

Palaeobiological implications of cuticle morphology, microstructure and formation in modern and fossil *Daira* (Decapoda, Brachyura, Dairoidea)

Implicaciones paleobiológicas de la morfología, microestructura y formación de la cutícula de *Daira* actual y fósil (Dairoidea, Brachyura, Decapoda)

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Abstract: The origin and function of peculiar mushroom-shaped cuticular structures in some decapod crustaceans remains unknown. This ornamentation has appeared several times in widely disparate clades (in podotreme and heterotreme crabs, and pagurids). These structures are analysed in the modern genus *Daira* and compared with fossil material from the Eocene of Huesca and the Miocene of Alicante and Mallorca. A morphological and petrographic study is carried out using conventional microscopy and Scanning Electron Microscopy to understand the microstructure in modern and fossil representatives. This provides a clear view of the mushroom-like structures that cover the carapace of *Daira* and the distribution of the different layers of the exoskeleton. The results reveal a complex morphology, which involves all layers of the cuticle, with changes in the thickness of the exocuticle in different areas, and the presence of conical structures that especially affect the outer layers. These convolutions form a network of channels connected to the outside by pores. Finally, possible anti-predatory functions of these complex structures are proposed.

Resumen: El origen y función de las peculiares estructuras cuticulares en forma de seta en algunos crustáceos decápodos sigue siendo desconocida. Estas estructuras han aparecido varias veces en clados que no están relacionados filogenéticamente (en cangrejos podotremas y heterotremas, y pagúridos). En este estudio, estas estructuras se analizan en el género actual *Daira*, y se comparan con material fósil del Eoceno de Huesca y del Mioceno de Alicante y Mallorca. Para ello se realiza un estudio morfológico y petrográfico mediante microscopía convencional y SEM en representantes modernos y fósiles. Esto proporciona una visión clara de las estructuras en forma de seta que cubren el caparazón de *Daira* y la distribución de las diferentes capas que forman el exoesqueleto. Los resultados revelan una morfología compleja, que implica todas las capas de la cutícula, engrosando y adelgazando la exocutícula en diferentes zonas y la presencia de estructuras cónicas que afectan especialmente a las capas externas. Estas convoluciones forman una red de canales conectados al exterior mediante poros. Finalmente, se revisan las posibles interpretaciones morfofuncionales de dichas estructuras y se propone una nueva hipótesis relacionada con la protección frente a posibles depredadores.

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INTRODUCTION

The shape and size of marine invertebrates are both genetically controlled and secondarily influenced by the environment; while internal parts or those that are weakly affected by the environment change less; those external parts that are in direct contact with the environment are more prone of morphological variation (*i.e.*, [Outomuro & Johansson, 2017](#), and references herein). Brachyuran decapod crustaceans fit well within such paradigm in which those conservative internal or ventral structures are useful in understanding clade relationships (*i.e.*, [Guinot & Tavares, 2003](#); [Davie *et al.*, 2015a, b](#)), while external sculpture of carapace helps

less in understanding the relationships between clades. In contrast, the latter offers important information about adaptations to different environments and protection against predators (*i.e.*, [Guinot, 1979](#); [Davie *et al.*, 2015b](#)).

The presence of mushroom-like tubercles in modern and fossil decapods has been documented in several clades that independently developed such peculiar structures ([Bittner, 1893](#); [Serène & Soh, 1976](#); [Guinot, 1976, 1979](#); [Haj & Feldmann, 2002](#); [Davie *et al.*, 2015b](#); [De Angeli & Caporiondo, 2017](#); [Ossó *et al.*, 2021](#); [Cluzaud & Ossó, 2022](#)). However, most of

these studies do not show sections (with microscopic details) that complement superficial descriptions (see exception in Haj & Feldmann, 2002). Guinot (1979) noted that this ornamentation is shared by groups that are phylogenetically distant suggesting convergent evolution. These structures evolved from simple tubercles that gradually increased complexity and finally overlapped each other (i.e., Guinot, 1979). The first appearance in the fossil record of mushroom-like tubercles was in some podotreme brachyurans during the Cretaceous (Ossó et al., 2021). However, it is not until the Eocene when they become widely distributed in several heterotreme brachyurans (i.e., Ossó et al., 2021 and references herein) and some anomurans (De Angeli & Caporiondo, 2017).

In order to understand the formation and function of such structure we have analysed the cuticle (micro- and macrostructure) in fossils of *Daira corallina* from the Arguís Formation, Eocene of Huesca (Spain) and *D. speciosa* from the Miocene of Alicante and Mallorca, Spain, together with the modern species *D. perlata* from Philippines. By using standard microscopy methods (binocular microscope and Scanning Electron Microscopy-SEM images) we describe its formation in detail. We also provide evidence that such singular morphology is the result of adaptation to very specific environments and perhaps has an antipredatory function.

MATERIAL AND METHODS

The dry samples were photographed after been coated with sublimated ammonium chloride. A detailed photograph of the surfaces was taken with a Nikon d7100 camera (Nikon, Tokyo, Japan) with a 60 mm macro-lens. A selection of 10 petrographic thin sections of fossils *Daira corallina*, *D. speciosa* and the extant *D. perlata* were prepared for standard transmitted light microscopy and carbonate staining with Alizarin Red S and potassium ferricyanide (following Dickson, 1965). A number of samples were selected and examined under SEM using a Jeol JSMT6400 at the Universidad del País Vasco/Euskal Herriko Unibertsitatea (UPV/EHU). The studied specimens (fossil specimens of *Daira corallina* and *D. speciosa*, and modern specimen of *D. perlata*) are deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza (Spain) under the acronym MPZ.

To test the action of octopod suckers on the cuticle of *Daira* and other crabs, a fresh specimen of white octopus (*Eledone cirrhosa* (Lamarck, 1798)) has been used (Fig. 1A–1B), and various traction tests have been applied in different species with different characteristics (Fig. 1C–1E); *Carpilius corallinus* (Herbst, 1790) with a smooth surface; *Euxanthus exsculptus* (Herbst, 1790), and *Daira perlata* (Herbst, 1790) with mushroom-like ornamentation. The size of the octopus (approx. 25 cm in normal extension) was chosen according to the size of a potential *Daira perlata* (3–4 cm wide) predator.

To carry out the experiment, a tentacle of the octopus was sectioned to place the strongest suckers on the surface of the different crabs (Fig. 1F–1H). Because the experiment was developed with died octopus, we applied tentacles on the surface of different carapaces and pulled from the tentacle on a flat surface. We developed the experiments in subaerial conditions and not under water because crab samples are dry. The experiment was repeated 13 times in each specimen, alternating each specimen in each try. Between trials 6 and 7 the tentacle was rehydrated to avoid dry. Based on observations of the traction experiment, the distance moved by the pull of the tentacle was calculated. The distances (in cm) are indicated in the Table 1.

MORPHOLOGY AND COMPARISON OF THE CUTICLE IN DAIRA

Microstructure of the cuticle in modern *Daira*

The dorsal surface of the carapace (Fig. 2A), pereopods (Fig. 2B, 2C) and pleon (Fig. 2F) of *Daira* are completely covered by complex mushroom-like tubercles of variable size and shape, whose flaps are in contact with each other (see Fig. 2). The studied thin sections show a thick endocuticle formed by thinner lamellar layers, which folds back to form the base of the tubercles, but also show a thickening of the exocuticle at the top of the tubercles, giving rise to most of the lateral expansions (Figs. 2E, 3). The epi- and exocuticle are present inside the folds (base of the channels), but very thin and without remarkable structures (Fig. 3).

The different longitudinal and transverse thin sections in different species of *Daira* show an average thickness of 0.95 mm, where the three different characteristic layers (epi-, exo- and endocuticle) present in all decapod crustaceans are recognized (i.e., Dalingwater & Mutvei, 1990; Dillaman et al., 2013), as well as the typical mushroom-like morphology of *Daira* (Guinot, 1979).

Both, the exocuticle and the endocuticle, are affected by mushroom-like tubercles, giving the sections a convoluted appearance and showing variable thickness (Fig. 2C). The epicuticle, with a homogeneous thickness ($\approx 5 \mu\text{m}$), covers the entire complex, including the outer margin and the interior of the basal channels, but it is poorly observed in some sections (Fig. 3). The exocuticle in particular shows the greatest variation in thickness, being very thin inside the channels and very thick on top of the tubercles (Fig. 3B, 3D).

The endocuticle is the thickest part ($\approx 200\text{--}300 \mu\text{m}$) and is characterized by its greater lateral continuity with a clear red-yellowish alternating lamination of fine sheets (lamellae). Without staining, they appear as light-dark sheets under polarized light (Fig. 3). The light coloured sheets contain higher carbonate content, while the dark ones are mostly protein.

The overgrowth of the upper part of the tubercles and their coalescence give rise to the formation of the aforementioned basal channels (apparent empty

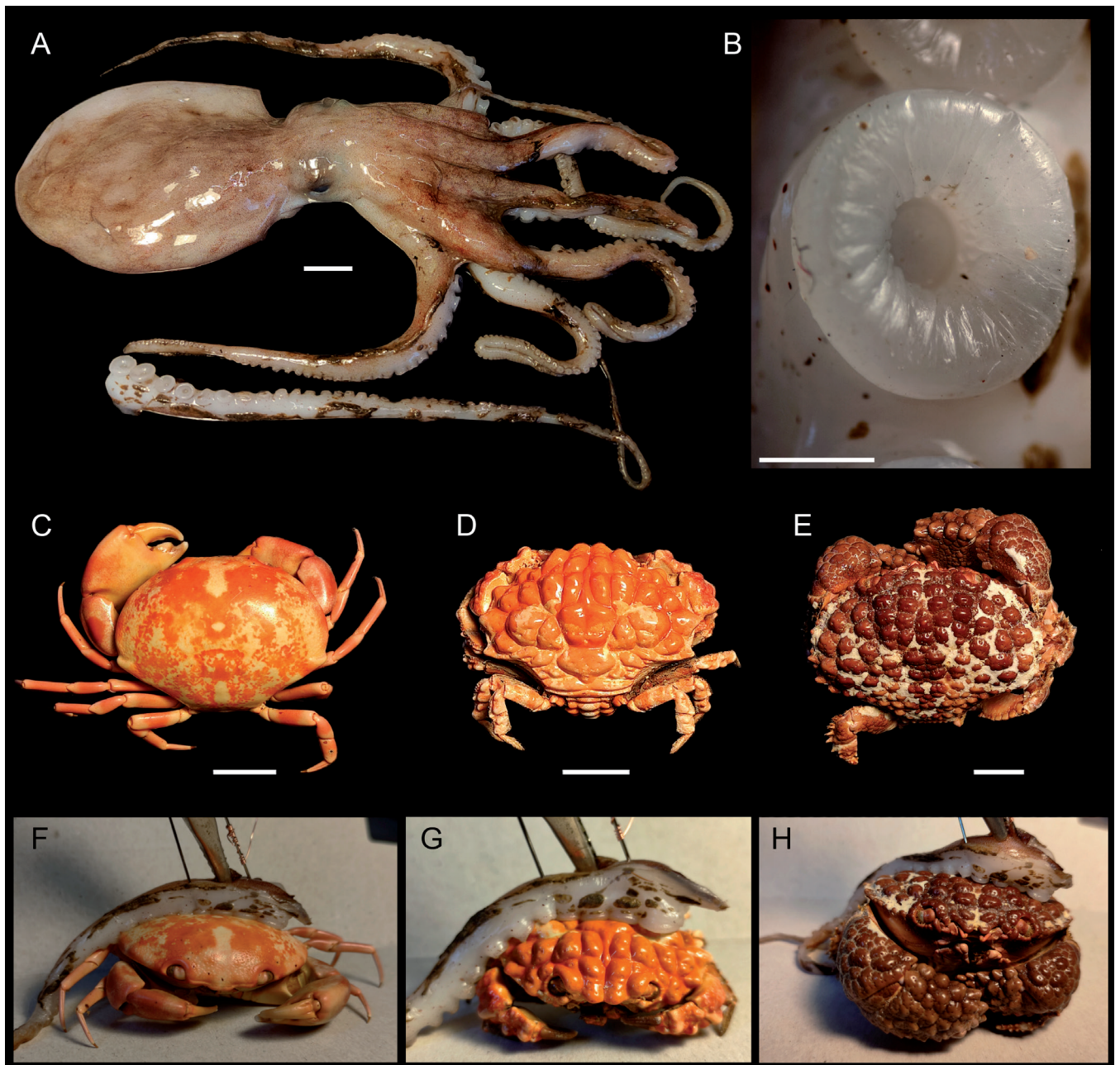


Figure 1. Specimens used for traction experiment. **A**, Specimen of white octopus *Eledone cirrhosa* (Lamarck, 1798); **B**, Detail of one of the suckers; **C**, *Carpilius corallinus* (Herbst, 1790); **D**, *Euxanthus exsculptus* (Herbst, 1790); **E**, *Daira perlata* (Herbst, 1790); **F–H**, Application of tentacle on crab surface; all scale bars = 1 cm, except B = 2 mm.

chambers in thin sections), limiting their upper margin. In the folds of the upper part of the mushroom-shaped tubercles (above the basal canals), the lateral expansions appear as rounded sections with fibrous-radial morphology, highlighted by dark organic-rich concentrations (Fig. 3).

Internally, these structures form a network of channels that crosses the entire carapace (Fig. 4A–4C). In dorsal view, tubercles are in contact (Figs. 2A, 4D), but the sutures between the tubercles and the pores that connect the channels with the outside are visible (Fig. 4D). The folds on the edge of each tubercle form the pores (pore channels) that connect the basal channels

with the exterior (Fig. 4D, 4E, 4F). These structures are also present in pereopods (Fig. 2D) and pleon (Fig. 2C, 2F).

Microstructure of the cuticle in fossil *Daira*

Most specimens of fossil *Daira* show poorly preserved cuticle (see Di Salvo, 1933; Portell & Collins, 2004; Beschin et al., 2007, 2012, 2015, 2016, 2018; De Angeli et al., 2010; Gatt & De Angeli, 2010; Tessier et al., 2011; Klompaker et al., 2015) but presumably with a very similar (if not identical) structure than modern representatives. In fact, the morphological structure

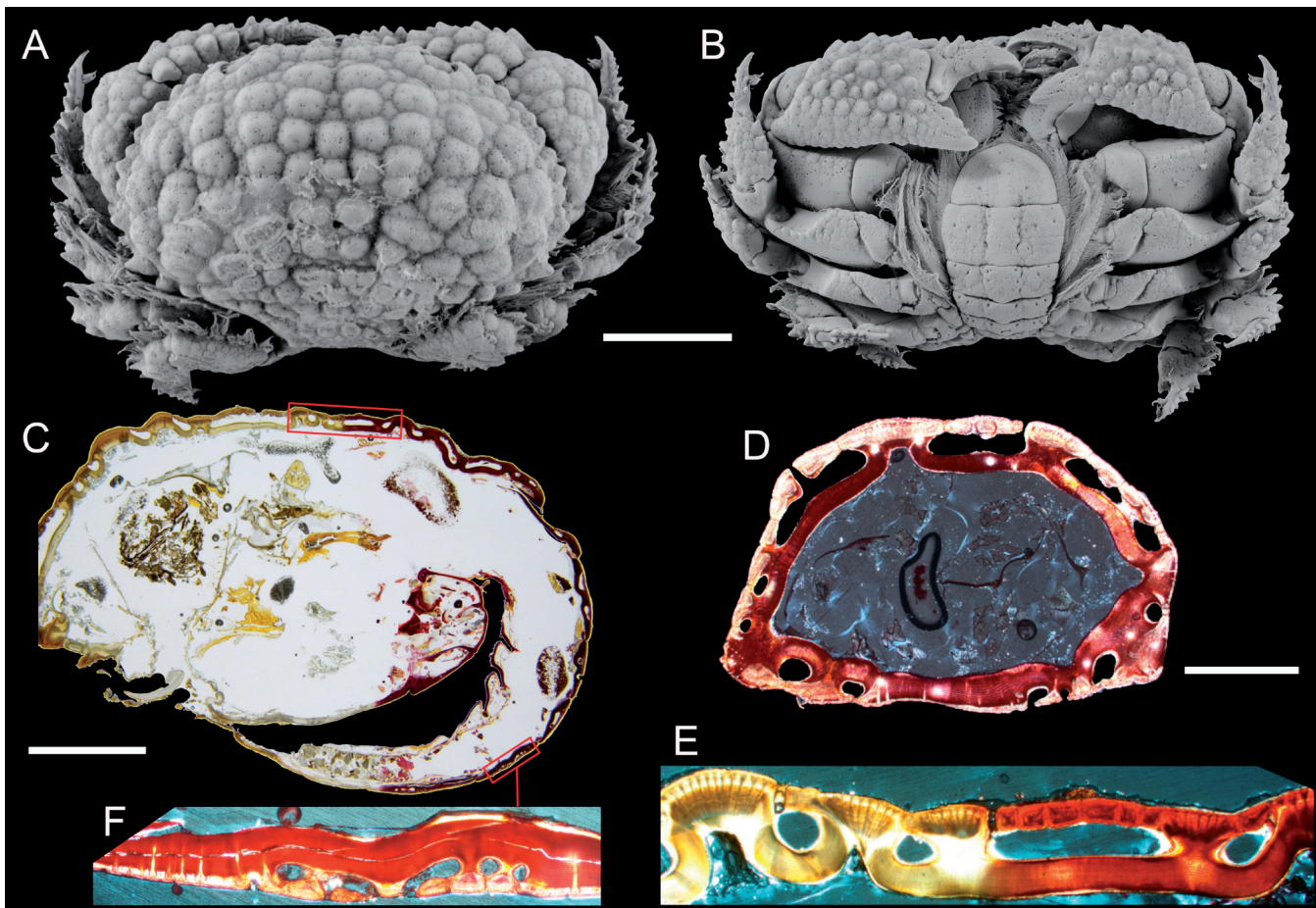


Figure 2. Modern specimen of *Daira perlata* (female) collected in Gato Island (Visayan sea), Cebu, Philippines (about 10 meters deep). **A**, Dorsal view; **B**, Ventral view. Specimen whitened with ammonium chloride sublimated; **C**, Longitudinal section of the same specimen, with the right part stained with Alizarin red S; **D**, Complete section of a tinted pereopod of the same specimen with the characteristic structure; **E**, Detail of the mushroom-shape tubercles of the dorsal carapace marked in C with a red box; **F**, Detail of the mushroom-shape tubercles of the pleon marked in C with a red box; scale bars A, B = 1 cm, C = 5 mm and D = 1 mm.

and microstructure in the studied fossil species of *Daira* (*D. corallina* and *D. speciosa*) is basically identical to that of the modern species *D. perlata*, both in the surface and thin sections (see Fig. 5).

In the examined material, fossil specimens preserve the exo- and endocuticle (Fig. 5). They show the same channel network (see Fig. 4) but filled with finer sediments than those present in the surrounding matrix (Fig. 5). In all species, the mushroom-shape tubercles have the same characteristics, with the presence of vertical pores (pore channels) and interprismatic septa or honeycomb (Figs. 3, 5). The development of the exocuticle is marked by fine discontinuous sheets of iron oxides (Fig. 5A–5C, 5E), probably as a result of pyrite alteration (FeS_2) formed by the decay of the organic matter, in a reducing environment during the fossil diagenetic phase.

Thin sections of *D. speciosa* from Mallorca are embedded in a microsparite matrix rich in bioclasts (Fig. 5D–5E), occasionally affected by diagenetic recrystallization (Fig. 5F). In some specimens from Alicante, the endocuticle shows strong diagenetic alteration with loss of lamination and development of

carbonate crystals (Fig. 5G–5H), and some show that the endocuticle has been cracked with displacement and even filled with spatic calcite.

The epicuticle, which was organic in origin, has been decayed and the recognizable surface in the fossils corresponds to the exocuticle. This allows observation of a honeycomb network in the outer margin of the cuticle (Fig. 6). In section, these structures correspond to cones that especially affect the exocuticle and penetrate the endocuticle at the top of the tubercles (see Figs. 3 and 5). Regarding the staining of the exocuticle by Alizarin red S, a coloration of lighter tones can be seen compared to the more reddish coloration of the endocuticle (Figs. 3C–3E, 5C). These variations can be justified by a higher organic content compared to the dominance of Ca as carbonate.

Distribution of mushroom-like tubercles in decapod crustaceans

This type of mushroom-like tubercles is not exclusive of the genus *Daira* and other fossil and extant taxa show this or a similar ornamentation, covering partial

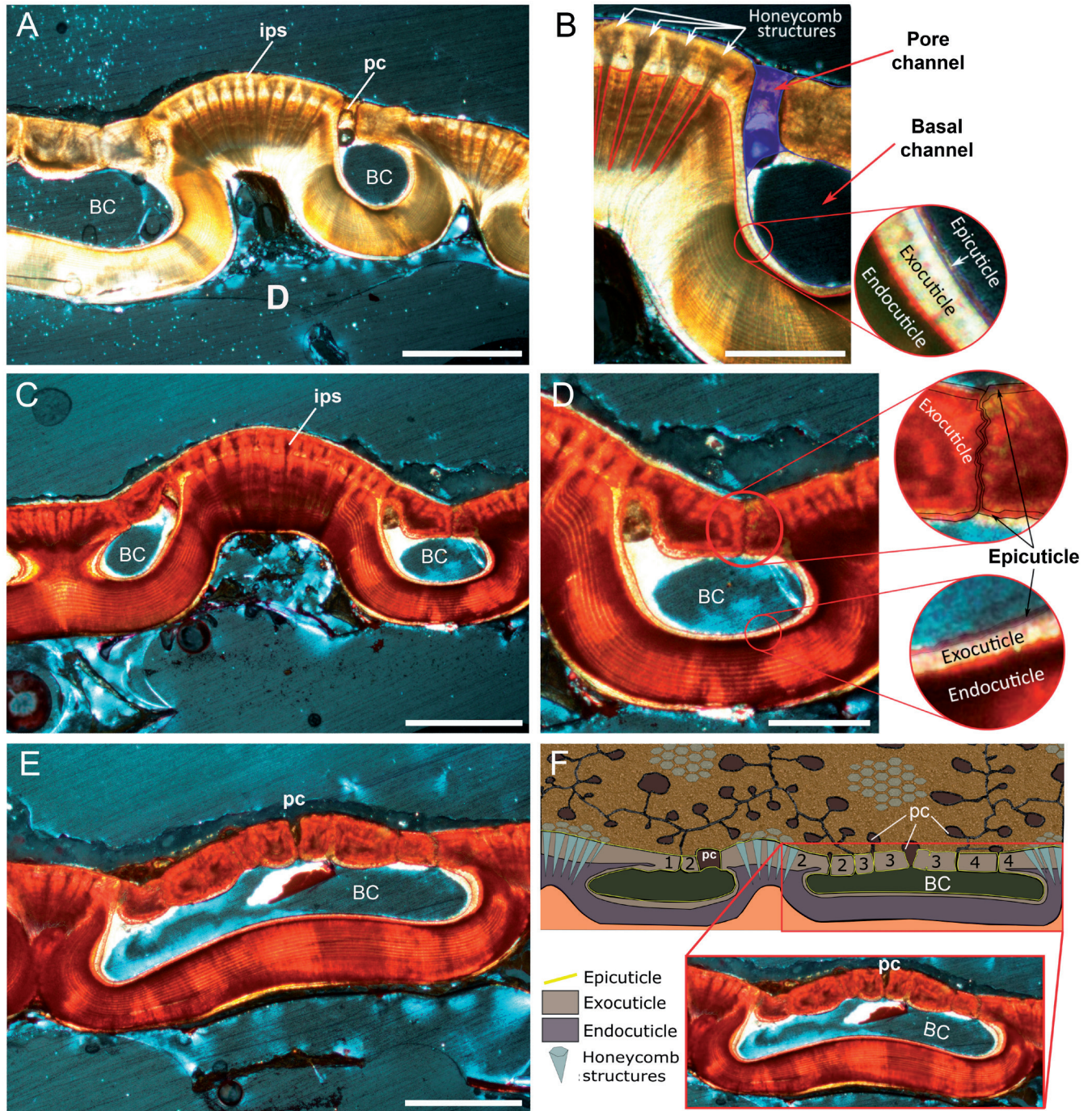


Figure 3. Details of specimen in the Figure 2E (A and C), showing the epi-, exo- and endocuticle (B and D), the robust interspersed mushroom-shape tubercles, the base of the channels, the interprismatic septa with honeycomb-type disposition and a thin alternating light-dark lamination mainly visible in the endocuticle. The great plasticity of the exocuticle is remarkable (B–D), with a strong thickening in the area compared to the base of the channel; E, Longitudinal section of base of the channel limited by three mushroom-shaped tubercles. The central tubercle is sectioned tangentially; F, Photomicrograph and interpretive diagram of the stained cuticle with the three recognized zones, channels, and the different sectioned tubercles (1, 2, 3, 4). Abbreviations: BC, base of the channel; ips, interprismatic septs; pc, pore channel; scale bars A, B, E = 5 mm, C = 1 cm and D = 2 mm.

or completely the dorsal carapace and pereiopods. Some fossil podotreme brachyurans from the Upper Cretaceous, like *Cuchiadromites* Ossó et al., 2021; *Marylireidus* Rathbun, 1935; *Eucorystes* Bell, 1863; *Ferroranina* van Bakel et al., 2012 and *Cretacorantina* Mertin, 1941, show similar fungiform ornamentation (see Haj & Feldmann, 2002; Waugh et al., 2009; van

Bakel et al., 2012; Ossó et al., 2021), or fungiform nodes according to Waugh et al. (2009), also present in some species of the modern genus *Symethis* (see Waugh et al., 2009). In the Eocene, some heterotreme brachyurans show this ornamentation (including the parthenopoids *Phrynolambrus* Bittner, 1893; and *Aragolambrus* Ferratges et al., 2019) in the dorsal

surface of the carapace (e.g., Bittner, 1893, figs. 3, 3a, 3b); some Neogene leucosid crabs, like *Aquitainotlos* (see Cluzaud & Ossó, 2022, fig. 4) and *Pterocarcinus* (see Blow, 2003, figs. 2–4) show a similar cuticular structure composed of mushroom-shaped tubercles, coalescing in some areas of the carapace. The fossil anomuran species *Lessinipagurus ornatus* De Angeli & Caporiondo, 2017 (Xylopaguridae Gašparič, Fraaije, Robin & De Angeli, 2016), exhibits the same cuticular ornamentation in the outer side of the propodus (see De Angeli & Caporiondo, 2017, fig. 16, tab. 6, 4a). In extant parthenopoids such as *Garthambrus* Ng, 1996 and *Dairoides* Stebbing, 1920; xanthids such as *Actaea* De Haan, 1833, and the aethrid *Drachiella* Guinot in Serène & Soh, 1976, similar fungiform tubercles are also present (McLay & Tan, 2009, figs. 9A–9B, 13B; Ng & Tan, 1999, fig. 5; Guinot, 1976, tab. 12, fig. 5, 5a; Guinot, 1967, fig. 3; Viswanathan et al., 2019, fig. 1).

ENVIRONMENTAL DISTRIBUTION OF *DAIRA*

The genus *Daira* is represented by a small number of species (both modern and fossil) adapted to reef environments and rocky bottoms in shallow waters (approx. 0–60 m depth). Modern representatives include only two species; *D. perlata* (Fig. 2) which is typical in shallow coral environments from the Indo-

Pacific (Peyrot-Clausade, 1989; Morgan & Berry, 1993; Davie & Short, 2001; Poupin, 2016); and *D. americana* Stimpson, 1860, typical of the rocky and coral bottoms from the Pacific coasts of Central America (Rathbun, 1930; Abele, 1979; Garth, 1991).

In the fossil record, the genus *Daira* is represented by twelve species generally associated with coral reef environments (see Ferratges et al., 2020 and references herein). The study of Ferratges et al. (2020) in the late Eocene of the Pyrenees, suggests that the genus *Daira* apparently showed preference for areas rich in branching corals, which were probably used as hiding places against predators. Environmental studies for most fossil species are lacking, so it is difficult to determine what type of environment inhabited other species of the genus.

It is noteworthy that in some Miocene reef environments *Daira speciosa* appears in high abundance representing mass-occurrences of carapaces (i.e., Górká, 2018). This species is widely distributed in the Miocene deposits of the Mediterranean and Paratethyan realms (see Lőrenthey in Lőrenthey & Beurlen, 1929; Yanakevich, 1977; Förster, 1979; Saint Martin & Müller, 1988; García-Socias, 1989; Müller, 1993, 1996; Górká & Jasionowski, 2006; Radwański et al., 2006; Górká, 2002, 2018; Gatt & De Angeli, 2010; Ossó & Stalennuy, 2011; Hyžný, 2016; Hyžný & Gross, 2016; Hyžný & Dulai, 2021).

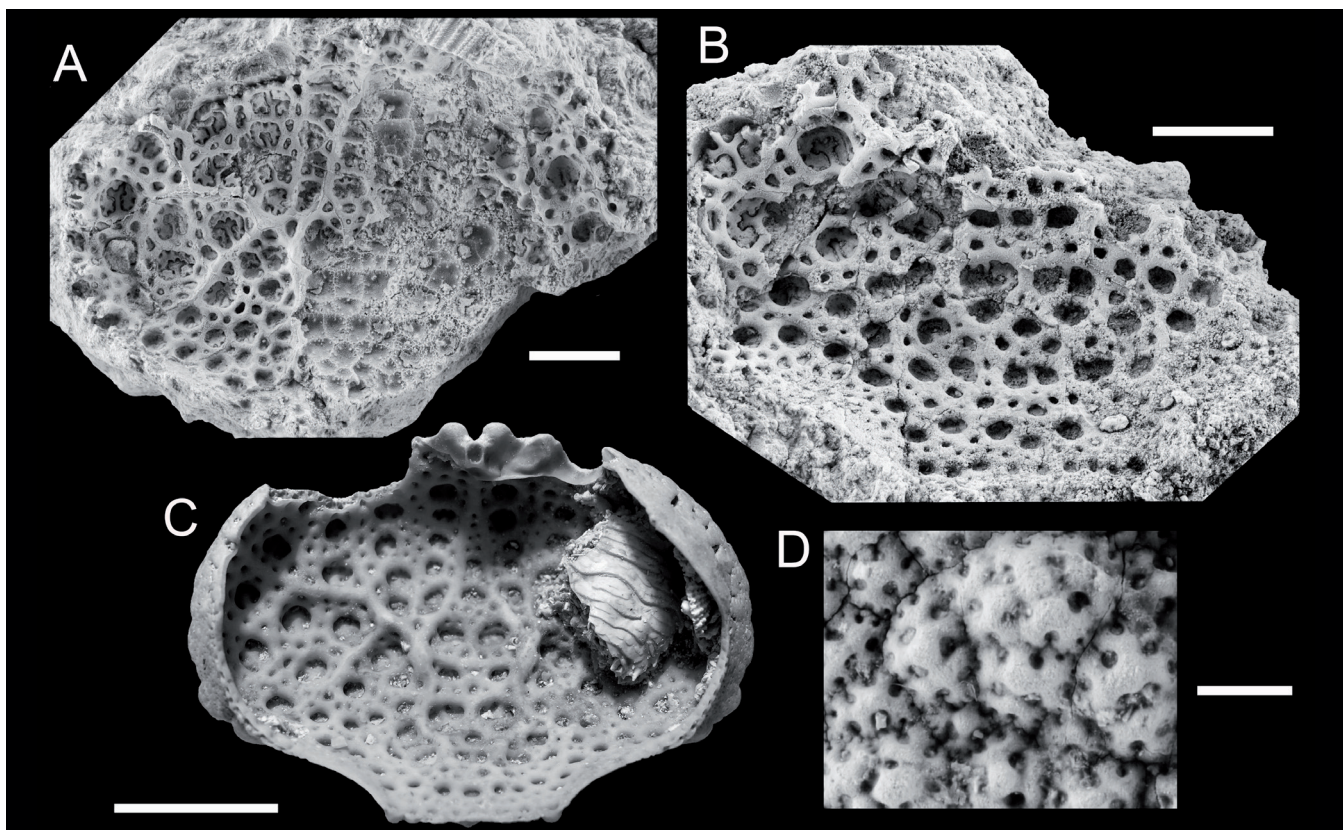


Figure 4. A–C, Internal carapace view of *Daira speciosa* Reuss, 1871, showing the internal channel network and tubercles (A–B specimens from Alicante, Spain (MPZ 2022/928 and MPZ 2022/929)), and C (C418.4) from Medobory Hills (Ukraine); image C courtesy of Àlex Ossó; D, Detail of the cuticle surface of the holotype of *Daira corallina* (MPZ 2019/1691); scale bars A, B = 1 cm, C = 5 mm and D = 1 mm.

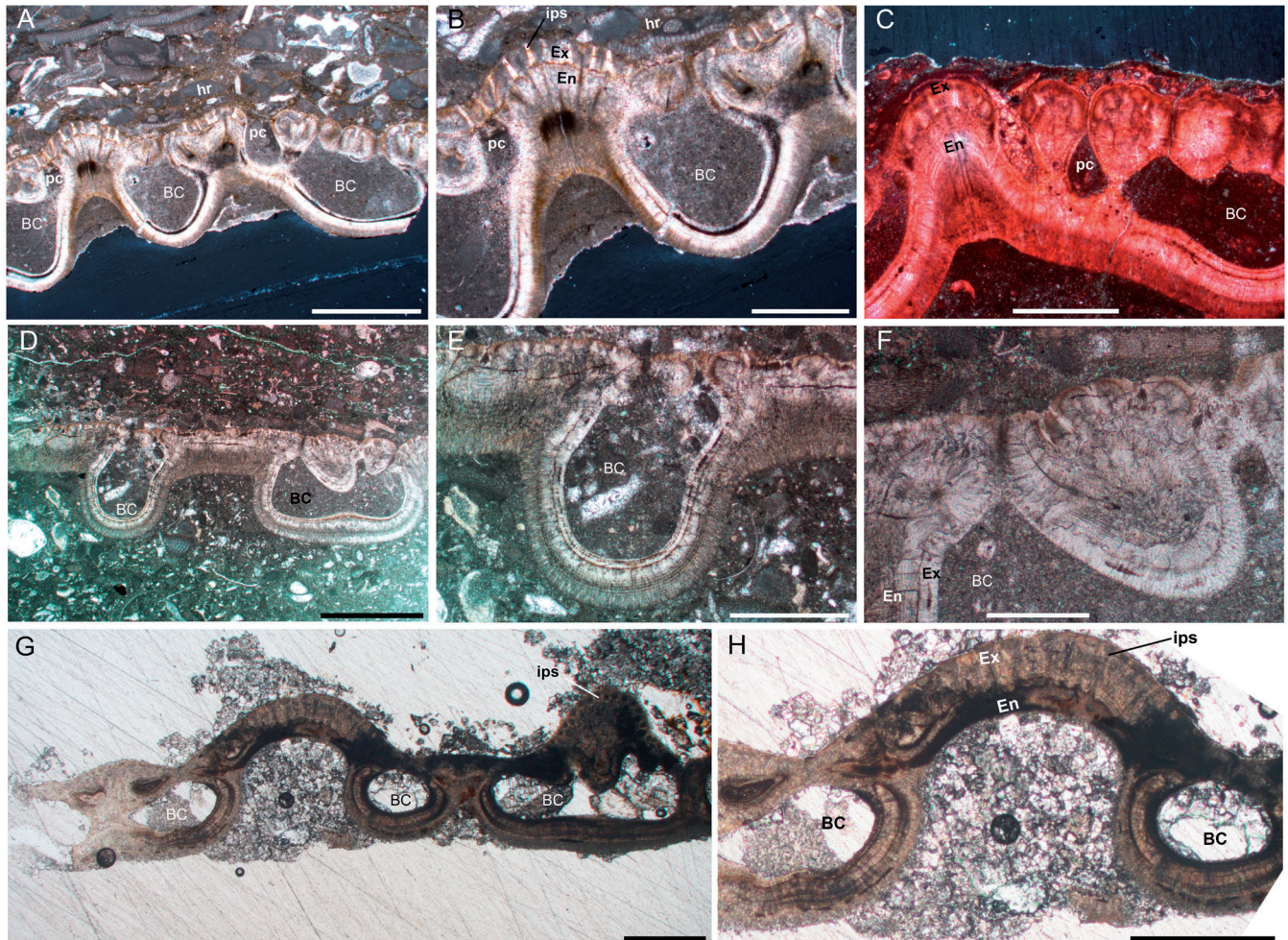


Figure 5. A–C, Longitudinal sections of *Daira corallina* (MPZ 2019/1698); B, Detail of picture A where the exo-, and endocuticle with intersprismatic sects (honeycomb structure in plan view) are recognized. The basal channels are filled with carbonate fine sediment compared to the coarser host rock; D–H, Microphotographs of the cuticle of *Daira speciosa* (D–F, from the Miocene of Mallorca; G–H, from the Miocene of Alicante), where the microstructure with mushroom-shape tubercles with well-developed channels is preserved. The diagenetic alteration maintains the fine laminations in some areas, but in others they appear recrystallized (left G and H); H, Details of the microstructure, partially recrystallized by the diagenesis, where the exo- and endocuticle are recognized. Abbreviations: BC, basal channel; Ex, exocuticle; En, endocuticle; hr, host-rock; ips, intersprismatic sects; pc, pore channel; scale bars A, D = 1 mm, B, C, E, G, H = 0.5 mm and F = 0.25 mm.

TRACTION TEST

Obtained results using different crabs of similar size and weight (see Fig. 1) show different values when dragging the specimens on a flat and horizontal surface before detaching from the octopus tentacle. This adherence seems to depend on the different surfaces of each crab (*Carpilius corallinus*, *Euxanthus exsculptus* and *Daira*

perlata). Values in *Carpilius corallinus* are higher than in the other two crabs, and lowest values are shown in *D. perlata*. Suckers of the octopus *Eledone cirrhosa* were more effective in smooth surfaces, and in the case of *Daira* they were not capable of moving specimen more than 10 cm (Tab. 1).

Table 1. Displaced distances (in cm) after traction experiments on the different taxa by octopus tentacle.

Taxa	Test 1	Test 2	Test 3	Test 4	Test 5	Test 6	Test 7	Test 8	Test 9	Test 10	Test 11	Test 12	Test 13
<i>Carpilius corallinus</i>	>50	42.4	40.7	45.2	37.6	41.6	>50	>50	38.4	35.2	29.4	33.5	34.9
<i>Euxanthus exsculptus</i>	27.3	24.3	32.4	34.7	31.1	32.5	34.6	28.7	26.4	19.2	20.3	18.6	19.4
<i>Daira perlata</i>	4.7	5.5	7.8	3.7	2.7	3.9	2.1	2	2.3	3.7	2.7	1.8	2.5

DISCUSSION

The detailed study of the cuticle in modern decapod crustaceans facilitates the recognition of the microstructures shown in fossil taxa, even in specimens poorly preserved due to diagenesis (Waugh & Feldmann, 2003; Waugh *et al.*, 2006; Klompaker *et al.*, 2015). In contrast to the studies that exhaustively describe the morphological differences in the carapace of different species, works on the microstructure-ultrastructure of the cuticle are rare (with some exceptions, see Taylor, 1973; Haj & Feldmann, 2002; Vega *et al.*, 2005; Waugh *et al.*, 2009; Waugh, 2013).

Mushroom-like tubercles were first examined by Guinot (1979) as a gradual growth of the tubercles up to the formation of mushroom-like structures, which finally appear in the outer part of the cuticle (Guinot, 1979, fig. 10A). However, details of their development are incompletely understood, and possible explanations are lacking. The microstructures observed in thin sections (both fossil and modern species) show a more complex arrangement than previously explained.

Morphofunctional significance of honeycomb structures

Honeycomb like structures are widespread in the animal kingdom (*i.e.*, bees, corals, lenses in insects) and are considered an important bioinspired design in human innovations (Zhang *et al.*, 2015). The analysis under binocular microscope and SEM of *Daira corallina* reveals honeycomb microstructures on the top of mushroom-like tubercles (Fig. 6). This structure, which is observed in plan view, has the shape of a polygon (honeycomb-type), and was previously observed in *Daira perlata* (see Guinot, 1979, fig. 13B). Similar structures (in surface and section) have been observed in other crabs (*i.e.*, Feldmann *et al.*, 2010, fig. 14). However, these structures (prismatic in section) appear much more densely packed in other taxa, and do not penetrate the lower layers of the cuticle, forming a prismatic layer on the outermost part of the cuticle.

Several works have studied the cuticle of various taxa demonstrating its bearing in the resistance of the carapace (*i.e.*, Hegdahl *et al.*, 1977a, 1977b, 1977c; Sachs *et al.*, 2008; Fabritius *et al.*, 2009, 2012; Erko *et al.*, 2013). Other crustaceans show modifications of the cuticle in order to resist stress and impacts (*i.e.*, Weaver *et al.*, 2012). In some other marine invertebrates (*i.e.*, oysters like *Crassostrea gigas*), honeycomb microstructures in plan view and prismatic in section with intercalations of calcite and protein material have been interpreted as buffers against waves (Higuera-Ruiz & Elorza, 2009, 2011). It is possible that these structures in crabs perform a defensive function against certain predators to minimize impacts produced by attacks (*i.e.*, Crane *et al.*, 2018), although an ecomorphological explanation cannot be ruled out.

Correlation of cuticle shape and microstructure with environment

Mushroom-like ornamentation has appeared independently in several groups of decapod crustaceans as explained above, and seems to be related with different functions and adaptations to different habits and environments, including camouflage (*i.e.*, Bittner, 1893; Lörenthey & Beurlen, 1929), burrowing or defence against predators (*i.e.*, Schmalfuss, 1978; Savazzi, 1982; Haj & Feldmann, 2002).

Guinot (1967), observed this type of ornamentation in some modern eubranchyurans (*Dairoides*, *Daira* and *Actaea*). Later, Guinot (1979) reviewed the descriptions and interpretations made by previous authors about this type of cuticular structure and re-interpreted its function (Guinot, 1979, p. 55–56). This author suggested the possible function of water circulation inside the carapace of *Dairoides* and *Daira* (see Guinot, 1979, figs. 12A, and 15A–15B, respectively), as well as its extension to the coxae of pereopods. This internal structure would allow water to penetrate through the pores on the outer surface of the mushroom-like tubercles circulating freely through the internal network of channels. According to Guinot (1979), this would allow circulation of oxygenated water and the maintenance of certain humidity in the body, but Guinot (1979) did not discard other functions.

The hypothesis of the maintenance of humidity in the carapace is weakly supported because *Daira* spend all time under water (*i.e.*, Peyrot-Clausade, 1989; Davie & Short, 2001), and is preferably found in front reef environments (*i.e.*, Poupin, 2016). On the other hand, dairoidids have never been observed having amphibian habits, so they do not need to maintain humidity. In addition, crabs with amphibious habits lack this structure, so it does not seem to be a significant improvement for maintaining humidity in the body.

Other authors (*i.e.*, Schmalfuss, 1978; Savazzi, 1982; Haj & Feldmann, 2002) related similar type of cuticular microstructure in raninoids (but with terraces and without dorsal porosities) with burrowing and/or defence. Furthermore, Haj and Feldmann (2002) suggested that the network laterally opened may have been exposed to the water/sediment interface, functioning as a pneumatic device to press the cuticle against the substrate.

These structures might allow water circulation under the sediment (“snorkel” function) to canalize oxygen-rich water into the branchial openings, or to facilitate vertical movements within the sediment, allowing water to flow between the sediment grains. Extant species of *Daira*, *Dairoides* or *Actaea* do not burrow into the sediment, so interpretations of burrowing raninoids are not applicable to this case. In addition, ornamentation in raninoids, although superficially similar, does not present exactly the same structure than in *Daira* (and

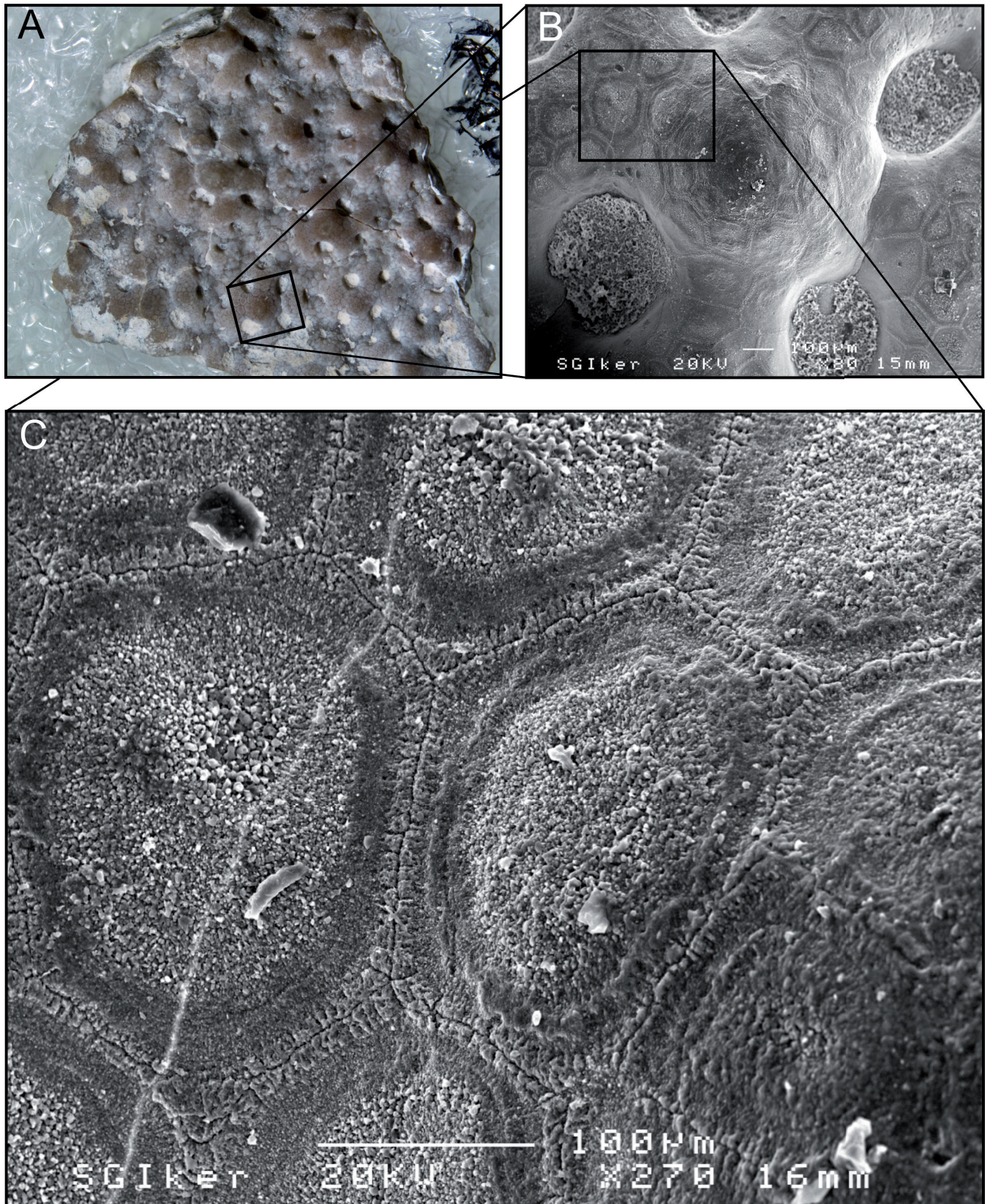


Figure 6. A, Detailed appearance of the polygonal cells in honeycomb-type present in the dorsal part of fossil *Daira corallina* (MPZ 2019/1712). Note the remarkable size of the pores that connect the inner net of channels with the exterior; B–C, Images under SEM, enlarged view of a mushroom-shape tubercle with the honeycomb cells that make up the exocuticle; C, Detail of the arrangement of the cells in honeycomb-type morphology; scale bars B, C = 100 μ m.

Dairoides). In raninoids it appears to be a convolution only on the external part of the exocuticle (Haj & Feldmann, 2002, fig. 8), with the exception of most derived taxa, in which the fungiform ornamentation would involve all layers of the cuticle (e.g., Guinot, 1967, figs. 7–8; 1979, figs. 10A, 11C, 13C, 14, 15; Ossó & Stalennuy, 2011, fig. 3.13; Cluzaud & Ossó, 2022, fig. 4; Ferratges et al., 2022, fig. 1D).

Possible anti-predation function

Some authors suggest that large accumulations of *Daira speciosa* could be the product of moults after accumulation or alternatively remains of predation and consumption by predators (Górka & Jasionowski, 2006; Radwański et al., 2006) or due to accumulations of similar size elements by hydrodynamic processes (Müller, 2004).

In modern coral reefs and rocky environments one of the main predators of crabs are octopuses (i.e., Ambrose, 1984; Villanueva, 1993; Anderson et al., 2008; Leite et al., 2009; Jordan, 2010; Bouth et al., 2011; Ossó & Stalennuy, 2011). Many small crabs are caught by octopuses while hiding under hard substrates and cavities (i.e., Leite et al., 2008; Jordan, 2010). To do this, octopuses use their suction cups on the surface of the carapace to generate suction allowing them to manipulate the crabs.

Modern *Daira perlata* is one of the octopus preys, despite they represents a small percentage of preys compared to other species (i.e., Scheel et al., 2017). Studies on the efficiency of octopus suckers on the surface of *Daira* are lacking, but based on our observations a possible explanation for the cuticle of *Daira* could be related with defence against this type of predator. This unique system of pores and channels generate a water flow that prevents the suction generated by the suction cups of the octopus (Fig. 7).

When the suckers of an octopus reach the surface of a crab (Fig. 7A) vacuum is created by contracting muscles, and this allows octopus to pull its prey (Fig. 7B). However, the channel system of *Daira* prevents sufficient adherence to create vacuum (Fig. 7C). It is possible that the function of this complex network work diminishing the suction produced by some predators, preventing the octopus and other predators (i.e., carnivore gastropods) from producing enough traction to extract the crab out of its hiding place.

Recently, Ossó and Stalennuy (2011) proposed octopuses as possible predators and generators of the large accumulations of Miocene *Daira* carapaces without any justification. Nevertheless, these authors did not record the presence of the specific holes that could be attributed to predation by octopuses (Arnold & Okerlund-Arnold, 1969; Klompaker et al., 2013;

Górka, 2018). These data support the hypothesis that octopuses are not the main predators of this genus.

The anti-predatory hypothesis would also explain why these structures are found in unrelated taxa, such as the hermit crab *Lessinipagurus ornatus* De Angeli & Caporiondo, 2017, in which mushroom-like tubercles are found on the outer side of the opercular claw, avoiding suction in the only exposed part of the body. Further work is necessary to corroborate such hypothesis and how these mushroom-shaped structures are developed independently in different taxa; but if our interpretation is correct, mushroom-like structures in *Daira* are a very conservative structure since the Cretaceous, with a clear anti-predatory function.

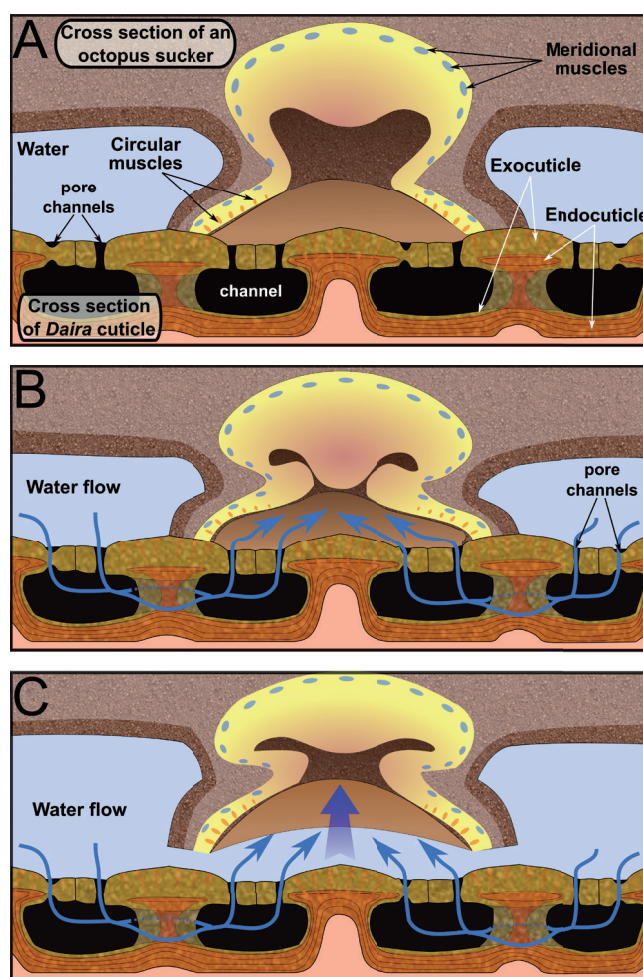


Figure 7. Schematic diagram of the possible anti-predatory function of the complex tubercles that cover the carapace of *Daira*. The lighter part of the cuticle (light brown) represents the exocuticle, the area with parallel lines (orange) corresponds to the endocuticle. The scheme shows the circulation of water through the pores and of internal channel network when the sucker of a predator (octopus) makes a vacuum on a part of the carapace (A–B). This mechanism would make adherence difficult or even impossible (C).

CONCLUSIONS

The microstructure of *Daira* cuticle shows that the mushroom-shaped tubercles that cover its dorsal surface are different from those of other taxa, such as *Ferroranina*. The “wings” of these mushroom-shaped tubercles are mainly formed by overgrowths of the epicuticle and exocuticle. Fossil remains indicate that these structures have appeared independently in different decapod crustaceans (anomurans, podotreme crabs and not closely related eubrachiuran crabs) since the Cretaceous, and have persisted up today. These complex folds of the cuticle form a network of basal-channels connected by pores to the outside allowing the free circulation of water. In addition, cone-shaped (honeycomb-type) structures have been observed crossing both the epi- and the exo-endocuticle. The latter are similar to those of other organisms, whose function has been interpreted as increasing resistance to stress and impacts. The morphology of these complex cuticular structures might correspond to anti-predatory function against predators, especially octopuses.

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REFERENCES

- Abele, L. G. (1979). The community structure of coral-associated decapod crustaceans in variable environments. In R. J. Livingston (Eds.), *Ecological Processes in Coastal and Marine Systems* (pp. 265–287). Springer. doi: [10.1007/978-1-4615-9146-7_13](https://doi.org/10.1007/978-1-4615-9146-7_13)
- Ambrose, R. F. (1984). Food preferences, prey availability, and the diet of *Octopus bimaculatus* Verrill. *Journal of Experimental Marine Biology and Ecology*, 77, 29–44. doi: [10.1016/0022-0981\(84\)90049-2](https://doi.org/10.1016/0022-0981(84)90049-2)
- Anderson, R. C., Wood, J. B., & Mather, J. A. (2008). *Octopus vulgaris* in the Caribbean is a specializing generalist. *Marine Ecology Progress Series* 371, 199–202. doi: [10.3354/meps07649](https://doi.org/10.3354/meps07649)
- Arnold, J. M., & Okerlund-Arnold, K. (1969). Some aspects of hole-boring predation by *Octopus vulgaris*. *American Zoologist*, 9, 991–996. doi: [10.1093/icb/9.3.991](https://doi.org/10.1093/icb/9.3.991)
- Bell, T. (1863). A monograph of the fossil malacostracous Crustacea of Great Britain. Part II. Crustacea of the Gault and Greensand. *Monograph of the Palaeontographical Society (London)*, 14, 1–40.
- Beschin, C., Busulini, A., De Angeli, A., & Tessier, G. (2007). I decapodi dell'Eocene inferiore di Contrada Gecchelina (Vicenza – Italia settentrionale) (Anomura e Brachiura). *Museo di Archeologia e Scienze Naturali “G. Zannato”, Montecchio Maggiore (Vicenza)*, 14, 9–76.
- Beschin, C., De Angeli, A., Checchi, A., & Zarantonello, G. (2012). Crostacei del giacimento eocenico di Grola presso Spagnago di Cornedo Vicentino (Vicenza, Italia settentrionale) (Decapoda, Stomatopoda, Isopoda). *Montecchio Maggiore (Vicenza). Museo di Archeologia e Scienze naturali “G. Zannato”, 1–100.*
- Beschin, C., Busulini, A., & Tessier, G. (2015). Nuova segnalazione di crostacei associati a coralli nell'Eocene inferiore dei Lessini orientali (Vestenanova–Verona). *Lavori Società veneziana di Scienze naturali*, 40, 47–109.
- Beschin, C., Busulini, A., Tessier, G., & Zorzin, R. (2016). I crostacei associati a coralli nell'Eocene inferiore dell'area di Bolca (Verona e Vicenza, Italia nordorientale). *Memorie del Museo civico di Storia naturale di Verona, Serie 2. Sezione Scienze della Terra*, 9, 1–189.
- Beschin, C., Busulini, A., Fornaciari, E., Papazzoni, C. A., & Tessier, G. (2018). La fauna di crostacei associati a coralli dell'Eocene superiore di Campolongo di Val Lione (Monti Berici, Vicenza, Italia nordorientale). *Bollettino del Museo di Storia naturale di Venezia*, 69, 129–215.
- Bittner, A. (1893). Decapoden des pannonischen Tertiäre. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien*, 102, 10–37.
- Blow, W. C. (2003). New brachiuran crabs (Crustacea: Decapoda) from the Upper Pliocene Yorktown Formation of south-eastern Virginia. *Proceedings–Biological Society of Washington*, 116(1), 168–189.
- Bouth, H. F., Leite, T. S., Lima, F. D. D., & Oliveira, J. E. L. (2011). Atol das Rocas: an oasis for *Octopus insularis* juveniles (Cephalopoda: Octopodidae). *Zoologia (Curitiba)*, 28(1), 45–52.
- Cluzaud, A., & Ossó, À. (2022). Note sur des crustacés décapodes du Rupélien de Gaas (Landes, France) avec description d'un nouveau crabe (Brachyura: Leucosiidae). *Nemus*, 12, 122–136.
- Crane, R. L., Cox, S. M., Kisare, S. A., & Patek, S. N. (2018). Smashing mantis shrimp strategically impact shells. *Journal of Experimental Biology*, 221(11), jeb176099. doi: [10.1242/jeb.176099](https://doi.org/10.1242/jeb.176099)
- Dalingwater, J. E., & Mutvei, H. (1990). Arthropod Exoskeletons. In J.G. Carter (Ed.), *Skeletal biomineralization: Patterns, Processes and Evolutionary Trends*. (pp. 83–96). Van Nostrand Reinhold.
- Davie, P. J. F., & Short, J. W. (2001). Decapod Crustacea of North East Cay, Herald Cays, Coral Sea. *Herald*

- Cays Scientific Study Report, Geography Monograph Series (pp. 75–86). The Royal Geographical Society of Queensland Inc.
- Davie, P. J., Guinot, D., & Ng, P. K. (2015a). Phylogeny of Brachyura. In P. Castro, P. J. F. Davie, D. Guinot, F. R. Schram, & J. C. von Vaupel Klein (Eds.), *Treatise on Zoology–Anatomy, Taxonomy, Biology. The Crustacea*, Volume 9, Part C (pp. 921–979). Brill Academic Pub.
- Davie, P. J., Guinot, D., & Ng, P. K. (2015b). Anatomy and functional morphology of Brachyura. In P. Castro, P. J. F. Davie, D. Guinot, F. R. Schram, & J. C. von Vaupel Klein (Eds.), *Treatise on Zoology–Anatomy, Taxonomy, Biology. The Crustacea*, Volume 9, Part C (pp. 11–163). Brill Academic Pub. doi: [10.1163/9789004190832_004](https://doi.org/10.1163/9789004190832_004)
- De Angeli, A., & Caporiondo, F. (2017). I granchi eremiti (Crustacea, Decapoda, Anomura, Paguroidea) dell'Eocene medio di cava "Main" di Arzignano (Vicenza, Italia settentrionale). *Studi Trentini di Scienze Naturali*, 96, 11–32.
- De Angeli, A., Garassino, A., & Ceccon, L. (2010). New report of the coral-associated decapods from the "Formazione di Castelgomberto" (early Oligocene) (Vicenza, NE Italy). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano*, 151(2), 145–177.
- De Haan, W. (1833) [1833–1850]. Crustacea. In P. F. von Siebold (Ed.), *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit*. J. Müller et Co., Lugduni Batavorum.
- Dickson, J. A. D. (1965). A modified staining technique for carbonates in thin section. *Nature*, 205(4971), 587–587.
- Dillaman, R., Roer, R., Shafer, T., & Modla, S. (2013). The crustacean integument: structure and function. In L. Watling, & M. Thiel, (Eds.), *Functional Morphology and Diversity* (pp. 140–166). Oxford University Press.
- Di Salvo, G. (1933). I crostacei del Terziario Inferiore della Provincia di Palermo. *Giornale di Scienze naturali ed economiche*, 37(3), 1–46.
- Erko, M., Hartmann, M. A., Zlotnikov, I., Serrano, C. V., Fratzl, P., & Politi, Y. (2013). Structural and mechanical properties of the arthropod cuticle: comparison between the fang of the spider *Cupiennius salei* and the carapace of American lobster *Homarus americanus*. *Journal of structural biology*, 183(2), 172–179. doi: [10.1016/j.jsb.2013.06.001](https://doi.org/10.1016/j.jsb.2013.06.001)
- Fabritius, H. O., Sachs, C., Triguero, P. R., & Raabe, D. (2009). Influence of structural principles on the mechanics of a biological fiber-based composite material with hierarchical organization: the exoskeleton of the lobster *Homarus americanus*. *Advanced materials*, 21(4), 391–400. doi: [10.1002/adma.200801219](https://doi.org/10.1002/adma.200801219)
- Fabritius, H. O., Karsten, E. S., Balasundaram, K., Hild, S., Huemer, K., & Raabe, D. (2012). Correlation of structure, composition and local mechanical properties in the dorsal carapace of the edible crab *Cancer pagurus*. *Zeitschrift für Kristallographie–Crystalline Materials*, 227(11), 766–776. doi: [10.1524/zkri.2012.1532](https://doi.org/10.1524/zkri.2012.1532)
- Feldmann, R. M., Schweitzer, C. E., & Encinas, A. (2010). Neogene decapod Crustacea from southern Chile. *Annals of Carnegie Museum*, 78(4), 337–366. doi: [10.2992/007.078.0404](https://doi.org/10.2992/007.078.0404)
- Ferratges, F. A., Zamora, S., & Aurell, M. (2019). A new genus and species of Parthenopidae MacLeay, 1838 (Decapoda: Brachyura) from the lower Eocene of Spain. *Journal of Crustacean Biology*, 39(3), 303–311. doi: [10.1093/jcobiol/ruz014](https://doi.org/10.1093/jcobiol/ruz014)
- Ferratges, F. A., Zamora, S., & Aurell, M. (2020). Systematics and distribution of decapod crustaceans associated with late Eocene coral buildups from the southern Pyrenees (Spain). *Neues Jahrbuch für Geologie und Paläontologie–Abhandlungen*, 296(1–2), 79–100. doi: [10.1127/njgpa/2020/0893](https://doi.org/10.1127/njgpa/2020/0893)
- Ferratges, F. A., Luque, J., Domínguez, J. L., Ossó, À., Aurell, M., & Zamora, S. (2022). The origin of Dairoidid crabs (Decapoda, Brachyura, Parthenopoidea). *8th Symposium on Fossil Decapod Crustaceans*, Abstract Book (pp. 47–48). Palaeontological Publications.
- Förster, R. (1979). Decapod Crustaceans from the Middle Miocene (Badenian) deposits of Southern Poland. *Acta Geologica Polonica*, 29, 89–106.
- García-Socias, L. (1989). *Daira speciosa* Reuss, 1871 (Crustacea, Decapoda, Xanthidae) en el Mioceno de la isla de Mallorca. *Bolletí de la Societat d'Història Natural de les Balears*, 33, 81–85.
- Garth, J. S. (1991). Taxonomy, distribution, and ecology of Galápagos Brachyura. In M. J. James (Ed.), *Galápagos marine invertebrates* (pp. 123–146). Springer.
- Gašparič, R., Fraaije, R. H. B., Robin, N., & De Angeli, A. (2016). The first record of paguroids from the Eocene of Istria (Croatia) and further phylogenetic refinement of the Paguroidea (Crustacea, Anomura). *Bulletin of Geosciences Geosciences* 91(3), 467–480. doi: [10.3140/bull.geosci.1616](https://doi.org/10.3140/bull.geosci.1616)
- Gatt, M., & De Angeli, A. (2010). A new coral-associated decapod assemblage from the upper Miocene (Messinian) Upper Coralline Limestone of Malta (central Mediterranean). *Palaeontology*, 53, 1315–1348. doi: [10.1111/j.1475-4983.2010.01008.x](https://doi.org/10.1111/j.1475-4983.2010.01008.x)
- Górka, M. (2002). The Lower Badenian (Middle Miocene) coral patch reef at Grobie (southern slopes of the Holy Cross Mountains, Central Poland), its origin, development and demise. *Acta Geologica Polonica*, 53, 521–534.
- Górka, M. (2018). Badenian (middle Miocene) decapod crustaceans from western Ukraine, with remarks on eco-taphonomy, palaeoecology and biogeography. *Acta Geologica Polonica*, 68(4), 511–535. doi: [10.1515/aggp-2018-0031](https://doi.org/10.1515/aggp-2018-0031)
- Górka, M., & Jasionowski, M. (2006). Badenian decapods of the Medobory Hills: their taxonomy and eco-taphonomy. In A. Wysocka, & M. Jasionowski (Eds.), *Przebieg i zmienność sedymentacji w basenach przedgórkich* (pp. 121). II Polska Konferencja Sedymentologiczna.
- Guinot, D. (1967). Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyours. III. A propos des affinités des genres *Dairoides* Stebbing et *Daira* de Haan. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 39(3), 345–374.
- Guinot, D. (1976). Constitution de quelques groupes naturels chez les Crustacés Décapodes Brachyours. I. La superfamille des Bellioidea Dana et trois sous-familles de Xanthidae (Polydectinae Dana, Trichiinae De Haan, Actaeinae 530 Alcock). *Mémoires du Muséum National d'Histoire Naturelle, Paris (A)*, 97, 1–308.
- Guinot, D. (1979). Données nouvelles sur la morphologie, la phylogénèse et la taxonomie des Crustacés Décapodes Brachyours. *Mémoires du Muséum National d'Histoire Naturelle, Paris (A)*, 112, 1–354.
- Guinot, D., & Tavares, M. (2003). A new subfamilial arrangement for the Dromiidae de Haan, 1833, with

- diagnoses and description of new genera and species (Crustacea, Decapoda, Brachyura). *Zoosystema*, 25, 43–129.
- Haj, A. E., & Feldmann, R. M. (2002). Functional morphology and taxonomic significance of a novel cuticular structure in Cretaceous raninid crabs (Decapoda: Brachyura: Raninidae). *Journal of Paleontology*, 76, 472–485. doi: [10.1666/0022-3360\(2002\)076<0472:FMATSO>2.0.CO;2](https://doi.org/10.1666/0022-3360(2002)076<0472:FMATSO>2.0.CO;2)
- Hegdahl, T., Silness, J., & Gustavsen, F. (1977a). The structure and mineralization of the carapace of the crab (*Cancer pagurus* L.). 1. The endocuticle. *Zoologica Scripta*, 6, 89–99.
- Hegdahl, T., Gustavsen, F., & Silness, J. (1977b). The structure and mineralization of the carapace of the crab (*Cancer pagurus* L.). 2. The exocuticle. *Zoologica Scripta*, 6, 101–105.
- Hegdahl, T., Gustavsen, F., & Silness, J. (1977c). The structure and mineralization of the carapace of the crab (*Cancer pagurus* L.). 3. The epicuticle. *Zoologica Scripta*, 6, 215–220.
- Herbst, J. F. W. (1790) [1790–1783]. *Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen*. Beschreibung ihrer verschiedenen Arten, 1–3, Gottlieb August Lange.
- Higuera-Ruiz, R., & Elorza, J. (2009). Biometric, microstructural, and high-resolution trace element studies in *Crassostrea gigas* of Cantabria (Bay of Biscay, Spain): Anthropogenic and seasonal influences. *Estuarine Coastal and Shelf Science*, 82(2), 201–213. doi: [10.1016/j.ecss.2009.01.001](https://doi.org/10.1016/j.ecss.2009.01.001)
- Higuera-Ruiz, R., & Elorza, J. (2011). Shell thickening and chambering in the oyster *Crassostrea gigas*: natural and anthropogenic influence of tributyltin contamination. *Environmental Technology*, 32(6), 583–591. doi: [10.1080/09593330.2010.506201](https://doi.org/10.1080/09593330.2010.506201)
- Hyžný, M. (2016). Diversity and distribution patterns of the Oligocene and Miocene decapod crustaceans (Crustacea: Malacostraca) of the Western and Central Paratethys. *Geologica Carpathica*, 67(5), 471–494. doi: [10.1515/geoca-2016-0030](https://doi.org/10.1515/geoca-2016-0030)
- Hyžný, M., & Dulai, A. (2021). *Badenian decapods of Hungary*. GeoLitera Publishing House.
- Hyžný, M., & Gross, M. (2016). From the palaeontological collection of the Universalmuseum Joanneum – The Cenozoic Decapod Crustaceans (Crustacea: Malacostraca: Decapoda). *Joannea Geologie und Paläontologie*, 12, 73–127.
- Jordan, T. S. (2010). *The role of behavioral temperaments on the ecology of the Caribbean reef octopus, Octopus briareus*. (Master Thesis, Clemson University, Clemson).
- Klomp maker, A. A., Karasawa, H., Portell, R. W., Fraaije, R. H. B., & Ando, Y. (2013). An overview of predation evidence found on fossil decapod crustaceans with new examples of drill holes attributed to gastropods and octopods. *Palaios*, 28, 599–613. doi: [10.2110/palo.2013.p13-026r](https://doi.org/10.2110/palo.2013.p13-026r)
- Klomp maker, A. A., Hyžný, M., & Jakobsen, S. L. (2015). Taphonomy of decapod crustacean cuticle and its effect on the appearance as exemplified by new and known taxa from the Cretaceous–Danian crab *Caloxanthus*. *Cretaceous Research*, 55, 141–151. doi: [10.1016/j.cretres.2014.11.011](https://doi.org/10.1016/j.cretres.2014.11.011)
- Lamarck, J. B. (1798). Extrait d'un Mémoire sur le genre de la Sèche, du Calmar et du Poulpe, vulgairement nommés, Polypes de Mer. *Bulletin des Sciences, par la Societe Philomatique de Paris*, 1(17), 129–131.
- Leite, T. S., Haimovici, M., Molina, W., & Warnke, K. (2008). Morphological and genetic description of *Octopus insularis* new species (Cephalopoda: Octopodidae), a cryptic species in the *Octopus vulgaris* complex from the tropical Southwestern Atlantic. *Journal of Molluscan Studies*, 74, 63–74. doi: [10.1093/mollus/eym050](https://doi.org/10.1093/mollus/eym050)
- Leite, T. S., Haimovici, M., & Mather, J. (2009). *Octopus insularis* (Octopodidae), evidences of a specialized predator and a time-minimizing hunter. *Marine Biology*, 156(11), 2355–2367. doi: [10.1007/s00227-009-1264-4](https://doi.org/10.1007/s00227-009-1264-4)
- Lőrenthey, E., & Beurlen, K. (1929). Die fossilen Dekapoden der Länder der Ungarischen Krone. *Geologica Hungarica, Series Palaeontologica*, 3, 1–420.
- McLay, C. L., & Tan, S. H. (2009). Revision of the crab genus *Garthambrus* Ng, 1996, with the description of two new genera and discussion of the status of *Tutankhamen* Rathbun, 1925 (Crustacea: Brachyura: Parthenopidae). *Zootaxa*, 2122(1), 1–50. doi: [10.11646/ZOOTAXA.2122.1.1](https://doi.org/10.11646/ZOOTAXA.2122.1.1)
- Mertin, H. (1941). Decapode Krebse aus dem subhercynen und Braunschweiger Emscher und Untersenon, sowie Bemerkungen über einige verwandte Formen in der Oberkreide. *Nova Acta Leopoldina, N. F.*, 10, 149–264.
- Morgan, G. J., & Berry, P. F. (1993). Decapod Crustacea of Ashmore Reef and Cartier Island. Marine and Faunal Surveys of Ashmore Reef and Cartier Island North-western Australia. *Western Australian Museum*, 44, 47–65.
- Müller, P. (1993). Neogene decapod crustaceans from Catalonia. *Scripta Musei Geologici Seminarii Barcinonensis*, 225, 1–39.
- Müller, P. (1996). Middle Miocene decapod Crustacea from southern Poland. *Prace Muzeum Ziemi*, 43, 3–16.
- Müller, P. (2004). History of reef-dwelling Decapod Crustaceans from the Palaeocene to the Miocene with comments about Mesozoic occurrences. *Földtani Közlöny*, 134(2), 237–255.
- Ng, P. K. L. (1996). *Garthambrus*, a new genus of deep water parthenopid crabs (Crustacea: Decapoda: Brachyura) from the Indo-Pacific, with description of a new species from the Seychelles. *Zoologische Mededelingen*, 70(10), 155–168.
- Ng, P. K. L., & Tan, S. H. (1999). The Hawaiian parthenopid crabs of the genera *Garthambrus* Ng, 1996, and *Dairoides* Stebbing, 1920 (Crustacea: Decapoda: Brachyura). *Proceedings of the Biological Society of Washington*, 112(1), 120–132.
- Ossó, A., & Stalennuy, O. (2011). Description of the first fossil species of *Bathynectes* (Brachyura, Polybiidae) in the Badenian (middle Miocene) of the Medobory Hills (Ukraine, Central Paratethys), with remarks on its habitat ecology. *Treballs del Museu de Geologia de Barcelona*, 18, 37–46.
- Ossó, À., van Bakel, B. W. M., & Ferratges, F. A. (2021). *Cuchiadromites jadeae*, a new genus and species of primitive crab (Crustacea: Decapoda: Podotremata) from the Aptian of Cantabria (Spain), with comments on its peculiar surface ornament. *Cretaceous Research*, 117, 104636. doi: [10.1016/j.cretres.2020.104636](https://doi.org/10.1016/j.cretres.2020.104636)
- Outomuro, D., & Johansson, F. (2017). A potential pitfall in studies of biological shape: does size matter? *Journal of Animal Ecology*, 86(6), 1447–1457. doi: [10.1111/1365-2656.12732](https://doi.org/10.1111/1365-2656.12732)

- Peyrot-Clausade, M. (1989). Crab cryptofauna (Brachyura and Anomura) of Tikehau, Tuamotu Archipelago, French Polynesia. *Coral Reefs*, 8(3), 109–117.
- Portell, R. W., & Collins, J. S. H. (2004). Decapod crustaceans of the Lower Miocene Montpelier Formation, White Limestone Group of Jamaica. *Cainozoic Research*, 3(1/2), 109–126.
- Poupin, J. (2016). First inventory of the Crustacea (Decapoda, Stomatopoda) of Juan de Nova Island with ecological observations and comparison with nearby islands in the Mozambique channel (Europa, Glorieuses, Mayotte). *Acta oecologica*, 72, 41–52. doi: [10.1016/j.actao.2015.04.001](https://doi.org/10.1016/j.actao.2015.04.001)
- Radwański, A., Górka, M., & Wysocka, A. (2006). Middle Miocene coralgall facies at Maksymivka near Ternopil (Ukraine): A preliminary account. *Acta Geologica Polonica*, 56, 89–103.
- Rathbun, M. J. (1930). The Cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. *United States National Museum Bulletin*, 152, 1–609.
- Rathbun, M. J. (1935). Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America Special Paper*, 2, 1–160.
- Sachs, C., Fabritius, H., & Raabe, D. (2008). Influence of microstructure on deformation anisotropy of mineralized cuticle from the lobster *Homarus americanus*. *Journal of Structural Biology*, 161(2), 120–132. doi: [10.1016/j.jsb.2007.09.022](https://doi.org/10.1016/j.jsb.2007.09.022)
- Saint Martin, J. P., & Müller, P. (1988). Les Crustacés décapodes du Messinien récifal d'Oranie (Algérie). *Geobios*, 21(2), 251–257.
- Savazzi, E. (1982). Burrowing habits and cuticular sculptures in Recent sand-dwelling brachyuran decapods from the Northern Adriatic Sea (Mediterranean). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 163(3), 369–388.
- Scheel, D., Leite, T., Mather, J., & Langford, K. (2017). Diversity in the diet of the predator *Octopus cyanea* in the coral reef system of Moorea, French Polynesia. *Journal of Natural History*, 51(43–44), 2615–2633. doi: [10.1080/00222933.2016.1244298](https://doi.org/10.1080/00222933.2016.1244298)
- Schmalzfuss, H. (1978). Structure, patterns, and function of cuticular terraces in Recent and fossil Arthropods. I. Decapod crustaceans. *Zoomorphologie*, 90, 19–40.
- Serène, R., & Soh, C. L. (1976). Brachyura crabs collected during the Thai–Danish expedition (1966) [the west coast of Thailand]. *Research Bulletin–Phuket Marine Biological Centre (Thailand)*, 12, 1–37.
- Stimpson, W. (1860). Prodromus descriptionis animalium evertibratorum, quae in expeditione ad oceanum Pacificum septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VIII. Crustacea Macrura. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 12, 22–47.
- Stebbing, T. R. R. (1920). XXIII. The Malacostraca of Durban Bay. *Durban Museum Novitates*, 2(6), 263–278.
- Taylor, B. J. (1973). The cuticle of *Cretaceous macrurous* Decapoda from Alexander and James Ross Islands. *British Antarctic Survey Bulletin*, 35, 91–100.
- Tessier, G., Beschin, C., & Busulini, A. (2011). New evidence of coral-associated crustaceans from the Eocene of the Vicenza Lessini (NE Italy). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 260(2), 211–220. doi: [10.1127/0077-7749/2011/0168](https://doi.org/10.1127/0077-7749/2011/0168)
- van Bakel, B. W. M., Guinot, D., Artal, P., Fraaije, R. H. B., & Jagt, J. W. M. (2012). A revision of the Palaeocorystoidea and the phylogeny of raninoidian crabs (Crustacea, Decapoda, Brachyura, Podotremata). *Zootaxa*, 3215(1), 1–216. doi: [10.11646/zootaxa.3215.1.1](https://doi.org/10.11646/zootaxa.3215.1.1)
- Vega, F. J., Dávila-Alcocer, V. M., & Filkorn, H. F. (2005). Characterization of cuticle structure in Late Cretaceous and Early Tertiary decapod Crustacea from Mexico. *Bulletin of the Mizunami Fossil Museum*, 32(3), 37–43.
- Villanueva, R. (1993). Diet and mandibular growth of *Octopus magnificus* (Cephalopoda). *South African Journal of Marine Science*, 3(1), 121–126.
- Viswanathan, C., Goutham, S., Samuel, V. K. D., Krishnan, P. Purvaja, R., & Ramesh, R. (2019). First record of two rare brachyuran crabs: *Drachiella morum* Alcock, 1896 and *Quadrella maculosa* Alcock, 1898 along the Tamil Nadu coast, India. *Journal of Threatened Taxa*, 11(10), 14358–14362.
- Waugh, D. A. (2013). *Utility of fossil cuticle morphology applied to the taphonomy and taxonomy of decapod crustaceans*. (PhD Thesis, Kent State University, Kent). Available in <https://www.proquest.com/openview/b8662bf361ae716cc1a5805abc6f0d16/1?pq-origsite=gscholar&cbl=18750>
- Waugh, D. A., & Feldmann, R. M. (2003). Cuticle microstructure as a new tool in systematic paleontology. *Contributions to Zoology*, 72, 191–193.
- Waugh, D. A., Feldmann, R. M., Schroeder, A. M., & Mutel, M. H. (2006). Differential cuticle architecture and its preservation in fossil and extant *Callinectes* and *Scylla* claws. *Journal of Crustacean Biology*, 26(3), 271–282. doi: [10.1651/S-2692.1](https://doi.org/10.1651/S-2692.1)
- Waugh, D. A., Feldmann, R. M., & Schweitzer, C. E. (2009). Systematic evaluation of raninid cuticle microstructure. *Bulletin of the Mizunami Fossil Museum*, 35, 15–41.
- Weaver, J. C., Milliron, G. W., Miserez, A., Evans-Lutterodt, K., Herrera, S., Gallana, I., Mershon, W. J., Swanson, B., Zavattieri, P., DiMasi, E., & Kisailus, D. (2012). The stomatopod dactyl club: a formidable damage-tolerant biological hammer. *Science*, 336(6086), 1275–1280. doi: [10.1126/science.1218764](https://doi.org/10.1126/science.1218764)
- Yanakevich, A. N. (1977). *Middle Miocene reefs of Moldavia*. Shtiintsa Publishers. [In Russian]
- Zhang, Q., Yang, X., Li, P., Huang, G., Feng, S., Shen, C., Han, B., Zhang, X., Jin, F., Xy, F., & Lu, T. J. (2015). Bioinspired engineering of honeycomb structure – Using nature to inspire human innovation. *Progress in Materials Science*, 74, 332–400. <https://doi.org/10.1016/j.pmatsci.2015.05.001>