

## BRYOZOAN EPIBIOSIS ON FOSSIL CRABS: A RARE OCCURRENCE FROM THE MIOCENE OF IRAN

MARCUS M. KEY, JR.,<sup>1</sup> MATÚŠ HYŽNÝ,<sup>2</sup> ERFAN KHOSRAVI,<sup>3</sup> NATÁLIA HUDÁČKOVÁ<sup>4</sup> NINON ROBIN,<sup>5</sup>  
AND MAJID MIRZAEI ATAABADI<sup>6</sup>

<sup>1</sup>Department of Earth Sciences, Dickinson College, P.O. Box 1773, Carlisle, Pennsylvania, 17013, USA

<sup>2</sup>Department of Geology and Palaeontology, Natural History Museum, Vienna, Burgring 7, A-1010 Vienna, Austria; Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, SVK-842 15, Bratislava 4, Slovakia

<sup>3</sup>Department of Animal Biosystematics, School of Biology, College of Science, University of Tehran, 16th Azar St., Enghelab Sq., Tehran, Iran

<sup>4</sup>Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, SVK-842 15, Bratislava 4, Slovakia

<sup>5</sup>Muséum National d'Histoire Naturelle, Centre de Recherches sur la Paléobiodiversité et les Paléoenvironnements (CR2P, UMR 7207),

Sorbonne Universités-MNHN, CNRS, UPMC-Paris6, 8 rue Buffon, F-75005, Paris, France

<sup>6</sup>Department of Geology, Faculty of Science, University of Zanjan, Zanjan, Iran  
email: [key@dickinson.edu](mailto:key@dickinson.edu)

**ABSTRACT:** Epibionts are uniquely valuable in their ability to constrain paleoecological hypotheses about their own as well as their host's behavior and environment. Rarely preserved epizoic bryozoans are here reported on fossil crabs from the Miocene Mishan Formation in the Zagros Basin of southwestern Iran. One-hundred-thirty-eight decapod crustaceans were recovered from the upper marly member of the Mishan Formation. Of those, seven decapods (5%) were fouled by bryozoans. Of these seven decapods, five had bryozoans growing attached to the cuticle of the hard outer surface of the exoskeleton of the host crabs and thus fouled while the host crab was potentially alive. Forty percent of the bryozoan colonies occurred on the host crab's dorsal carapace, and 60% were found on chelipeds. On average, 30% of the surface area of the host crabs' fouled skeletal components were covered by bryozoan colonies. The brachyurans were mostly leucosiids, including *Leucosia persica* and *Myra* sp. The bryozoans were all cheilostomes and included *Acanthodesia* sp., *Thalamoporella* sp., and an indeterminate ascophoran. These bryozoans are all the first reported occurrences in the Mishan Formation. The low incidence of crabs fouled by bryozoans is attributed to preservational bias. The results from this study are compared to those of fossil and extant host crabs reported in the literature. The bryozoan-crab relationship documented here is best described as commensalism.

### INTRODUCTION

The purpose of this paper is to quantitatively describe the commensal relationship between epizoic bryozoans and their host crabs from the Miocene of Iran and to compare it to those reported from the literature of fossil and living crabs. Symbioses (Bary 1879; Paracer and Ahmadjian 2000), such as mutualism, commensalism, and parasitism, correspond to a variety of prolonged interspecific associations (Robin et al. 2016a). These associations are crucial factors for evolutionary strategies and species innovations. Although *syn-vivo* associations are particularly difficult to document in the fossil record, fossilized epizoans warrant consideration as they may directly document past symbioses involving a diversity of ancient invertebrates (e.g., Key et al. 2010; Misaki et al. 2014; Topper et al. 2014; Wyse Jackson et al. 2014; Siveter et al. 2015; Robin et al. 2015, 2016a, 2016b). Here, colonies of cheilostome bryozoans are found on several decapod specimens. 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 such associations on these crustaceans when fossilized is generally only about 1.5% (see Robin 2015), thus the importance of documenting the present bryozoans observed on their host crabs.

In general, symbiotic relationships are rarely preserved in the fossil record (Feldmann 2003a; Klompmaker et al. 2016). In particular, epizoans, including bryozoans, are rarely found on fossil crabs (Waugh et al. 2004). This rarity of bryozoan epibiosis on crabs is partly a function of the hosts'

biology. Crabs are motile, which creates deterrents for fouling bryozoans (Key et al. 1996a, 1996b). Living on a crab results in water flow around the moving substrate, which can positively or negatively affect the ability of epibionts to feed (Glasby 2001; Fernandez-Leborans 2010). 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 substrates, which is a deterrent for fouling bryozoans (Key et al. 1996a, 1996b). Many crabs exhibit burrowing/burying behavior which can reduce the incidence of fouling (Mori and Zunino 1987). More importantly, the vagaries of fossilization of the host crab's epicuticle makes the preservation of any attached epibionts uncommon and probably 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.

Fouling of fossil crabs by non-bryozoan epizoans include foraminifera (Feldmann et al. 2006a; Schweitzer and Feldmann 2009a), clionaid sponges (Jakobsen and Feldmann 2004), scleractinian corals (Jakobsen and Feldmann 2004; Collins et al. 2014), serpulid worms (Feldmann and Fordyce 1996; Jakobsen and Feldmann 2004; Waugh et al. 2004; Collins et al. 2014), thecidean brachiopods (Jakobsen and Feldmann 2004), and most commonly, balanid barnacles (Glaessner 1960, 1969; Rémy 1960; Feldmann 2003a, 2003b; Waugh et al. 2004; Schweitzer 2005; Feldmann et al. 2006b; Collins et al. 2014). Bryozoans have a fossil record of fouling

other (non-crab) motile hosts such as hyolithids (Galle and Parsley 2005), trilobites (Key et al. 2010), gastropods (Taylor and Schindler 2004), cephalopods (Baird et al. 1989; Wyse Jackson and Key 2014; Wyse Jackson et al. 2014), and echinoids (Schneider 2003). Extant (non-crab) motile hosts encrusted by modern bryozoans include cephalopods (Landman et al. 1987), pycnogonids (Key et al. 2013), horseshoe crabs (Key et al. 2000), isopods (Key and Barnes 1999), sea snakes (Key et al. 1995), and sea turtles (Frazier et al. 1992).

Although fossil decapod crustaceans of Iran have been the subject of scientific research since at least the interwar period (Glaessner 1933), only recently have they received renewed and more systematic attention. Decapods were reported from Cretaceous (Feldmann et al. 2007; McCobb and Hairapetian 2009; Yazdi et al. 2010; Jagt et al. 2014), Eocene (Khodaverdi Hassan-vand et al. 2016), and Miocene strata (Toraby and Yazdi 2002; Dehbozorgi et al. 2010a, 2015; Vega et al. 2010, 2012; Heidari et al. 2012; Hyžný et al. 2013; Yazdi et al. 2013). The Miocene Mishan Formation yields rather diverse decapod assemblages, including ghost shrimps (Hyžný et al. 2013) and various brachyurans (Vega et al. 2010, 2012; Heidari et al. 2012; Yazdi et al. 2013). This study adds further information on the Miocene decapods of the Mishan Formation and for the first time reports epizoic bryozoans in direct association with the crabs from this formation. By crabs in this study, we mean true crabs (i.e., brachyuran decapod crustaceans); we exclude paguroid hermit crabs, which include an intermediary host as a substratum (a gastropod shell), even though they are often fouled by bryozoans (e.g., Taylor et al. 1989; Taylor 1994; McDermott 2001; Taylor and Schindler 2004; Tilbrook and Grischenko 2004; Carter and Gordon 2007; Balazy and Kuklinski 2013).

#### GEOLOGICAL SETTING

The Zagros fold-thrust belt is world famous for its whaleback anticlines, seismic activity, textbook modern carbonate system, and its giant petroleum reserves. The Zagros basin of southwestern Iran has been the site of almost continuous sedimentation from the Triassic to the Pleistocene (Fig. 1A). The Cenozoic formations in the Zagros basin accumulated over two sedimentary cycles: the Paleocene to early Miocene sediments were deposited in the Jahrom and Asmari cycles, while the early Miocene to Pliocene–Quaternary sediments were deposited in the Fars cycle. The latter includes the three formations of the Fars Group (i.e., the basal Gachsaran Formation, the middle Mishan Formation, and the upper Aghajari Formation) which represent syn-orogenic deposition in a generally regressing sea (James and Wynd 1965; Stocklin and Setudehnia 1991; Alavi 2004; Pirouz et al. 2011).

The Fars Group was deposited in the proforeland megasequence XI of Alavi (2004). The paleoenvironmental conditions during deposition of the Fars Group were not consistent across the entire Zagros basin. Due to differential regional uplift across the basin, different sedimentation regimes developed. Evaporites of the Gachsaran Formation were deposited in sabkha and supratidal environments to the southwest, while the deeper marine deposits of the upper marly member of the Mishan Formation accumulated in the more open sea of a foreland basin to the northeast (Pirouz et al. 2011). The “Marly member” was informally proposed by Fanati Rashidi et al. (2014a) for the previously unnamed upper member of the Mishan Formation that is dominated by marls (Vega et al. 2010, 2012). Around the uplifted areas (e.g., the Fars platform), shallow marine limestone of the Guri Member of the Mishan Formation formed (Aghanabati 2004; Fanati Rashidi et al. 2014a).

The “Marly member” of the Mishan Formation is dominated by grayish green marl deposits from the deeper part of the basin. Mishan marls are regionally sandier toward the Fars platform and toward the southern parts of Iran. Although the general depositional trend since the early Miocene in the Zagros basin has been regressive, a brief period of transgression at the

end of the Burdigalian caused the deposition of the Mishan Formation (James and Wynd 1965; Pirouz et al. 2011).

The marls of the Mishan Formation play a significant role in the local geomorphology. They usually outcrop in the sides of anticlines, and in the plains they appear as low marly foothills (Fig. 1B). The exposed sediments form a badland area (Vega et al. 2010, fig. 4; Pirouz et al. 2011, fig. 5d; Hyžný et al. 2013, fig. 2c; Yazdi et al. 2013, fig. 3) with clearly visible folds. The Mishan Formation is well exposed in different parts of the Zagros basin and is most widespread in the southern parts of Iran. However, its thickness gradually decreases from the southeast in Hormozgan Province, where it is more than 3,000 m thick, to the northwest, where it is only 100 m in Khuzestan Province, and it disappears in Lorestan Province (James and Wynd 1965; Motiei 1995; Heidari et al. 2012, fig. 2).

There are two facies in the Mishan Formation: a clastic and a carbonate one. The carbonate facies (Guri Member) preserves open lagoon shallow subtidal environments with a diverse macrofauna and restricted lagoon microfossils (Kalantari 1992). The clastic facies (Marly member) mainly consists of green and gray marls frequently intercalated with thin to medium bedded limestone, marly limestone, or calcareous marl (Fig. 1C). These interbedded limestones and marly limestones sometimes contain eolian quartz grains reflecting the extreme weathering and active tectonics in the Zagros region during deposition of the Mishan Formation. The marls also contain exogenetic quartz grains as sand and silt transported from land. The clastic microfacies are highly diverse in large benthic, e.g., *Neorotalia viennoti* (Greig 1935), *Ammonia beccarii* (Linnaeus 1758), *A. stachi* (Asano 1951), and pelagic foraminifera, e.g., *Globigerinoides* sp., *G. trilobus* (Reuss 1850), and *G. sicamus* De Stefani 1952 as well as *Globigerina* sp. and *G. bulloides* d’Orbigny 1826. Based on lithological, microfacies analysis, and paleontological evidence, it is clear that the clastic Marly member was deposited in a deeper setting than the carbonate Guri Member (James and Wynd 1965; Pirouz et al. 2011; Fanati Rashidi et al. 2014b).

The Mishan Formation is highly fossiliferous, but there have been few studies on its diverse fauna. Kani and Feshki (2004) briefly described the calcareous nannofossil biostratigraphy in southern Iran. More recently in the Bandar Abbas area, in southern Iran, Kroh et al. (2011) and Daneshian et al. (2016) studied the echinoids and bivalves as well as the foraminifera, respectively. Dehbozorgi et al. (2010b) reported on the oysters southwest of Firuzabad. Vega et al. (2010, 2012), Heidari et al. (2012), Hyžný et al. (2013), and Yazdi et al. (2013) studied the decapod fauna in various parts of the Zagros basin. Chanet and Armoon (1999) described flatfish. Rahmani et al. (2010), Heidari et al. (2014a), and Fanati Rashidi et al. (2015) synthesized the formation’s paleoecology.

#### MATERIALS AND METHODS

Specimens were collected from the Marly member of the Mishan Formation in the Konar-Takhteh area of Fars Province in the Zagros Mountains (Fig. 1A), 40 km southwest of Kazeroon and 50 km from Mishan Village, where the type section is located. This area is in the southern foothills of the folded Zagros basin. Though the thickness of the Mishan Formation in its type locality (E50°45’34” N30°13’08”) is 710 m (Aghanabati 2004), the section measured in Konar-Takhteh is ~ 500 m. The underlying Gachsaran Formation, and the basal part of the Mishan Formation (Guri Member), which is medium to thick bedded limestone, are either absent or covered in the Konar-Takhteh area. The section here exposes the upper marly member of the Mishan Formation. Nevertheless, the geology of the area is generally comparable to the upper part of the Mishan Formation in the type locality, with soft gray and green marls and bands of limestone (James and Wynd 1965; Aghanabati 2004). The contact between the Mishan Formation and the overlying Aghajari Formation is gradational and extends from ~ 400 m to 480 m from the base of the

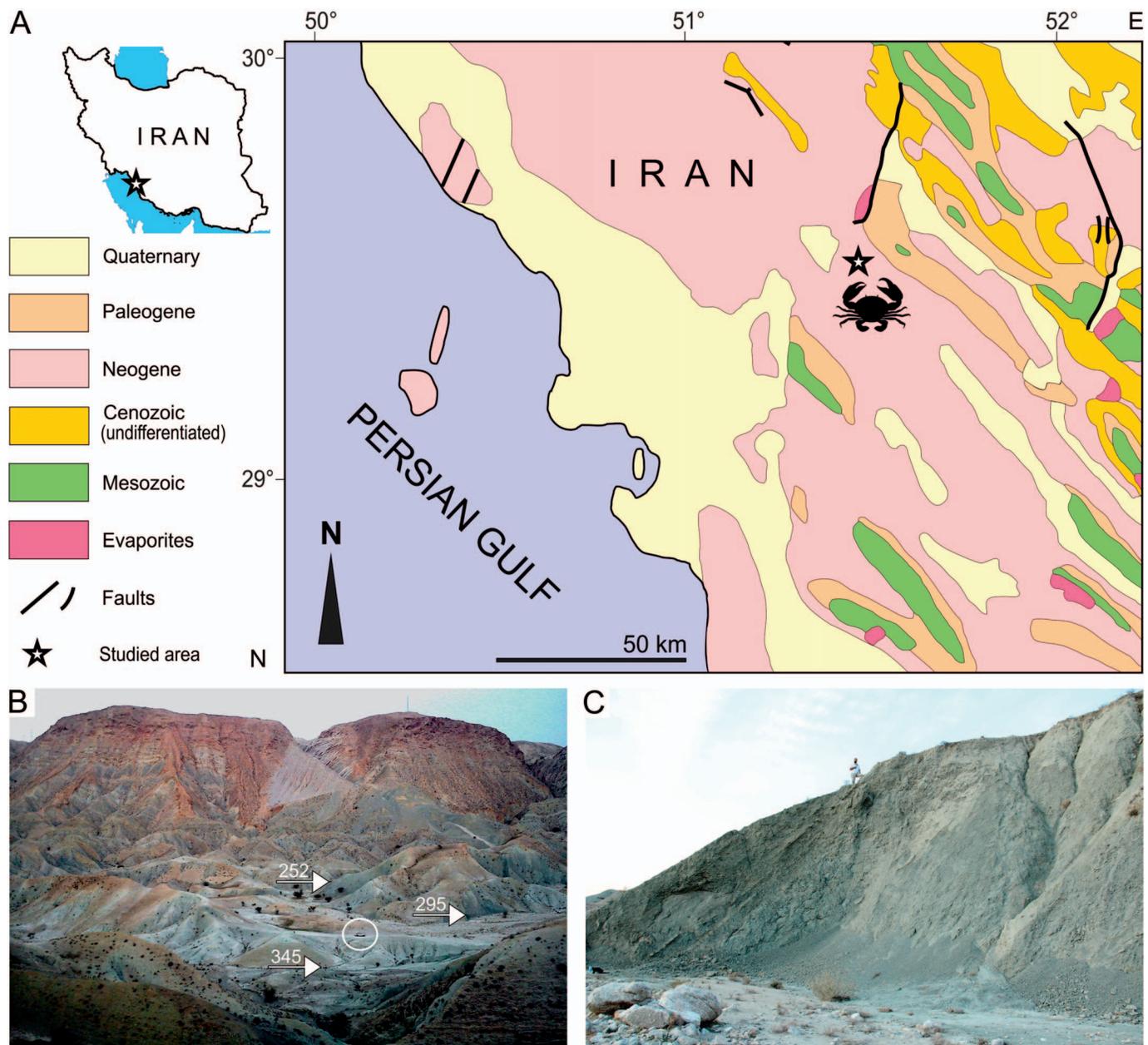


FIG. 1.—Konar-Takhteh area of the Fars Province, southwestern Iran. **A**) Regional geologic map showing the study area in the Zagros Fold Belt geologic province from Pollastro et al. (1999). **B**) Badlands topography of study area. Arrows indicate crab-bearing beds in meters above base of the measured composite section (Fig. 2). Note circled pickup truck for scale. **C**) Outcrop of the upper marly member of the Miocene Mishan Formation showing the crab-bearing bed at 295 m. Note person at ridge top for scale.

section. The Aghajari Formation *sensu stricto* starts at  $\sim 480$  m in the section with reddish sandy limestone and mud beds. Thus, the purely marine marly facies of the Mishan Formation grade upward into the terrestrial sandy facies of the Aghajari Formation, and hence the greenish color changes up section to reddish brown.

A composite stratigraphic section of the three sample locations is shown in Figure 2. The base of the section begins in the core of an anticline high on a hill and extends downhill across a badland landscape of valleys and hills (Fig. 1B). At 295 m up the section, wadi alluvial sediments in a river bed obscure the outcrop (Fig. 2). The last bed before this covered section has a strike of  $N40^{\circ}W$  and dip of  $30^{\circ}SW$ . Another 50 m of the section are partly covered under a dirt road before the section resumes as the beds rise

above the floodplain. At the Mishan/Aghajari contact, the layers get higher and finally form another high hill, opposite the base of the anticline.

Three different calcareous marl beds yielded fossil crab specimens with epizoic bryozoans (Figs. 2, 3). The lowermost bed with a single specimen (ZUTC 6397; Zoological Museum, University of Tehran, Tehran, Iran) is 252 m above the base, with coordinates  $E51^{\circ}28'34.8''$   $N29^{\circ}33'56.3''$ . Three other specimens (ZUTC 6394-6396) were collected at 295 m in the last layer before the flood plain cover, with coordinates  $E51^{\circ}28'32.5''$   $N29^{\circ}33'52.6''$ . The uppermost bed at 345 m is the first fossiliferous layer with crabs above the dirt road, with three specimens (ZUTC 6391-6393) found at a spot with coordinates  $E51^{\circ}28'26.8''$   $N29^{\circ}33'52.5''$ .

After collecting, the crab specimens were prepared using an air scribe. They were photographed dry and uncoated or/and coated with ammonium

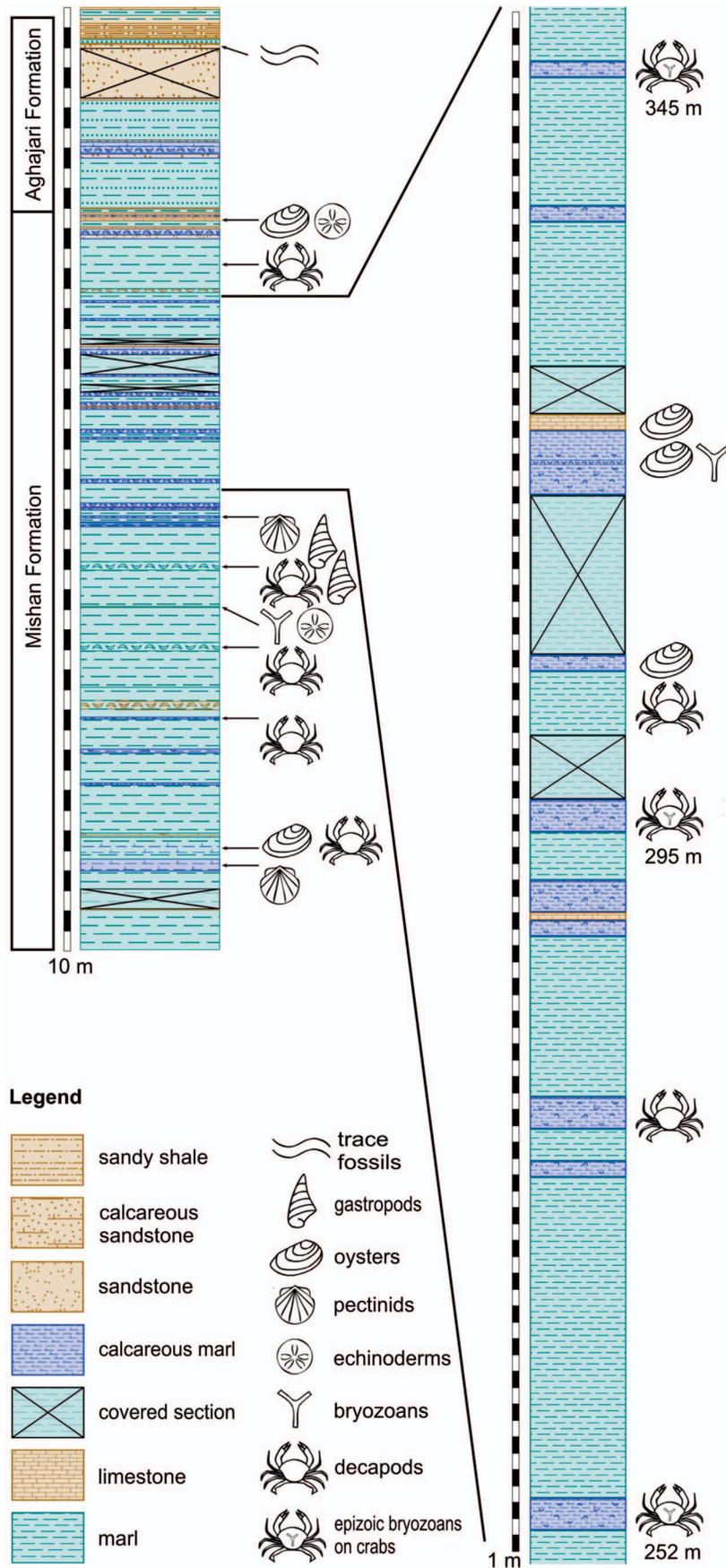
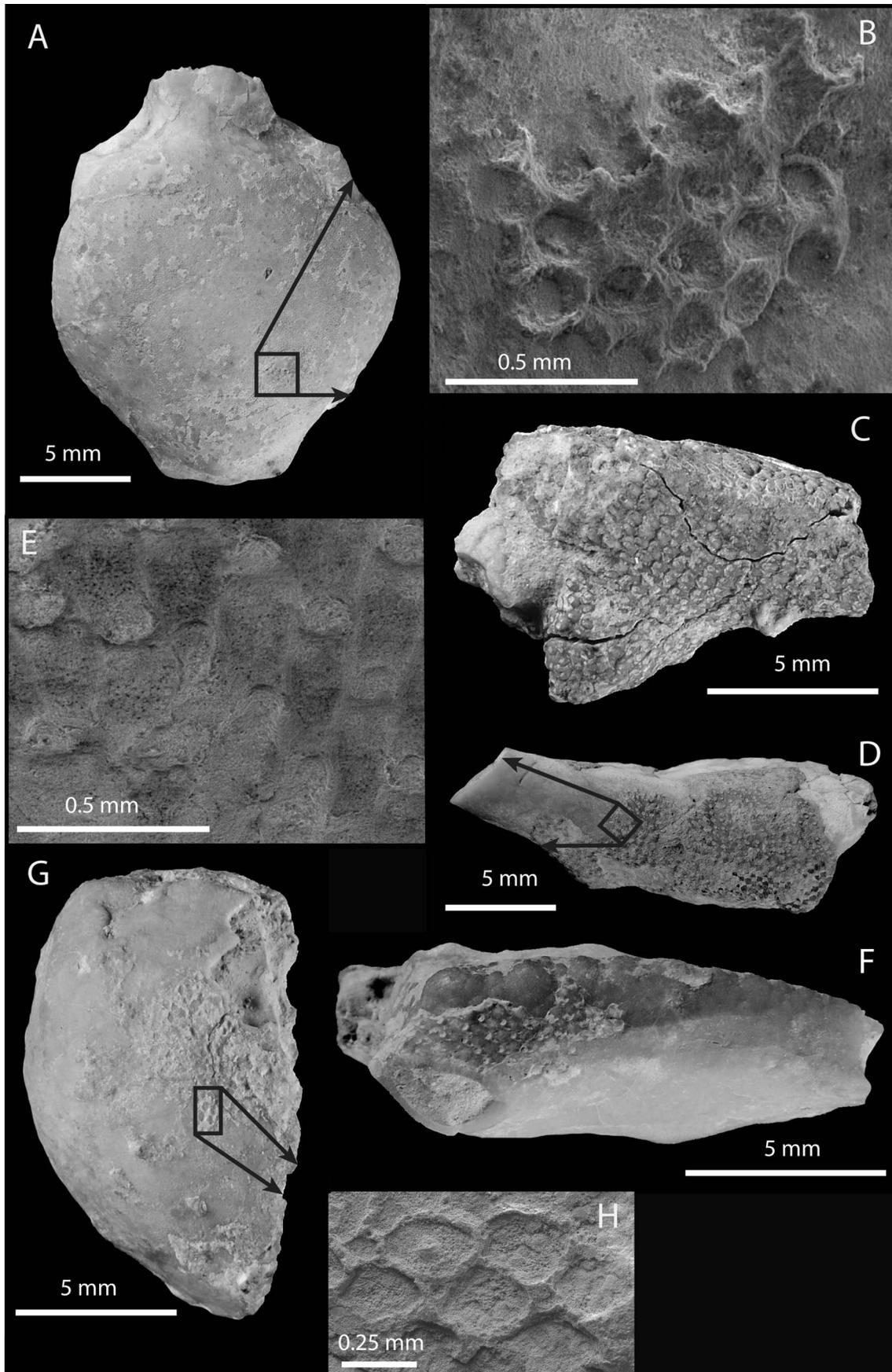


FIG. 2.—Composite stratigraphic section showing where crabs were collected in the Konar-Takhteh area of the Fars Province, southwestern Iran (Fig. 1).



chloride. SEM-images were made using a JEOL JSM-6610 under high-vacuum settings. To quantify the morphology of the epizoic bryozoans, we counted the number of zooecia per colony from the SEM images. Using ImagePro Express 5.0 software (Media Cybernetics 2004) with the SEM images, we measured colony area and area of host crab's fouled skeletal component to the nearest 0.1 mm<sup>2</sup>.

Four foraminifera samples were obtained from the three crab horizons. Two came from the crab horizon 295 m above the base of the section. One each came from the crab horizons at 252 m and 345 m. The samples were disaggregated with hydrogen peroxide and wet-sieved through 0.071 mm and 1 mm mesh.

Foraminifera were identified and imaged using a combination of an Olympus SZ75 binocular stereoscopic microscope, a biological polarizing microscope, and a QUANTA FEG 250 scanning electron microscope. Immersion oil was used with the optical microscope to see the inner structure of the foraminiferal tests and specify which are agglutinated taxa. Identification of foraminifera followed Loeblich and Tappan (1992) and Holbourn et al. (2013). Paleoecological parameters of the foraminiferal assemblage were evaluated based on the presence and dominance of those morphogroup taxa with environmental significance (Boltovskoy 1976; Boltovskoy and Wright 1976; Murray 2006).

## RESULTS

### *Foraminifera Assemblages*

All three crab horizons yielded foraminiferal tests and calcite molds. Foraminiferal determination was difficult due to strong secondary calcification of foraminiferal tests which often covered the original ornamentation and obscured the chamber organization. Due to poor preservation of the tests, some remain in open nomenclature. Beside foraminifera, bryozoans, echinoid spines, as well as articulated and disarticulated ostracod shells were the most common fossils in the wash residuum. In the sample from the crab horizon 345 m above the base of the section, almost all ostracod shells were articulated and fish remnants also occurred.

Foraminiferal assemblages were not very diverse; most were dominated by just a few taxa. Only extremely rare planktonic foraminifera occurred in the crab horizon at 295 m, including *Globigerina* sp. indet. and *Globigerinoides* cf. *trilobus* Reuss 1850 which serves as a Miocene index taxon (Gradstein et al. 2012). This biostratigraphic age can be further constrained by the recent work of Kroh et al. (2011) and Daneshian et al. (2016), who determined the age of the underlying Guri Member of the Mishan Formation in southern Iran as late Burdigalian to Langhian.

The benthic foraminiferal assemblage (Fig. 4) is dominated by tests of the oxic, epiphytic morphogroup, i.e., *Ammonia beccarii*, *A. parkinsoniana* (d'Orbigny 1839), *Rotalia aculeata* (d'Orbigny 1846), *Cibicides* cf. *boueanus* (d'Orbigny 1846), *Lobatula lobatula* (Walker and Jacob 1798), *Elphidium crispum* (Linnaeus 1758), *E.* sp. cf. *flexuosum* (d'Orbigny 1846), and rare *Quinqueloculina* molds. The shallow infaunal morphogroup is also present (i.e., *Ammonia* and *Pararotalia*) in all studied samples except for the crab horizon at 345 m above the base of the section. In this sample, the agglutinated taxa *Clavulina* cf. *angularis*

d'Orbigny 1826, *C. multicamerata* Chapman 1907, *Pseudoclavulina tricarinata* (Leroy 1941), and *Eggerelloides scabra* (Williamson 1858) prevail.

The foraminiferal assemblage from these horizons suggests a shallow water, well aerated oligotrophic paleoenvironment of seagrass meadow or macroalgae (Boltovskoy 1976; Murray 2006; Schmidt 2015). The foraminiferal assemblage from the top crab horizon, i.e., 345 m from the base of the section, is typical of a deeper environment (i.e., the "Marly member" of the Mishan Formation). In this horizon, there is also evidence for assemblages dominated by *Clavulina* and other agglutinated taxa affected by acid dissolution of dead assemblages originally dominated by infaunal *Stainfortia* (Alve and Murray 1995). *Clavulina multicamerata* is common in tidal flats, where it grows on seagrasses and macroalgae (Lacuna and Gayda 2014); thus, we cannot exclude a shallow water origin for this sample as well.

Brachyuran Systematic Paleontology  
 Infraorder Brachyura Linnaeus 1758  
 Section Eubrachyura Saint-Laurent 1980  
 Subsection Heterotremata Guinot 1977  
 Superfamily Leucosioidea Samouelle 1819  
 Family Leucosiidae Samouelle 1819

**Remarks.**—The present specimens are a portion of a larger decapod crustacean assemblage collected in the Konar-Takhteh area, which is currently under study for a future taxonomic report. The taxonomic identification of the specimens presented below is preliminary, pending a revision of the Miocene leucosiid crabs of Iran. The attribution to the genera (i.e., *Leucosia* and *Myra*) follows Vega et al. (2010) and Yazdi et al. (2013) and is provisional, since the recent taxonomic re-evaluations of these taxa (Galil 2001, 2003, 2005, 2006a, 2006b) resulted in a complete re-classification and erection of several distinct genera; for a summary of a recent classification, see De Grave et al. (2009). Additionally, the fossil record of Leucosioidea as a whole needs more revisionary work, as already pointed out by Artal and Hyžný (2016).

Genus *Leucosia* Weber 1795  
*Leucosia persica* Vega, Gholamalian, and Bahrami 2010

**Material.**—ZUTC 6395 (near-complete carapace), from the crab horizon at 295 m.

**Remarks.**—Although not complete, the material fully conforms to *Leucosia persica* as described by Vega et al. (2010).

Genus *Myra* Leach 1817  
*Myra* sp.

**Material.**—ZUTC 6397 (complete carapace), from the crab horizon at 252 m.

**Remarks.**—The specimen fully conforms to *Myra* sp. as reported and figured by Yazdi et al. (2013, p. 230, fig. 4.14). The material probably represents a new species, as already suggested by Yazdi et al. (2013). More specimens attributable to this taxon are currently under study.

FIG. 3.—Reflected light and scanning electron microscope images of the crabs fouled by bryozoans in this study. **A**) Outer surface of near-complete dorsal carapace of *Myra* sp. ZUTC 6397 (coated with ammonium chloride prior to photography) encrusted by the cheilostome bryozoan *Acanthodesia* sp. **B**). **C**) Outer surface of fragmentary dactylus (lateral view) of an indeterminate brachyuran crab ZUTC 6391 encrusted by an indeterminate ascophoran cheilostome bryozoan. **D**) Outer surface of fragmentary propodus (ventral view) of an indeterminate brachyuran crab ZUTC 6392 encrusted by the cheilostome bryozoan *Thalamoporella* sp. **E**). **F**) Outer surface of fragmentary propodus (ventral view) of an indeterminate brachyuran crab ZUTC 6393 encrusted by an indeterminate ascophoran cheilostome bryozoan. **G**) Outer surface of incomplete dorsal carapace (lateral view) of Leucosiidae indet. ZUTC 6394 encrusted by the cheilostome bryozoan *Acanthodesia* sp. **H**).

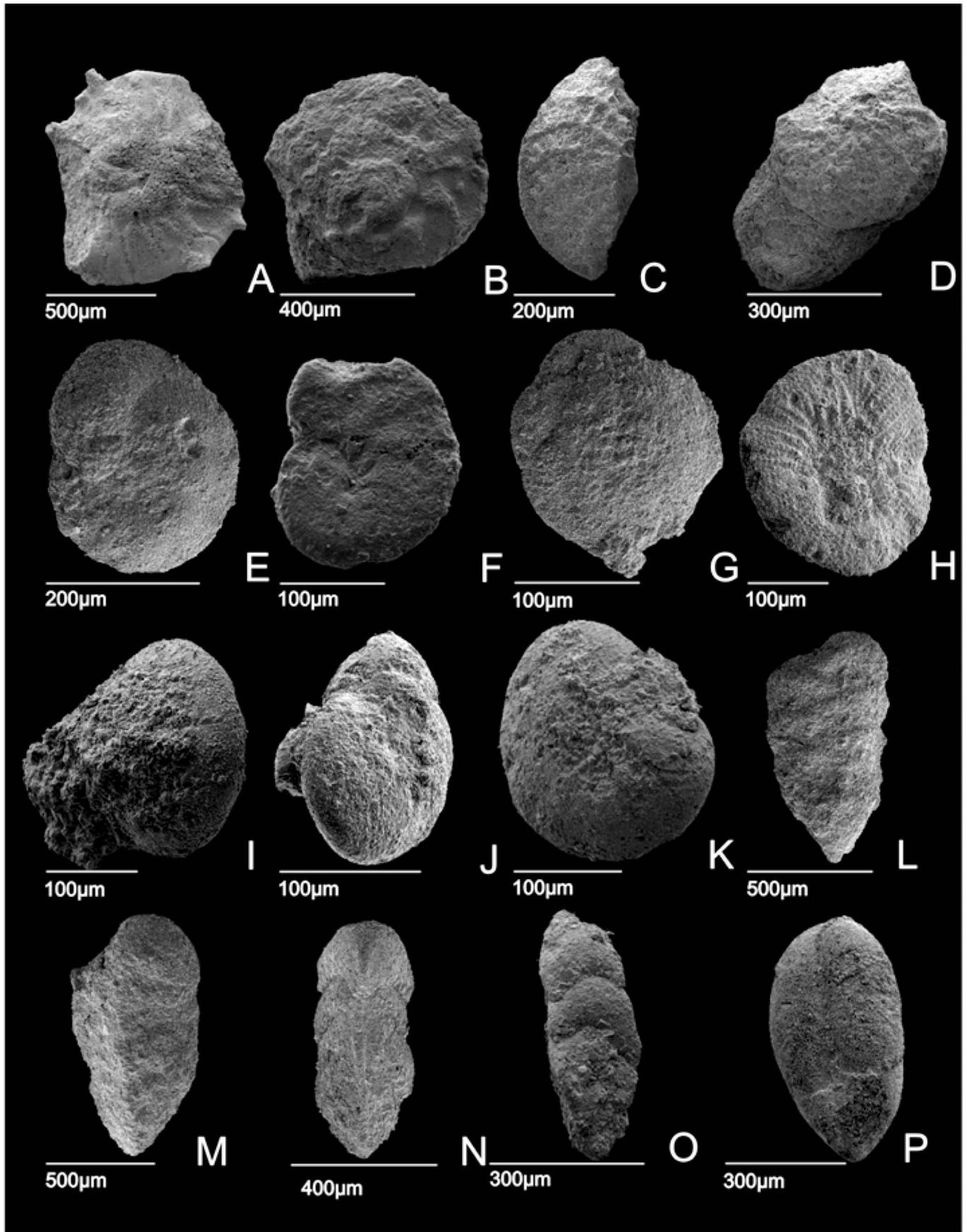


TABLE 1.—Potentially *syn-vivo* epizoic bryozoans on fossilized crabs discovered in this study.

Specimen number*	Bryozoan	# of colonies	Host crab species	Host crab family	Where on host	Figure #
ZUTC 6397	Cheilostome <i>Acanthodesia</i> sp.	1	<i>Myra</i> sp.	Leucosiidae	Outer surface of carapace	3A, 3B
ZUTC 6391	Indeterminate ascophoran cheilostome	1		Brachyura indeterminate	Outer surface of dactylus	3C
ZUTC 6392	Cheilostome <i>Thalamoporella</i> sp.	1		Brachyura indeterminate	Outer surface of propodus	3D, 3E
ZUTC 6393	Indeterminate ascophoran cheilostome	1		Brachyura indeterminate	Outer surface of propodus	3F
ZUTC 6394	Cheilostome <i>Acanthodesia</i> sp.	1	Leucosiidae indeterminate	Leucosiidae	Outer surface of carapace	3G, 3H

\* ZUTC = Zoological Museum, University of Tehran, Tehran, Iran

#### Leucosiidae indeterminate

**Material.**—ZUTC 6394 (incomplete carapace), ZUTC 6396 (incomplete carapace), both from the crab horizon at 295 m.

**Remarks.**—More leucosiid taxa are apparently present at the studied locality (E. Khosravi and M. Hyžný personal observation 2016) and there are several distinct leucosiids already known from the Miocene strata of the Mishan Formation (Vega et al. 2010; Yazdi et al. 2013). The studied specimens are clearly leucosiid crabs, but closer identification is not possible due to incompleteness of the remains.

#### Brachyura indeterminate

**Material.**—ZUTC 6391 (fragmentary dactylus), ZUTC 6392 (fragmentary propodus), ZUTC 6393 (fragmentary propodus), all from the crab horizon at 345 m.

**Remarks.**—The specimens are too fragmentary for confident taxonomic identification.

#### Bryozoan Epibiosis

Most of the decapod specimens collected at the studied section do not possess epizoans. A single fouled specimen from the crab horizon at 252 m from the base of the section (Fig. 2) comes from a collection of six crabs. From the crab horizon at 295 m, three individuals out of 97 collected specimens were fouled. From the crab horizon at 345 m, 35 specimens were collected; however, only three of them were fouled. This represents a fouling rate (or incidence) of 5% for all horizons together.

Seven bryozoan colonies were discovered with the fossilized crabs. Two were not potentially *syn-vivo* (ZUTC 6395, ZUTC 6396)—they were not attached to the outer surface of the host crab's cuticle and were simply found in association with the crabs. These include an indeterminate cheilostome belonging to the suborder Flustrina or Ascophorina and the cheilostome *Thalamoporella*.

Five of the seven colonies were epizoic bryozoans that grew attached to the cuticle of the hard outside surface of the exoskeleton of the host crabs (Fig. 3). The membraniporid cheilostome bryozoan *Acanthodesia* was identified based on its distinctive twinned ancestrula (Fig. 3B). The diagnostic spatulate avicularium at a row bifurcation permitted identification of the thalamoporellid cheilostome *Thalamoporella* (Fig. 3E). Due to poor preservation, the other colonies could not be identified as precisely. One was an ascophoran cheilostome with abundant interzooidal avicularia (Fig. 3C), which are found in numerous genera including *Trematoeocia*, *Rhynchozoon*, and *Pleisioleidochasma*. The remaining colony was also probably an ascophoran cheilostome (Fig. 3F).

The locations of these five potentially *syn-vivo* epizoic bryozoans are reported in Table 1. All five colonies are cheilostome bryozoans. Two of the five potentially *syn-vivo* epizoic bryozoans occurred on the host crab's dorsal carapace, and the remaining three were found on chelipeds (i.e., two on the propodus and one on a dactylus).

The sizes of these five potentially *syn-vivo* epizoic bryozoans are reported in Table 2. The bryozoan colonies range in size from 0.9–69.0 mm<sup>2</sup> (mean: 22.7 mm<sup>2</sup>, standard deviation: 25.9 mm<sup>2</sup>). The colonies contained 22 to 504 zoecia (mean: 170, standard deviation: 186). There was no evidence of sexual ovicell formation in any of the bryozoan colonies. The bryozoan colonies covered 0.4–71.7% of the surface area of the host crabs' fouled skeletal component (mean: 30.0%, standard deviation: 29.8%).

#### DISCUSSION

The three cheilostomes reported in this study (*Acanthodesia*, *Thalamoporella*, and an indeterminate ascophoran) are the first records of Mishan Formation bryozoans since James and Wynd (1965) reported the presence of the cheilostome genus *Tubucellaria* (now referred to as *Margaretta*). Ordovician (Ross et al. 2000), Devonian (Brice et al. 1978; Ernst and Mohammadi 2009; Tolokonnikova et al. 2011; Ernst et al. 2012, 2017), Carboniferous (Gorjunova 2006; Tolokonnikova and Yazdi-Moghadam 2013), and Permian (Sakagami 1980; Ernst and Gorgij 2013; Ernst et al. 2006a, 2006b, 2008, 2009a, 2009b, 2010, 2011) bryozoan faunas have been described from the Paleozoic of Iran. Schäfer et al. (2003) described the only Iranian Mesozoic bryozoans from the Triassic. In the Cenozoic, Berning et al. (2009) described an Oligocene bryozoan fauna from Iran.

The decapod assemblage of the studied section is comparable with that already reported from other localities within the exposed Mishan Formation (Vega et al. 2010; Heidari et al. 2012; Yazdi et al. 2013). When comparing examined specimens with and without epizoans, the ratio of fouled specimens is relatively low. However, this is likely attributed to aspects of preservation (Waugh et al. 2004) since most of the 138 studied specimens do not retain the outer layers of cuticle. The bryozoans in the Mishan Formation experienced periods of micritization, cementation, and pyritization (Heidari et al. 2014b). Thus it is no wonder that few epizoic bryozoans were found.

Another potential cause for the low incidence of epizoic bryozoans is that crab behavior such as burrowing/burying can affect the settling, growth, and preservation of epizoans on host carapaces (Waugh et al. 2004). Most leucosiids are burrowers (e.g., Schembri 1981, fig. 3), and burrowing/burying behavior in crabs reduces the incidence of fouling (Mori and Zunino 1987). Additionally, burrowing decapods have a higher chance of preservation than pelagic ones (Bishop 1986). Thus, the burrowing behavior of the leucosiid crabs in this study may have: (1)

FIG. 4.—Benthic foraminiferal assemblage from the study site. A, B) *Rotalia aculeata* (d'Orbigny 1846). C, D) *Elphidium crispum* (Linnaeus 1758). E, F) *Cibicides cf. boueanus* (d'Orbigny 1846). G) *Ammonia beccarii* (Linnaeus 1758). H) *Glabrata* sp. I) *Ammonia beccarii* (Linnaeus 1758). J, K) *Ammonia parkinsoniana* (d'Orbigny 1839). L) *Dorothia* sp. M) *Pseudoclavulina tricarinata* (Leroy 1941). N, O) *Clavulina cf. angularis* d'Orbigny 1826. P) *Quinqueloculina* sp. indet.

TABLE 2.—Morphometric data of potentially *syn-vivo* epizoic bryozoans on fossilized crabs discovered in this study.

Specimen number*	No. of zoecia in bryozoan colony	Colony area (mm <sup>2</sup> )	Area (mm <sup>2</sup> ) of host crab's fouled skeletal component	% of host crab's skeletal area covered by colony
ZUTC 6397	22	0.9	246.4	0.4
ZUTC 6391	243	33.3	46.5	71.7
ZUTC 6392	504	69.0	114.7	60.2
ZUTC 6393	35	4.7	39.8	11.8
ZUTC 6394	43	5.4	93.6	5.7
N:	5	5	5	5
Minimum:	22	0.9	39.8	0.4
Mean:	170	22.7	108.2	30.0
Maximum:	504	69.0	246.4	71.7
Standard deviation:	186	25.9	74.6	29.8

\* ZUTC = Zoological Museum, University of Tehran, Tehran, Iran

reduced the incidence of bryozoan fouling by limiting access of bryozoan larvae to the host crabs' exoskeletons; (2) reduced survival of the settled bryozoan colonies through sediment abrasion; and (3) increased the preservation potential of the burrowing crabs. However, only two of the five crabs with potentially *syn-vivo* epizoic bryozoans are leucosiids (Table 1). The other three crabs are isolated cheliped remains and do not belong to burrowing taxa. Therefore, burrowing behavior by the host crabs is not the only cause for the low incidence of epizoic bryozoans.

To put the bryozoan fouling of these crabs into context, we reviewed recently published (i.e., 1990–present) reports of extant epizoic bryozoans on crabs where we know that *syn-vivo* fouling occurred. We only included reports that contain information of where on the host crab the *syn-vivo* fouling occurred. There is a pre-1990 compilation of bryozoan fouling of crabs (Ingle 1983, p. 176), but it lacks information on where the bryozoans were growing on their host crabs. We found 34 published occurrences (Table 3). The bryozoans include two classes: Gymnolaemata (79% of the reported occurrences and represented by two orders: Ctenostomata and Cheilostomata) and Stenolaemata (12% and represented by one order: Cyclostomata). The most common fouling bryozoans were ctenostomes (44% of the cases) and cheilostomes (35%). The host crabs represent 12 different brachyuran decapod families, the most common being Portunidae (18%), Varunidae (15%), and Epialtidae (15%).

From all documented cases of epizoic bryozoans on fossil crabs, there are only nine previous studies involving 19 crabs and 30 bryozoan colonies (Table 4). They range from the Bathonian (Middle Jurassic) to the Pleistocene, with a majority in the early Paleogene. Of these 19 cases, seven were clearly *post-mortem* as the fouling bryozoan was found on the inner surface of the host crab's dorsal carapace. Of the remaining 12 crabs, all the bryozoans were found on the cuticle of the outer surface of the dorsal carapace or chelipeds and, thus, the hosts were potentially fouled while alive. We could not rule out the fouling occurring on a corpse or a molt, so in Table 4, they are listed as potentially *syn-vivo* fouling.

It is challenging to determine if epibionts found on fossil hosts were growing on the hosts when they were alive (i.e., *syn-vivo*) or dead (i.e., *post-mortem*) (e.g., Key et al. 2010; Robin et al. 2015). One way is to compare the exposure time of the host's carapace before being buried to the time of growth of the colonies. Here, most of the specimens are isolated carapaces and cheliped fragments, which impedes knowing how fast they were buried. For the cases of carapaces, none display any appendages or pleonites preserved in connection, which also impedes any deduction on the duration of exposure of these crabs' carcasses before burial, and thus, to exclude a *post-mortem* colonization. Regardless, in the terminology of

Taylor and Wilson (2002), these bryozoans are considered episkeletozoans on the basibiont host crabs.

In addition to the articulation of the body, the fragility of the preserved carapace may help constrain the time of exposure of the crab carcass. For instance, in many brachyuran groups, the extreme fragility of the carapace would likely exclude long exposure before burial and thus *post-mortem* colonization (Robin et al. 2015). Here, cheilostome colonies reach up to about 500 zoecia (Table 2) corresponding to a rather significant time of growth of at least several weeks (Hermansen et al. 2001; Amui-Vedel et al. 2007; Kuklinski et al. 2013). This timing remains difficult to compare to the carapaces' state of preservation. Indeed, little is known about the resistance of extant leucosioid crab carapaces, but the rather compact carapace morphology of these animals may promote their preservation.

At the present stage of study, we do not know if the carapaces were large for these species, although the specimens are within the same size ranges as conspecific individuals reported by Vega et al. (2010) and Yazdi et al. (2013). Thus, we cannot determine if they many have been mature individuals, possibly in their terminal molt, with the fouling occurring while the host was alive. However, there are two pieces of circumstantial evidence that at least some of the host crabs may have been fouled while alive: (1) the bryozoans were found on the cuticle of the outer surface of the dorsal carapace and the chelipeds and, thus, the hosts were potentially fouled while alive; and (2) in two of the host crabs, the bryozoan colonies surround the dactylus and propodus (Fig. 3C, 3D). This suggests the cheliped was not fouled while the crab was partially buried in the substrate following death or molting of the host, unless the *post-mortem*/molt claw rolled around on the substrate before burial.

Of the 12 potentially *syn-vivo* fossil fouling cases in the literature, all are on the outer surface of the dorsal carapace (Table 4). The number of potentially *syn-vivo* bryozoan colonies per host crab ranged from one to five (mean: 1.6, standard deviation: 1.2). The potentially *syn-vivo* fouling bryozoans include two classes: Gymnolaemata (represented by one order: Cheilostomata) and Stenolaemata (represented by one order: Cyclostomata). The most common fouling bryozoans were cheilostomes (92% of the cases in the literature). The host crabs represent nine different brachyuran decapod families (Table 4), the most common being Dromiidae (18% of the cases) and Majidae (18%).

Why is there such a discrepancy between the types of bryozoans fouling crabs today (Table 3) versus those in the fossil record (Table 1, 4)? Today, the most common fouling bryozoans on crabs are the ctenostomes (42% of published occurrences) and cheilostomes (36%), but in the fossil record they are cheilostomes (92% in the literature and 100% in this study). This probably reflects a preservational bias as ctenostomes are unmineralized and thus less likely to be fossilized (Wilson and Taylor 2013).

Of the potentially *syn-vivo* epizoic bryozoans found in this study, 40% of the colonies occurred on the host crab's dorsal carapace, and 60% were found on chelipeds (Table 1). Based on the total number of zoecia counted, 8% occurred on the host crab's dorsal carapace, and 92% were found on chelipeds. Is this spatial distribution of the bryozoans on the host fossil crabs typical of extant crabs? Based on extant epizoic bryozoans on host crabs where *syn-vivo* fouling can be demonstrated, bryozoans occur on all parts of hosts' exoskeletons, but there are more occurrences on the carapace than the pereopods. Settlement specifically on chelipeds is rarely mentioned in extant crabs (Table 3), but this may be an observational bias (Bishop 1986). No evidence was found for spatial competition among the bryozoan colonies on host crabs (sensu Taylor 2016).

Why were the majority of the bryozoan colonies in this study found on the chelipeds? These are the first descriptions of a bryozoan fouling a non-carapace skeletal component in a fossil crab. No fossil epizoic bryozoans have been reported in previously published literature on any appendages (Table 4). This could be a bias of relative surface areas of carapaces versus appendages: In a typical crab (e.g., the well-studied *Callinectes sapidus* Rathbun 1896), the chelipeds represent a small portion of the outer surface

TABLE 3.—List of recently published reports of extant epizoic bryozoans that contain information of where on the host crab syn-vivo fouling occurred.

Fouling bryozoan	Host crab family, species	Where on host	Reference
Ctenostome <i>Triticellopsis</i> sp.	Homolidae, <i>Paromola cuvieri</i>	Carapace	Mori and Manconi 1990
Cheilostome <i>Turbicellopora</i> sp.	Homolidae, <i>Paromola cuvieri</i>	Carapace	Mori and Manconi 1990
Cylostome <i>Tubulipora</i> sp.	Homolidae, <i>Paromola cuvieri</i>	Carapace	Mori and Manconi 1990
Ctenostome <i>Nolella annectens</i>	Polybiidae, <i>Bathynectes piperitus</i>	Carapace	Gili et al. 1993
Ctenostome <i>Alcyonidium mamillatum</i>	Goneplacidae, <i>Goneplax rhomboides</i>	Carapace and chelipeds	Abelló and Corbera 1996
Cheilostomes <i>Cellepora pumicosa</i> , <i>Celleporina hassali</i> , <i>Chartella papiracea</i> , <i>Electra pilosa</i> , <i>Scruparia chelata</i>	Majidae, <i>Maja squinado</i>	Carapace	Parapar et al. 1997
Cylostome <i>Tubulipora plumosa</i>	Majidae, <i>Maja squinado</i>	Carapace	Parapar et al. 1997
Ctenostomes <i>Alcyonidium</i> sp., <i>Triticella</i> sp.	Oregoniidae, <i>Chionoecetes bairdi</i>	All parts of exoskeleton	Dick et al. 1998
Cyclostome indeterminate lichenoporiid	Oregoniidae, <i>Chionoecetes bairdi</i>	Carapace	Dick et al. 1998
Cylostome <i>Crisia</i> sp.	Oregoniidae, <i>Chionoecetes bairdi</i>	Pereiopods	Dick et al. 1998
Cheilostome <i>Conopeum tenuissimum</i>	Varunidae, <i>Hemigrapsus sanguineus</i>	Carapace	McDermott 1998
Ctenostome <i>Alcyonidium</i> sp.	Varunidae, <i>Hemigrapsus sanguineus</i>	Carapace	McDermott 1998
Ctenostomes <i>Alcyonidium albescens</i> , <i>Triticella elongata</i>	Portunidae, <i>Callinectes sapidus</i>	Carapace	Key et al. 1999; Winston and Key 1999
Cheilostome <i>Membranipora arborescens</i>	Portunidae, <i>Callinectes sapidus</i>	Carapace	Key et al. 1999
Ctenostome <i>Triticella capsularis</i>	Portunidae, <i>Ovalipes catharus</i>	All parts of exoskeleton	Gordon and Wear 1999
Ctenostome <i>Bowerbankia</i> sp.	Epialtidae, <i>Libinia dubia</i>	Carapace	Stachowicz and Hay 2000
Cheilostome <i>Bugula neritina</i>	Epialtidae, <i>Libinia dubia</i>	Carapace	Stachowicz and Hay 2000
Ctenostome <i>Triticella flava</i>	Goneplacidae, <i>Goneplax rhomboides</i>	All parts of exoskeleton	Fernandez-Leborans 2003
Cheilostome <i>Membranipora membranacea</i>	Cancridae, <i>Cancer productus</i> , <i>C. magister</i>	All parts of exoskeleton	McGaw 2006
Cheilostome <i>Schizoporella unicornis</i>	Cancridae, <i>Cancer magister</i>	All parts of exoskeleton	McGaw 2006
Ctenostome <i>Flustrellidra cormiculata</i>	Cancridae, <i>Cancer productus</i> , <i>C. magister</i>	All parts of exoskeleton	McGaw 2006
Ctenostome <i>Triticella capsularis</i>	Portunidae, <i>Ovalipes catharus</i>	All parts of exoskeleton	Miller et al. 2006
Cheilostome <i>Acanthodesia tenuis</i>	Majidae, <i>Libinia ferreirae</i>	Mainly pereiopods	Winter and Masunari 2006
Cheilostomes <i>Conopeum tenuissimum</i> , <i>Membranipora tenuis</i>	Varunidae, <i>Hemigrapsus sanguineus</i>	Most parts of exoskeleton	McDermott 2007
Ctenostome <i>Alcyonidium albescens</i>	Varunidae, <i>Hemigrapsus sanguineus</i>	Most parts of exoskeleton	McDermott 2007
Cheilostome <i>Conopeum tenuissimum</i>	Portunidae, <i>Carcinus maenas</i>	All parts of exoskeleton	McDermott 2007
Ctenostomes <i>Anguinella</i> sp., <i>Triticella capsularis</i>	Portunidae, <i>Carcinus maenas</i>	All parts of exoskeleton	McDermott 2007
Ctenostomes <i>Alcyonidium albescens</i> , <i>Triticella capsularis</i>	Panopeidae, <i>Panopeus herbstii</i>	Pereiopods	McDermott 2007
Ctenostomes <i>Triticella flava</i> <i>Arachnoidea</i> sp.	Geryonidae, <i>Geryon longipes</i>	All parts of exoskeleton	Di Camillo et al. 2008
Cheilostome <i>Conopeum reticulum</i>	Varunidae, <i>Cyrtograpsus angulatus</i> , <i>Neohelice granulata</i>	Carapace	Alda et al. 2011
Indeterminate bryozoans	Inachidae, <i>Podocheila hemphilli</i>	Pereiopods	Hultgren and Stachowicz 2011
Cheilostome <i>Bugula neritina</i>	Epialtidae, <i>Loxorhynchus crispatus</i>	All parts of exoskeleton	Hultgren and Stachowicz 2011
Indeterminate bryozoans	Epialtidae, <i>Pteromaja maklayi</i>	Carapace	Ng and Anker 2014
Indeterminate bryozoans	Epialtidae, <i>Loxorhynchus crispatus</i>	All parts of exoskeleton	Guinot and Wicksten 2015

area of the host crab's exoskeleton (Key et al. 1997, 1999). Alternatively, this could be a bias from crab paleontologists collecting carapaces in preference of appendages, as they supply most of the morphologic characters used in crab taxonomy (Glaessner 1969; Schweitzer 2003; Jagt

et al. 2015). There is also a taphonomic bias towards preservation of the more robust chelipeds and dorsal carapaces (Bishop 1986; Jakobsen and Feldmann 2004; Waugh et al. 2004; Stempien 2005). Whether the lack of previous reports of epizoic bryozoans on crab appendages is due to

TABLE 4.—List of all known fossil occurrences of epizoic bryozoans on crabs.

Fouling bryozoan	# of colonies	Host crab family, species	Where on host	Fouling occurred <i>syn-vivo</i> or <i>post-mortem</i>	Age	Location	Reference
Indeterminate cheilostome	1	Menippidae, <i>Menippe frescoensis</i>	Outer surface of carapace	Potentially <i>syn-vivo</i>	Eocene	Ivory Coast	Rémy (1960, fig. 4, 5)
Ctenostome <i>Terebripora</i>	2	Raninidae, <i>Rogueus orri</i>	Inner surface of carapace	<i>Post-mortem</i>	Eocene	Oregon, U.S.A.	Berglund and Feldmann (1989, fig. 2)
Indeterminate cheilostome	2	Calappidae, <i>Calappilia sitzi</i>	Outer surface of carapace	Potentially <i>syn-vivo</i>	Eocene	North Carolina, U.S.A.	Feldmann et al. (1998, fig. 7)
Indeterminate cheilostome	1	Majidae, <i>Wilsonimaia ethelae</i>	Outer surface of carapace	Potentially <i>syn-vivo</i>	Eocene	North Carolina, U.S.A.	Feldmann et al. (1998, fig. 19)
Indeterminate cheilostome	3	Parthenopidae, <i>Acantholambrus baumi</i>	Outer surface of carapace	Potentially <i>syn-vivo</i>	Eocene	North Carolina, U.S.A.	Feldmann et al. (1998, fig. 21)
Indeterminate cheilostome	1	Mathildellidae, <i>Coeloma</i> sp.	Outer surface of carapace	Potentially <i>syn-vivo</i>	Miocene	Denmark	Feldmann (2003a, fig. 6.2)
Indeterminate cheilostome	1	Dromiidae, <i>Dromiopsis rugosa</i>	Inner surface of carapace	<i>Post-mortem</i>	Paleocene	Denmark	Jakobsen and Feldmann (2004, fig. 5)
Indeterminate cheilostome	1	Dromiidae, <i>Dromiopsis rugosa</i>	Outer surface of carapace	Potentially <i>syn-vivo</i> , but probably a molt	Paleocene	Denmark	Jakobsen and Feldmann (2004, fig. 6.2)
Indeterminate cheilostome	4	Dromiidae, <i>Dromiopsis rugosa</i>	Inner surface of carapace	<i>Post-mortem</i>	Paleocene	Denmark	Jakobsen and Feldmann (2004, fig. 7.1)
Indeterminate cheilostome	1	Dromiidae, <i>Dromiopsis rugosa</i>	Outer surface of carapace	Potentially <i>syn-vivo</i> , but probably a molt	Paleocene	Denmark	Jakobsen and Feldmann (2004, fig. 7.3)
Indeterminate cheilostome	1	Dromiidae, <i>Dromiopsis rugosa</i>	Inner surface of carapace	<i>Post-mortem</i>	Paleocene	Denmark	Jakobsen and Feldmann (2004, fig. 7.4)
Cheilostome <i>Allantopora</i>	1	Dromiidae, <i>Dromiopsis rugosa</i>	Inner surface of carapace	<i>Post-mortem</i>	Paleocene	Denmark	Jakobsen and Feldmann (2004, fig. 7.7)
Indeterminate cheilostome	1	Cancridae, <i>Metacarcinus tenax</i>	Outer surface of carapace	Potentially <i>syn-vivo</i>	Pliocene	Belgium	Van Bakel et al. (2006, fig. 1.6)
Indeterminate cheilostome	1	Majidae, <i>Mithrax acuticornis</i>	Outer surface of carapace	Potentially <i>syn-vivo</i>	Pleistocene	Jamaica	Collins et al. (2009, pl. 2, fig. 7)
Indeterminate cheilostome	1	Glaessneropsidae, <i>Glaessneropsis heraldica</i>	Outer surface of carapace	Potentially <i>syn-vivo</i>	Jurassic	Austria	Schweitzer and Feldmann (2009b, fig. 4.3)
Indeterminate cheilostome	5	Portunidae, <i>Callinectes danae</i>	Outer surface of carapace	Potentially <i>syn-vivo</i>	Pleistocene	Texas, U.S.A.	Collins et al. (2014, pl. 3, fig. 4)
Cyclostome “ <i>Berenicea</i> ”	1	Tanidromitidae, <i>Tanidromites raboefi</i>	Outer surface of carapace	Potentially <i>syn-vivo</i>	Jurassic	France	Robin et al. (2015, fig. 3.A.1, 3.B, 4)
Cyclostome “ <i>Berenicea</i> ”	1	Tanidromitidae, <i>Tanidromites raboefi</i>	Inner surface of carapace	<i>Post-mortem</i>	Jurassic	France	Robin et al. (2015, fig. 3.A.2, 3.C, 5)
Cyclostome “ <i>Berenicea</i> ”	1	Dromiidae <i>Dromiopsis rugosa</i>	Inner surface of carapace	<i>Post-mortem</i>	Paleocene	Denmark	Robin et al. (2015, fig. 7)

preservational or worker bias or represents an accurate picture of bryozoan settlement on crabs, the Mishan specimens shed new light on the relationship between these two groups in the fossil record.

The spatial distribution of epizoic bryozoans on host crabs is further complicated in some species by bryozoan larval preference and host decorator crab preference. Bryozoan larvae often choose where to settle based on the composition of the biofilm community on the substrate (Dahms et al. 2004) and/or the mechanical properties of the surface on which bryozoan larvae settle (Gray et al. 2002). Some epizoic bryozoans (e.g., *Triticella*) are obligate symbionts whose larvae prefer to settle on specific parts of their host crabs (Eggleston 1971; Key et al. 1999; Miller

et al. 2006). We found no evidence for or against bryozoan larval site preference in this study. Some decorator crabs, e.g., *Podochela hemphilli* (Lockington 1877) purposely decorate their pereopods with bryozoans (Hultgren and Stachowicz 2011). Others, e.g., *Loxorhynchus crispatus* Stimpson 1857, purposely decorate with the chemically noxious bryozoan *Bugula neritina* (Linnaeus 1758) (Hultgren and Stachowicz 2011). This use of sessile epibionts as camouflage by decorator crabs is well known (e.g., Parapar et al. 1997; Fernández et al. 1998, Stachowicz and Hay 2000; Guinot and Wicksten 2015). In this study, we found no evidence for or against the host crabs preferentially selecting or placing bryozoans.

The bryozoans covered on average 30% of the surface area of the host crab's fouled skeletal components (Table 2). This epizoan infestation density is well below that of crabs that use epizoans for camouflage (Fernandez-Leborans 2010). The bryozoan colonies contained on average 170 zooecia (Table 2). This epizoan load is well below that of crabs that use epizoans for camouflage (Fernandez-Leborans 2010). Camouflage is just one of the benefits that can accrue to the fouled hosts which more often experience the negative costs of epibiosis to the hosts (Fernandez-Leborans 2010).

There was no evidence of sexual ovicell formation in any of the bryozoan colonies. This may be a preservational artifact or simply a function of the small sizes of the colonies. Bryozoan colonies, like most clonal animals, typically require some minimum size before sexually reproducing (Harvell and Grosberg 1988). The colonies in this study may simply have been too small to reach the stage of sexual reproduction (Table 2). If so, there was no benefit to the bryozoans of sexual reproduction by living on the host crabs (i.e., a potentially mutualistic relationship). If not a preservational bias, then the lack of ovicells suggests that the bryozoan-crab relationship is best described as commensalism.

It is interesting to note the temporal distribution of fossil occurrences of epizoid bryozoans on crabs (Table 4). The oldest occurrences of the crab families are Jurassic with the majority from the Late Cretaceous to the Eocene. This is to be expected as this is when brachyurans were diversifying (Schweitzer and Feldmann 2005, table 4; Tsang et al. 2014, fig. 2B). But this also matches the temporal distribution of cheilostomes which also originated in the Jurassic and diversified through the Cretaceous and Eocene (Lidgard et al. 1993, fig. 6; Taylor and Waesenbach 2015, fig. 12). Could this apparent simultaneous timing be linked in a co-evolutionary host substrate-fouling bryozoan relationship? Competing hypotheses for the radiation of cheilostomes in the Cretaceous and Eocene include the evolution of larval brooding, the evolution of features that protect the colony from predation, and the advent of biomineralogical diversity (Taylor 1988; Taylor et al. 2009; Taylor and Waesenbach 2015). Perhaps increasing bryozoan fouling of motile crabs could have provided an additional way to avoid predation and enhanced the evolutionary success of cheilostomes.

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