

## Bryozoan Fouling Pattern on the Horseshoe Crab *Tachypleus gigas* (Müller) from Singapore

Marcus M. Key, Jr., William B. Jeffries, Harold K. Voris, and Chang M. Yang

**Abstract**—Bryozoans are common fouling organisms on sessile, inorganic, hard substrates. They are also epizoans on a variety of living substrates including both nektonic and motile benthic hosts. Epizoic bryozoans are less common on motile ephemeral substrates where the host regularly discards its outer surface. Two cheilostome bryozoans, *Biflustra savartii* (Audouin) and *Electra angulata* (Levinsen), are reported on 56 specimens of the horseshoe crab, *Tachypleus gigas* (Müller), from the seas adjacent to Singapore. This study attempts to quantify the relationships between the number, size, and spatial distribution of the epizoic bryozoan colonies and the size, gender, behavior, and morphology of the hosts. A total of 376 bryozoan colonies were found on 43 fouled horseshoe crabs. Compared to female horseshoe crabs, the males had more and larger bryozoan colonies as well as more total and percent cover by bryozoans. What makes these gender differences so dramatic is that the females had much larger surface areas than the males. Other factors affecting these patterns include the host's molting frequency and burrowing. More and larger epizoic bryozoan colonies grew on the dorsal surface as well as on the opisthosoma of the horseshoe crabs than on the ventral surface, prosoma, telson, or on the walking legs. As expected, the spatial distribution of epizoic bryozoan colonies on the host horseshoe crabs was bilaterally symmetrical. These bryozoan settlement patterns may reflect pre-settlement larval choice and/or post-settlement differential mortality. Bryozoans on these horseshoe crabs may experience post-settlement mortality due to subaerial exposure and abrasion from host amplexus and burrowing. Understanding the spatial distribution of bryozoans on extant hosts, will permit more effective evaluation of similar patterns on extinct hosts in the fossil record.

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### Introduction

Because epizoans are preserved precisely in their life positions, they provide natural experiments that may shed light on the autecology of the epizoans and their hosts. Preserved epizoans provide a valuable means by which inferences regarding the life habits of the epizoans (e.g., substrate selection, larval settling behavior, gregariousness, intraspecific spacing, overgrowth interactions, etc.) and the hosts (e.g., burrowing, molting, post-mortem taphonomic histories of skeletons, etc.) may be inferred in detail (e.g., Alexander and Brett, 1990).

Bryozoans tend to be poor competitors for substrate space and, as a result, they tend to occur frequently as epizoans, especially on ephemeral host substrates (McKinney and

Jackson, 1989). Bryozoan epibiosis has been well documented on several ephemeral motile hosts that shed (e.g., Key et al., 1995, 1996a) and molt (e.g., Key et al., 1996a,b, In press). This study investigated how the characteristics (e.g., morphology, behavior, etc.) of a motile host organism affect the spatial distribution of epizoic bryozoans. The specific goals of this study were: (1) to quantitatively describe the prevalence, abundance, and intensity of ectosymbiotic bryozoans on the horseshoe crab *Tachypleus gigas* from Singapore; (2) to compare the number and size of bryozoan colonies on male and female horseshoe crabs; (3) to compare the number and size of bryozoan colonies on various parts of the host's carapace; and (4) to use horseshoe crabs as an analogy for examining epizoic bryozoan settlement patterns on fossilized trilobites.

## Materials and Methods

Between December 1985 and May 1987, 56 specimens of the horseshoe crab *Tachypleus gigas* were collected from the shallow marine waters around Singapore. These specimens consisted of 38 males and 18 females. All material is housed in the Zoological Reference Collection (ZRC) in the Department of Zoology of the National University of Singapore. Four specimens (ZRC.1986.9–ZRC.1986.12) were collected on 2 December 1985 and one specimen (ZRC.1986.13) was collected on 18 December 1985 from the Singapore Straits near Sentosa Island, Singapore (1°15'N 103°50'E). Six specimens (ZRC.1986.3–ZRC.1986.8) were collected on 18 January 1986 and two specimens (ZRC.1986.1–ZRC.1986.2) were collected on 4 April 1986 off Kusu Island, south of Singapore (1°14'N 103°52'E). Three specimens (ZRC.1987.54–ZRC.1987.56) were collected on 14 May 1987 and 40 specimens (ZRC.1987.876–ZRC.1987.915) were collected on 15 May 1987 at Tuas, Singapore (1°19'N 103°40'E).

The dorsal and ventral surfaces of the host horseshoe crab exoskeletons were divided up into three dorsal sectors (prosoma, opisthosoma, and telson) as well as 29 ventral sectors (prosoma, left and right chelicera, left and right walking legs 1–5, left and right chilidia, left and right genital opercula, left and right branchial appendages 1–5, opisthosoma, and telson) (Figure 1).

The location and size of epizoic bryozoan colonies on the host horseshoe crabs were recorded in each of these 32 sectors. Due to the difficulty in classifying all the bryozoan colonies to the species level in the field, these data were not determined separately for the various bryozoan species. The surface area of each colony was measured using a personal computer-based image analysis system. The maximum measurement error was calculated at 3.7% based on repeatability experiments. Host size was measured using prosoma length and width (Figure 1) which are the standard morphometric proxies for size in horseshoe crabs (Shuster, 1982; Yamasaki, 1988).

## Results

A total of 56 specimens of *Tachypleus gigas* were collected. All host size and bryozoan fouling data are summarized in Table 1. Of the 56 hosts, 43 (76.8%) were fouled by either or both of two species of anascan cheilostome, gymnolaemate bryozoans: *Biflustra savartii* (Audouin) and *Electra angulata* (Levinsen). These species are known as epizoans on a variety of nektonic substrates such as sea snakes, crustaceans, and cephalopods. Both bryozoan species have been previously reported on motile benthic substrates such as horseshoe crabs (Key et al., 1996a, b) and are common fouling organisms that can be found encrusting surface-drift objects such as seeds, wood, and plastic trash (e.g., Winston et al., 1997).

A total of 376 bryozoan colonies were found on the 43 fouled horseshoe crabs. The abundance of bryozoans ranged from zero (for the 13 unfouled hosts) to 32 (mean = 6.7). The intensity of bryozoans ranged from one to 32 (mean = 8.7). The size of colonies ranged from 2 to 2,616 mm<sup>2</sup> (mean = 141 mm<sup>2</sup>). The percentage of the fouled host's surface area covered by bryozoans ranged from 0.03 to 12.31% (mean = 2.51%).

Of the 56 horseshoe crabs collected, 38 (68%) were males and 18 (32%) were females. Of the 38 males, 29 (76.3%) were fouled. Of the 18 females, 14 (77.7%) were fouled. Of the 376 colonies, 260 were found on male hosts whereas 116 were found on female hosts. Male horseshoe crabs tended to have a higher abundance (mean = 6.9) and intensity (mean = 9.0) of fouling bryozoan colonies than the females (mean = 6.4, mean = 8.3, respectively). The colonies on male hosts were slightly larger (mean = 143 mm<sup>2</sup>) than those on females (135 mm<sup>2</sup>). None of these differences between the fouling of male and female hosts were significant (t-tests,  $P > 0.05$ ) because they do not take into account the relative surface areas of the hosts. As with all horseshoe crabs, sexual dimorphism is most obviously expressed as larger body size in females (e.g., Botton et al., 1996). The *T. gigas* females collected were significantly larger (82%, Table 1) than the males (t-test,  $P < 0.0001$ ). Because male horseshoe crabs are much smaller than females, they are

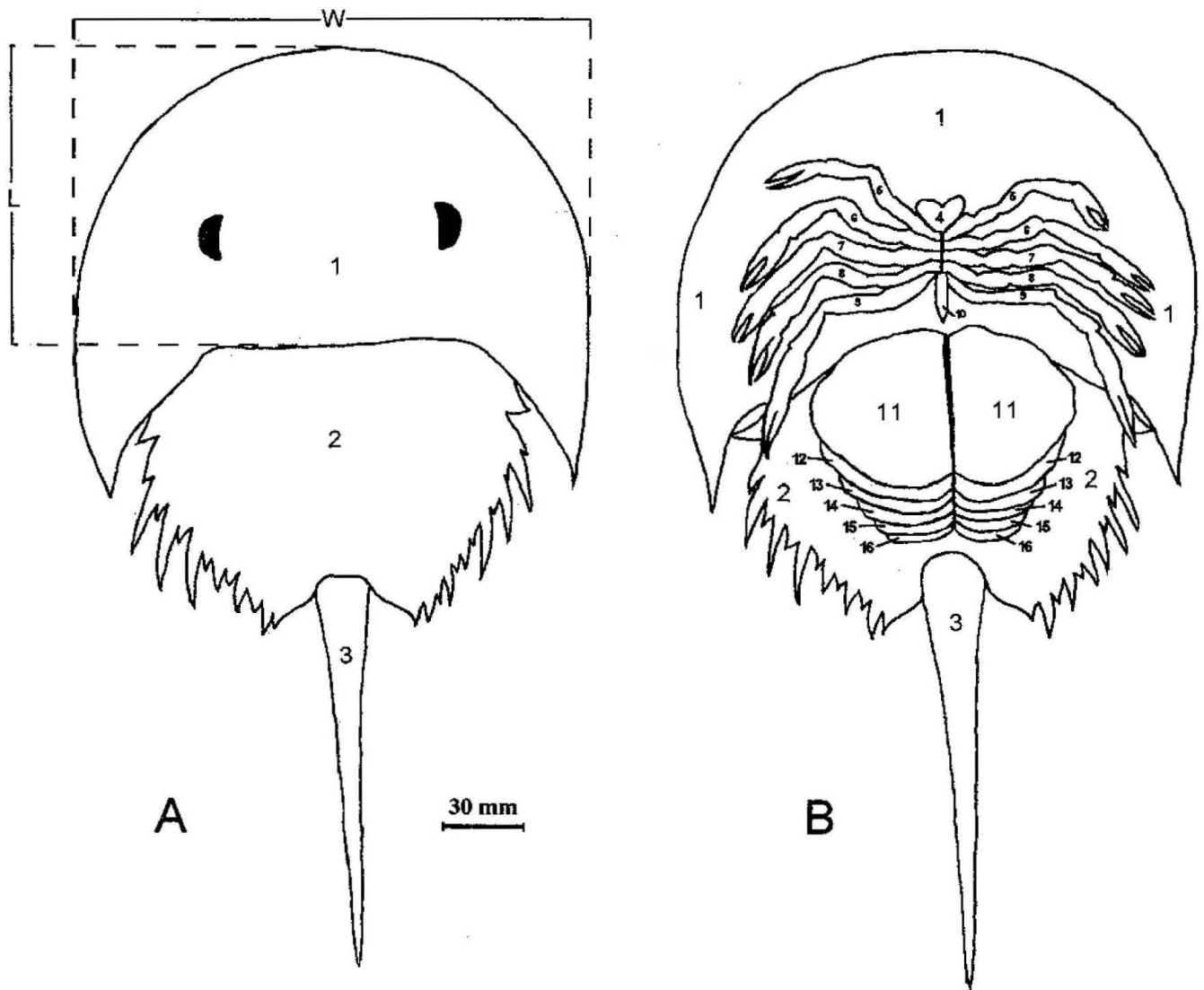


FIGURE 1. Dorsal (A) and ventral (B) surfaces of *Tachypleus gigas* showing the various sectors examined for bryozoans and the prosoma dimensions measured. 1 = prosoma. 2 = opisthosoma. 3 = telson. 4 = chelicera. 5-9 = walking legs 1-5, respectively. 10 = chilaria. 11 = genital opercula. 12-16 = branchial appendages 1-5, respectively. L = prosoma length. W = prosoma width. Modified from Debnath (1992, figs. 4 and 5).

relatively more fouled by bryozoans. This is evidenced in the male hosts having a significantly higher percentage cover (mean = 3.2%) than females (mean = 1.6%) (t-test,  $P < 0.05$ ).

More epizoic bryozoan colonies grew on the dorsal surface as well as on the opisthosoma of the hosts than on the ventral surface or the prosoma and telson whereas fewer grew on the walking legs (Table 2). Chi-squared tests revealed that these differences in number of colonies were not statistically significant ( $P > 0.05$ ). This is in contrast to the size distribution of epizoic bryozoan colonies on the hosts (Table 3). Chi-squared tests revealed that there were significantly ( $P < 0.05$ ) larger epizoic bryozoan colonies on the dorsal surface compared to the ventral surface. There were also

significantly larger colonies on the opisthosoma than on the prosoma, telson, and walking legs.

As expected, the spatial distribution of epizoic bryozoan colonies on the host horseshoe crabs was bilaterally symmetrical (Tables 2 and 3). There was no statistically significant ( $P > 0.05$ ) difference in the number or in the percent cover of colonies on the left and right appendages of the hosts.

### Discussion

The 76.8% prevalence of fouled hosts for *Tachypleus gigas* is similar to that found by previous studies. Jeffries et al. (1989) examined the exact same specimens of *T. gigas* and found that 70% were fouled by epizoic barnacles.

TABLE 1. Host carapace size and bryozoan colony fouling data for *Tachypleus gigas* ( $\pm$ SD). Numbers in parentheses indicate percentage distribution.

Character	Males	Females	Total
No. of hosts collected	38 (67.9)	18 (32.1)	56 (100)
Mean prosoma length (mm) of hosts	88.1 $\pm$ 5.3	123.2 $\pm$ 5.9	99.4 $\pm$ 17.4
Mean prosoma width (mm) of hosts	156.7 $\pm$ 8.8	204.2 $\pm$ 11.1	172.0 $\pm$ 24.3
Mean dorsal and ventral surface area (mm <sup>2</sup> ) of hosts	39,845 $\pm$ 4,269	72,573 $\pm$ 7,218	50,365 $\pm$ 16,317
No. of hosts fouled	29	14	43
Prevalence of fouling (% of hosts fouled)	76.3	77.8	76.8
No. of colonies found	260 (69.1)	116 (30.9)	376 (100)
Abundance of colonies (mean number per host)	6.8 $\pm$ 8.1	6.4 $\pm$ 8.4	6.7 $\pm$ 8.1
Intensity of colonies (mean number per fouled host)	9.0 $\pm$ 8.1	8.3 $\pm$ 8.7	8.7 $\pm$ 8.2
Mean surface area of each colony (mm <sup>2</sup> )	143 $\pm$ 236	135 $\pm$ 236	141 $\pm$ 235
Mean total surface area of colonies (mm <sup>2</sup> ) per fouled host	1,285 $\pm$ 1,447	1,116 $\pm$ 1,107	1,230 $\pm$ 1,335
Mean % cover of fouled hosts	3.2 $\pm$ 3.6	1.6 $\pm$ 1.6	2.5 $\pm$ 3.1

Though *T. gigas* females compared to males had on average 82% more surface area available for fouling, they were less fouled (Table 1). Compared to males, the females had 8% fewer bryozoan colonies per fouled host individual, 6% smaller bryozoan colonies, and 50% less cover by bryozoans. These results are similar to those from previous studies (Roonwal, 1944; Saha, 1989; Debnath, 1992; and Debnath and Choudhury, 1991), which also reported that *T. gigas* males are more fouled than females. Why are males of *T. gigas* more

heavily fouled than females? Perhaps females molt more frequently or later in ontogeny than males. This has been suggested by Debnath and Choudhury (1991) based on Sekiguchi et al.'s (1988) data that *T. gigas* males molt 12 times before reaching adulthood and females 13 times.

Another explanation for the more extensive fouling of *T. gigas* males is that females spend more time buried in the substrate. Horseshoe crabs frequently burrow during feeding and breeding (e.g., Shuster, 1982). Fouling inten-

TABLE 2. Number of epizoic bryozoan colonies on various sectors of *Tachypleus gigas* carapaces. Expected values are based on relative surface area of each sector. Numbers in parentheses indicate percentage distribution.

Sector	Males observed	Females observed	Total observed	Total expected
Dorsal	139 (53.5)	67 (57.8)	206 (54.8)	188 (50.0)
Ventral	121 (46.5)	49 (42.2)	170 (45.2)	188 (50.0)
Prosoma	138 (53.1)	54 (46.5)	192 (51.1)	229 (61.0)
Opisthosoma	115 (44.2)	59 (50.9)	174 (46.3)	128 (33.9)
Telson	7 (2.7)	3 (2.6)	10 (2.6)	19 (5.1)
Dorsal Prosoma	73 (28.1)	26 (22.4)	99 (26.3)	115 (30.5)
Dorsal Opisthosoma	59 (22.7)	38 (32.8)	97 (25.8)	64 (17.0)
Dorsal Telson	7 (2.7)	3 (2.6)	10 (2.7)	9 (2.5)
Ventral Prosoma	65 (25.0)	28 (24.1)	93 (24.7)	115 (30.5)
Ventral Opisthosoma	56 (21.5)	21 (18.1)	77 (20.5)	64 (17.0)
Ventral Telson	0 (0.0)	0 (0.0)	0 (0.0)	9 (2.5)
All Appendages	19 (7.3)	15 (12.9)	34 (9.0)	68 (17.9)
Left Appendages	8 (3.1)	7 (6.0)	15 (4.0)	34 (8.9)
Right Appendages	11 (4.2)	8 (6.9)	19 (5.1)	34 (8.9)
Chelicera	0 (0.0)	0 (0.0)	0 (0.0)	4 (1.0)
Walking Legs 1-5	18 (6.9)	12 (10.3)	30 (7.9)	42 (11.3)
Chilaria	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.3)
Genital Opercula	1 (0.4)	0 (0.0)	1 (0.3)	13 (3.4)
Branchial Appendages 1-5	0 (0.0)	3 (2.6)	3 (0.8)	9 (1.9)

TABLE 3. Percentage of total epizoic bryozoan surface area on various sectors of carapaces of *Tachypleus gigas*. Expected values are based on relative surface area of each sector.

Sector	Males observed	Females observed	Total observed	Total expected
Dorsal	60.5	61.5	60.7	50.0
Ventral	39.5	38.5	39.3	50.0
Prosoma	39.9	38.3	39.6	61.0
Opisthosoma	59.4	61.4	59.8	33.9
Telson	0.7	0.3	0.6	5.1
Dorsal Prosoma	29.3	19.0	27.3	30.5
Dorsal Opisthosoma	30.5	42.2	32.8	17.0
Dorsal Telson	0.7	0.3	0.6	2.5
Ventral Prosoma	10.6	19.3	12.3	30.5
Ventral Opisthosoma	28.9	19.2	27.0	17.0
Ventral Telson	0.0	0.0	0.0	2.5
All Appendages	1.7	2.5	1.9	17.9
Left Appendages	1.1	1.2	1.1	8.9
Right Appendages	0.6	1.3	0.7	8.9
Chelicera	0.0	0.0	0.0	1.0
Walking Legs 1-5	1.5	2.1	1.7	11.3
Chilaria	0.0	0.0	0.0	0.3
Genital Opercula	0.2	0.0	0.2	3.4
Branchial Appendages 1-5	0.0	0.4	0.0	1.9

sities of burrowing hosts are partly a function of how much time they spend on the surface of the substrate (Hartnoll, 1972). Hosts that burrow extensively are less available for larval settlement (e.g., Abelló et al., 1990). *T. gigas* females do more burrowing, especially in the breeding season during amplexus when the males clasp onto the dorsal surface of the females (Roonwal, 1944; Saha, 1989). As a result, the male is more exposed to settling epizoic larvae. Brockmann and Penn (1992) studied the related horseshoe crab *Limulus polyphemus* and also attributed the higher prevalence of fouling in males to lower burrowing frequency.

The results of this and other studies (Rao and Rao, 1972; Debnath, 1992) indicate the dorsal surface of *T. gigas* is more fouled than the ventral surface. This may be due to differential larval substrate selection and/or differential post-settlement mortality. Why would the dorsal surface be more fouled? Perhaps the bryozoan larvae are not negatively phototropic at the time of settlement like many bryozoan larvae (Ryland, 1960), and as a result they settle on the dorsal surface. Unfortunately, there is no published information on the larval settlement preferences for the two bryozoan species in this study. The host's burrow-

ing and feeding in the substrate as well as normal motion along the substrate as discussed above probably prohibit epizoan larvae from settling on the ventral surface. Any larvae that do settle on the ventral surface may be abraded by rubbing along the substrate. This is especially obvious on the telson where the ventral surface was completely devoid of bryozoans.

Why would the opisthosoma be more fouled than the prosoma and telson? Compared to the opisthosoma, the dorsal and ventral surfaces of the prosoma and the ventral surface of the telson are more subject to abrasion with the substrate. Small hair-like bristles occur on various parts of the carapace of *T. gigas* (Yamasaki, 1988). These may hinder colony growth in the encrusting, sheet-like bryozoans in this study. The spatial distribution of epizoans on hosts may also be associated with host-generated breathing and/or feeding currents that influence epizoic larval settlement. Apparently the water currents generated by the gills of the host (Yamasaki, 1988) do not pull in bryozoan larvae to the ventral surface of the opisthosoma as the branchial appendages are less fouled than expected (Tables 2 and 3). Perhaps larvae preferentially settle on or preferentially survive on the opisthosoma. Due to the elevated nature of the prosoma in horseshoe crabs, water flow over the prosoma creates turbulent eddies above the downcurrent-sloping opisthosoma (Nascimento and Alexander, 1994). It has been suggested that this is why bryozoans are often concentrated on the opisthosoma of *Limulus polyphemus* (Nascimento and Alexander, 1994). These eddies could cause preferential larval settlement on the dorsal surface of the opisthosoma or cause preferential survival of larvae there due to slower currents and better feeding.

Thus, there are several factors which can affect the spatial distribution of epizoic bryozoans on their hosts. They include pre-settlement host availability (e.g., parts of host unavailable to settling larvae due to burial, sub-aerial exposure, amplexus, previous epizoan cover, etc.), larval preference (e.g., phototropism, geotropism, rheotropism, host microflora, host ornamentation/texture, etc.), and post-settlement larval mortality (e.g., due to

differential abrasion, predation, food availability, subaerial exposure, etc.).

Interpreting such processes in the fossil record is even more complicated. The first problem is determining if the epibiosis occurred when the host was alive or dead. For example, Snajdr (1983) described epizoic bryozoans on what he considered to be dead trilobite exoskeletons, probably exuviae. If it can be determined that the bryozoans settled on the host when it was alive, then the spatial distribution patterns of the bryozoans on their hosts may provide useful information about the host. For example, a 100% colonization rate by sessile invertebrates suggest terminal anecdyosis in the host, whereas prevalences not surpassing 30% suggest the absence of terminal anecdyosis in the host (Abelló et al., 1990).

A similar approach focusing on the spatial distribution of epizoans has recently been applied in the fossil record to interpret host behavior (e.g., Mikulic, 1990; Tetreault, 1992; Brandt, 1996). Brandt (1996) found several trestome bryozoan species encrusted on Ordovician trilobites that were interpreted to be living at the time of bryozoan larval settlement. The bryozoans were site specific in their settlement location, and Brandt (1996) interpreted this as indicating either the preferentially fouled area was the only part of the host exposed above the substrate and/or the bryozoan/host relationship was commensal and the bryozoans were exploiting the hosts as hard substrate and also perhaps benefitting from host-generated feeding currents.

The data from this present study suggest several possible alternatives. A bryozoan settlement pattern similar to Brandt (1996) could be produced by other factors: (1) nonrandom larval settlement due, not to the part of the host that was exposed above the substrate, but to morphological characteristics of parts of the host that make it unavailable or unattractive to settling larvae; and (2) random larval settlement and differential colony survival due to food availability or abrasion from activities such as burrowing and amplexus.

### Conclusions

The factors controlling the spatial distribution of epizoans such as bryozoans on a host

such as a horseshoe crab are complex. They involve characteristics of the settling larvae as well as the host. The biology of the epizoic bryozoans and the host must be known before the spatial distribution of the bryozoans can be used to infer host behavior. This is especially true when examining the fossil record. Before interpreting epizoans on extinct organisms such as trilobites, it would be useful to examine extant modern host analogs, such as horseshoe crabs, if possible.

### Acknowledgments

We thank the National University of Singapore for access to specimens. Dr. Judith Winston helped with bryozoan species identifications, Dr. Alan Cheetham assisted with the bryozoan literature review, and Dr. Carl Shuster helped with the horseshoe crab literature review. Jessica Ustick did the drafting. This research received financial support from Dickinson College and a National Science Foundation grant (BSR-8917108) to MMK.

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