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Barnacle taphonomy and ultrastructure: comparing modern and fossil shells from the western Mediterranean

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Fossil acorn barnacles are excellent palaeoenvironmental proxies in shallow-marine settings. However, the impact of post-depositional and diagenetic alterations on the barnacle shell remains poorly understood. Opercular plate preservation and observations on abrasion and fragmentation of the wall plates are the most valued taphonomic indicators. Although the shell microstructure of marine invertebrates usually provides useful insights for understanding these processes, conventional microscopic observations are often insufficient for assessing the degree of micro- and ultrastructural alteration in fossil barnacles. This study compares the ultrastructure of modern and fossil (Pliocene and Pleistocene) barnacle shells from the western Mediterranean to explore their ultrastructure and investigate the impact of taphonomic and diagenetic processes. Under Scanning Electron Microscopy (SEM), modern barnacles show a porous 'dragon-scale pattern'. SEM and cathodoluminescence analyses reveal microstructural changes in fossil barnacles, including dissolution features and diagenetic imprints. Evidence of microbial activity is also observed, in both modern and fossil specimens, in the form of microbioerosion traces made by cyanobacteria. Despite their stable low-magnesium calcite composition, barnacle shells from coarse-grained deposits usually show significant diagenetic alteration. In contrast, specimens from fine-grained sediments typically exhibit minimal alteration, preserving ultrastructural features almost comparable to those of their modern counterparts. This study underscores the importance of high-resolution analytical approaches in palaeontological research to advance our understanding of barnacle ultrastructure, taphonomy and diagenesis. □ *Fossil-diagenesis, microstructure, cathodoluminescence,* Chelonibia, Concavus, Perforatus

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Fossil acorn barnacles (Cirripedia, Balanomorpha) are valuable proxies for palaeoecological and palaeoenvironmental studies in shallow-marine settings due to their wide distribution and abundance, high growth rates, and low-magnesium calcite shell.

Today, large acorn barnacle accumulations are typically found at middle and high latitudes (Raymond & Stetson 1932; Hoskin & Nelson 1969; Newman & Ross 1971; Milliman 1972; Müller & Milliman 1973; Farrow *et al.* 1978; Hottinger 1983; Domack 1988; Nelson *et al.* 1988; Scoffin 1988; Wilson 1988; Henrich *et al.* 1995; Frank *et al.* 2014), though they can also occur in low-latitude regions, especially in nutrient-rich water (Glynn & Wellington 1983; Halfar *et al.* 2006; Westphal *et al.* 2010; Michel *et al.* 2011; Reijmer *et al.* 2012; Klicpera *et al.* 2013; Reymond *et al.* 2016; Bialik *et al.* 2023). In spite of a general paucity of palaeontological studies on barnacles, these sessile crustaceans are common in the Cenozoic fossil record, especially in Neogene and Quaternary deposits (Darwin 1854; De Alessandri 1895; Davadie-Suaudeau 1952; Newman *et al.* 1969; Menesini 1971; Pajaud 1976; Foster & Buckeridge 1987; Menesini & Casella 1988; Donovan 1989; Doyle *et al.* 1996; Collins *et al.* 2014; Buckeridge 2015; Gale & Sørensen 2015; Coletti *et al.* 2018, 2021, 2024; Collareta *et al.* 2019; Buckeridge *et al.* 2020; Hoffmann *et al.* 2020; Gale 2021; Gale *et al.* 2021; Kočí *et al.* 2024a).

Most barnacle shells exhibit relatively high growth rates (Newman *et al.* 1967; Bourget & Crisp 1975; Crisp & Bourget 1985; Anderson 1994; Lopez *et al.* 2012), enabling them to effectively record short-term fluctuations of the environmental conditions such as seasonal variations (Buckeridge 1975; Killingley & Newman 1982). A fast growth rate can also lead to the accumulation of high numbers of shells in short time spans (Hoskin & Reed 1984; Buckeridge 1999, 2015). Consequently, barnacle shells serve as valuable and detailed indicators of environmental dynamics, providing insights into the ecological conditions during their growth (e.g. Burgess *et al.* 2010; Coletti *et al.* 2018, 2024), provided that diagenesis does not alter the original shell structure.

Barnacle shells are composed of low-Mg calcite, which is diagenetically more stable and less soluble compared to aragonite and high-Mg calcite (Clarke & Wheeler 1917; Chave 1954; Hall *et al.* 1967; Bourget 1974; Hover *et al.* 2001; Borromeo *et al.* 2017; Ullmann *et al.* 2018). Its structure consists of thin layers of calcite crystals embedded within an organic matrix – a complex, hierarchically organized structure (Bourget 1987; Khalifa *et al.* 2011; Lewis *et al.* 2014; Gal *et al.* 2015; Checa *et al.* 2019, 2020; Shaw *et al.* 2024). Biomineralization is controlled by this organic matrix that determines the type, size and orientation of the crystals that form the shell (Rodríguez-Navarro *et al.* 2006; Khalifa *et al.* 2011). This layered arrangement is not homogeneous, but rather varies in response to seasonal shifts and ontogenetic development, both of which influence the shell growth rate (Nishizaki & Carrington 2015), and thus its geochemical characteristics. Killingley & Newman (1982) found that the calcite of recent balanomorph barnacle shells exhibits systematically higher $\delta^{18}O$ values than those expected under equilibrium conditions, whereas Burgess *et al.* (2010), Bojar *et al.* (2018) and Ullmann *et al.* (2018) suggested that the cirripede shells form at isotopic equilibrium with the surrounding seawater. Furthermore, the mineralogy of barnacle shells is extremely variable not only in comparison to other marine invertebrates, but also within the Cirripedia, which also includes species with shells made of chitin and/or hydroxyl-apatite (Carpenter & Lohmann 1992; Buckeridge & Newman 2006; Khalifa *et al.* 2011; Iglikowska *et al.* 2018; Ullmann *et al.* 2018).

Therefore, although acorn barnacles present an attractive opportunity for palaeoenvironmental studies, the aforementioned 'grey areas' highlight how the few microstructural and geochemical analyses that have been conducted on extant (Murdock & Currey 1978; Dougherty *et al.* 1990; Fernández *et al.* 2001; Rodríguez-Navarro *et al.* 2006; Khalifa *et al.* 2011; Raman & Kumar 2011; Lewis *et al.* 2014; Bojar *et al.* 2018; Mitchell *et al.* 2019; Checa *et al.* 2019, 2020; Shaw *et al.* 2024) and fossil forms (e.g. Buckeridge 1975; Roskowski *et al.* 2010; Gale & Schweigert 2016; Collareta *et al.* 2018; Taylor *et al.* 2019; Bosio *et al.* 2020; Paces *et al.* 2023; Coletti *et al.* 2024) severely limits the potential of barnacles as (palaeo)environmental indicators, which contrasts with the attention that is given to the micro- and ultrastructure of other groups of fossil invertebrates (e.g. Barbin & Gaspard 1995; Barbin 2000; Machel 2000; Vinn *et al.* 2008a,b; Vinn & Kupriyanova 2011; Angiolini *et al.* 2012; Vinn 2013, 2020; Crippa *et al.* 2016, 2020; Casella *et al.* 2018; Bosio *et al.* 2020; Sanfilippo *et al.* 2021; Guido *et al.* 2024).

Furthermore, only few taphonomic studies are available (Donovan 1988; Donovan 1993; Doyle *et al.* 1996; Nielsen & Funder 2003; Nomura & Maeda 2008; Coletti *et al.* 2024). Based on mascroscopic observations, Doyle *et al.* (1996) and then Nomura & Maeda (2008) recognized seven and four different types of macroscopic taphonomic preservation of barnacle shells, respectively. Nielsen & Funder (2003) described three grades of alteration of barnacle shells based on the extent of abrasion and fragmentation. Overall, well-preserved, complete barnacle shells with articulated or associated opercular plates seems to be typically associated with sheltered, low-energy environments, while disarticulated, fragmented and abraded specimens are related to high-energy settings (e.g. Nielsen & Funder 2002; Coletti *et al.* 2024).

To address these gaps in knowledge, this work analyses modern and fossil barnacles specimens from the Western Mediterranean using cathodoluminescence (CL) and scanning electron microscopy (SEM), with the aim of (i) investigating the barnacle ultrastructure and (ii) developing a standardized taphonomic protocol in fossil barnacles. The fossil specimens come from various Pliocene-Pleistocene barnacle-rich deposits of central and northwestern Italy, and represent different (palaeo)environmental settings (ranging from coastal and very shallow to open shelf), burial types (fine-grained versus coarse-grained deposits), geological time intervals (including the Early and Late Pliocene, and Early Pleistocene), barnacle taxa (numbering four species in two families), and ecological adaptations (including epizoic as well as non-epizoic forms). Together with fossil samples, modern barnacles from the central Mediterranean Sea were analysed for comparison.

Geographical and stratigraphical setting

The fossils analysed in this work come from deposits that span the Lower Pliocene to Lower Pleistocene

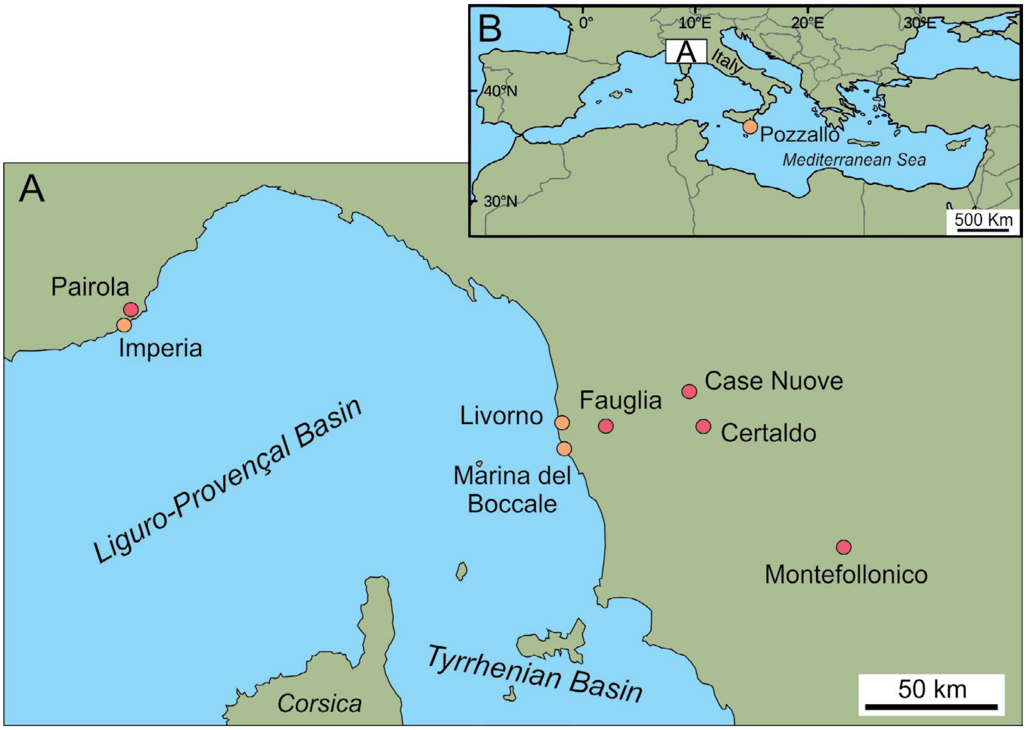

Fig. 1. Geographic position of the sampled localities. A, location of the studied Pliocene and Pleistocene outcrops (red circles) and sampling sites of all modern barnacles but *Chelonibia testudinaria* (orange circles). B, location of the study area in the Mediterranean region and sampling site of the modern *C. testudinaria* specimens.

(Fig. 1).The oldest such deposits are those of the Lower Pliocene succession cropping out at the western Ligurian locality of Pairola (Imperia Province) (Fig. 2A, B) (Giammarino *et al.* 2010; Dalla Giovanna 2016; Coletti *et al.* 2021). Three main coarse-grained, mixed siliciclastic-bioclastic facies are identified in the studied succession, which are mainly composed of calcirudites: a barnacle-dominated facies that developed in a shallow (less than 15 m deep), nearshore palaeoenvironment; a foraminifera-dominated facies from deeper waters (ranging between 40–100 m); and an intermediate facies situated in-between (Coletti *et al.* 2021). The barnacle-rich layers date back to the early–middle Zanclean and originated in a semi-enclosed, high-energy coastal environment at water depths of less than 30 m (Coletti *et al.* 2021).

The mid-Pliocene succession of Certaldo (Florence Province) is located in the Valdelsa Basin of central Tuscany (Benvenuti *et al.* 2014). The deposits comprise mainly shelf mudstones belonging to the Argille Azzurre Formation, where several shell beds host barnacles as well as molluscs and fish remains (Fig. 2C, D). These deposits have been referred to the upper Zanclean – lower Piacenzian interval, and interpreted as resulting from offshore deposition at depths of a few tens metres (Benvenuti *et al.* 2014; Dominici *et al.* 2018).

The succession exposed at Case Nuove (also known as Casenuove - Pozzale; Florence Province) (Fig. 2E) includes mid-Piacenzian paralic sequences that deposited along the northern edge of the Valdelsa Basin (Dominici *et al.* 1995; Benvenuti *et al.* 2014) (Collareta *et al.* 2020, 2021; Merella *et al.* 2023). Within this succession, a balaenid skeleton was preserved along with many epizoic barnacles (Bianucci 1996; Collareta *et al.* 2016). The palaeoenvironment is reconstructed as a very shallow setting, likely less than 10 metres water depth, and possibly an interdistributary bay (Dominici *et al.* 1995).

Another Upper Pliocene succession is found at Montefollonico (Siena Province), in the Siena-Radicofani Basin of eastern Tuscany (Martini *et al.* 2021). The fossil-rich calcirudites exposed at this locality (Fig. 2F) are thought to have deposited in a low-energy setting along a sheltered coast (Nalin *et al.* 2016). Here, a barnacle-dominated facies has been recognized (Coletti *et al.* 2024).

Finally, the Lower Pleistocene Fauglia succession is located in the northern sector of the Tora-Fine Basin, one of the westernmost Neogene extensional basins of Tuscany (Bossio *et al.* 1999). At the Montalto Quarry, highly fossiliferous marine siltstones and sandstones are exposed (Fig. 2G). They are attributed to the Calabrian Sabbie di Nugola Vecchia Formation (Bosio

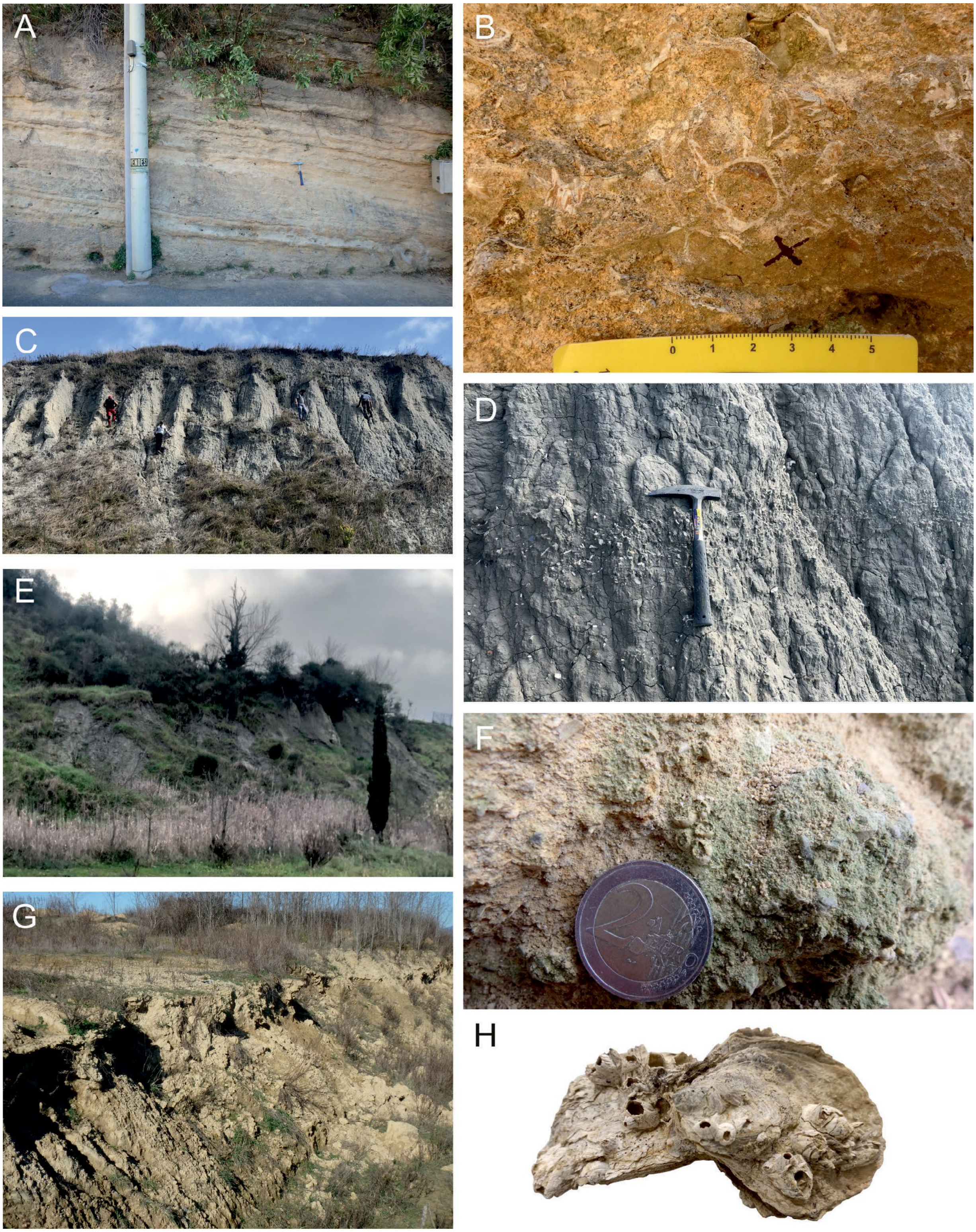

Fig. 2. Field photos of the studied outcrops. A, the Lower Pliocene succession exposed at Pairola. B, close-up of the barnacle-dominated facies of Pairola. C, the mid-Pliocene succession exposed at Certaldo. D, barnacle-rich shell bed cropping out at Certaldo. E, the Case Nuove locality, where an Upper Pliocene succession crops out in an abandoned quarry. F, detail of the Upper Pliocene, barnacle-dominated facies exposed at Montefollonico. G, the Lower Pleistocene succession cropping out at Fauglia. H, detail of a barnacle-encrusted oyster from the barnacle-rich oyster reef exposed at Fauglia.

et al. 2021). These deposits indicate a protected, marginal-marine setting, featuring a *Posidonia oceanica* meadow, a *Cladocora caespitosa* bank and an *Ostrea edulis* reef (Bosio *et al.* 2021; Mariani *et al.* 2022). The barnacle-rich layer coincides with the oyster reef horizon (Fig. 2H), which originated at some 5-10 m water depth (Bosio *et al.* 2021; Collareta *et al.* 2024).

Material

Fossil specimens of *Concavus concavus* (Bronn, 1831) were collected at Pairola (43.94°N; 8.09°E), Certaldo (43.56°N; 11.03°E) and Montefollonico (43.13°N; 11.73°E) (Fig. 1). Specimens of *Perforatus perforatus* (Bruguière, 1789) were collected at Fauglia (43.56°N; 10.53°E) (Fig. 1). Both the extinct *C. concavus* and the extant *P. perforatus* belong in the same subfamily of Balanidae, namely, Concavinae (Menesini 1965; Newman 1982; Zullo 1992). In addition, specimens of the common turtle barnacle, *Chelonibia testudinaria* (Linnaeus, 1758), were collected at Case Nuove (43.69°N; 10.95°E) (Fig. 1, 4) (Table 1).

Concavus concavus specimens were collected from the Lower Pliocene rudstones and packstones of Pairola (Fig. 4A), the oldest studied succession. According to Coletti *et al.* (2024), they are often fragmented, and usually exhibit a poor preservation state, corresponding to Type 7 of Doyle *et al.* (1996) and Type D of Nomura & Maeda (2008). Some shells are found in small clusters of relatively well-preserved specimens that have been dislodged from their substrate (Fig. 4A), matching Type 2 of Doyle *et al.* (1996) and Type C of Nomura & Maeda (2008). Opercular plates are very rare and invariably separated from their corresponding shells (Coletti *et al.* 2024).

Barnacle specimens from the mid-Pliocene deposits of Certaldo were collected from open shelf mudstones (Coletti *et al.* 2024) (Fig. 4B). According to Coletti *et al.* (2024), these barnacles are mostly found as displaced individuals, which conforms to Type 2 (Doyle *et al.* 1996) and Type C (Nomura & Maeda, 2008). In addition, rare individuals occur attached to their original shelly substrate, though the latter are no longer found in life position (see Fig. 4B; Type B of Nomura & Maeda, 2008). Disarticulated and fragmented plates, representing Type 7 of Doyle *et al.* (1996) and Type D of Nomura & Maeda (2008), were also collected. In all these cases, whole barnacle shells as well as shell fragments are typically well preserved, retaining the original pigmentation and showing no signs of abrasion (Fig. 4B), being classified in the Grade 0 of Nielsen & Funder (2003). In addition, the fragile opercular plates (both scuta and terga) are usually abundant, being still articulated to the corresponding shells in most cases.

Table 1. List of the analysed barnacle-rich and barnacle-dominated facies and localities. Modified after Coletti *et al.* (2024)

Site	**Age**	**Type of barnacle accumulation**	**Setting**	**Water depth**	**Lithology**	**Barnacle species**
Pairola	lower-middle Zanclean	Barnacle-dominated facies	High-energy, nearshore coastal setting	0–15 m	Coarse-grained, mixed siliciclastic bioclastic	*Concavus concavus*
Certaldo	upper Zanclean-lower Piacenzian	Barnacle-rich layer	Low-energy, open shelf setting	> 40 m	Shell-rich calcareous mudstone	*Perforatus perforatus*
Case Nuove	middle Piacenzian	Barnacle-rich layer	Low-energy, nearshore coastal embayment	0–10 m	Shell-rich calcareous sandy siltstone	*Chelonibia testudinaria*
Montefollonico	Piacenzian	Barnacle-dominated facies	Moderate-energy, nearshore coastal setting	20–40 m	Coarse-grained, mixed siliciclastic bioclastic	*Perforatus perforatus*
Fauglia	Calabrian	Barnacle-rich oyster reef	Moderate-energy, nearshore coastal setting (possibly a coastal embayment)	5–10 m	Coarse-grained, mixed siliciclastic bioclastic	*Perforatus perforatus*

In the Upper Pliocene deposits of Case Nuove, a bioclastic sandstone to siltstone layer hosts a partial mysticete (baleen whale) skeleton, in close proximity of which tens of turtle barnacle shells have been found (Fig. 4E). This association suggests that the barnacles lived as epibionts on the baleen whale, from

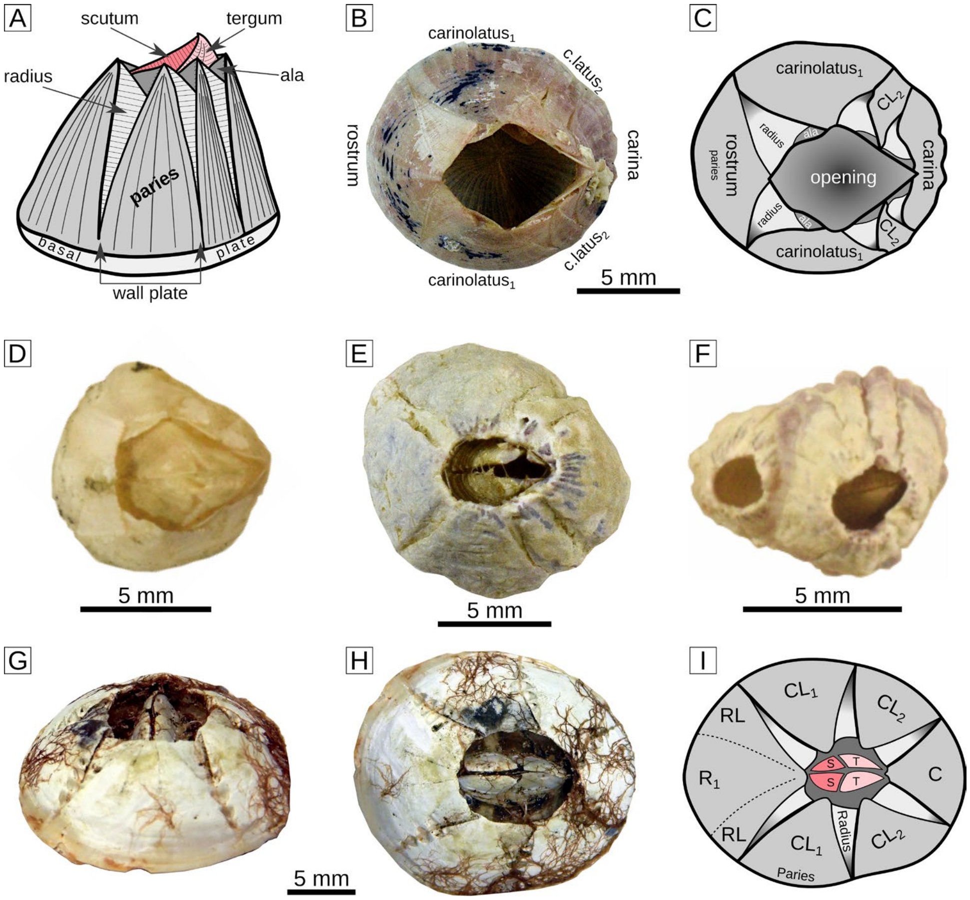

Fig. 3. Macroscopic images of the barnacle shells. A, generalized structure of a balanid barnacle shell in external view (modified after Buckeridge 1983). B, modern *Amphibalanus amphitrite* specimen from Imperia. C, interpretative structure of the barnacle shown in panel B. D, modern *A. amphitrite* specimen from Livorno. E, modern *Perforatus perforatus* specimens from Imperia. F, modern *P. perforatus* specimen from Marina del Boccale. G, H, modern *Chelonibia testudinaria* specimen from Pozzallo. I, generalized structure of a chelonibiine shell modified from Collareta *et al.* (2022).

which they detached after death as the cetacean soft tissues decayed (Collareta 2020; Coletti *et al.* 2024). The specimens are found both as disarticulated valves and as complete or nearly complete shells (Fig. 4E); however, the taphonomic classifications of Doyle *et al.* (1996) and Nomura & Maeda (2008) cannot be applied due to the epizoic nature and membraneous base of *C. testudinaria*. In any case, the shell morphology is very well preserved and evidence of abrasion was not detected (Fig. 4E), thus conforming to Grade 0 of Nielsen & Funder (2003) (Coletti *et al.* 2024).

At Montefollonico, *C. concavus* specimens are found in Late Miocene fine-grained calcirudite deposits. The analysed specimens usually exhibit a moderate to good preservation state, with some retaining the original pigmentation of the shell. According to Coletti *et al.* (2024), they are usually found as displaced clusters, but some are still attached to the corresponding substrate (e.g. pebbles and rhodoliths), though not in life position, thus corresponding to Type 2 of Doyle *et al.* (1996) and Type C of Nomura & Maeda (2008), respectively (Fig. 4C). Disarticulated and fragmented plates are also common, conforming to Type 5 of Doyle *et al.* (1996) and Type D of Nomura & Maeda (2008). Shells also exhibit some evidence of abrasion and fragmentation, allowing for identifying Grades 0 and 1 of Nielsen & Funder (2003). Opercular plates (mainly scuta) are also commonly found sparse within the sediment.

Coletti et al. (2024) recorded *P. perforatus* from the Lower Pleistocene oyster reef of Fauglia, from which some specimens were essentially complete, including the delicate opercula (Fig. 4D). In light of this, they can be classified as Type 1 of Doyle *et al.* (1996) and Type A of Nomura & Maeda (2008)

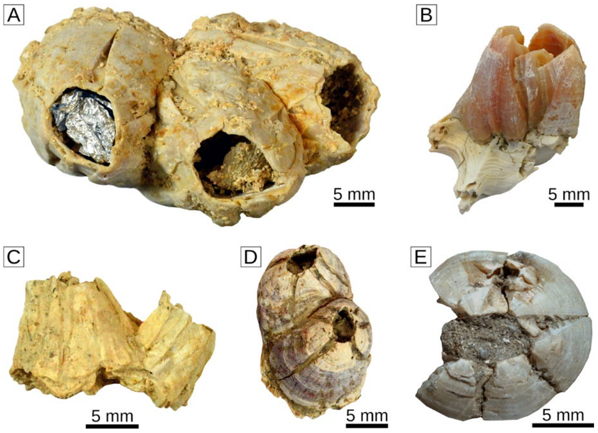

Fig. 4. A, cluster of fossil *Concavus concavus* specimens from Pairola. B, fossil *C. concavus* specimen from Certaldo, retaining its pink pigmentation. C, fossil *C. concavus* specimens from Montefollonico. D, cluster of fossil *Perforatus perforatus* specimens from Fauglia. E, fossil *Chelonibia testudinaria* specimen from Case Nuove. For detailed images of the opercular plates see Coletti *et al.* (2024).

(Coletti *et al.* 2024). Moreover, shells do not display any evidence of abrasion or fragmentation (Grade 0 of Nielsen & Funder, 2003). Though the macroscopic preservation state is good overall, shells are distinctly compressed diagenetically (Fig. 4D).

As a reference point, Recent specimens of *Amphibalanus amphitrite* (Darwin, 1854) were collected from Imperia, western Liguria (43.88°N, 8.05°E), and Livorno, southern Tuscany (43.56°N, 10.31°E) (Figs 1, 3A–D). *Perforatus perforatus* was also collected at Imperia, western Liguria (43.88°N, 8.05°E) and at Marina del Boccale, southern Tuscany (43.47°N, 10.32°E) (Figs 1, 3E,F). Finally, *C. testudinaria* was obtained at Pozzallo, southern Sicily (36.72°N, 14.85°E) (Figs 1, 3G–I). All specimens apart from *C. chelonibia* – which were removed from a beached loggerhead turtle, *Caretta caretta* (Linnaeus, 1758) – come from water depths of less than one metre.

Analytical methods

Twenty-three thick and thin sections were prepared following the method outlined by Coletti *et al.* (2019) and Collareta *et al.* (2019), embedding repeatedly the barnacle shell in epoxy resin, and then proceeding with cutting transversally the shell at various heights (near the base of the shell, just above the base of the sheath and close to the apex of the shell) by using a Buehler IsoMet, low-speed, precision-cutting machine at the Università degli Studi di Milano-Bicocca.

Thin sections were observed under a Leica transmitted-light optical microscope at the Università degli Studi di Milano-Bicocca. Seven such sections, including both modern and fossil specimens from all the studied localities, were examined using a CITL Optical CL microscope stage at the Università degli Studi di Milano-Bicocca. The microscope was operated at a voltage of 6.3 kV, with a current intensity of about 1.1 mA, under a vacuum of about 7.3 Pa.

Following Crippa *et al.* (2016), thick sections were first polished with 400- and 1000 SiC abrasive powder, and then briefly etched with diluted HCl for less than 15 seconds for highlighting structures. These sections were carbon-coated and observed for morphological analyses through a Zeiss FEG Gemini 500 SEM operating at 3.0 kV at the Università degli Studi di Milano-Bicocca. SEM images were examined in order to characterize and compare the micro- and ultrastructure of fossil and modern specimens as well as for identifying possible evidences of erosion, dissolution and recrystallization during biostratinomic and diagenetic processes.

Results

Microscopic structure

All studied barnacle shells feature an inner and an outer lamina (Fig. 5). Between the inner and outer laminas are distinct longitudinal tubes. The longitudinal tubes are separated from each other by septa, which in transverse section can be seen to form interlaminate figures (Fig. 5). Except for *Chelonibia*, these reflect the complex interlocking between the wall plates and the calcareous base, which articulate with each other without being cemented to each other to allow for the growth of the shell (Bourget 1977). The parietal tubes are partially or entirely infilled secondarily (during life) by concentric rings of biogenic carbonate. The sheath usually exhibits concentric laminations (Fig. 5F, G.) The internal sutural edges, where the wall plates meet each other, do typically display interlocking tooth-like projections with different degrees of complexity. These structures provide strength and durability to the shell while permitting the growth of the body chamber. Although these first-order structural elements are shared by all the investigated specimens, both recent and fossil, some microtaphonomic considerations are still possible. In the barnacle specimens from Montefollonico, Pairola and Fauglia, the large parietal tubes are diagenetically filled by drusy crystals of carbonate cement (Fig. 5D, E, H), which suggests that they have been rather severely affected by diagenesis. In contrast, specimens from Case Nuove and Certaldo are typified by empty parietal tubes, suggesting that diagenetic alteration was minor overall (Fig. 5G, I, J). In addition, modern specimens of both *Chelonibia testudinaria* and *Perforatus perforatus* and one fossil specimen from Certaldo have the outer lamina perforated by microborings, which however are best visible under the SEM (see paragraph below).

Ultrastructure

SEM observation of modern shells reveal that different species of epizoic and non-epizoic barnacles exhibit a similar ultrastructure, without variations at different shell heights or among the inner lamina, the outer lamina and the sheath. In particular, the modern species *Amphibalanus amphitrite* from Livorno

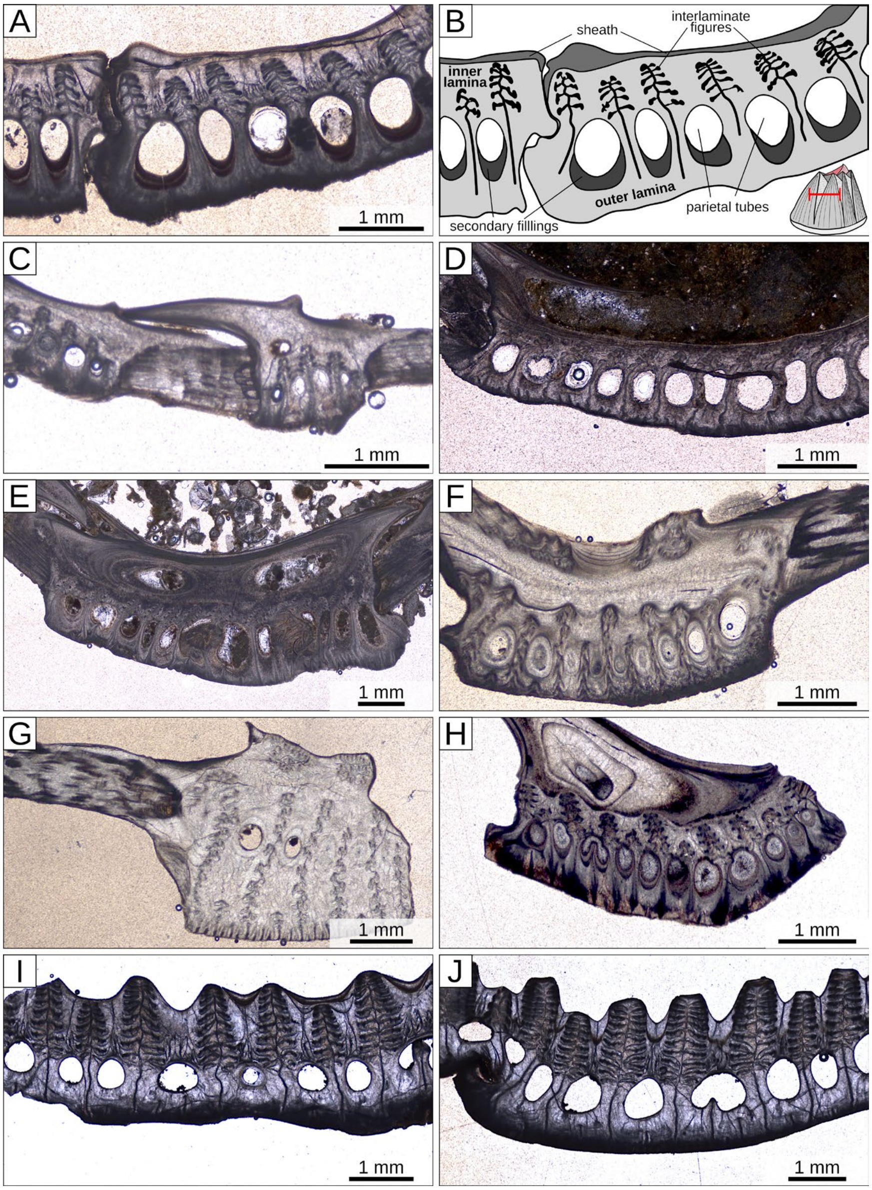

Fig. 5. Recent and fossil barnacle shells in transverse thin section. A, microstructure of a modern *Perforatus perforatus* specimen from Imperia. B, internal structure of the wall plate and the sheath as interpreted by the transverse section shown in panel A. C, microstructure of a modern *Amphibalanus amphitrite* specimen from Livorno. D, microstructure of a fossil *P. perforatus* specimen from Fauglia. E, microstructure of a fossil *Concavus concavus* specimen from Pairola. F, microstructure of a modern *Chelonibia testudinaria* specimen from Pozzallo. G, microstructure of a fossil *C. testudinaria* specimen from Case Nuove. H, microstructure of a fossil *C. concavus* specimen from Montefollonico. I. microstructure of a fossil *C. concavus* specimen from Certaldo. J, microstructure of the same *C. concavus* specimen as in panel I, observed along a cut slightly closer to the apex of the barnacle shell.

(Fig. 6A–C) and Imperia (Fig. 6D–F), and *Perforatus perforatus* from Imperia (Fig. 6G–I) and Marina del Boccale (Fig. 6J–L) exhibit the same crystal pattern in transverse section. At the micro-scale, the lamellar structure is revealed to consist of loosely packed, scale-like elements measuring from 1 to 5 μm in length and about 1 μm in thickness (Fig. 6). These scales are arranged in a complex 3D disposition with irregular spaces and crevices ('dragon-scale pattern' *sensu* Coletti *et al.* 2024). This structural arrangement results in the growth lines that are visible under an optical microscope at low magnification. At the nanoscale, porosity can be detected both in-between the scales and within the scales themselves (Fig. 6), thus confirming the porous nature of the barnacle shell at all levels.

Low-magnification (1.4k×) SEM observations reveal no significant differences between the modern and fossil specimens (Figs 6–8). However, at higher magnification (2.8k and 9.3k×), specimens of *Concavus concavus* from Certaldo (Fig. 7A–C) and Montefollonico (Fig. 7D–F) possess bulkier scales with more poorly defined margins than modern specimens. Fossil specimens from these localities show indeed the best-preserved shell structure at different magnifications. On the other side of the preservational spectrum, in the *C. concavus* specimens from Pairola, the dragon-scale pattern is entirely obliterated, with no discernible microstructural and ultrastructural patterns (Fig. 7G–I). The *P. perforatus* specimens from Fauglia exhibit variable degrees of ultrastructural preservation, with some displaying a

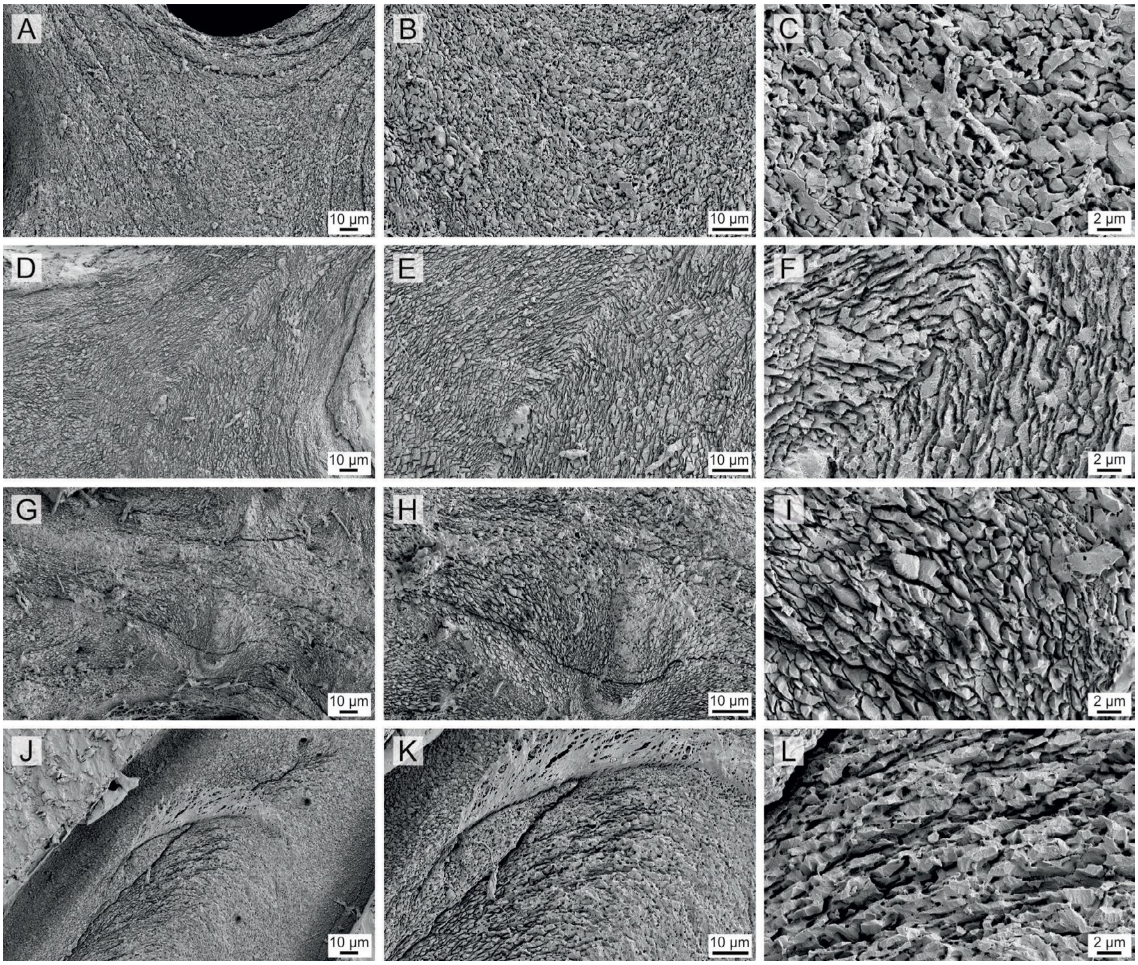

Fig. 6. SEM images of recent barnacles. A–C, ultrastructure of the wall plate of a modern specimen of *Amphibalanus amphitrite* from Livorno at different magnifications. D–F, ultrastructure of the wall plate of a modern specimen of *A. amphitrite* from Imperia at different magnifications. G–I, ultrastructure of the wall plate of a modern specimen of *Perforatus perforatus* from Imperia at different magnifications. J–L, ultrastructure of the sheath of a modern specimen of *P. perforatus* from Marina del Boccale at different magnifications.

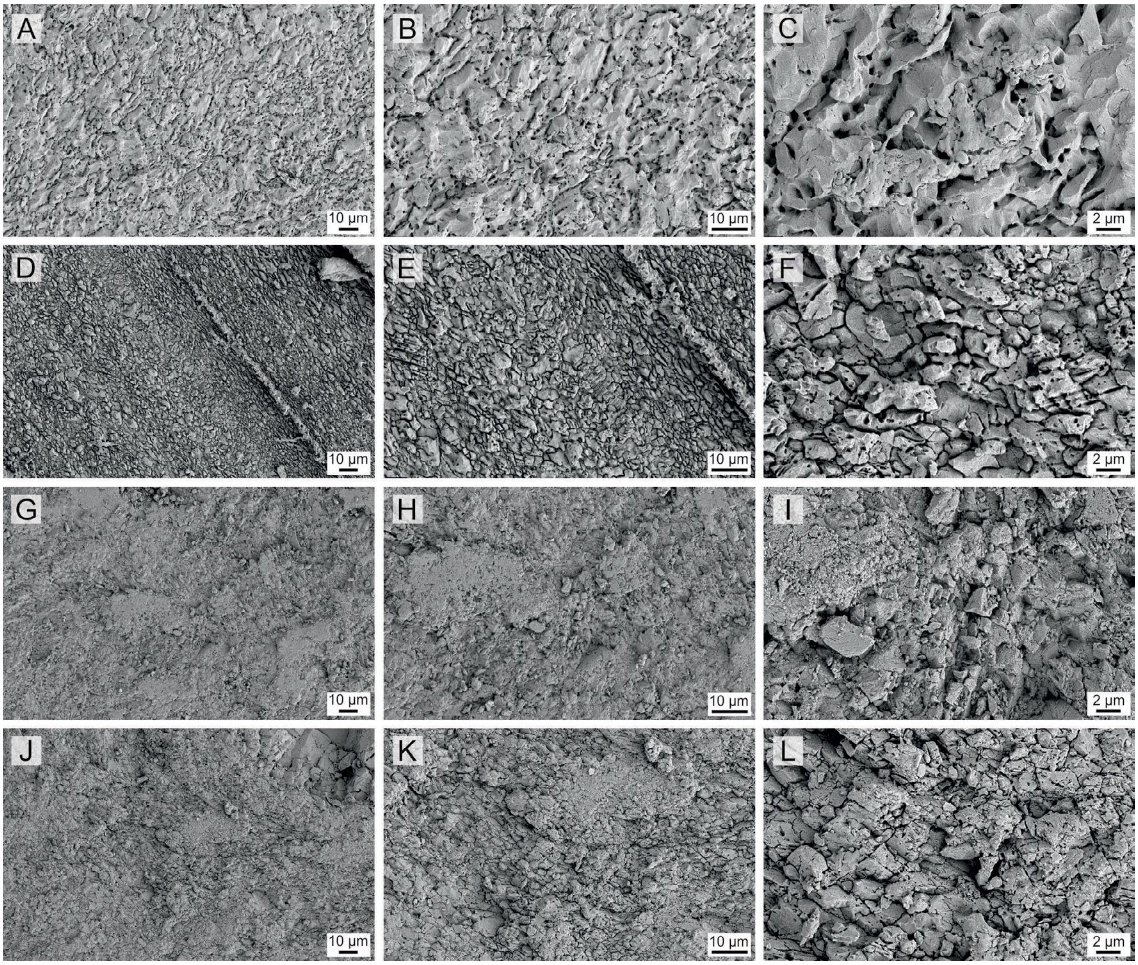

Fig. 7. SEM images of well-preserved and poorly preserved fossil barnacles. A–C, ultrastructure of the wall plate of a well-preserved fossil specimen of *Concavus concavus* from Certaldo at different magnifications. D–F, ultrastructure of the sheath of a well-preserved fossil specimen of *C. concavus* from Montefollonico at different magnifications. G–I, ultrastructure of the wall plate of a poorly preserved fossil specimen of *C. concavus* from Pairola at different magnifications. J–L, ultrastructure of the wall plate of a poorly preserved fossil specimen of *P. perforatus* from Fauglia at different magnifications.

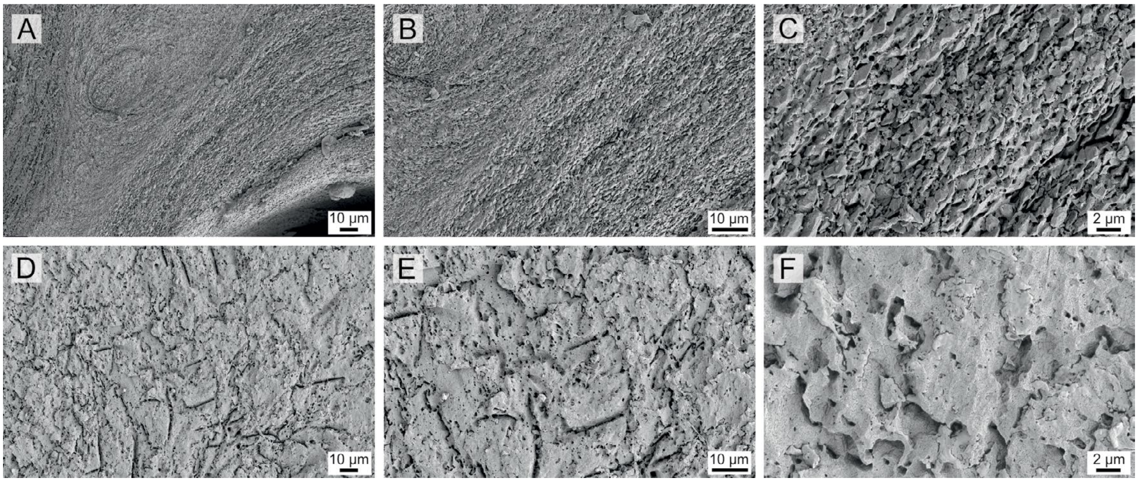

Fig. 8. SEM images of recent and fossil *Chelonibia testudinaria* shells. A–C, ultrastructure of the wall plate of a modern specimen from Pozzallo at different magnifications. D–F, ultrastructure of the wall plate of a moderately well-preserved fossil specimen from Case Nuove at different magnifications.

complete obliteration of the micro- and ultrastructure (Fig. 7J–L), thus resembling the Pairola specimens. The dragon-scale pattern is also clearly present in the modern *Chelonibia testudinaria* specimen from Pozzallo, resembling the non-epizoic barnacle samples in terms of both scale arrangement and scale size (Fig. 8A–C). In the fossil *C. testudinaria* specimen from Case Nuove, the ultrastructure is poorly preserved, but not totally obliterated. Scales are larger, more irregular, and have poorly defined margins compared to its modern counterpart (Fig. 8D–F). Consistent with these microstructural observation, the modern specimens exhibit intact interlaminate figures and empty parietal tubes (Fig. 9G), whereas some fossil samples such as the *P. perforatus* specimen from Fauglia show widepsread recrystallization and parietal tubes that are partly filled by very large crystals in a drusy-like fashion (Fig. 9H). SEM images reveal interesting shell modification patterns. The modern specimens of *C. testudinaria* from Pozzallo (Fig. 9A–D) and *P. perforatus* from Imperia (Fig. 9E) feature the pervasive occurrence of several resin-casts of microborings that penetrate into the outer wall. They occur as filamentous structures, 2–5 μm across and up to hundreds microns long, ranging from almost straight to strongly bent in shape, which may (or may not) branch (Fig. 9A–E). Thinner microboring casts, down to less than 1 μm across, can also be observed in one specimen of *C. concavus* from Certaldo (Fig. 9F).

Cathodoluminescence

Along with the SEM observations, the cathodoluminescence analyses allowed for the recognition of different degrees of alteration in the fossil specimens compared to their modern counterparts. Recent barnacle shells, including both epizoic and non-epizoic forms, display a very weak luminescence lining the interlaminate figures, the inner wall of the parietal tubes, the outer surface of the inner lamina and the growth lines of both laminae, ranging in colour from blue to very light reddish (Figs 10A–D, 11E,F). In particular, *Perforatus perforatus* from Imperia shows a predominant low blue and purple luminescence lining the interlaminate figures and the parietal tubes (Fig. 10A, B), whereas the modern *Amphibalanus amphitrite* from Livorno exhibits a general low blue luminescence and a low reddish luminescence that concentrates around the inner wall of the parietal tubes (Fig. 10C, D). As regards the epizoic forms, the modern specimen of *Chelonibia testudinaria* from Pozzallo shows a predominant low blue luminescence, similar to that observed for the non-epizoic barnacles (Fig. 11E, F).

Fossil specimens span across a broad spectrum of luminescence types. The least luminescent sample, namely, the *C. concavus* specimen from Certaldo, displays a low purple luminescence of the interlaminate figures and a moderate red luminescence of the outer wall (Fig. 10E, F). The conspecific fossil specimen from Montefollonico shows a moderate purple to red luminescence along the inner lamina and the interlaminate figures, and luminescent (red-coloured) parietal tubes that have been filled by diagenetic calcite (Fig. 10G, H). On the other hand, the *C. concavus* specimen from Pairola displays a high, fully red-coloured luminescence, and a diagenetic filling of the parietal tubes consisting of sparitic and drusy calcite crystals (Fig. 11A, B). The *P. perforatus* specimen from Fauglia is the most luminescent: it displays a very strong, red to orange and yellow luminescence throughout the shell and parietal tubes, the latter being filled by drusy sparitic calcite (Fig. 11C, D). Similar to the moderately well-preserved barnacle specimens from Certaldo and Montefollonico, the fossil *C. testudinaria* shell from Case Nuove exhibits a moderate purple to red luminescence that concentrates along the growth lines and interlaminate figures (Fig. 11G, H).

Discussion

Macroscopic observations provide useful insights into the preservation of barnacle specimens and their depositional environments. Well-preserved, complete specimens, when not related to rapid burial, tend to be associated with sheltered, low-energy settings, whereas poorly preserved, disarticulated, fragmented remains are the rule in more exposed settings (Nielsen & Funder 2002; Coletti *et al.* 2024). A key indicator is provided by the presence/absence of the opercular plates, because these delicate structures are often displaced and lost in high-energy environments. According to Coletti *et al.* (2024), fossil barnacles from coarse-grained deposits characterized by high values of primary porosity, such as sandstones, packstones and rudstones, display a poor (at Pairola and Fauglia) to intermediate (at Montefollonico) preservation at all scales. The *Concavus concavus* specimens from Pairola and those of *Perforatus perforatus* from Montefollonico are mostly fragmented, with poor to moderate macroscopic preservation and some indications of abrasion, thus indicating moderate energy conditions, with the exception of barnacles found attached to their own substrate (at Fauglia). On the contrary, in fine-grained sediments

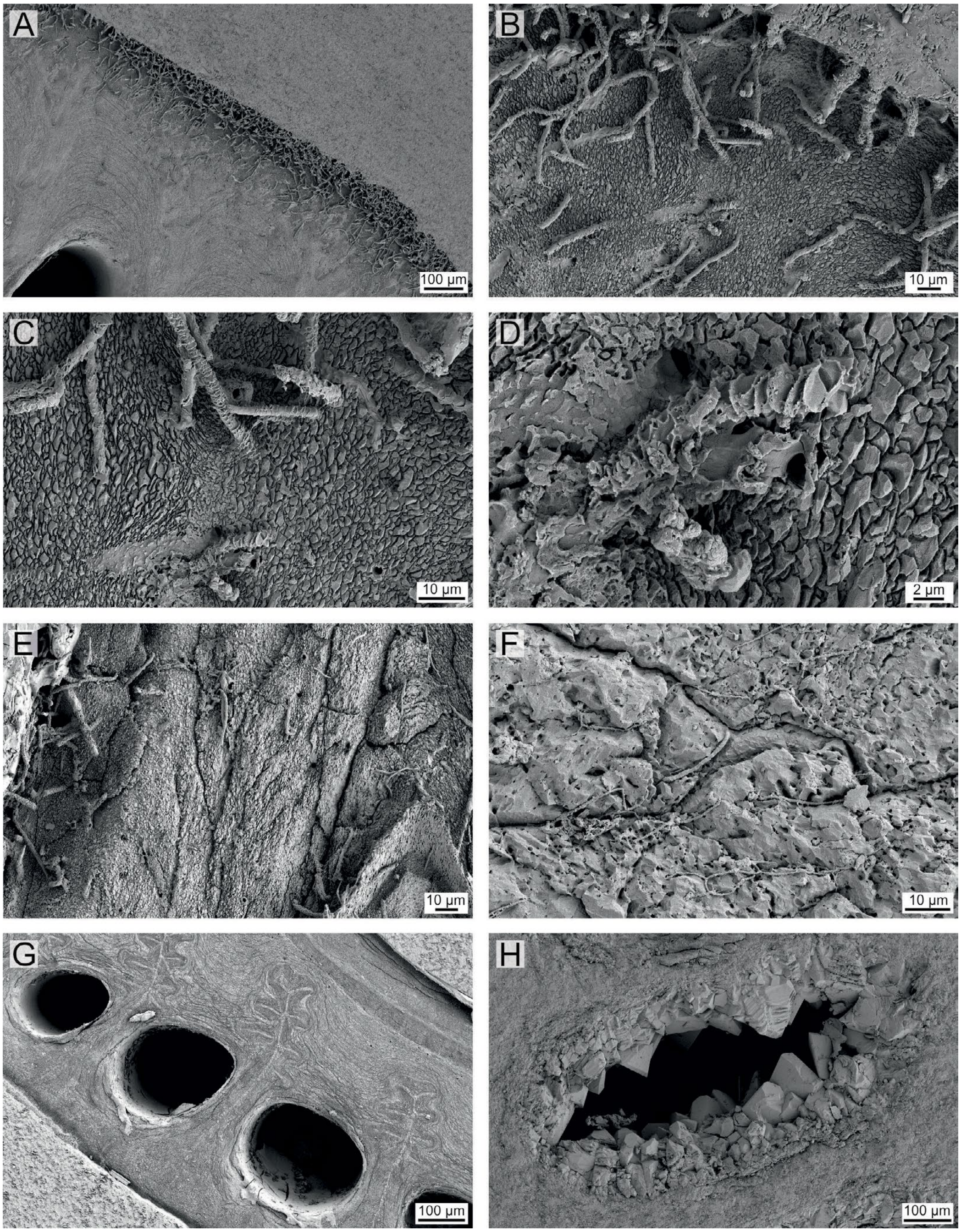

Fig. 9. SEM images showing taphonomic details of the analysed barnacle shells. A, microborings along the outer wall of the modern *Chelonibia testudinaria* shell from Pozzallo. B, resin-cast of the microborings occurring along the outer wall of the modern *C. testudinaria* shell from Pozzallo; they are tentatively assigned to the ichnogenera *Fascichnus*, *Scolecia* and *Eurygonum*. C, close-up of the microborings in Figure 8B. D, close-up of the microborings in Figure 8C. E, resin-cast microborings characterizing modern *Perforatus perforatus* from Imperia; they are tentatively assigned to the ichnogenera *Fascichnus*, *Scolecia* and *Eurygonum*. F, microborings occurring along the outer wall of a fossil *Concavus concavus* shell from Certaldo. G, shell ultrastructure of *Amphibalanus amphitrite* from Imperia, showing the interlaminate figures and empty parietal tubes. H, parietal tube of a fossil *P. perforatus* specimen from Fauglia filled with a drusy carbonate cement forming very large crystals.

such as those that entombed the *Chelonibia testudinaria* specimens from Case Nuove and the *P. perforatus* specimens from Certaldo, the shell morphology and original colour are well preserved, with no signs of abrasion. In summary, the macroscopic expression of barnacle preservation is strongly controlled by the hydrodynamic conditions of the depositional environment as well as by the subsequent diagenetic processes.

At the microscale, all specimens consist of an inner and an outer lamina, in-between are characteristic tree-like interlaminate figures and parietal tubes (Bourget 1977). The preservation of these internal structures has major consequences on all aspects of (acorn) barnacle palaeontology as their highly diagnostic value has been well known since the pioneering studies of Cornwall (1956, 1958, 1959, 1960, 1962) and Davadie (1963).

No significant differences were found among the analysed fossil and recent specimens. However, the barnacles from Montefollonico, Pairola and Fauglia exhibit drusy carbonate crystals filling the parietal tubes, thus highlighting a diagenetic imprint (Fig. 5D, E, H). On the other hand, the shells from Case Nuove and Certaldo display empty parietal tubes that suggests no precipitation from the diagenetic fluids (Fig. 5G, I, J). Though microscopical observations under conventional optical microscopy are not sufficient to differentiate between pristine and altered samples, analyses at higher magnification such as SEM imaging can help in this issue. Previous studies have shown that crystals are arranged massively in the outer shell wall, whereas in the inner wall they form an oriented disposition (Rodríguez-Navarro *et al.* 2006), and the same is true for the opercular plates (Khalifa *et al.* 2011). On the other hand, the radii and alae are formed by elongated fibrous crystals (Murdock & Currey 1978; Mitchell *et al.* 2019; Checa *et al.* 2019, 2020) permeated by a pore network of likely organic channels and pockets involved in the biomineralization process (Mitchell *et al.* 2019). Some variations among barnacle genera might exist (Mitchell *et al.* 2019), but recent investigations suggest that the same heterogeneous mix of crystallite dimensions and morphologies should invariantly occur across different barnacle species (Shaw *et al.* 2024). Our exploration of the ultrastructure of the wall plates reveals a consistent pattern across the studied barnacle species, both extinct and extant. At the ultrastructural level, the modern specimens of both epizoic and non-epizoic barnacles exhibit loosely packed scale-like crystals arranged in the 'dragon-scale pattern' described by Coletti *et al.* (2024) (Figs 6–8). The studied fossil specimens reflect different degrees of preservation of this pattern. The Pliocene specimens of *P. perforatus* from Montefollonico and Certaldo preserve a dragon-scale ultrastructure where the scales retain their original arrangement (Fig. 7). However, they are bulkier and exhibit poorly defined margins compared to the modern samples, thus suggesting a slight alteration due to diagenesis. In contrast, specimens from the coarse-grained sediments of Pairola and Fauglia are more strongly altered, their original ultrastructural pattern being entirely obliterated in some cases (Fig. 7). This indicates that these fossil shells underwent more extensive diagenetic changes, likely due to exposure to unfavourable post-depositional conditions such as the percolation of diagenetic fluids through the sediment pores. An intermediate degree of preservation is observed for the Case Nuove chelonibiids (Fig. 8).

Erosional microstructures are found in both modern and fossil barnacles. In the first case, they are preserved in both epizoic and non-epizoic forms. In the latter case, they have only been recognized in a well-preserved specimen from Certaldo. The observed features are interpreted as microbial borings, which are produced by a wide array of endolithic prokaryotes and eukaryotes, including phototrophic (e.g. cyanobacteria, algae) as well as heterotrophic (e.g. fungi, foraminifera) forms (e.g. Chacón *et al.* 2006; Glaub *et al.* 2007; Färber *et al.* 2015; Salamon *et al.* 2019; Golubic *et al.* 2019; Kočí *et al.* 2024b). In particular, the microborings observed in the modern examples (Fig. 9A–E) are reminiscent of the morphological diversity of the ichnogenera *Fascichnus*, *Scolecia* and *Eurygonum* (Radtke 1991; Perry & Macdonald, 2002; Försterra *et al.* 2005; Seuss *et al.* 2015; Wisshak *et al.* 2019; Mono *et al.* 2023), which are produced by cyanobacteria (e.g. Radtke & Golubic 2005, 2011). Comparable microbioerosional features have recently been described on barnacles from the polar regions, highlighting the occurrence of microborings of phototrophic euendoliths in shells from the shallow euphotic zone (Meyer *et al.* 2020, 2021). A putative attribution to phototrophic endoliths is supported by the very shallow-water (< 1 m) setting inhabited by one of the microbored modern specimens (*P. perforatus*). The microborings observed in the fossil specimen of Certaldo are similar to those of the modern barnacles, suggesting a well-preserved outer wall and a microbial activity due to photosynthesising bioeroders on a relatively sunlit offshore seafloor.

The cathodoluminescence (CL) response of carbonate biogenic shells correlates with their Mn^{2+}content (Glover 1977, Barbin *et al.* 1991). In barnacle shells, the latter reflects the Mn^{2+} availability in the seawater inhabited by the calcifying animals (Gordon *et al.* 1970; Blanchard & Chasteen 1976). Barbin (2000) considered the orange luminescent bands exhibited by barnacle shells to be related to the internal growth bands. However, the author noted that data are insufficient to positively link the CL emission to environmental factors. Based on our results,

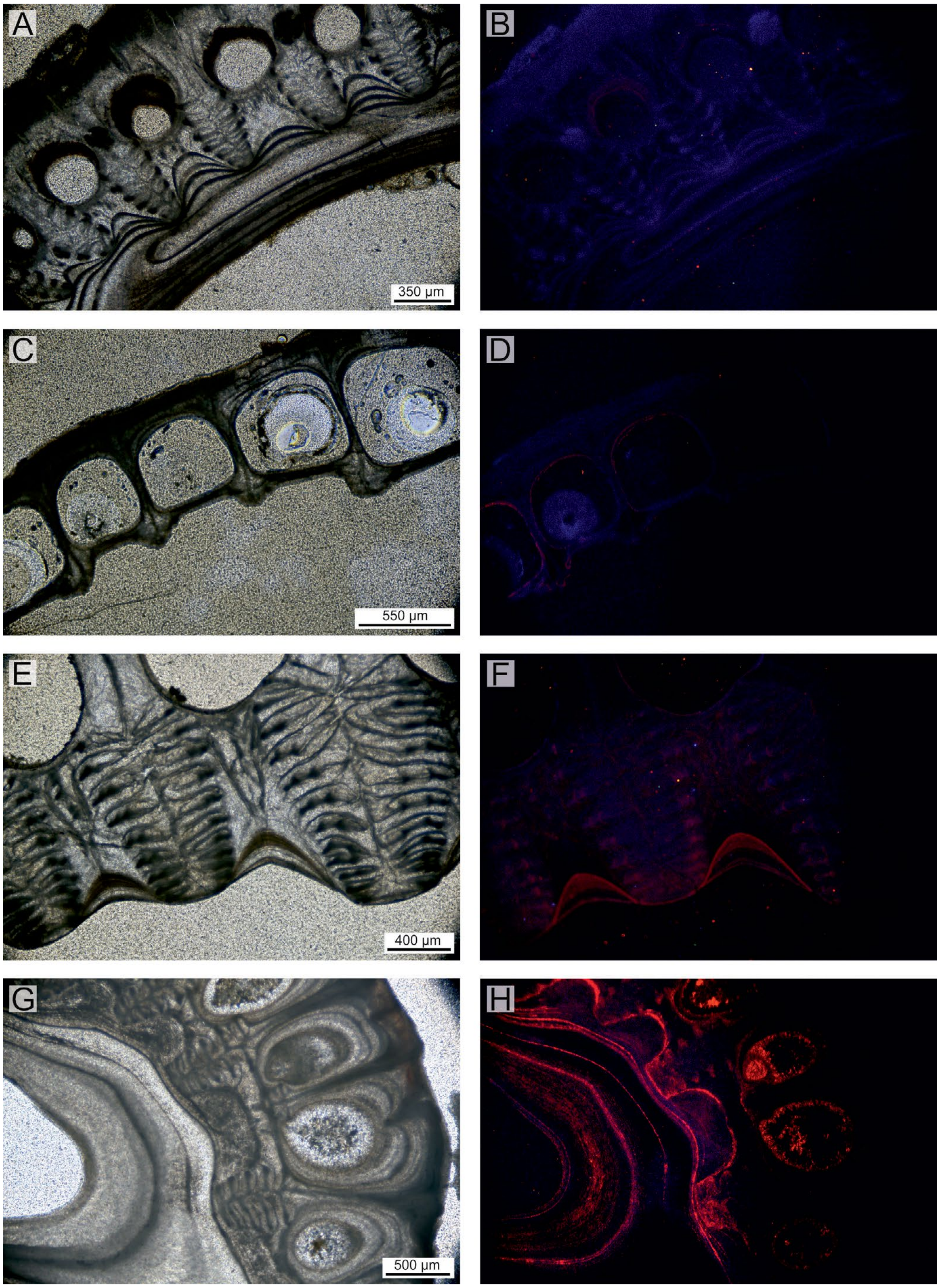

Fig. 10. Transmitted light and cathodoluminescence photomicrographs of barnacle shells. A, B, modern specimen of *Perforatus perforatus* from Imperia, showing a predominant low blue luminescence and a low reddish luminescence around the parietal tubes. C, D, modern specimen of *Amphibalanus amphitrite* from Livorno, showing a predominant low blue luminescence and a low reddish luminescence around the parietal tubes. E, F, fossil specimen of *Concavus concavus* from Certaldo, exhibiting a low purple luminescence of the interlaminate figures and a moderate red luminescence of the outer wall. G, H, fossil specimen of *C. concavus* from Montefollonico, exhibiting a moderate purple to red luminescence.

we can conclude that CL analysis have the potential to provide further insights into the diagenetic alteration in fossil barnacle shells. All the modern barnacle examples exhibit a very weak luminescence, primarily in blue and light reddish tones. This luminescence concentrates along the interlaminate figures, the

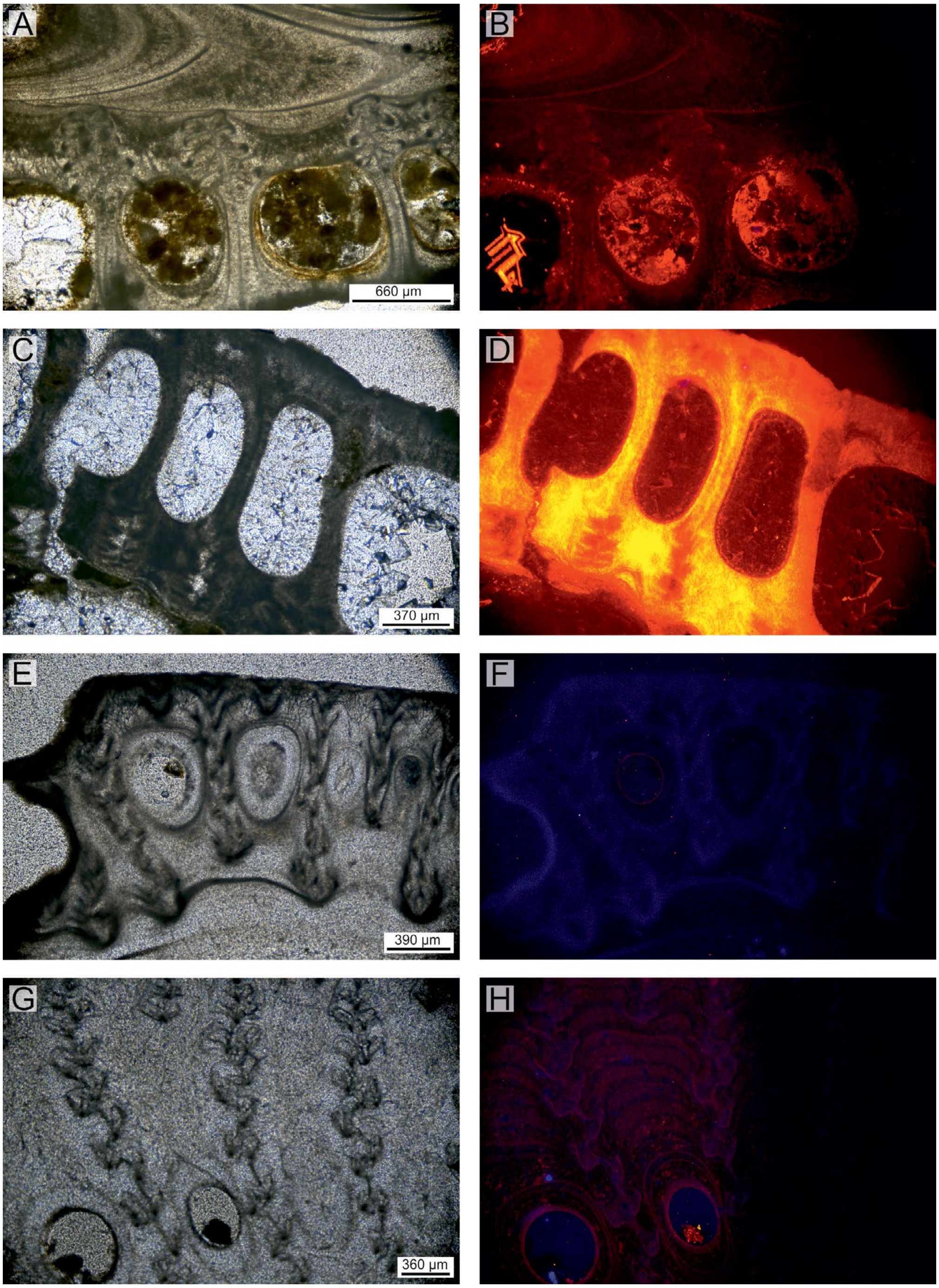

Fig. 11. Transmitted light and cathodoluminescence photomicrographs of barnacle shells. A, B, fossil specimen of *Concavus concavus* from Pairola, showing a high red luminescence and a diagenetic cement fill of the parietal tubes. C, D, fossil specimen of *Perforatus perforatus* from Fauglia, exhibiting a very high red to orange luminescence and a diagenetic cement-fill of the parietal tubes. E, F, modern specimen of *Chelonibia testudinaria* from Pozzallo, showing a predominant low blue luminescence. G, H, fossil specimen of *C. testudinaria* from Case Nuove, exhibiting a moderate purple to red luminescence.

inner walls of parietal tubes, the outer surface of the inner lamina and the growth lines (Figs 10, 11). This is recognizable as the intrinsic luminescence of the CL bands, which in turn correlate with the growth lines (Barbin 1992; Langlet *et al.* 2006). In contrast, the fossil specimens reveal a broader range of luminescence intensities, reflecting the extent of their diagenetic alteration (Figs 10, 11). The *C. concavus* specimen from Certaldo, which is among the least altered samples, displays a low purple luminescence of the interlaminate figures and a moderate red luminescence of the outer wall. Specimens from Case Nuove and Montefollonico exhibit moderate luminescence, transitioning from purple to red along the inner lamina and interlaminate figures, with luminescent parietal tubes that are partially filled with diagenetic calcite in the case of the latter locality. On the other hand, the specimens from Pairola and Fauglia reveal significant diagenetic imprints, with high-intensity red to orange to yellow luminescence permeating the entire shell, thus suggesting substantial diagenetic infilling by sparitic and drusy calcite. This luminescent response is particularly evident in the parietal tubes, which are filled with diagenetic cement, thus indicating extensive post-depositional diagenetic processes. In conclusion, the best-preserved fossil shells exhibit a low to moderate luminescence, from blue to purple to light reddish in colour, similar to the modern counterparts; whereas the poorly preserved specimens with a high diagenetic imprint display a high red to orange to yellow luminescence.

From the field to the laboratory, macroscopic and microscopic analyses helped to establish a protocol for the taphonomic evaluation of fossil barnacle shells. Overall, the integration of taphonomic macroscopic classifications, optical microscopy, SEM observations on the shell ultrastructure and CL analyses allows for a detailed evaluation of the degree of diagenetic alteration of fossil barnacles. On a general note, our results confirm that burial in fine-grained sediments is much less detrimental to the shell preservation at all scales – from the macroscopic features to the micro- and ultrastructure. This is also supported by a better preservation of the original C and O stable-isotope signatures of shells embedded in fine-grained sediments characterized by low permeability (Coletti *et al.* 2024). Barnacle shells from coarse-grained deposits such as those from Fauglia and Pairola exhibit a more impactful diagenetic imprint, including widespread recrystallization of the shell carbonates and the infilling of parietal tubes with diagenetic carbonate cement. These changes are likely the result of exposure to diagenetic fluids and/or meteoric waters, which can lead to the dissolution and recrystallization of the shell materials (e.g. Flügel 2004; Pederson *et al.* 2019).

Conclusions

This study demonstrates that a combined approach, including a macroscopic taphonomic assessment, microscopic (optical and SEM) ultrastructural analyses and cathodoluminescence (CL) investigations, provides a robust framework for evaluating fossil barnacle preservation and diagenetic alteration. Macroscopic observations reveal that well-preserved specimens are typically associated with fine-grained sediments indicative of low-energy sedimentary environments, while poorly preserved, fragmented specimens occur in coarse-grained sediments typical of higher-energy depositional settings. Microscopic and SEM analyses of the transverse section of the wall plates reveal that well-preserved fossil specimens share a distinctive 'dragon-scale' ultrastructure with their modern counterparts. Diagenetic alteration is more pronounced in specimens from coarse-grained, highly porous sediments, where recrystallization can lead to the obliteration of the original ultrastructure. CL analyses indicate that modern barnacle shells exhibit a weak, predominantly blue luminescence, while the fossil specimens display a broader luminescence spectrum, from blue to purple to red to yellow, reflecting different degrees of diagenesis. Despite their low-magnesium mineralogical stability and seemingly pristine preservation, many barnacle shells from coarse-grained deposits were found to be altered from a micro- and ultrastructural point of view as a likely consequence of the interaction with the diagenetic fluids and/or meteoric waters. Conversely, shells from fine-grained deposits exhibit little signs of diagenetic alteration compared to their modern counterparts. Overall, these results underscore the importance of the depositional environment and diagenetic processes in barnacle preservation, thus enhancing our understanding of the fossilization pathways of cirripede shells.

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