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RESEARCH PAPER

Cheilostome bryozoan epibiosis on brachyuran crabs in the Paratethys Sea during the late Badenian (middle Miocene)

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Abstract

This study quantifies the prevalence of a rarely documented occurrence of bryozoans encrusting fossil brachyuran crabs. Over 500 crab fossils were examined from the reef facies of the Rákos Limestone Member of the Leitha Limestone Formation in the quarry at Diósd, Hungary. They were deposited in the upper part of the regional Badenian stage (i.e., lower part of the international Serravallian stage) of the middle Miocene. Nine bryozoan colonies were found encrusting five dorsal carapaces of three different crab species: *Panopeus wronai*, *Dromia neogenica*, and *Cancer styriacus*. The bryozoans were restricted to the exterior surface of the preserved carapaces of the host crabs, so the epibiosis was most likely *syn-vivo*. The prevalence was calculated at 1%. The bryozoans were all cheilostome gymnolaemates identified as a cribrilinid, a calloporid, *Onychocella*? sp., and two indeterminate membraniporiform species. The low prevalence of bryozoan-encrusted crabs is consistent with other fossil-based bryozoan-crab studies but much lower than similar studies in today's faunas. This discrepancy was attributed to both colony spalling-induced preservational bias and differences in carapace size. The bryozoan-crab symbiosis was described as phoretic hitchhiking.

Keywords Bryozoa · Epibiosis · Brachyura · Pannonian Basin · Miocene · Hungary

Introduction

Epibiosis refers to the ecological association between organisms growing attached to a living surface (Wahl, 1989) such as the bryozoans on the crabs in this study. Understanding epibiosis is important because epibionts include organisms also capable of attaching on non-living surface, thereby degrading the functionality of ship hulls, heat exchangers, and water intake pipes (Hellio & Yebra, 2009) as well as the marketability of their commercial host animals (Zha et al., 2017). Bryozoan epibiotic associations range from opportunistic and facultative to the epibionts, in which the epibionts settle by chance on crab carapaces as they do on other acceptable substrata, to deliberate and obligatory, as in the case of some hermit crabs and commensal actinians (Ates, 1995; Gili et al., 1993; Gordon & Wear, 1999). In habitats with no conventional hard substrata, crabs can serve as motile hard "islands" for settlement in an otherwise inhospitable muddy habitat (Gordon & Wear, 1999). Some crabs, especially decorator crabs, purposely attach bryozoans, usually erect branching colonies, to essentially cover all parts of their exoskeleton for camouflage (Guinot & Wicksten,

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2015; Ng & Anker, 2014; Tanduo et al., 2021; Wicksten, 1979, 1992).

In general, symbiotic relationships involving crabs are rarely preserved in the fossil record (Feldmann, 2003a; Klompmaker et al., 2016). In particular, epizoans, including bryozoans, are rarely found on fossil crabs (Key et al., 2017; Waugh et al., 2004). This rarity of bryozoan epibiosis on crabs is partly a function of the hosts' biology. Crabs are motile, which creates advantages and deterrents for encrusting bryozoans (Key et al., 1996a, 1996b). Living on a crab results in water flow around the moving substratum, which can positively or negatively affect the ability of epibionts to feed (Fernandez-Leborans, 2010; Glasby, 2001). The effect of currents generated by the host on bryozoans has been documented in the fossil record (Wyse Jackson et al., 2014). Crabs molt, which results in their exoskeletons being ephemeral substrata, which is a deterrent for encrusting bryozoans (Key et al., 1996a, 1996b, 1999). Some crabs groom (Bauer, 1981) which is a deterrent to epizoans (Tashman et al., 2018). Many crabs exhibit burrowing/burying behavior which can reduce the prevalence of epibionts (Mori & Zunino, 1987). More importantly, the vagaries of fossilization of the host crab's epicuticle makes the preservation of any attached epibionts under-represented in the crab fossil record (Feldmann, 2003a, 2003b; Waugh et al., 2004). This has been attributed to the epicuticle being lightly calcified (Waugh et al., 2004). Thus, the occurrence of the epizoic bryozoans on the crabs in this study merits mention due to its rarity and paleoecological significance.

According to recent meta-analyses of epibiosis, bryozoans are the most diverse group of animal epibionts (Wahl, 2009), also largely settling on non-living marine debris (Haram et al., 2023). But few studies report epizoic bryozoans on crabs (Key et al., 2017). This may be a function of bryozoans being overlooked due to their removal in the aim of identifying the host (McDermott, 2005, 2009), the lack of researchers to identify the bryozoans, and/or their small size (e.g., Hendrickx & Ramírez-Félix, 2019: fig. 2). Bryozoan zooids are on the order of ~ 1 mm^3 and thus require SEM imaging to identify the species. As crabs are much larger, the crab workers are not typically taking SEM images of their specimens, so the bryozoans remain unidentified, which sometimes leads to them being referred to as "moss" in epibiont studies (Savoie et al., 2007).

Bryozoans have a fossil record of growing on other (non-crab) motile hosts such as hyolithids (Galle & Parsley, 2005), trilobites (Key et al., 2010), lobsters (Feldmann et al., 1977), gastropods (Buttler et al., 2022; Taylor, 1994; Taylor & Schindler, 2004), cephalopods (Baird et al., 1989; Wyse Jackson & Key, 2014; Wyse Jackson et al., 2014), and echinoids (Schneider, 2003). Extant (non-crab) motile hosts encrusted by modern bryozoans include gastropods (Schwaha et al., 2019), cephalopods (Landman et al., 1987), pycnogonids (Key et al., 2013a), horseshoe crabs (Key et al., 1996a, 1996b, 2000), isopods (Key & Barnes, 1999), shrimps (Farrapeira & Calado, 2010; Giri & Wicksten, 2001), crayfishes (Ďuriš et al., 2006), lobsters (Key & Decker, 2023; Key & Hendrickx, 2022; Key & Schorr, 2023; Key et al., 2023), sea snakes (Key et al., 1995, 1996b), and sea turtles (Frazier et al., 1992). In all these cases, the permanence/longevity of the host's external surface affects the occurrence of bryozoans. The more frequently a host molts its exoskeleton or sheds its skin, the less common encrusting bryozoans are (Gili et al., 1993). As the time since the last molt or shed increases, more time accrues for bryozoan larvae to settle on the host crab, and the more overgrown the host crab becomes (Gili et al., 1993).

Although Miocene fossil crabs of Hungary have been the subject of scientific research since the nineteenth century (e.g., Brocchi, 1883; Hyžný & Dulai, 2021; Lőrenthey & Beurlen, 1929; Müller, 1984), this study for the first time reports epizoic bryozoans in direct association with the crabs from this fauna. By crabs in this study, we mean true crabs (i.e., brachyuran decapod crustaceans); we exclude hermit crabs, which include an intermediary host as a substratum (a gastropod shell), even though they are often encrusted themselves by bryozoans (e.g., Balazy & Kuklinski, 2013; Carter & Gordon, 2007; McDermott, 2001; Taylor, 1994; Taylor & Schindler, 2004; Taylor et al., 1989; Tilbrook & Grischenko, 2004).

The goal of this study is to quantitatively describe the relationship between epizoic bryozoans and their host crabs from the Miocene of Hungary and to compare it to those reported from the literature on living and fossil crabs.

Geological setting

The fossils for this study came from Müller's (1984) Diósd locality in the southern part of the Tétény plateau on the southwestern edge of Budapest, Hungary (47.4°N, 18.9°E) (Fig. 1). The decapod-bearing horizons are not accessible anymore in this abandoned and now filled-in quarry (Hyžný & Dulai, 2021; Saint Martin et al., 2000). The crabs that we examined were collected from the reef facies of the Rákos Limestone Member of the Leitha Limestone Formation (Müller's, 1984 code MDZ), in particular from the interstices of the coral reefal framework along with bivalves, gastropods, echinoids, and bryozoans (Dulai et al., 2010; Saint Martin et al., 2000).

The Rákos Limestone Member of the Leitha Limestone Formation (Selmeczi et al., 2023) was deposited in the upper part of the regional Badenian stage (Harzhauser & Piller, 2007; Kováč et al., 2007) (Fig. 2). This is equivalent to the lower part of the international Serravallian stage of the middle Miocene, 12.7–13.8 Ma (Raffi et al., 2020: fig. 29.8; Hyžný & Dulai, 2021: fig. 3; Piller & Harzhauser, 2023:

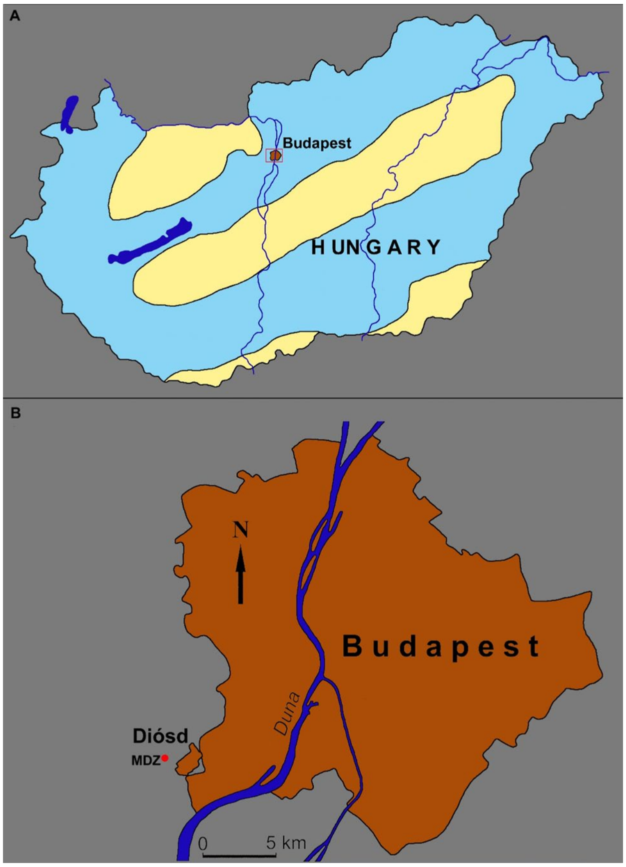

Fig. 1 Simplified maps of the fossiliferous locality. **a** Hungary showing the distribution of Badenian (middle Miocene) marine (light blue) and nonmarine (yellow) deposits. **b** Budapest (brown) showing location of reef facies in this study (locality code MDZ from Müller (1984)) relative to Diósd. Surface water in both maps shown in dark blue. Modified from Hyžný and Dulai (2021: fig. 7)

fig. 1) (Fig. 2). The compact hard Leitha skeletal packstones contain abundant reef-building corals, mollusks, decapods, and bryozoans (Hyžný & Dulai, 2021; Saint Martin et al., 2000). The Leitha Limestone is the dominant shallow-water carbonate formation in the Central Paratethys Sea during the middle Miocene Badenian stage (Piller et al., 1996, 1997; Riegl & Piller, 2000). With African-Eurasian convergence, the Paratethys became an epicontinental relict sea of the Tethys Ocean that existed from the end of the Eocene to the middle Miocene (Dulai, 2015; Meulenkamp & Sissingh, 2003; Palcu & Krijgsman, 2022). The fossils in this study accumulated in the Pannonian Basin of the Central Paratethys Sea, the sediments of which are exposed in present-day Austria, Bulgaria, Croatia, Czech Republic, Hungary, Poland, Romania, Serbia, Slovakia, Slovenia, and Ukraine (Harzhauser & Piller, 2007; Hudáčková et al., 2020; Hyžný, 2016; Hyžný & Dulai, 2021; Jiménez-Moreno et al., 2005; Key et al., 2013b; Kováč et al., 2007, 2017a, 2017b; Sant et al., 2017; Zágoršek, 2010). Paleogeographically, the Diósd locality would have been at a paleolatitude of ~ 46°N (Popov et al., 2004, map 6).

Materials and methods

We follow the terminology of Wahl (1989) and refer to the crabs as basibionts (i.e., the motile host arthropod substrata) and the bryozoans as epibionts (i.e., the sessile organisms attached to the basibiont's outer surface without trophically depending on it). Some use the term fouling in a more restrictive sense to refer to organisms growing on substrata where they are unwanted, such as bryozoans growing on fishing nets, navigation buoys or commercial ship hulls (Chae & Seo, 2019; Cuesta et al., 2016; El-Komi et al., 1998; Godwin, 2003; Liu et al., 2017). We follow Wahl's (1989) definition of epibiosis as a non-symbiotic, facultative association between epibionts and basibionts. Thus, epibiosis is more restrictive than sclerobiosis (Romero et al., 2022) where sclerobionts colonize any kind of hard substrate (Taylor & Wilson, 2002, 2003).

All the basibiont specimens for this study are part of the Pál Müller Badenian Decapoda Collection in the invertebrate paleontology collection of the Hungarian Natural History Museum (HNHM) in Budapest, Hungary (Dulai & Hyžný, 2022). The preserved skeletal components of the crab fossils were examined under a binocular reflected light microscope. Each component (i.e., carapace, sternum/pleon, or appendages) was checked for bryozoans and noted. When complete, carapace length and width were measured to the nearest 0.1 mm using digital calipers. We mapped the amount of host cuticle preserved and the locations of bryozoan colonies on to the template used in McGaw's (2006: fig. 2) *Cancer* epibiont study. This template (Fig. 3) divides a host crab exoskeleton into dorsal and ventral surfaces. The dorsal surface is subdivided into anterior and posterior sectors defined by a transversal line passing through the lateral spines cutting the carapace in two. The ventral surface is subdivided into three sectors: underside (a.k.a., inferior surface of carapace), chelae, and legs/appendages. Adjacent colonies were counted as separate if they had different ancestrula or different zooid growth directions.

To distinguish *post-mortem* from *syn-vivo* growth (sensu Robin et al., 2015: fig. 6), we made note of where each bryozoan colony was attached to its host crab. Was it on a calcified layer of the host cuticle (i.e., epicuticle, exocuticle, or endocuticle) or on an internal mold (see Waugh et al., 2004: fig. 7; Robin et al., 2015: fig. 6)? The area of the encrusted sectors of the host crabs and the areas of the bryozoan colonies were measured to the nearest 0.01 mm^2 with ImagingSource's IC Measure software version 2.0.0.286 with < 2.2% measurement error. Host carapace area was calculated from carapace length × width. This assumes the

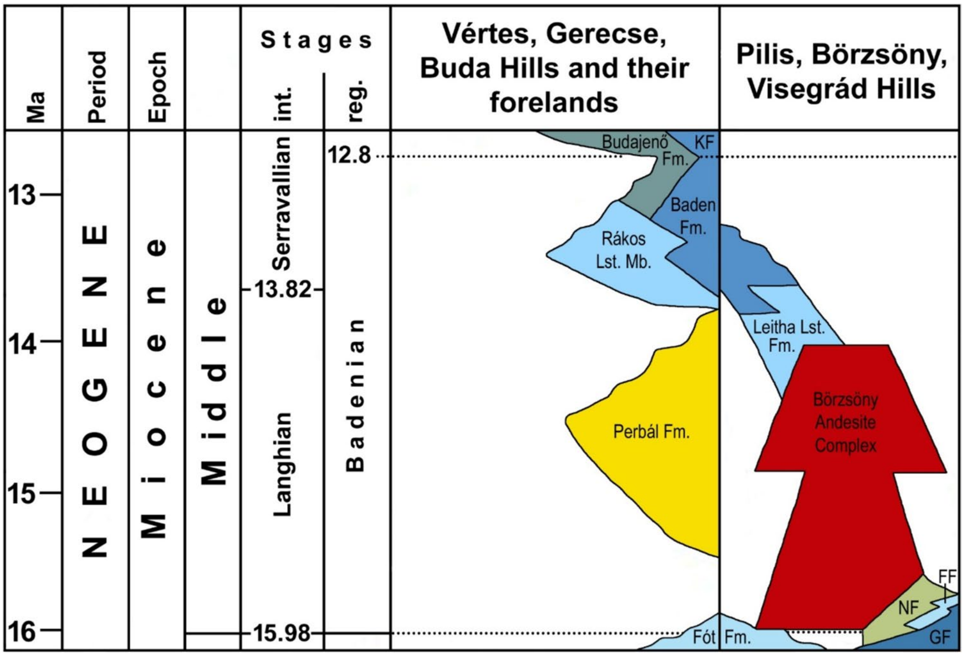

Fig. 2 Stratigraphy of the Badenian (middle Miocene) formations in the Budapest, Hungary area. Abbreviations: int—international; reg—regional; KF—Kozárd Formation; Fm.—Formation; Lst. Memb.—Limestone Member; FF—Fót Formation; NF—Nagyoroszi Formation; GF—Garab Formation. Modified from Selmeczi et al. (2023: 54)

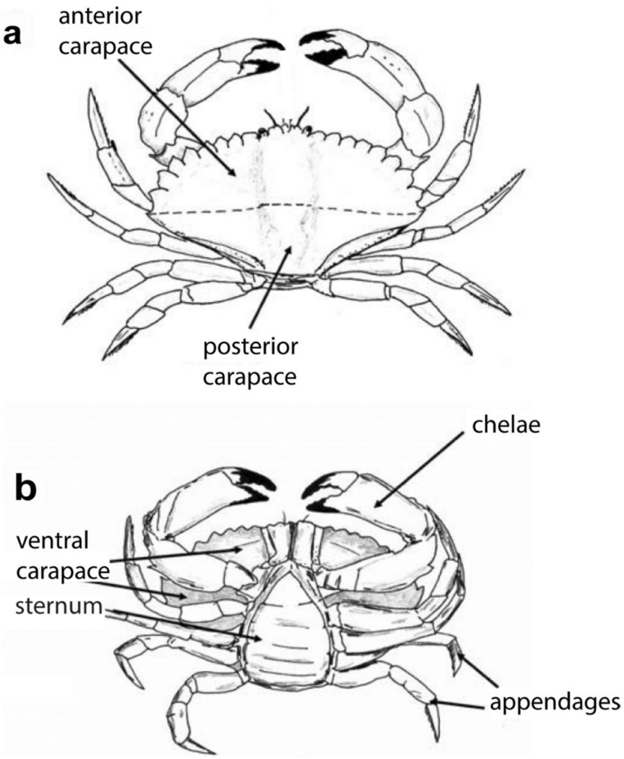

Fig. 3 Template used to map the amount of host cuticle preserved and the locations of any epizoic bryozoan colonies on the dorsal (**a**) and ventral (**b**) surfaces. Modified from McGaw's (2006: fig. 2) *Cancer* epibiont study

carapace is rectangular and over-estimates area more on less "boxy" crabs (e.g., *Cancer styriacus*).

Key's (2020) power function growth curve model was used to estimate colony age based on the number of zooids in the colony. For this, we counted the number of complete zooids in each colony to estimate colony age. Finally, the relative area of the bryozoan colony to the area of the encrusted sector of the host crab was calculated. Shall some colonies be incomplete or bearing broken edges, the collected values represent only minima to their colonial extension.

At the exception of those present on type crab specimens, bryozoan colonies were cut out of the host crab fossil using a Dremel diamond cutting wheel in order to observe them under the SEM for species identification. To remove loose sediment, the more robust colonies were cleaned in an EMAG Technologies Emmi-40HC ultrasonic vibrator water bath at 30 °C for 1 min. Due to the sufficiently preserved relief of its frontal walls, one specimen (HNHM INV 2019.914.1) was gold coated with a Quorom SC7620 spudder coater for more effective SEM imaging. Scanning electron imaging of bryozoans was performed with a Thermo Scientific Phenom Pro G6 Desktop SEM. Reflected light optical imaging was performed with a binocular Olympus SZ61 microscope with a Promicra Promicam 3-3CP color digital camera. We used previous compilations on bryozoan species reported from the same general time and place by Saint Martin et al. (2000: table 1), Moissette et al. (2006: table 1; 2007: table 2), and Dulai et al. (2010: 54) to help constrain the bryozoan identifications. These were chosen as they had access to more and better-preserved material, including from the exact same locality as this study, and the bryozoans were identified by P. Moissette, the bryozoologist most familiar with this fauna. The presence of other epibionts was also noted.

Finally, we did a thorough review of the literature of published reports identifying extant epizoic bryozoans encrusting host brachyuran crabs. We made note of which bryozoan order and species, which crab family and species, and where on the host crab the bryozoans were growing (Suppl. Table 1). We did the same for the fossil record (Suppl. Table 2).

Results

We screened 1,055 decapod crustacean fossils for bryozoans from the entire Pál Müller collection and identified 617 brachyuran crab fossils from Diósd as the best locality for our study. Of those, 569 were from the reef (MDZ) facies, the focus of this study. The 569 examined brachyuran remains represented 89% dorsal carapaces (n = 504), 11% appendages (n = 65), and no sterna (Suppl. Table 3). Nine bryozoan colonies were found encrusting the outer surface of the dorsal carapaces of five crabs (Table 1). This represents a prevalence (proportion of colonized carapaces) of 1% (i.e., 5/504*100). No bryozoans were found on the appendages. The five encrusted carapaces were from three different brachyuran crab species: one individual of *Panopeus wronai* Müller, 1984, two individuals of *Dromia neogenica* Müller, 1979, and two individuals of *Cancer styriacus* Bittner, 1884 (Fig. 4; Table 1).

Host crabs

Cancer styriacus Bittner, 1884 (Fig. 4a) is characterized by transversely ovate carapace, narrow orbitofrontal margin (~40% of carapace maximum width), trilobed front and anterolateral margins with nine finely denticulate lobes. From other Miocene cancrids of Europe it differs in having a relatively smooth carapace surface, a rather narrow posterior portion of the carapace and distinctly shaped anterolateral teeth (Hyžný & Dulai, 2021). *Cancer styriacus* is known from the middle Miocene (Badenian) of Austria (Bittner, 1884; Müller, 1998), Hungary (Hyžný & Dulai, 2021; Müller, 1984), and Poland (Müller, 1996). Its assignment to the genus *Cancer* within the family Cancridae fits the revised concept as presented by Schram and Ng (2012).

Panopeus wronai Müller, 1984 (Fig. 4b) is characterized by a transversely hexagonal carapace with straight front, an orbitofrontal margin attaining more than half of carapace width, anterolateral margins with four teeth, well defined carapace regions, and elevated transversal ridges (consisting of fine tubercles) on the epigastric, protogastric, hepatic and epibranchial regions. The species is known from the middle Miocene (Badenian) of Austria (Collins, 2014; Müller, 1984, 1998), Hungary (Hyžný & Dulai, 2021; Müller, 1984) and

Table 1 Potentially *syn-vivo* cheilostome bryozoans found on dorsal carapaces of fossil brachyuran crab specimens used in this study from the Hungarian Natural History Museum (HNHM) collected from the Badenian reef facies of the Rákos Limestone Member of the Leitha Limestone Formation exposed in the Diósd, Hungary quarry

Host crabs					Bryozoans				
HNHM inventory number	Species	Carapace length (mm)	Carapace width (mm)	Carapace area (mm^2)	Species	Number of colonies	Minimum number of complete zooids in colonies	Minimum area of colonies (mm^2)	Minimum % of host covered by bryozoans
INV 2007.100.1	*Panopeus wronai*	19.5	30.4	429.02	Indeterminate membraniporiform sp. 1	5	6, 23, 7, 5, 3	1.47, 2.12, 6.59, 1.81, 1.43	3.1
INV 2019.914.1	*Cancer styriacus*	57.0	72.0	845.65	Cribrilinid, similar to *Cribrilaria innominata*	1	121	15.99	1.9
INV 2019.914.2	*Cancer styriacus*			302.78	Indeterminate membraniporiform sp. 2	1	93	18.31	6.0
INV 2019.1012.1	*Dromia neogenica*	47.9	52.0	3476.32	*Onychocella*? sp.	1	37	17.27	0.5
M.89.72.1	*Dromia neogenica*			1078.57	Calloporid	1	77	21.20	2.0

Host crab species listed as on specimen label. Data sorted by HNHM inventory number

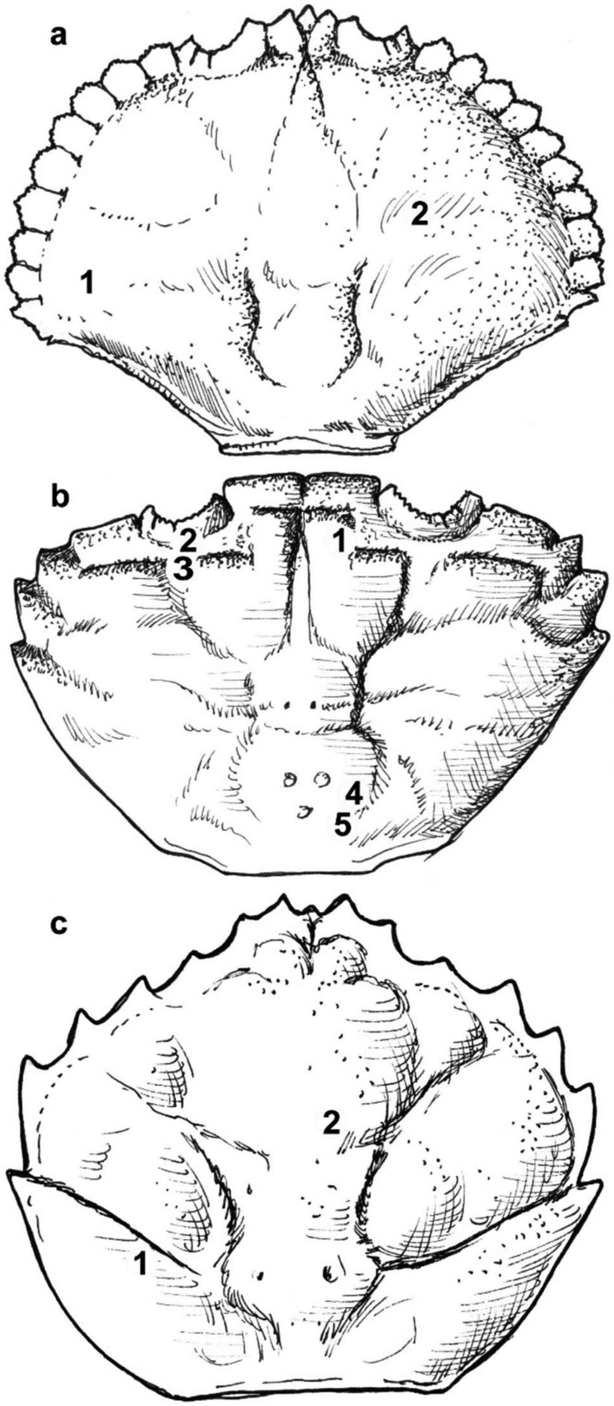

Fig. 4 Dorsal carapace reconstructions of the three species of brachyuran crabs in this study showing the numbered locations of the encrusting bryozoan colonies. All are from the reef facies of the upper Badenian (middle Miocene) Rákos Limestone Member of the Leitha Limestone Formation in Diósd, Hungary. **a** *Cancer styriacus* Bittner, 1884, **b** *Panopeus wronai* Müller, 1984. **c** *Dromia neogenica* Müller, 1979. The reconstructions are not to the same scale

Ukraine (Górka, 2018). Müller (1993: 17) opined that the Miocene *Panopeus* species from Europe could belong to a separate genus, differing from extant species. Nevertheless, the assignment to the family Panopeidae seems secured.

Dromia neogenica Müller, 1979 (Fig. 4c) is characterized by a subcircular, strongly convex carapace with bilobed rostrum, an orbitofrontal margin attaining about one-third of the total carapace width, and anterolateral margins with four well-developed teeth. Even though the carapace surface is smooth, and regions are delineated only faintly, the carapace outline is very distinctive and therefore also fragments can be identified. As for Paratethyan occurrences, the species is known from the middle Miocene (Badenian) of Austria (Müller, 1998), Hungary (Hyžný & Dulai, 2021; Müller, 1984), and Ukraine (Górka, 2018). It has been reported also from the middle Miocene (Langhian) of Spain (Müller, 1993); the upper Miocene (Messinian) of Malta (Gatt & De Angeli, 2010) and Algeria (Saint Martin & Müller, 1988); the upper Miocene/lower Pliocene of Belgium (Fraaije et al., 2010); and the lower Pliocene (Zanclean) of Italy (Garassino et al., 2012). *Dromia neogenica* is morphologically very close to the extant *Dromia personata*.

Epibionts

The bryozoans were all cheilostome gymnolaemates (Fig. 5; Table 1). They were all found growing on their host crab's epicuticle surface (Fig. 5a) which is compatible with potentially *syn-vivo* growth. The nine bryozoan colonies were identified as a cribrilinid, a calloporid, *Onychocella*? sp., and two indeterminate membraniporiform species. Identifying the bryozoans to even the genus level was challenging due to the often poor preservation and limited number of colonies (Saint Martin et al., 2000) with recrystallized or highly corroded frontal walls being common (Fig. 5d). The colonies easiest to identify were those found on the outer surface of the host crab's epicuticle and when the colony surface was visible (Fig. 5a). The colonies hardest to identify were those preserved as the thin basal portion found on the outer surface of the host crab's epicuticle but only the colony base was visible through the underlying crab cuticle (Fig. 5b, c). This style of preservation was referred to as a basal imprint by Robin et al., (2015, figs. 5, 7). In all cases, the bryozoans were collected from the host's carapace with epicuticle preserved, and in no case from internal casts. The cheilostome ichnogenus *Finichnus* Taylor et al., 2012 was not found.

The cribrilinid is an encrusting colony visible on the host crab's epicuticle surface (Fig. 5a). Cribrimorph grade frontal walls with 9–14 costae are highly corroded. Proximal margin of the orifice reveals a small apertural bar. Non-brooding zooids have five to six oral spines. When ovicells are present, all but two of the oral spines are covered by fertile

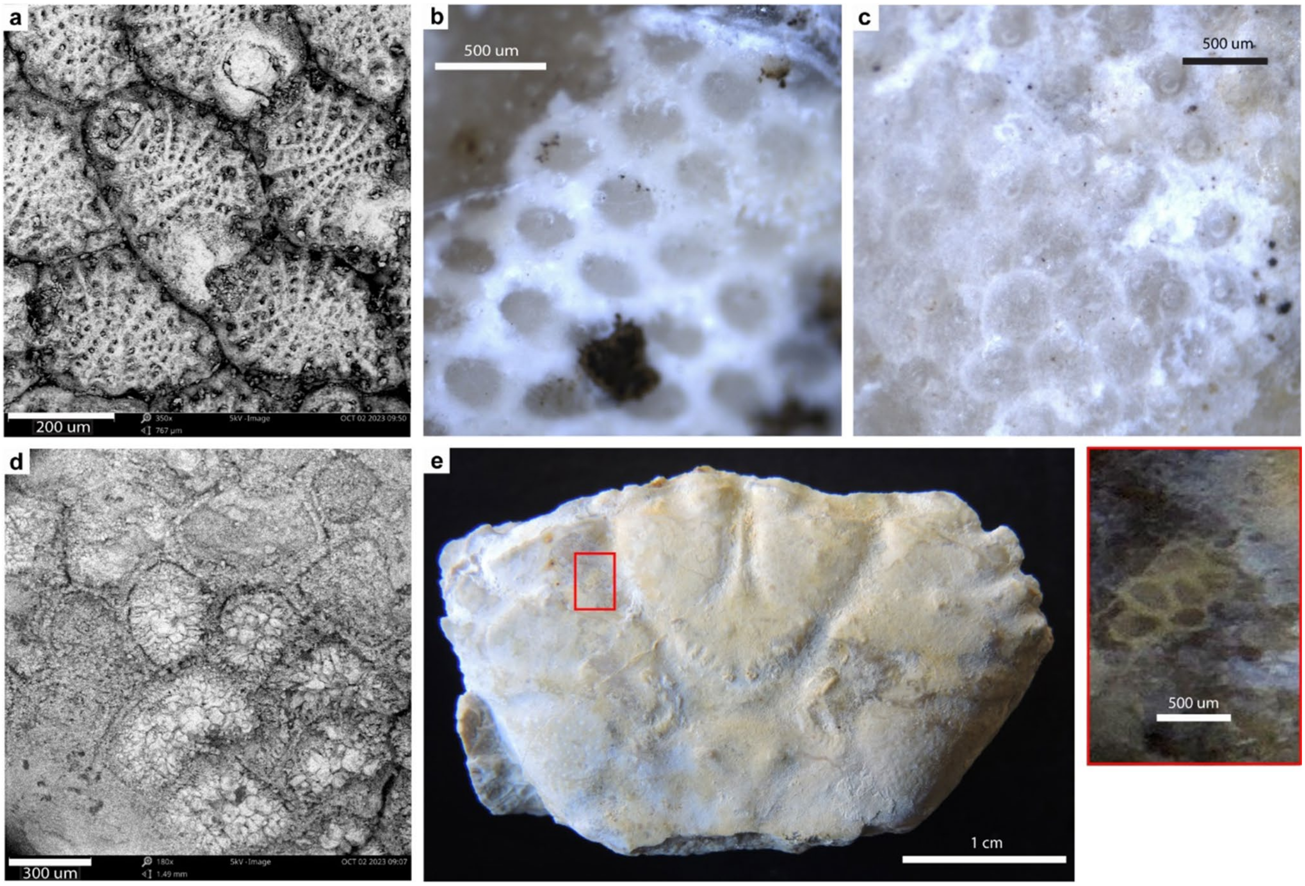

Fig. 5 The five cheilostome bryozoan species discovered on fossil crabs from the reef facies of the upper Badenian (middle Miocene) Leitha Limestone Fm. in Diósd, Hungary. **a** Cribrilinid (HNHM INV 2019.914.1). **b** Calloporid (HNHM M.89.72.1). **c** *Onychocella*? sp. (HNHM INV 2019.1012.1). **d** Indeterminate membraniporiform sp. 1 (HNHM INV 2019.914.2). **e** Indeterminate membraniporiform sp. 2, close-up of the bryozoan colony in red insert on paratype of the crab *Panopeus wronai* Müller, 1984 (HNHM INV 2007.100.1)

maternal zooids. Ovicells lack keels; they are smooth, quite small, not very convex with areolar pores around the margin. Maternal zooids have only two oral spines, instead of 4–5 in non-brooding zooids. No avicularia could be seen. These different features suggest a cribrilinid, similar to *Cribrilaria innominata* (Couch, 1844) which Dulai et al. (2010) reported from the same locality.

The calloporid is an encrusting colony visible from below through the crab cuticle internal structure on the host's epicuticle surface (Fig. 5b). Taking into consideration the size and rounded-polygonal outline shape of the base of the zooids, this anascan-grade cheilostome is probably a calloporid, several of which were reported from this same locality (Dulai et al., 2010).

Onychocella? sp. is an encrusting colony visible from below through the crab cuticle internal structure on the host's epicuticle surface (Fig. 5c). The general outline of the base of the zooids, with their rounded distal part and more rhomboidal proximal part corresponds to the outline of an onychocellid zooid. The autozoecia observed in the colony (Fig. 5c) have the characteristic outline very typical for *Onychocella*. This genus is also typically characterized by the presence of vicarious avicularia. Unfortunately, the small colony found in this study lacked them. Only one onychocellid has been described from the Diósd locality: *Onychocella angulosa* (Dulai et al., 2010).

Indeterminate membraniporiform sp. 1 is an encrusting colony visible on the host crab's epicuticle surface (Fig. 5d). This is compatible with potentially *syn-vivo* growth. The calcite crystals of the zooidal walls are different in size and shape from the calcite crystals of the zooidal cavity infilling. The zooidal walls are heavily recrystallized. The poor preservation limits identification to an unidentified membraniporiform/encrusting grade bryozoan (Fig. 5d).

Indeterminate membraniporiform sp. 2 is an encrusting colony with much smaller (1/2 ×) zooids than sp. 1. It is visible on the host crab's epicuticle surface (Fig. 5e), which is also compatible with potentially *syn-vivo* growth. This small size of the colony and its poor preservation limits identification to an unidentified membraniporiform/encrusting grade bryozoan.

The nine bryozoan colonies contained 3–121 zooids (mean = 41, standard deviation = 42). The colonies ranged from 1.4 to 21.2 mm^2 (mean = 9.6 mm^2, standard deviation = 7.9 mm^2). These colonies collectively covered 0.5–6.0% of the exposed (not the whole carapace) epicuticle of each crab (mean = 2.7%, standard deviation = 1.9%) (Table 1). These are all minimum values as some of the colonies are incomplete and have broken edges (e.g., Fig. 5b). All nine of the colonies might have encrusted their host crab *syn-vivo*. This was because the colonies were preserved on the epicuticle surface (Fig. 5d), not the exocuticle or endocuticle.

Of the 504 fossil crab carapaces from the reef facies of the Diósd locality, 23 were complete enough to measure carapace length and width (Table 1). The larger the surface of the crab carapaces, the more likely they were to be encrusted by bryozoans (Fig. 6). The carapaces of crabs encrusted by bryozoans were on average twice as long and wide as the crabs not encrusted, but the differences were insignificant (t-Tests with $p = 0.167$ and 0.137, respectively). Other than *Necronectes*, the three encrusted crabs (i.e., *Cancer styriacus*, *Dromia neogenica*, and *Panopeus wronai*) are among the largest crabs from Diósd.

Three of the crabs also had epibiotic serpulid worms growing on their carapaces (HNHM INV 2007.100.1, HNHM INV 2019.914.1, HNHM INV 2019.1024). Two of those crabs also had bryozoans. One of the crabs also had an encrusting foraminiferan growing on its carapace (HNHM INV 2019.914.1) and another a non-clionid sponge (HNHM M.89.72.1).

In our literature review, we found 63 published reports identifying 157 extant epizoic bryozoans growing on host brachyuran crabs (Suppl. Table 1). These included 68 different bryozoan species found on 47 different crab species. The most commonly reported bryozoans were *Triticella elongata* (Osburn, 1912) (n = 22 reports), *T. flava* Dalyell, 1848 (n = 6), *Bugula neritina* (Linnaeus, 1758) (n = 5), and *Conopeum tenuissimum* (Canu, 1908) (n = 5). The most commonly reported host crabs were *Maja squinado* (Herbst, 1788) (n = 20 reports), *Callinectes sapidus* Rathbun, 1896 (n = 18), *Hyas araneus* (Linnaeus, 1758) (n = 12), and *Chionoecetes opilio* (Fabricius, 1788) (n = 11). For the fossil record (Suppl. Table 2), we found 14 published papers reporting 29 instances of extinct epizoic bryozoans growing on host brachyuran crabs. Of those 29 reports, only five bryozoan species were identified as 72% of the reports did not identify the bryozoans below the order level. The fossil bryozoans were found on 16 different crab species. The most commonly reported bryozoans were *Berenicea* sp. (n = 3) and *Acanthodesia* sp. (n = 2). The most commonly reported host crabs were *Dromiopsis rugosa* (Schlotheim, 1820) (n = 9) and *Tanidromites raboeufi* Robin et al., 2015 (n = 2).

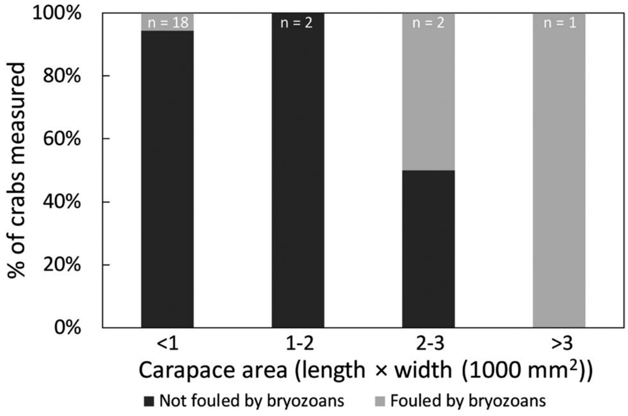

Fig. 6 Bar chart showing proportion of crabs in this study free of bryozoan colonies versus those encrusted by bryozoans relative to host crab total surface area represented by carapace area (i.e., length × width)

Discussion

Prevalence

Although 22 different invertebrate taxa, ranging from phyla to infra-classes, are known to be epizoans of extant decapods, only seven have been reported on fossil representatives (Feldmann, 2003a; Fernandez-Leborans, 2010). The prevalence of organisms growing on fossil decapod crustaceans is generally only about 2% (Robin, 2015). Other than this study, only four other studies of bryozoan epibionts on modern and fossil crabs are known. The fossil prevalence of 1% documented here is similar to Key et al.'s (2017) reported rate of 5% in similar aged Miocene crabs from Iran. In contrast to these low prevalences, extant crabs have a higher bryozoan prevalence. Abelló and Corbera (1996) reported 18% of the specimens of the extant crab *Goneplax rhomboides* (Linnaeus, 1758) encrusted by bryozoans. Gordon and Wear (1999) reported bryozoans on 17% of the extant crab *Ovalipes catharus* (White, 1843). Key et al. (1999) reported 16% of the extant blue crab *Callinectes sapidus* Rathbun, 1896 were encrusted by bryozoans. The prevalence of bryozoans on extant crabs is on average six times higher than in the fossils (mean 17% versus 3%, respectively).

There are several competing hypotheses for why bryozoan epibiosis is more prevalent on extant crabs. The most likely explanation is due to preservational bias against preservation of epibionts on the epicuticle of crabs (Waugh et al., 2004). Loss of fossil bryozoans by spalling-off their hard substrates has also been documented in the Ordovician (Wilson et al., 2024). It is impossible to know how important bryozoan dislodgement was in these fossils and to what extent it impacts epibiont size, distribution, and prevalence.

Alternatively, there are different species of bryozoans involved, so perhaps the fossil bryozoan species were more selective about what substrata their larvae settled on. Modern bryozoan larvae show preferences for specific substrata which are often based on the orientation of the substratum (e.g., Pomerat & Reiner, 1942), how cryptic or well-lit the substratum is (e.g., Lescinsky, 1993; Ryland, 1960), or the presence of a certain microflora (e.g., Scholz & Krumbein, 1996). There are also different species of crabs involved, so perhaps the microflora of the carapaces of the fossil crab species were less attractive to bryozoan larvae. Finally, it may be that the three well-studied extant crab species are simply larger targets for settling larvae sensu the Target Area Hypothesis (Lomolino, 1990). Larger crabs should have more epibionts, including bryozoans. This hypothesis, derived from MacArthur and Wilson's (1967) Theory of Island Biogeography, argues that larger targets (e.g., islands or in the case of this study, molting carapaces of crabs) should have more epibionts simply because they are a larger target for 'propagules' (Stracey & Pimm, 2009).

The mean available carapace surface area of the encrusted hosts in this study is 1,226 mm^2. In the other fossil study on Miocene crabs from Iran (Key et al., 2017), it is 246 mm^2. The surface areas of the encrusted extant crabs, *Goneplax rhomboides* (274 mm^2), *Ovalipes catharus* (6529 mm^2), and *Callinectes sapidus* (10,435 mm^2) are on average eight times larger than the fossil species. Therefore, the lower prevalence of bryozoans growing on fossil crabs compared to extant crabs is likely due to both preservational bias and the Target Area Hypothesis.

The epibiotic bryozoans in this study were all cheilostome gymnolaemates (Table 1). This follows the trend shown in previous studies of fossil bryozoans encrusting brachyuran crabs (Suppl. Table 2) which found 83% of the reports were cheilostomes, 10% cyclostomes, and 7% ctenostomes. Of the studies identifying extant epizoic bryozoans growing on host brachyuran crabs (Suppl. Table 1), 50% of the reports involved cheilostome bryozoans, 42% ctenostomes, and 8% cyclostomes. This difference between extinct and extant epibiotic bryozoans may simply be a function of ctenostomes lacking mineralized skeletons (Bogdanov et al., 2022; Taylor, 2020) so they are less likely to be preserved as fossils. The fossil ctenostomes reported on crabs in the literature (e.g., *Terebripora* sp. in Suppl. Table 2) are shallow endolithic boring/etching bryozoans (Decker et al., 2023) preserved as voids in the host crab carapaces (Pohowsky, 1974). The fact that cheilostome bryozoans are the most common and diverse type of bryozoan encrusting crabs has been attributed to a coevolutionary relationship existing between them (Key & Schweitzer, 2019).

Badenian crab and bryozoan faunas

The middle Miocene Badenian decapod fauna of the Central Paratethys of central and eastern Europe is diverse with at least 120 species reported (Dulai & Hyžný, 2022; Hyžný, 2016; Hyžný & Dulai, 2021; Müller, 1984; Saint Martin et al., 2000). The three crab species reported here (*Panopeus wronai*, *Dromia neogenica*, and *Cancer styriacus*) have been found previously in the Badenian of Hungary (Hyžný & Dulai, 2021; Müller, 1984, 1998; Saint Martin et al., 2000), Austria (Collins, 2014; Müller, 1984, 1998), Poland (Müller, 1984, 1996, 1998), and Ukraine (Górka, 2018; Ossó & Stalennuy, 2011).

The middle Miocene Badenian bryozoan fauna of Hungary is also diverse with at least 238 species (Dulai et al., 2010; Moissette et al., 2006; Saint Martin et al., 2000). *Onychocella* is an extant genus from the Indo-Pacific and the Pacific (Bock, 2024) to the eastern Atlantic and Mediterranean (Moissette et al., 2006) that also occurs to the northwest in the Vienna Basin and the Carpathian Foredeep (Zágoršek, 2010). The Diósd coral reef facies in Hungary is more depauperate with 20 bryozoan species, dominated by membraniporiform (encrusting) representatives (Dulai et al., 2010; Moissette et al., 2007; Saint Martin et al., 2000), like five species found growing on the crab carapaces in this study.

In decapod crustaceans, grooming behavior of sensory appendages and respiratory surfaces is widespread throughout various groups, while cleaning of the other body surfaces, observed mostly in shrimps and lobsters, is less common in brachyuran crabs (Bauer, 1981; Tashman et al., 2018). Nevertheless, not all brachyurans exhibit the same degree of epizoic growth. For instance, burrowing behavior of some crab taxa may act as an antifouling behavior (Becker & Wahl, 1996). Among published records of extant brachyurans with epizoic bryozoans, majoid and portunoid crabs dominate (Suppl. Table 1). Up to 29 genera of bryozoans have been observed as attached to the exoskeleton of various representatives of the superfamily Majoidea. This is not surprising, because majoid crabs, also known as decorator crabs, possess unique stiff-hooked setae which are actively used for attaching various organic matter as a camouflage (Guinot & Wicksten, 2015). In portunoid crabs, which often exhibit active swimming behavior (Spiridonov et al., 2014) as many as 9 epizoic bryozoan genera have been reported (Suppl. Table 1). Other documented encrusted crabs include inhabitants of the intertidal zone (Eriphioidea: *Sphaerozius*) and shallow-marine environments (Xanthoidea) to inhabitants of deep-water environments, including carrying crabs (Homoloidea: *Paromola*) and burrowers (Goneplacoidea: *Goneplax*) (Poore & Ahyong, 2023). For example, McGaw (2006: 91) reported that bryozoans were found on *Cancer productus* and *C. magister*, but since bryozoans are susceptible to sedimentation, they did not occur on *C. gracilis*, which is confined to muddy areas (Orensanz & Galluci, 1988). Interestingly, crabs exhibiting burying behavior (e.g., raninoids and calappoids) have not been reported as being encrusted by bryozoans.

Fossil occurrences of crabs with epizoic bryozoans are limited to a handful of occurrences (Suppl. Table 2) without any recognizable pattern. Data are too limited to draw any major conclusions. At least for some decapod groups, molts are more often found than corpses in the fossil record (Mertin, 1941; Müller, 2004). As for Badenian bryozoan epibiosis reported from Diósd herein, they are more common on the larger individuals compared to other crabs found at the same locality (Fig. 6).

Spatial distribution of bryozoan colonies on host crabs

All nine of the bryozoan colonies were found encrusting the crabs' dorsal carapaces, none on the ventral appendages or sterna/pleons. There are several competing hypotheses to explain this. It could simply be a function of their relative surface areas as individual carapaces are larger (Fig. 3). It could be a preservation bias as the crab fossils from the reef facies of the Diósd locality were 89% dorsal carapaces, 11% appendages (pereopods), and no sterna (Table 1). There is preservation bias towards claws (Klompmaker et al., 2017; Krause et al., 2011; Mutel et al., 2008), which often are heavily calcified (Waugh et al., 2006). It could be a collection bias against appendages as they typically contain fewer taxonomically diagnostic features than the carapace and sternum (Hyžný & Dulai, 2021). It may be a grooming bias as crabs generally can more easily groom epibionts from their appendages (Bauer, 1981; Tashman et al., 2018).

Regardless, bryozoans are most often found encrusting the carapaces of their host crabs. Of the studies identifying where on extant host crab the bryozoan colony was found (Suppl. Table 1), 93% of the studies reported them on the carapace and 63% on the appendages. In contrast to the fossil record (Suppl. Table 2), where 86% were on the carapace and 14% on the appendages. This disparity of reduced prevalence of encrusted appendages in the fossil record supports the argument of a preservational bias.

Timing of epibiosis

It is a challenge to know for certain if the extant bryozoan growth on the host crab occurred *syn-vivo*, *post-mortem* or *post-molt* (Bogdanov et al., 2022). Many terrestrial arthropods eat their shed cuticle after molting. These include insects (Guthrie & Tindall, 1968; Mira, 2000; Sands et al., 1997) and crustaceans such as isopods (Luquet & Marin, 2004; Steel, 1993) and land crabs (Greenaway, 1985, 1993; Skinner, 1985). This behavior is more common in terrestrial arthropods where Ca^{2+} is less available than in marine environments (Luquet & Marin, 2004). But even some marine decapod crustaceans also eat their exuviae including multiple species of crabs (Berrill, 1982; Breteler, 1975; Lovrich & Sainte-Marie, 1997; Williams, 1981).

It is even more challenging to determine if the fossil bryozoan-crab relationship is *syn-vivo*. Sometimes bryozoan colonies are simply preserved adjacent to, but not on, a fossilized crab (e.g., *Steginoporella* sp. deposited next to the carapace of *Hebertides jurassica* (Ossó & Gagnaison, 2019: fig. 3J)), and this can be confused with epibiosis. Other times, the epibiosis is potentially *syn-vivo*, but the bryozoan was not identified even though it would have been possible with an SEM image (e.g., Ossó & Gagnaison, 2019: figs. 5L, M which is probably the cheilostome *Porella* or *Perigastrella*). The most challenging situation is when the growth occurred on the exterior of a preserved internal mold (Waugh et al., 2004: fig. 7; Robin et al., 2015: fig. 6).

Based on this discussion and the location of all the bryozoan colonies on the host crabs' epicuticle surfaces, it is possible the epibiosis was *syn-vivo*.

Sexual reproduction of bryozoan colonies

Bryozoan colonies must be able to sexually reproduce before the host crab molts or dies to make growing on their host crab selectively advantageous. Bryozoan colonies must reach a size large enough to invest in sexual reproduction (Harvell & Grosberg, 1988; Herrera et al., 1996; Hughes, 1989). Assuming the epibiosis occurred *syn-vivo*, this growth must be fast enough to be completed before the host crab molts or dies. On some crabs, this does not happen until the host crab reaches maximum size following terminal molt (Gordon & Wear, 1999). Only one of the nine colonies in this study was well enough preserved to show evidence of the delicate ovicell structures indicative of sexual reproduction. It occurred on the largest encrusted crab (i.e., *Cancer styriacus*, INV 2019.914.1). The bryozoan was a cribrilinid, similar to *Cribrilaria innominata*, and it had many ovicells, indicative of at least female sexual reproduction. One of its ovicells is visible upper right of Fig. 5a. Just because the one colony that is well enough preserved to show ovicells does show them, that does not mean that all the colonies were sexually reproducing. In fact, some probably could not because they were quite small.

The nine bryozoan colonies discovered in this study contained 3–121 zooids (mean = 41, standard deviation = 42). These are minimum values as some of the colonies are incomplete and have broken edges (e.g., Fig. 5b). We estimated the ages of the bryozoan colonies using Key's (2020) power function growth curve model for encrusting cheilostomes based on the number of complete zooids in the colony (Table 1). The colony ages ranged from 3 to 169 days (mean = 45 days, standard deviation = 57 days). Colonial organisms like bryozoans typically delay reproduction until attaining some minimum size (Wood & Seed, 1992; Nekliudova et al., 2019). Colony size and age at sexual reproduction varies widely by cheilostome species and location, but published values range from < 10 zooids to 4600 and from 16 to 550 days (Kuznetzov, 1941; Gordon, 1970; Hayward & Ryland, 1975; Jackson & Wertheimer, 1985; Winston & Håkansson, 1986; Herrera et al., 1996; Grishenko et al., 2018). Therefore, the smallest and youngest colonies encrusting the host crabs in this study may not have been capable of sexual reproduction.

Conclusions

The low prevalence (1%) of bryozoan epibiosis on these Badenian crabs is attributed to preservational bias and the relatively small size of these reefal crabs compared to the range of size reached in modern crabs. The bryozoans were restricted to the preserved carapaces of the host crabs, and the epibiosis was compatible with a *syn-vivo* association. In this case, at least one of the colonies was large enough to sexually reproduce before its host crab molted or died. Thus, at least some of the sessile bryozoans were able to derive the benefits of living on a motile host which include expanding their geographic range and avoiding both substratum competition and predation on conventional hard benthic substrata. The symbiosis documented here is best described as phoresy by small encrusting bryozoan colonies on brachyuran crabs living in patch reefs.

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Data availability Not applicable as all the data is being made available in the tables and supplemetary files.

Declarations

Conflict of interest The authors declare no conflicts of interest with this manuscript.

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