arda and Stirone River marine successions, located in Northern Italy, belong to the Castell'Arquato wedge-top basin, that developed from the late Messinian to the Pleistocene after the north-eastward migration and the fragmentation of the Po Plain-Adriatic foredeep (Roveri & Taviani 2003; Ghielmi *et al.* 2013).

These sections belong to the upper part of the Castell'Arquato Formation (Pliocene-lower Pleistocene), cropping out along the homonym rivers, respectively close to the towns of Castell'Arquato and Salsomaggiore Terme at the margin of the northern Apennines facing the Po plain (Fig. 1 A-D). The marine sediments (Fig. 1 C, D) correspond to a subaqueous extension of a fluvial system affected by hyperpycnal flows triggered by river floods, whose terrigenous input is mainly supplied by an increase in the Apennine uplift and erosion, especially starting from 1.80 Ma (e.g. Amorosi *et al.* 1996; Bartolini *et al.* 1996; Argnani *et al.* 1997, 2003; Dominici 2001, 2004; Crippa *et al.* 2016a, 2018, 2019).

Marine deposits are composed by an alternation of siltstones, sandstones and mudstones, recording lower order transgressive and regressive cycles with shifts from lower foreshore-shoreface to offshore transition settings and water depths ranging between 5 and 50 m (Crippa *et al.* 2018). The marine succession ends with alluvial conglomerates, that represent a sea-level drop and the establishment of a continental environment with freshwater molluscs and vertebrate faunas (Cigala Fulgosi 1976; Pelosio & Raffi 1977; Ciangherotti *et al.* 1997; Esu 2008; Crippa & Raineri 2015; Esu & Girotti 2015; Crippa *et al.* 2018, 2019). Based on calcareous nannofossil and foraminifera biostratigraphy these successions have been given a Calabrian age (early Pleistocene), ranging from ~1.8 to 1.2 Ma (Crippa *et al.* 2016a, 2019).

Materials and methods

14 Recent and fossil specimens of the species *Xenophora crispa* were analysed in this study. The material is housed in the Dipartimento di Scienze della Terra “A. Desio” and registered with reference numbers consisting of a prefix MPUM followed by a five digit number.

Recent specimens [(id numbers: #35450 (MPUM 11857), #35453 (MPUM 11858), #35459 (MPUM 11859)] were trawled by fishing boats at 100-120 m water depth in muddy substrates of the Mediterranean Sea, offshore from Sant Carles de la Ràpita (Spain) (Fig. 1A).

Fossil specimens were collected from the lower Pleistocene (Calabrian) part of the Castell’Arquato Formation, cropping out along the Arda and Stirone Rivers in northern Italy [id numbers, Arda section: ACG11 (MPUM 11846), ACG24 (MPUM 11847), ACG133 (MPUM 11848), ACG199 (MPUM 11849), ACG236 (MPUM 11850); Stirone section: STR1 (MPUM 11851), STR2 (MPUM 11852), STR3 (MPUM 11853), STR4 (MPUM 11854), STR5 (MPUM 11855), STR6 (MPUM 11856)]. Specimens of *Xenophora crispa* were sampled in situ from several stratigraphic beds along the sections mainly in fine-grained massive siltstones and mudstones, rarely in massive sandstones (Fig. 1 C, D); these sediments were deposited around 20-40 metres of water depth, according to the sedimentary structures and the associated fauna (Crippa *et al.* 2016a, 2018, 2019).

Fossil specimens were first cleaned from the sediment using a scalpel and a brush, then washed and air dried, being careful to preserve the attached objects to the shell. Recent and fossil shells were then described, focusing on the types and numbers of agglutinated material. To characterise the microstructure shell sections were investigated using the Scanning Electron Microscope [(SEM Cambridge S-360 with lanthanum hexaboride (LaB_6) cathodes], and to define the mineralogical composition shell powders were analysed at the X-Ray Powder Diffraction (XRD, Panalytical X'pert Powder Diffractometer). For SEM sample preparation we follow the procedure proposed by Crippa *et al.* (2016b) for brachiopod shells, with a few modifications (i.e. higher exposure time to hydrochloric acid). Five specimens (ACG11, ACG199, STR1, STR6 and #35450) were cut in half longitudinally along the major axis and one section of each shell was embedded in a transparent bicomponent epoxy resin forming small blocks; further transversal sections were then obtained from each block, to analyse the microstructure along the growth direction. Every block was ground smooth using Silicon Carbide (SiC) powder of two different granulometries and etched with 5% hydrochloric acid for 15-20 seconds in order to reveal the detail of the microstructure. After washing with demineralised water and drying, each block was coated with gold and observed using SEM at Dipartimento di Scienze della Terra 'A. Desio', Università di Milano.

Small amounts of powders (~0.1 gr) were collected from six specimens (ACG11, ACG199, STR1, STR6, #35450 and #35459) and from different parts of the shell (columella, inner surfaces of different whorls, ornamentation on the adapical and abapical surface, surface of the object casts and peripheral edge) using a microdrill (Dremel 3000) equipped with a 300-μm tungsten carbide drill bit. Powders collected from the columella and the peripheral edge were sampled in the sectioned surface (beneath the shell surface). The powders were then deposited on low-background sample holders (made with specifically cut silicon single crystals), fixed with acetone and then analysed using XRD at Dipartimento di Scienze della Terra 'A. Desio', Università di Milano. The X-ray tube (Cu Kα wavelength) was set at 40 kV and 40 mA, and data were collected between 5 and 90° 2θ, with a step size of about 0.02° 2θ and a counting time per step of 30 sec. The incident slit was fixed at 1/2°, with an antiscatter of 1/2°; the detector is a multistrip X'Celerator.

Results

Specimen descriptions

Recent and fossil specimens of *Xenophora crispa* have a dextral, trochoid shell of small size [Arda specimens, height: (9)21-26 mm, diameter: (12)35-38 mm; Stirone specimens, height: 22-34 mm, diameter: 34-52 mm; Recent specimens, height: 21-22 mm, diameter: 32-38 mm] with a pointed apex, narrow peripheral flange and generally 6-8 whorls progressively increasing in size (Fig. 2). The spiral angle is 90°-95°. The suture varies from shallow to deep and the whorl profile – observable only where attached objects are missing – ranges from flat to slightly convex. The shell surface is ornamented by irregular and curved collabral and spiral costellae, sometimes forming a net. The base is flat to slightly convex, ornamented by thin and dense collabral growth lines and spiral grooves, crossing each other and giving a granular appearance to the surface. A deep umbilicus is visible in Recent specimens, but in nearly all the fossil ones is covered by a variably thick callus. The basal ornamentation is sometimes visible where the callus layer is thin. 70-80% of the spire surface is covered by objects or object scars (from 20 to 30 in number for each specimen). Fossil specimens generally preserve the agglutinated objects, but when these are absent the shapes of their casts usually allow the type of object to be determined. The casts of agglutinated objects are usually deep, although a few specimens show poor preservation and weak corrasion (ACG236, STR1, STR3). Agglutinated objects may be small or proportionally very large and consist predominantly of valves or shell fragments of bivalves [*Aequipecten opercularis* (Linnaeus, 1758), *Chamelea gallina* (Linnaeus, 1758), *Timoclea ovata* (Pennant, 1777), *Corbula gibba* (Olivi, 1792), *Astarte sulcata* (da Costa, 1778), *Anadara* sp., *Nucula* sp., *Acanthocardia* sp.], together with a few lithoclasts, and numerous fragments of determinable (*Ditrupa* sp.) and undeterminable taxa (e.g. gastropods, echinoids). Bivalve shells are agglutinated with the concavity-upward and increase in size along the growth vector, but there is no preferential orientation with respect to the umbo. Encrusting bryozoans, serpulids and corals are present on both the original gastropod shell surface and on attached objects in fossil specimens.

Shell microstructure

SEM analyses of longitudinal and transversal sections of specimens of *Xenophora crispa* show that Recent and fossil shells have the same microstructure. Almost all of the shell of *Xenophora* consists of the most common fabric among molluscs, that is an aragonite crossed lamellar microstructure (Fig. 3 A-E), occurring as alternating layers of simple crossed lamellae (SCL) and irregular complex crossed lamellae (ICCL).

The hierarchical organization of simple crossed lamellae, which defines a sort of "zebra pattern", is easily discernible. First order lamellae (~20-30 μm thick) appear as a series of linear oriented lenses, rarely branching, that frequently change their orientation (Fig. 3 A). These are easily recognised on SEM images thanks to the alternating brightness - linked to differences in electron scattering (Tschudin 2001) - of the adjacent first order lamellae, inclined in two opposite directions (Crippa 2013). The boundary between simple crossed lamellae and irregular complex crossed lamellae is usually well defined (Fig. 3 B, C). It is difficult to find a particular pattern in the distribution of the alternating layers of SCL and ICCL; these alternate irregularly without any specific organization. In some cases, a three-layered pattern occurs from the inner to the outer part of the shell, passing from ICCL to SCL and then again to ICCL; in others there is a two-layered distribution of ICCL and SCL (Fig. 3 B,C).

In this otherwise monotonous crossed lamellar shell, we have noted the presence of additional fibrous to spherulitic prismatic layers in the thickest parts of the shell, in area such as the columella and the peripheral edge, in both Recent and fossil specimens (Fig. 3 D-H; Fig. 4 A-C). These are sometimes interleaved with crossed lamellar layers (Fig. 3 E; Fig. 4 C). The prisms composing these layers are very narrow, 0.2-0.5 μm. In the inner part of the peripheral edge, these layers follow the curvature of the shell (Fig. 3 H). The fibrous prismatic layers are not always distinct in both the columella and the peripheral edge of all the specimens; in some of them a fine crossed lamellar fabric with a banded appearance occurs, like if the fibrous prismatic fabric is superimposed on, slightly masking, the crossed lamellar fabric (Fig. 3 G; Fig. 4 B). This is particularly evident in the transitional zones between fibrous prismatic and CL fabrics, indicating a gradual passage between the two microstructures. In the contact region between two different shell whorls, which has usually an undulose appearance, the fibrous prismatic fabric may grade into a spherulitic prismatic microstructure (Fig. 3 D).

The objects attached to *Xenophora* shell are firmly included in the shell itself (Fig. 4 D). The attachment area of the object to the shell comprises a thin irregular prismatic layer of variable thickness (~2-6 μm) between the agglutinated object and the underlying crossed lamellar fabric; this layer is present along the entire contact surface. Similar layers are present in both Recent and fossil specimens, although not always so clearly defined; they are formed by a stockade of parallel elongated irregular simple prisms in which the prism cross sections are highly variable along their lengths (Carter *et al.* 2012) and are arranged perpendicularly to the contact surface (Fig. 4 E-H).

Mineralogical composition

XRD analysis allows us to differentiate aragonite and calcite. Aragonite is a metastable form of calcium carbonate that is commonly replaced by calcite during diagenesis (Casella *et al.* 2017). XRD analyses of both Recent and fossil specimens of *X. crispa*, indicate that aragonite is the major mineral component of the shell; however, calcite occurs sporadically in both Recent and fossil specimens, although mainly restricted to the thickest parts of the shell (columella and peripheral edge; Figs. 5, 6, Table 1). Indeed, a low-intensity peak corresponding to the (210) peak of calcite (d=3.037 Å, 2Θ=29.45° with Cu Kα) is present in the XRD patterns of almost all specimens, including the Recent ones. Table 1 shows the approximate weights % of calcite in the samples. The area of calcite main peak (with d=3.037 Å) was divided by the sum of the peak areas of calcite and aragonite (with d=3.401 Å) and then multiplied by 100. As these are the only two components of the mixture and because calcite and aragonite have the same chemical composition (and therefore the same X-ray absorption coefficient), this can be considered a valid approximation.

Calcite is found in every specimen in both the columella, except in STR6, and the peripheral edge. A large amount of calcite is present in the peripheral edge of fossil specimens (ACG11, ACG199, STR1), and also in Recent ones (#35450 and #35459). A small amount of calcite, but still well above the detection limit, is present in the peripheral edge of STR6. The columella is particularly rich in calcite in samples ACG11, ACG199, STR1 and #35450. Calcite is less abundant or not detected in the other analysed shell parts (cast surface in STR1; columella and ornamentation on adapical surface in STR6). There are, however, exceptions in the cast surface in ACG11 and ACG199, and the ornamentation on adapical surface in ACG11, ACG199 and #35450 where calcite is more abundant.

Discussion

Shell microstructure and the agglutination process

The microstructural organization of the shell of *Xenophora crispa* is complex and irregular; it consists of several alternating layers of crossed lamellar fabric (simple and irregular complex crossed lamellae) without a definite distribution pattern. According to Bøggild (1930) this complexity mainly reflects the irregular form of the shells that causes a great variation in the distribution of the shell layers in the different regions of the same specimen. Two important features where missing from the Bøggild (1930) description of the microstructure of the Xenophoridae and are here recorded for the first time in both Recent and fossil specimens: i) the presence of fibrous to spherulitic prismatic layers in the columella and peripheral edge and ii) the presence of a thin prismatic layer (~2-6 μm in thickness) beneath agglutinated objects.

Carter (1990) suggested that the shells of most gastropods consists of an aragonitic crossed lamellar microstructure, in agreement with our observations in *X. crispa* shells. He also observed that many gastropod taxa (e.g. *Strombus*) show intercalations of fibrous prismatic layers with crossed lamellar ones, structurally continuous with overlying and underlying crossed lamellar fabrics. This fibrous prismatic microstructure may grade into a spherulitic prismatic fabric, especially in areas where the shell is thickened (e.g. in apertural lips and within the shell interior). This feature is also recorded in *Xenophora crispa*, where the columella and peripheral edge, which represent the thickest parts of the shell, consist of fibrous to spherulitic prismatic layers.

The second important character reported here has important implications for the agglutination process of *Xenophora crispa*. Below the cemented object there is an irregular prismatic layer (~2-6 µm thick), which then gives origin towards the shell interior to the crossed lamellar microstructure (Bandel 1979; Carter 1990; Wilmot *et al.* 1992). As pointed out by several authors (e.g. Taylor *et al.* 1969; Waller 1980; Crippa 2013), in bivalve shells the irregular simple prismatic fabric is commonly associated with muscle-attachment areas (e.g. adductor and pedal retractor muscles, pallial line); here, it is associated with object attachment to the shell. This led us to hypothesize that this fabric may represent the most functional microstructure for such areas. The prismatic fabric has a higher organic content than the crossed lamellar microstructure (Taylor & Layman, 1972; Checa *et al.* 2005; Esteban Delgado 2008; see also next paragraph); considering the same shell volume, it has a higher organic/inorganic ratio and thus more space (volume) occupied by the organic content than by the mineral. Also, the prisms are arranged perpendicularly with respect to the contact surface; as each prism is surrounded by an organic envelope a greater organic volume is exposed than if the prisms were parallel oriented. This may create a larger surface area/volume available for the mucus secreted by the mantle (Zhu 1984) to promote and strengthen the attachment of the object to the shell.

In the case of *X. crispa*, after having glued the bio/lithoclasts with organic material, the organism continues the biomineralization of new carbonate shell to solidly cement and embed the object (see Fig. 4 D). Our data suggest that *Xenophora crispa* attaches foreign particles to its shells in a way that is different from that observed by Shank (1969) in *Xenophora conchyliophora*. The latter species fills the gaps between the mantle and the agglutinated object with grains of sands, whereas no sand grain has been detected between the attached object and the shell in *Xenophora crispa*.

Linsey & Yochelson (1973) observed that the methods of manipulation and implantation of foreign material in *X. conchyliophora* and *X. neozelanica* is completely different, suggesting that the agglutination process may differ from species to species and is a species-specific behaviour.

Occurrence of calcite in Xenophora crispa *shell*

The major mineral component of the shell of *Xenophora crispa* is aragonite, as indicated by XRD analysis; however, calcite, which is rarely found in gastropod shells and is generally limited to the outer shell layers (Blandel in Carter 1990; Taylor & Reid 1990), has been found to occur in both Recent and fossil analysed specimens. Calcite has also been detected in species of the order Littorinimorpha (Lowenstam 1954; Taylor & Reid 1990), the same order to which *Xenophora* belongs.

However, the presence of calcite in fossil shells may not be of primary origin. Aragonite is a metastable form of calcium carbonate and when the shell undergoes diagenetic alteration it is commonly replaced by calcite (Casella *et al.* 2017). Nevertheless, the occurrence of calcite in the same parts of the shell of Recent specimens, implies that it may be of primary origin also in fossils. Furthermore, samples from the columella and the peripheral edge in both Recent and fossil specimens were collected on the sectioned innermost surfaces (beneath the shell surface) which are supposed to have lacked a direct contact with diagenetic fluids. So, the presence of calcite in the columella and peripheral edge in fossil specimens should have a primary origin. However, we take into account the possibility that traces of calcite occurring in other parts of the shell, as in the surface of the inner whorl, of the abapical and adapical ornamentation and below casts of attached objects in fossil specimens, may be due to diagenetic alteration. As testified also by studies on other fossil organisms (e.g. brachiopods; Romanin *et al.* 2018) the shell outermost parts may be more directly affected by diagenetic fluids and thus be more prone to be altered. However, it is not possible to discern between primary or diagenetic calcite and quantify the different proportion of the two.

Most of the shell of *X. crispa* consists of a crossed lamellar fabric, a typically aragonitic microstructure (e.g., Bøggild 1930; Taylor *et al.* 1969; Carter 1990), in agreement with the results of XRD. However, the columellas and the peripheral edges, of both Recent and fossil specimens, include fibrous prismatic layers. Notwithstanding the difficulty of precisely relating the presence of calcite to a particular microstructural type using only SEM, we suggest that these fibrous prismatic layers are probably made of calcite. Taylor & Reid (1990) and Carter (1990) suggested that this microstructural type is of aragonite, although Pérez-Huerta *et al.* (2011) recorded calcite forming fibrous prismatic fabric in the gastropod genera *Haliotis* and *Concholepas*. To try to explain why calcite occurs in specific parts of the shells, we need to consider the physical properties of the two polymorphs, the organic contents of the different shell microstructures and the ecological behaviour of *X. crispa*. Calcite is less dense and less hard compared to aragonite (2.71 g/cm^3 and 3 Mohs' scale compared to 2.95 g/cm^3 and 3.5-4 Mohs' scale) (MacDonald 1956; Table 1 in Thenepalli *et al.* 2015). In addition, the prismatic fabric has a higher organic content than the crossed lamellar microstructure that has only 1 wt% of organic content, most of which is present as thin organic sheaths enveloping the third order lamellae (e.g. Uozumi *et al*. 1972; Suzuki *et al.* 2011; Rodríguez-Navarro *et al.* 2012). Organic content values reported by Taylor & Layman (1972) and Checa *et al.* (2005) for prismatic fabrics are higher (4–6 wt%) (Esteban Delgado 2008), with each prism surrounded by an organic envelope. Rhoads & Lutz (1980) suggest that the porosity and the percentage of organic matrix significantly affect shell density, and observe, together with Taylor & Layman (1972), that, despite differences in organic content in the shell microstructures, calcitic shell layers are generally less dense than aragonitic ones.

Thus the presence of the less dense polymorph (calcite) in the thickest parts of the shell (columella and peripheral edge) may have a functional and adaptative significance. *Xenophora crispa* lives on loose muddy substrate, commonly below the photic zone, where the use of object attachment as visual camouflage is unlikely. Instead, a snowshoes strategy would be more beneficial together with tactile and olfactory camouflage. As observed by Copper (1992), epibenthic organisms adapt in different ways to soft muddy bottoms mainly finding strategies to prevent sinking; one of these includes the increase of the surface area. Through object attachment, *Xenophora crispa* enlarges the area of the shell base (see Fig. 2 D, F and specimens figured by Nappo & Nappo, 2014) and lifts itself from the sea bottom, avoiding sinking in soft sediment and, at the same time, creating a protected feeding area where the animal can graze; also, although *Xenophora* has a sedentary lifestyle (Feinstein & Cairns, 1998), the shell lifting allows the animal's body to remain suspended from the substrate and to leave, when it moves, discontinuous scent trails to protect itself from predators.

In addition, secretion in the columella and in the peripheral edge of a less dense, less hard and more organic rich calcitic microstructure, lighten these thickest parts of the shell, possibly representing a further adaptation to muddy substrates and aiding the lifting of the shell for feeding and olfactory camouflage. The scattered presence of calcite in other parts of the shell may indicate further attempts to locally lighten the shell. A similar strategy is followed by another deep water species of Xenophoridae, *Stellaria solaris* (Linnaeus, 1764), which possesses long and hollow, thus light, spines on the edge of the shell that lift the animal from the muddy substrate.

The same behaviour has been recorded in Pleistocene and Recent specimens of *X. crispa* living in muddy environments, suggesting that object attachment was a strategy pursued and beneficial to the species for over 2 million of years.

Understanding why *Xenophora* attaches objects to its shells still remain a complex issue. According to Feinstein & Cairns (1998) camouflage was possibly the original function, but the degree to which the other functions are derived is still unknown; as above mentioned, this is likely a species-specific behaviour, where different species exposed to different predation pressure and environmental conditions may have adapted the basic attachment to various purposes. The new findings here presented (i.e., the occurrence of calcite) can help to add another piece to this intriguing puzzle.

Conclusion

The study of biominerals of marine organisms provides invaluable information in different fields of palaeontology (e.g. the comprehension of evolutionary taxonomy and of biomineralization processes, the detection of shell diagenetic alteration, palaeoclimatic and palaeoenvironmental reconstructions), so it has to be applied more often. The present study, besides providing new and taxonomically useful data on *Xenophora crispa* shell microstructure, has implications for the understanding of the agglutination process and its significance through time.

The analyses of Recent and fossil *Xenophora crispa* specimens using the SEM and XRD indicate that:

a) *Xenophora crispa* has a predominantly aragonitic crossed lamellar shell, although calcite is present in the thickest parts of the shell (i.e. the columella and peripheral edge). In these regions a fibrous to spherulitic prismatic fabric occurs, suggesting this fabric to be made by calcite.

b) Object attachment requires a prismatic microstructure, which may be thus the most functional fabric in attachment areas in molluscs, although further studies are required to confirm this hypothesis.

c) The functional significance of the attachment of foreign material is species-specific and linked to different ecological behaviours. For *Xenophora crispa* a snowshoe strategy is suggested, coupled with tactile and olfactory camouflage. This species secretes in the columella and in the peripheral edge a less dense, less hard and more organic rich calcitic microstructure, possibly to lighten these thickest parts of the shells in order to adapt to muddy substrates and to lift the aperture from the substrate.

d) *Xenophora crispa* shell microstructure and the agglutination purpose do not changed in the last 2 millions of years.

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Captions

Figure 1. A) Schematic map showing collection sites of Recent (star with stripes; offshore from Sant Carles de la Ràpita, Spain) and fossil (white star; Arda and Stirone River sections, Italy) specimens of *Xenophora crispa*. B) Geological map of northern Italy, showing the position of the Arda and Stirone River sections (modified after Crippa *et al.* 2018). C) Log of the Arda river section (base at 44°51′18.52″N, 9°52′26.7″E) with position of shell layers (modified after Crippa *et al.* 2016a). D) Log of the Stirone River Section (base at 44°50′38.87″N; 9°58′38.37″E) with position of shell layers (modified after Crippa *et al.* 2019).

Figure 2. Fossil (A-C, E) and Recent (D) specimens of *Xenophora crispa*. A1-3) Fossil specimen, Arda River section; apical, abapical and apertural views respectively (ACG133). B1-3) Fossil specimen, Arda River section; apical, abapical and apertural views respectively (ACG236). C1-3) Fossil specimen, Stirone River section; apical, abapical and apertural views respectively (STR5). D1-3) Recent specimen, offshore from Sant Carles de la Ràpita, Spain, Mediterranean Sea; apical, abapical and apertural views respectively (#35453). E1-3) Fossil specimen, Stirone River section, apical, abapical and apertural views respectively (STR3). F1-3) Recent specimen, offshore from Sant Carles de la Ràpita, Spain, Mediterranean Sea; apical, abapical and apertural views respectively (#35459).

Figure 3. Scanning electron microscope images showing the microstructure of *Xenophora crispa* shells; CL: crossed lamellar fabric; Fp: fibrous prismatic fabric; ICCL: irregular complex crossed lamellar fabric; SCL: simple crossed lamellar fabric; Sph: spherulitic prismatic fabric.
A) First order lamellae changing in orientations in the simple crossed lamellar fabric. Recent specimen (#35450). B) Alternation of irregular complex crossed lamellae and simple crossed lamellae. Recent specimen (#35450). C) Boundary between simple crossed lamellar and irregular complex crossed lamellar fabric. Recent specimen (#35450). D) Contact between two different

whorls; the contact is undulose and a spherulitic prismatic fabric is present. The lower dark contact is in correspondence of a growth line. Growth lines are organic rich; in fossil specimens the decay of the organic matrix leave many voids making this part more delicate and prone to fracture (e.g. during specimens cutting). Fossil specimen, Stirone River section (STR6). E) Spherulitic band crossing the simple crossed lamellar fabric, possibly representing a growth band. Fossil specimen, Stirone River section (STR6). F) Fibrous prismatic fabric in the columella. Fossil specimen, Arda River section (ACG199). G) Fibrous prismatic fabric to banded crossed lamellar fabric in the columella. Fossil specimen, Arda River section (ACG199). H) Fibrous prismatic fabric in the innermost part of the peripheral edge. Fossil specimen, Stirone River section (STR6).

Figure 4. Scanning electron microscope images showing the microstructure of *Xenophora crispa* shells; CL: crossed lamellar fabric; Fp: fibrous prismatic fabric; Pr: prismatic fabric; Obj: object agglutinated; SCL: simple crossed lamellar fabric. A) Fibrous prismatic fabric in the innermost part of the peripheral edge. Fossil specimen, Stirone River section (STR6). B) Banded crossed lamellar fabric in the innermost part of the peripheral edge. Recent specimen (#35450). C) Alternated layers of fibrous prismatic and crossed lamellar fabrics in the innermost part of the peripheral edge. Fossil specimen, Stirone River section (STR6). D) Object cemented to the shell. Fossil specimen, Arda River section (ACG11). E-H) Prismatic layer below the agglutinated object. Fossil specimens, Arda River section (ACG11, Fig. E; ACG199, Fig. F), Stirone River section (STR6, Fig. H), Recent specimen (#35450, Fig. G).

Figure 5. Diffractograms of Recent specimens showing the main peaks of calcite and aragonite. Legend: C: columella; OAS: ornamentation on the abapical surface; PE: peripheral edge.

Figure 6. Diffractograms of fossil specimens showing the main peaks of calcite and aragonite. Legend: CS: cast surface; PE: peripheral edge; WIS: whorl inner surface.

Table 1. Distribution and approximate % weight of calcite in the different parts of the shell of *Xenophora crispa*. X: no calcite.