PALEOECOLOGY OF COMMENSAL EPIZOANS FOULING
FLEXICALYMENE (TRILOBITA) FROM THE UPPER ORDOVICIAN,
CINCINNATI ARCH REGION, USA

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ABSTRACT—Commensal epizoans and episkeletozoans are rarely preserved attached to the external exoskeleton of the Late Ordovician trilobite Flexicalymene. Of nearly 15,000 Flexicalymene specimens examined, 0.1% show epizoans or episkeletozoans. Factors limiting Flexicalymene fouling include a shallow burrowing life style, frequent molting of the host, larval preference for other substrates, observational bias caused by overlooking small fouling organisms, and the loss of the non-calciﬁed, outermost cuticle prior to fossilization or as the trilobite weathered from the encasing sediment. Trepostome bryozoans, articulate and inarticulate brachiopods, cornulitids, and a tube-dwelling/boring nonbiomineralized organism represent the preserved members of the Late Ordovician marine hard substrate community fouling Flexicalymene. This assemblage of organisms is less diverse than the hard substrate community fouling Late Ordovician sessile epibenthic organisms. Fouling is not restricted to only large Flexicalymene specimens as observed in previous studies but occurs in medium to large individuals interpreted as early to late holaspid specimens. Epizoans fouling the carcasses or molt ensembles of 16 Flexicalymene specimens provide insight into the life habits of the host and these fouling organisms. Trepostome bryozoans, articulate and inarticulate brachiopods, and cornulitids preferentially attached to elevated portions of the dorsal exoskeleton, and preferentially aligned in either the direct line or lee side of currents generated by Flexicalymene walking on the sea ﬂoor or swimming through the water column.

INTRODUCTION

Fossil and modern marine hard substrate communities contain a diverse assemblage of organisms. Among them are algae, annelids, barnacles, brachiopods, bryozoans, coccoliths, echinoderms, foraminifera, hydroids, mollusks, serpulid polychaetes, poriferans, protoctists, ascidian tunicates, rugose and tabulate corals, cornulitids, and various echinoderms such as edrioasteroids, cystoids, and blastoids (Taylor and Wilson, 2003). Larvae of these organisms colonize rocks, plants, and the skeletons of living and dead animals by cementing themselves to surfaces or boring into them (Taylor and Wilson, 2002). Larvae are more likely to either settle on sessile epibenthic hosts than on motile benthic or nektonic hosts, or to cement themselves to previously settled members of the hard substrate community (Taylor, 1990). Motile benthic and nektonic mollusks, arthropods, echinoderms, and vertebrates are less frequent sites of colonization (Key et al., 1995, 1996a, 1996b, 1997). Lower colonization rates exhibited by motile hosts may reﬂect host behaviors developed to remove fouling organisms. For example, modern arthropods can molt their exoskeletons or burrow into the sediment to cleanse themselves of epibionts (e.g., Ross, 1983; Mikulic, 1990; Gili et al., 1993).

In this study, we investigate organisms of the marine hard substrate community that have fouled carcasses and articulated exuviae of the calymenid trilobite Flexicalymene spp. Shirley, 1936, which occurs throughout Upper Ordovician rocks of the Cincinnati arch region of southwestern Ohio, southeastern Indiana, and northern Kentucky (Hunda and Hughes, 2007). This is a period when the evolution of epibiotic relationships played an important role in the Great Ordovician Biodiversity Event (Servais et al., 2009). We restrict our investigation to those organisms that cemented themselves to the external skeletons of living or dead Flexicalymene spp. or that live within bryozoan colonies fouling Flexicalymene spp. We apply the nomenclature for marine organism-hard substrate relationships proposed by Taylor and Wilson (2002). An organism interpreted as colonizing a living Flexicalymene spp. host is termed an epizoan, and an organism living on a Flexicalymene spp. skeleton, whether it belonged to a living animal or a corpse, is termed an episkeletozoan.

Fossil episkeletozoans are valuable resources in the paleoecologic study of ancient hard substrate communities and provide vital information for addressing the life habits of host organisms (Alexander and Brett, 1990; Powers and Ausich, 1990; Lescinsky, 1996; Taylor and Wilson, 2002). Ecologic data commonly lost by preservational bias and destructive taphonomic processes is preserved because fouling episkeletozoans are fossilized in life position on the exoskeletons of host organisms. Thus, hard substrate communities provide opportunities to study the composition, abundance, density, intraspecific spacing, species interactions, larval settling behavior, and overgrowth interactions of its members (Taylor and Wilson, 2003). Examination of episkeletozan-host interactions also provides information about feeding habits of episkeletozoans and host organisms, the substratum selection of episkeletozoans, and strategies used by living hosts to remove epizoans.
Well-preserved trilobite carcasses and articulated exuviae are common fossils in many Paleozoic marine stratigraphic sequences. However, studies describing episkeletozoans on trilobites are relatively few in number (e.g., Brandt, 1996; Kloc, 1997). Moreover, most studies involve few encrusted trilobites (e.g., Prokop, 1965; Kesling and Chilman, 1975; Clarkson and Tripp, 1982; Snajdr, 1983; Mikulic, 1990; Tetreault, 1992, 1997; Budil and Saric, 1995; Kácha and Saric, 1995; Taylor and Brett, 1996; Brett and Taylor, 1997; Pratt, 2001). Exceptions are Kloc (1992, 1993, 1997) and Brandt (1996) who documented the frequency, stratigraphic occurrence, and paleoecology of trilobite episkeletozoans from sizeable collections of articulated specimens. Kácha and Saric’s (2009) recent study examined a large population of trilobites, but they were all incomplete, disarticulated and transported exoskeletons.

Kloc (1992, 1993, 1997) discovered that 14 (100%) carefully prepared articulated specimens of the Lower Devonian odontopleurine trilobite Dicranurus hamatus elegantus Campbell, 1977 from Oklahoma contained a diverse assemblage of encrusting bryozoans, brachiopods, corals, foraminifera, worm tubes, and unknown nonbionomineralized organisms. Episkeletozoans were present on trilobites of varying holaspid sizes. Episkeletozoans generally encrusted the cephalon, genal, pleural, and occipital spines more than they encrusted the thorax or pygidium. Kloc (1992, 1993, 1997) suggested that a mutualistic relationship existed between the host and the episkeletozoans. D. hamatus elegantus provided the necessary hard substrate as well as increased feeding opportunities and mobility for the sessile episkeletozoans, whereas the episkeletozoans produced a living camouflage that functioned to make the outline of the host less conspicuous to predators.

Tetreault (1992, 1997) examined the autecology of several trilobite species from the Rochester Shale (Silurian) of Ontario and New York. Numerous specimens of the large lichid Arctinus boltoni (Bigsby, 1825) supported Cornulites sp. Schlotheim, 1820 tubes on the doublure and brachiopods, cyclostome bryozoans, and Cornulites sp. tubes elsewhere on the dorsal exoskeleton. Apertures of Cornulites sp. on the doublure were oriented posteriorly, suggesting a rheophilic response to persistent water circulation patterns beneath the trilobite. Tetreault (1992, 1997) concluded that the upper part of the exoskeleton of Arctinus sp. remained mud free because of the large number of epizoozoans fouling that area. Further support for the interpretation was provided by the presence of individuals representing several age classes of the brachiopod Stegerhynchus sp. Foerste, 1909a. Tetreault (1992, 1997) concluded that molting had either slowed or stopped in these large holaspid specimens of A. boltoni allowing sufficient time for colonization by epizoans.

Brandt (1996) reported that only 8 (0.4%) of 2,030 Flexicalymene specimens in museum collections from the Upper Ordovician rocks of the Cincinnati, Ohio, area were fouled with trepostome bryozoans and cornulitid worm tubes. These episkeletozoans preferentially attached to the elevated areas of the anterior/medial portion of the cephalic doublure and the glabella, the axial rings of the thorax, and the medial portion of the pygidium. However, the bryozoans and cornulitids did not exhibit a preferred orientation on the fouled trilobites. Only large Flexicalymene spp. specimens interpreted as late adult (holaspid) molt stages contained epizoans and episkeletozoans. Brandt (1996) suggested that a commensal relationship existed between Flexicalymene and associated episkeletozoans. As interpreted, the exoskeleton of Flexicalymene spp. served as a hard substrate for bryozoans and cornulitids that filtered food from the feeding currents of the host. Flexicalymene spp. was interpreted by Brandt (1996) as a semi-infaunal, burrowing organism that inhabited shallow burrows at or near the sediment-water interface.

Over the past two decades, 16 additional fouled specimens of Flexicalymene spp. have been found in Upper Ordovician rocks of the Ohio-Indiana-Kentucky area. These specimens form the basis of this study and provide important new information that supports some of Brandt’s (1996) conclusions, but they also suggest some alternative explanations. Our objectives are to: 1) describe the paleoenvironmental setting and lateral distribution of selected Upper Ordovician shale beds of the Ohio-Indiana-Kentucky area containing encrusted Flexicalymene spp. trilobites; 2) quantitatively describe the community composition, prevalence, abundance, and spatial distribution of epizoozoans and episkeletozoans on Flexicalymene spp.; 3) document preserved epizoan biotic interactions; 4) document preferred larval settling and alignment of epizoozoans; 5) discuss the feeding habits of epizoans and the host Flexicalymene spp.; and 6) describe the commensal relationships between these organisms.

MATERIALS AND METHODS

Nearly 15,000 articulated, relatively undeformed Flexicalymene spp. specimens were examined for epizoans and episkeletozoans from nine localities in the Cincinnati arch region of southwestern Ohio, southeastern Indiana, and northern Kentucky (Fig. 1). Most specimens probably belong to F. meeki (Foerste, 1910) or F. retrorsa retrorsa (Foerste, 1910) (see Hunda and Hughes, 2007). However, species-level identification was not attempted on non-figured specimens because numerous people, who were not all trilobite taxonomists, examined 1,000s of specimens for epizoans. Thus, the non-figured material is left under open nomenclature (i.e., Flexicalymene spp.) and from here on will be referred to simply as Flexicalymene.

The largest collection came from Mt. Orab, Ohio, where ~14,500 specimens were excavated during extensive quarrying of the trilobite shale bed (Ferre, 1994; Hunda et al., 2006). These specimens were examined for episkeletozoans with only the naked eye. Surface exposures at the remaining eight locations yielded 458 more specimens. These specimens were more carefully examined under a binocular microscope. All specimens were collected from six stratigraphic intervals, referred to as trilobite shale beds, within the Upper Ordovician Katian Stage (Maysvillian and Richmondian Stages of the historic North American Cincinnatian Series succession [Bergström et al., 2009]; Fig. 2). Prevalence of fouling was calculated as the percentage of fouled specimens at each location (Table 1). We also examined a smaller collection of well preserved specimens from the Treptoceras duseri shale exposed at Bevis, Ohio. In these specimens, width of the lp preoccipital lobe was measured to the nearest 1 mm as a proxy for host size (Fig. 3).

We classified each fouled Flexicalymene as a carcass or exuvium using the criteria of Brandt (1993). A Flexicalymene carcass is characterized by intact librigenae and hypostome, and by thoracic segments that are not telescoped, displaced, or unevenly spaced. All 13 thoracic segments should be evident. Complete spheroidal enrollment is considered conclusive evidence of a carcass. Flexicalymene exuviae meet one or more of the following conditions: missing sclerites such as librigenae, hypostome, or other cephalic elements; incomplete enrollment or sharply bent cephalia; displaced, disarticulated,
telescoped, or unevenly spaced thoracic segments; or rotated pygidia or cephalon.

For the fouled specimens, the degree of specimen compaction and its attitude (i.e., enrolled versus outstretched) were recorded. Width of the 1p preoccipital lobe and the dorsal surface area of the exoskeleton were measured on each fouled Flexicalymene. Epizoozoans and episkeletozoans were identified, counted, and examined for biotic interactions and preferred orientation. The surface area of each colonial or solitary episkeletozoan was measured. All 1p preoccipital lobe width measurements were made to the nearest 0.01 mm, and all surface area measurements were made to the nearest 0.01 mm². Area measurements were done with a digital image analysis system with measurement errors of less than 3%.

All fouled trilobite specimens of Flexicalymene are reposited in the Orton Geological Museum, The Ohio State University, Columbus, Ohio (OSU). They have been assigned catalog numbers OSU 53684 through OSU 53699 inclusive.

PALEOENVIRONMENTAL SETTING

The trilobite Flexicalymene ranges throughout the approximately 230 m of thin, interbedded limestone and shale beds characterizing the Cincinnatian succession (Caster et al., 1961; Holland and Patzkowsky, 2007; Hunda and Hughes, 2007; Meyer and Davis, 2009). Flexicalymene and other trilobites commonly occur as disarticulated sclerites and average 9% of the bioclast fraction in Cincinnatian limestones (Martin, 1975). Trilobite bioclasts, ranging from 10 to 14% of fossil bioclasts, are most abundant in the deeper water, offshore environments of the Kope and Waynesville Formations and the intermediate water depths of the transitional, shoreface environments of the Fairview Formation, Corryville Member of the Grant Lake Formation, Corryville Member of the Grant Lake Limestone, and Liberty Formation. Trilobite bioclasts represent only 5 to 7% of fossil bioclasts in the shallower water, upper shoreface environments of the Bellevue and Mount Auburn Members of the Grant Lake Formation, the Bellevue and Straight Creek Members of the Grant Lake Limestone, the Arnheim Formation, and the Whitewater Formation, and represent only 1% of fossil bioclasts present in the lagoonal environments of the Saluda Formation (Martin, 1975).

Articulated Flexicalymene carcasses and exuviae occur throughout the Cincinnatian shales and limestones. However, the frequency of articulated Flexicalymene specimens is generally low in most stratigraphic intervals. So called...
“trilobite shale beds” are an exception to the general pattern of occurrence because these beds are characterized by abundant articulated trilobite carcasses and exuviae, complete crinoid crowns, butterfly bivalves, and complete articulated ostracodes (Brandt, 1985; Frey, 1987a, 1987b; Schumacher and Shrake, 1997; Hughes and Cooper, 1999; Hunda et al., 2006). These shales are thick-bedded, laminated claystones to lime mudstones with occasional, thin, fining upward laminae and beds of skeletal debris. Most articulated fossils and disarticulated fossil debris occur in clusters or patches separated by largely unfossiliferous claystone or mudstone. Trilobite shale beds occur as localized beds having limited geographic distribution (e.g., Hughes and Cooper, 1999), or beds that are regionally persistent and laterally traceable for tens of kilometers (e.g., Frey, 1987a, 1987b; Schumacher and Shrake, 1997). Brandt (1985), Frey (1987a, 1987b), Schumacher and Shrake (1997), Hughes and Cooper (1999), Babcock (2005), and Hunda et al. (2006) viewed storm related sedimentation as responsible for smothering benthic communities that are now preserved in trilobite shale beds. Rapid burial apparently inhibited scavenging and skeletal disarticulation, resulting in excellent preservation of trilobites and other fossils.

SAMPLE LOCATIONS AND STRATIGRAPHY

Flexicalymene specimens examined in this study occur in six discrete trilobite shale beds exposed at nine locations (Fig. 1). The stratigraphic interval containing the trilobite shale beds ranges from the basal Corryville Member of the Grant Lake

Table 1—Prevalence of episkeletozoans on Flexicalymene from Cincinnatian trilobite shale beds.

<table>
<thead>
<tr>
<th>Number of Flexicalymene specimens examined</th>
<th>Number of fouled Flexicalymene specimens</th>
<th>Prevalence (%)</th>
<th>Trilobite shale bed</th>
<th>Location</th>
<th>Reference</th>
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<tr>
<td>2,030</td>
<td>8</td>
<td>0.39</td>
<td>Multiple beds</td>
<td>Cincinnati, OH region</td>
<td>Brandt (1996)</td>
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<td>−14,500</td>
<td>3</td>
<td>0.02</td>
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<td>Georgetown, OH</td>
<td>This study</td>
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<tr>
<td>383</td>
<td>5</td>
<td>1.3</td>
<td>Treptoceras duseri</td>
<td>Bevis, OH</td>
<td>This study</td>
</tr>
<tr>
<td>37</td>
<td>2</td>
<td>5.4</td>
<td>Treptoceras duseri</td>
<td>Caesar Creek, OH</td>
<td>This study</td>
</tr>
<tr>
<td>12</td>
<td>1</td>
<td>8.3</td>
<td>Treptoceras duseri</td>
<td>Madison, IN</td>
<td>This study</td>
</tr>
<tr>
<td>11</td>
<td>1</td>
<td>9.1</td>
<td>Western Hills</td>
<td>Queenswood Road, OH</td>
<td>This study</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>17</td>
<td>Western Hills</td>
<td>Quail Hill Road, OH</td>
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</tr>
<tr>
<td>4</td>
<td>1</td>
<td>25</td>
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</tr>
<tr>
<td>3</td>
<td>1</td>
<td>33</td>
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<td>Maysville, KY</td>
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</tr>
<tr>
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<td>1</td>
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<td>16</td>
<td>0.11</td>
<td></td>
<td>Total this study</td>
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</table>

Figure 2—North American stratigraphic nomenclature of Upper Ordovician rocks of southwestern Ohio, southeastern Indiana, and northern Kentucky illustrating the positions of the Flexicalymene Shirley, 1936 trilobite shale beds and the number of fouled specimens collected.
Limestone to the middle Waynesville Formation of Schumacher et al. (1991). In terms of historic North American stratigraphic nomenclature, the trilobite shale beds range from the middle Maysvillian Stage to the lower Richmondian Stage of the Cincinnatian (C3 to C5 third order sequences of Holland and Patzkowsky, 1996; Fig. 2). This interval correlates to the Katian Stage of the Upper Ordovician Series as now used globally (Bergström et al., 2009).

The Moranburg trilobite shale bed is exposed in two roadcuts along U.S. Route 62, 3.2–3.7 km northeast of the junction of Kentucky Routes 9 and 10 near Maysville, Kentucky (Fig. 1). An 11 cm thick claystone, containing scattered pockets of well preserved Glyptocrinus sp. Hall, 1847, occurs in the basal Corryville Member, about 1 m above the top of the Bellevue Member of the Grant Lake Limestone (Fig. 2). The total lateral extent of this bed is unknown but it is easily traced for 0.5 km along the high ridge traversed by U.S. Route 62.

The Western Hills trilobite shale bed crops out in natural stream exposures and construction site excavations in the Cincinnati, Ohio, area (Fig. 1). This shale occurs in the upper part of the Corryville Member of the Grant Lake Formation between 2 and 3 m below the Corryville-Mount Auburn Member contact (Fig. 2). This 1 m claystone is traceable for at least 20 km from the Quail Hill and Queenswood locations northward to Bevis, Ohio.

The Dent trilobite shale bed (Glyptocrinus sp. beds of Caster, 1961) is a 1 m thick, medium- to thick-bedded mudstone interbedded with thin limestones in the basal Arnheim Formation (Fig. 1). The base of this shale occurs about 1.5 m above the top of the Mount Auburn Member of the Grant Lake Formation (Fig. 2). This shale has a lateral distribution similar to the Western Hills trilobite shale bed (Fig. 1).

The informal Mt. Orab shale bed of Hunda et al. (2006) has been quarried from extensive excavations adjacent to Flat Run north of Georgetown, Ohio (Fig. 1). This trilobite shale bed consists of 0.46 m of gray lime mudstone interbedded with nodular- and wavy-bedded calcisiltite and limestone. The Arnheim Formation index fossils, Retrorsirostra carleyi (Hall, 1860) and Leptaena richmondensis Foerste, 1909b, are present in the overlying nodular limestone and shale beds (Ferree, 1994; Hunda et al., 2006). Geologic mapping of Brown and Highland counties places the base of the Mt. Orab shale bed approximately 10 m above the Arnheim-Grant Lake Limestone formational contact (e.g., Schumacher et al., 2000). Weir et al. (1980) described a similar shale bed containing abundant, articulated trilobites (Flexicalymene and Isotelus sp. Dekay, 1824) overlain by a thin interval of nodular-bedded limestones and shales containing R. carleyi and L. richmondensis from stream exposures of the Arnheim Formation at its type section in Straight Creek near Arnheim, Ohio (Fig. 1). The Mt. Orab shale bed has a lateral distribution of at least 15 km from Flat Run Creek to Straight Creek.

The Madison trilobite shale bed is exposed in roadcuts of U.S. Route 421 approximately 2 km northeast of the intersection of Indiana Route 56 and U.S. Route 421 near Madison, Indiana. The 1.5 m thick blue shale is located near the top of the Arnheim Formation (Hattin et al., 1961), which is also correlated to the middle of the Dillsboro Formation (Brown and Lineback, 1966). The lateral distribution of this shale is unknown.

The Treptoceras duseri shale of southwestern Ohio (sensu Flower, 1946) and its lateral equivalent, the trilobite shale unit of southeastern Indiana (sensu Frey, 1987a, 1987b), is exposed at Bevis, Ohio, Caesar Creek, Ohio, and Weisburg, Indiana (Fig. 1). This unit consists of approximately 1.5 m of thick-bedded claystone with thin-bedded limestone capped by the Onniella meeki Miller, 1875 zone consisting of 1.5 to 2.5 m of interbedded shale and limestone. Frey (1997) determined the base of the T. duseri shale to be 10 to 11 m above the Arnheim-Waynesville formational contact in southwestern Ohio (Fig. 2). The trilobite shale unit occurs in the upper Dillsboro Formation in southeastern Indiana. Frey (1997) traced the T. duseri shale, O. meeki zone, and trilobite shale unit for 135 km through southwestern Ohio and southeastern Indiana (Fig. 1).

**RESULTS**

Of the ~14,958 Flexicalymene specimens examined, 16 (0.1%) were fouled. Eleven (69%) of these were preserved enrolled or semi-enrolled, and five (31%) were outstretched. Thirteen (81%) of the fouled specimens are considered carcasses, and three (19%) are interpreted as nearly intact exuviae (Table 2). Fouled specimens of Flexicalymene have cephalas ranging from 6.61 to 12.90 mm (mean = 9.50 mm) across the width of the 1p preocciptal lobe. This size range suggests that these specimens ranged from early holaspids to gerontic specimens well past their terminal molt. Of the 383 Flexicalymene specimens collected from the Bevis, Ohio, location, 313 were not deformed, and their 1p widths could accurately be measured. These ranged from 2 to 14 mm, and all are holaspids (Fig. 3).

The community of commensal episkeletozoans consisted of three trepostome bryozoan genera, three brachiopod species, one annelid species, and a tube-dwelling/boring organism. Nine of the Flexicalymene specimens were fouled by a total of 50 trepostome bryozoan colonies (Table 2) belonging to Parvohallopora sp. Singh, 1979 (40 colonies), Amplexopora sp. Ulrich, 1882 (6 colonies), and Heterotrypa sp. Nicholson, 1879 (4 colonies). More bryozoans occurred on carcasses than exuviae but the differences are not significant because of the small number of fouled exuviae (t-test, P = 0.167). By contrast, more brachiopods occurred on exuviae than
carcasses but the differences are not significant (t-test, $P = 0.422$).

Two *Flexicalymene* exoskeletons were encrusted with a total of six specimens of the inarticulate brachiopods *Schizocrania filosa* Hall, 1847 and *Petrocrania scabiosa* (Hall, 1868; Table 2). One *Flexicalymene* was colonized by at least 124 individuals of the articulate brachiopod *Zygospira modesta* (Say in Hall, 1847). Five *Flexicalymene* specimens were encrusted with 22 calcareous *Corulites corrugatus* (Hall, 1888) annelid tubes. More *C. corrugatus* occurred on carcasses than exuviae but the differences are not significant because of the small number of fouled exuviae (t-test, $P = 0.111$).

On average there were more brachiopods (mean = 8.1 per fouled host) than bryozoans (mean = 3.1) or worm tubes (mean = 1.3). These numbers are skewed by one exuvium that was fouled by 124 brachiopods. Excluding all the exuviae (i.e., using the remaining 13 carcasses), there were more bryozoans per host (mean = 3.8) than worm tubes (mean = 1.5) or brachiopods (mean = 0.4). On average bryozoans covered more of their hosts’ dorsal surface area (mean = 38.7 mm$^2$) than worm tubes (mean = 1.24 mm$^2$) or brachiopods (mean = 0.92 mm$^2$). The cumulative percent of the host carcass’ dorsal surface area that was covered by all epizoozoans ranged from 0.1% to 39.1% (mean = 8%). Overall, the amount of surface area of hosts that were covered by epizoozoans was positively and significantly correlated with the 1p preoccipital lobe width ($R^2 = 0.014$, $P = 0.035$). This suggests that larger fouled trilobites provided more area for the epizoozoans to grow.

Sizes (as measured by both 1p preoccipital lobe width and dorsal surface area) of fouled carcasses and exuviae are not significantly different (t-tests, $P > 0.05$). Therefore any differences in the prevalence of fouling of carcasses and exuviae are not a function of different size targets for larval settlement.

We excluded exuviae from the following analyses because the shed molts may represent older substrates that were fouled by larvae at various times. The carcasses were more likely to be fouled while the hosts were alive. The carcasses of fouled hosts were significantly larger (mean 1p width = 10.25 mm) than the non-fouled carcasses (mean = 6.75 mm; t-test, $P = 0.043$), indicating that the larger trilobites were more likely to be fouled by settling larvae. This is expected because larger trilobites molted less frequently than smaller (i.e., younger) trilobites (Hunt, 1967; Chatterton et al., 1994; Clarkson et al., 2003). Also, larger trilobites provided larger targets for settling larvae.

The prevalence of epipoozoans and episkeletozoans fouling *Flexicalymene* varied between collection localities from 0.02% to 50% (Table 1). We suggest that encrustation frequencies of less than 2% reflect the normal rate of fouling for *Flexicalymene* in the Late Ordovician. Frequencies greater than 2% are most likely due to sampling bias resulting from small samples. The *Heterotrypa* sp. and *Amplexopora* sp. epipoozoans fouling *Flexicalymene retrorsa retrorsa* specimens collected from two Ohio localities (Mt. Orab and Bevis) contain numerous cylindrical tubes or borings incorporated in the bryozoan colonies (Fig. 4). The tubes/borings are oriented perpendicularly to the surface of the colony, and range in diameter from 0.2 to 0.8 mm. The bryozoan zooids parallel the tube/boring boundaries. Some tube/boring openings are surrounded by zooids forming an elevated ring around each tube/boring. The elevated rims suggest the bryozoan was still alive when the tube/boring formed. If so, this is an example of a bioclaustration (Tapanila, 2005). The borings without the elevated rims are similar to the trace fossil *Sanctum* sp. Erickson and Bouchard, 2003 (Wyse Jackson and Key, 2007). Identification of the exact trace fossil is not certain as thin sections of the bryozoan colony was not possible. If it is *Sanctum* sp., this is the first reported fossil occurrence of a sessile organism (*Heterotrypa* sp.) encrusting a live motile host (*Flexicalymene*) that itself is bored by a presumed filter feeding polychaete, the probable tracemaker of *Sanctum* sp. (Wyse Jackson and Key, 2007).

The Mt. Orab *Heterotrypa* sp. colony (Fig. 4.1, 4.2) incorporated 25 tubes/borings concentrated on the elevated portion of the colony encrusting the cranidium of one *Flexicalymene retrorsa retrorsa* specimen and the upper part of the single branch of the bryozoan colony. The *Amplexopora* sp. colony from Bevis (Fig. 4.3) incorporated five tubes/borings along the anterior margin of the doublure. The tubes/borings point forward, not upward, as observed in the Mt. Orab *Heterotrypa* sp. colony.

Epipoozoans and episkeletozoans are not randomly distributed on the 16 fouled *Flexicalymene* specimens, but...
preferentially encrust the elevated regions of the exoskeleton. On the 13 carcasses, 55 (65%) of the epizoans encrusted the glabella, fixigenae adjacent to the glabellar furrow, occipital ring, eye ridges, axial rings, fulcra of the pleurae, and axial rings of the pygidium (Table 3; Figs. 5, 6). Sixteen (19%) epizoans were attached to the anterior margin of the cephalon and doublure. The remaining 13 (15%) epizoans were preserved fouling the librigena, pleural field, distal portions of individual pleura, or the axial furrows (Table 3; Fig. 7).

The three inferred exuviae of *Flexicalymene* display a pattern of episkeletozoan fouling similar to that on the carcasses. Ninety one (72%) episkeletozoans encrusted the elevated regions of the glabella, fixigenae adjacent to the lateral glabellar furrows, axial rings, and fulcra of the pleurae (Table 3; Figs. 5, 6). Thirty five (28%) episkeletozoans were preserved attached to the lower regions of the librigena, pleural fields, or within the axial furrows (Table 3; Figs. 8, 9).

*Parvohallopora* sp. and *C. corrugatus* display preferred alignment of individual colony branches or individual tube apertures. One *Flexicalymene retrorsa retrorsa* specimen (Fig. 6) has five parallel, aligned *Parvohallopora* sp. colonies. The colonies are centered on the eye ridges, the glabella, and either side of the doublure. The colony branches did not grow vertically from the cephalon, but instead grew more or less horizontally beyond the anterior margin of the cephalon (Fig. 6.1, 6.2).

One *Flexicalymene meeki* specimen (Fig. 5) contains 30 *Parvohallopora* sp. colonies of which 28 (90%) occur on the elevated regions of the glabella, eye ridges, pleural fulcra and fields, and axial rings immediately adjacent to the glabellar, axial, and pleural furrows. On the pleurae, each colony grew along the axis of a pleuron but did not extend to the neighboring pleuron. Fourteen (45%) of these colonies contain 1–3 mm long branches that grew laterally at angles ranging from 30° to 45° above horizontal. Branches of all 14 colonies are aligned parallel to the axis of each pleuron, each occipital or axial ring, or the posterior margin of the cephalon. They also extend laterally into the area above the glabellar, axial, and pleural furrows or from the pleural fulcra toward a lateral margin of the specimen.

The tubes of *C. corrugatus* display a variety of orientations at their initial attachment site on the cephalons of the five fouled *Flexicalymene* specimens. Fourteen (70%) of 20 specimens bend so that the aperture opens posteriorly and parallel to the sagittal axis (Fig. 7). Five (25%) specimens are oriented with the aperture opening anteriorly, and one (5%) is oriented with the aperture oriented perpendicularly to the sagittal axis.

**DISCUSSION AND CONCLUSIONS**

The diversity of marine hard substrate encrusters on *Flexicalymene* is somewhat less than the hard substrate community encrusting sessile epifaunal organisms of the Cincinnati sea floor. Previous studies of Cincinnati fossils have documented that sessile epifaunal organisms were fouled by articulate and inarticulate brachiopods, trepostome bryozoans, cornulitids, rugose and tabulate corals, crinoids, edrioasteroids, and stromatoporoids (Richards, 1972; Alexander and Scharpf, 1990; Meyer, 1990). Motile Cincinnati organisms interpreted as having been fouled by encrusting and ramose bryozoans and cornulitids while living include cephalopods, gastropods, monoplacophorans, and trilobites (Morris and Rollins, 1971; Baird et al., 1989; Morris and Felton, 1993; Brandt, 1996). Our investigations add inarticulate and articulate brachiopods and an undetermined tube-dwelling/boring organism, probably *Sanctum* sp., to the hard substrate community living on Late Ordovician *Flexicalymene*.

Why are epizoans so rare on trilobites in general and on *Flexicalymene* in particular? Brandt (1996), who previously reported a 0.4% prevalence of encrustation from a large museum collection of *Flexicalymene* specimens, concluded that the low prevalence of fouling is a function of opportunistic larval settlement, preservational bias resulting from the loss of nonbiomineralized epizoans, and a semi-infaunal, shallow burrowing lifestyle of *Flexicalymene*. Studies of antifouling mechanisms in modern crabs have shown that burrowing plays the largest role in antifouling (e.g., Becker and Wahl, 1996). Shallow burrowing by *Flexicalymene* no doubt limited the amount of area of the dorsal exoskeleton available for larval settling, in part because of the scouring action of sediment (Smith and Nelson, 2003).
Conceivably, the low prevalence of fouling of *Flexicalymene* by bryozoans, brachiopods, and annelid worms reflects a larval preference for, or a greater opportunity to settle on, other substrates. Larvae are known to respond to various aspects of substrates including mechanical properties (e.g., Gray et al., 2002) and/or the presence of microbial biofilms (e.g., Kitamura and Hirayama, 1987). The larval settlement on these trilobites may have been purely accidental and phoretic (i.e., hitchhiking). A low intensity of fouling has been found with bryozoans on extant sea snakes (0.8%: Key et al., 1995).

### Table 3—Number and spatial distribution of episkeletozoans on dorsal surfaces of *Flexicalymene* exoskeletons.

<table>
<thead>
<tr>
<th>Episkeletozoan</th>
<th><em>Flexicalymene</em> specimen number</th>
<th>Topographically elevated regions of carapace</th>
<th>Topographically depressed regions of carapace</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Cephalon</td>
<td>Thorax</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Glabella</td>
<td>Fixigena</td>
</tr>
<tr>
<td><em>Amplexopora, Heterotrypa, and Parvohallopora</em></td>
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<td>1</td>
<td>1</td>
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<tr>
<td></td>
<td>OSU 53687</td>
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<tr>
<td></td>
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</tr>
<tr>
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<td>OSU 53699</td>
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<tr>
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<td><em>Cornulites corrugatus</em></td>
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<td><em>Schizocrania filiosa and Petrocrania scabiosa</em></td>
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<td></td>
<td>OSU 53691</td>
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<td>0</td>
</tr>
<tr>
<td>Sum:</td>
<td>OSU 53685</td>
<td>13</td>
<td>5</td>
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</table>

*a* colony covers most of cephalon, *b* colony extends onto doublure, *c* aperture facing anterior, *d* aperture facing posterior, *e* aperture facing perpendicular to host's sagittal axis.
but most bryozoan fouling rates are higher on extant arthropods such as blue crabs (16%: Key et al., 1999), isopods (42%: Key and Barnes, 1999), and horseshoe crabs (57–77%: Key et al., 1996a, 1996b, 2000). Studies by Richards (1972), Alexander and Scharpf (1990), and Meyer (1990) show that in the Cincinnatian, encrusters colonized any available hard substratum whether pebbles or cobbles, motile or sessile organisms, or living or dead hosts. If so, larval settlement on Flexicalymene was probably greatly influenced by exposure of its exoskeleton above the sediment water interface and chemical signaling. As a motile, burrowing animal, exoskeletons of Flexicalymene may have been only intermittently available for larval settlement.

Is the low prevalence of fouling of Flexicalymene related to frequent molting? With a sample size of roughly 15,000 in all holaspisid size ranges showing low rates of encrustation, this possibility can largely be ruled out.

There is a possibility that the low prevalence of fouling is an observational bias. Lescinsky (1996) noted that epiceteletozoans are commonly overlooked because of small size or because of removal along with matrix adhering to fossil specimens during preparation. Waugh et al. (2004) stated that epiceteletozoans can go unreported in taxonomic studies because the presence of epiceteletozoans seems irrelevant to those studying the hosts. Observational bias may have contributed to the apparent low prevalence of fouling among Flexicalymene specimens collected from Mt. Orab, Ohio, as these specimens were inspected only with the naked eye and not thoroughly examined under a binocular microscope. Some tiny epiceteletozoans were undoubtedly overlooked.

Preservational bias is another possible cause of the apparent low prevalence of fouling. Some epiceteletozoans were almost certainly lost from Flexicalymene specimens as they weathered from the soft Cincinnatian shales. Further taphonomic bias could result from the degradation of Flexicalymene epicutele, something that has been observed in fossil decapods (Waugh et al., 2004). Dalingwater et al. (1993) argued that the thin, outermost layer of trilobite exoskeleton was an epicutele similar to that of decapods. Low prevalence of fouling observed in Flexicalymene may reflect the loss of the epicutele along with its epiceteletozoans before fossilization.
Epibionts can serve to camouflage animals. Vance (1978) reported predation rates by starfish on clams were reduced when the clams were covered by bryozoans. It could be speculated that epizoozoans camouflaged *Flexicalymene* individuals from their predators, or alternatively from their prey. The low percentage of the hosts’ dorsal surface area covered by epizoozoans in this study (mean = 8%) and the low incidence of epizoozoan encrustation, however, suggests this benefit did not accrue to *Flexicalymene*. Another more speculative idea is that *Flexicalymene* harbored microbial symbionts that tended to discourage larval settlement. This is essentially untestable from fossil material however.

Successful larval settlement on Cincinnati *Flexicalymene* shows a clear preferred pattern. Brandt (1996) observed that epizoozoans and episkeletozoans consistently fouled the elevated central regions of the dorsal exoskeleton and the anterior cephalic margin. Our results are consistent with those of Brandt (1996). Epizoozoans and episkeletozoans on
Flexicalymene preferred the elevated portions of the exoskeleton or the anterior cephalic margin. On Flexicalymene carcasses, 81% of the epizoans were preserved attached either to the elevated regions of the glabella, fixigenae, occipital rings, eye ridges, axial rings, and fulcra of individual pleura, or the anterior margin of the librigena, fixigenae, and doublure. On Flexicalymene exuviae, 77% of episkeletozoans were preserved attached either to the elevated areas of the glabella, fixigenae, axial rings, pleura fulcra, or the anterior regions of the librigena. The fouling pattern is similar on both carcasses and exuviae of Flexicalymene, suggesting that the exuviae were not subject to extensive additional colonization by episkeletozoans prior to burial and preservation.

Did epizoans fouling Flexicalymene preferentially align or colonize preferred areas of the exoskeleton to take advantage of currents created by locomotion or other life activities of the host? Previous studies of Morris and Rollins (1971), Baird et al. (1989), Morris and Felton (1993), and Galle and Parsley (1995) concluded that aligned epizoans preserved on motile cephalopods, tergomyans, gastropods, and hyolithids displayed preferential orientation to take advantage of the movement or feeding currents generated by the hosts.
Flexicalymene classically has been interpreted as having a benthic, semi-infaunal suspension feeder habit. This trilobite is presumed to have excavated shallow concave burrows that were used as filter chambers under the dorsal exoskeleton (Osgood, 1970; Seilacher, 1985; Brandt, 1996). If true, the epizoans on Flexicalymene were possibly oriented to take advantage of feeding currents generated by the trilobite (Brandt, 1996). Examination of Rusophyus pudicum Hall, 1852 trace fossils, which were constructed by Cincinnatian Flexicalymene, however, has revealed that the trilobite-constructed traces often truncate traces left by infaunal worms. This suggests the Flexicalymene was an active nektobenthic swimmer and burrower. Preferential disposition of epizoans therefore likely reflects sites on the trilobite exoskeleton that were inflexible or weakly flexible. This same pattern is seen among epizoans on a variety of extant hosts (Kny et al., 1995, 1996a, 1996b, 1997). Apertures and commissures of the encrusters may have aligned to either take advantage of currents generated while the host swam, or to help prevent fouling by sediment while the host dug into the substrate.

Nascimento and Alexander (1994), who conducted flume analyses on a model of Calyme ne celeb ro Raymond, 1916, discovered that at water velocities exceeding 8 to 10 cm/sec, turbulent flow was distinctly visible across the glabellar furrows and behind the occipital ring and pygidium. If we assume that similar turbulent water flows would have occurred across the exterior exoskeleton of Flexicalymene, then most epizoans would have preferred locations on the elevated areas adjacent to the zones of turbulent flow. Many animals minimize the energy required to feed by taking advantage of natural turbulent flow created by obstructions hindering water currents (Vogel, 1981). Thus, organisms would preferentially gather to take advantage of food suspended in the water column by eddies created downstream from the obstructions. It is possible that epizoans observed in our study preferentially settled in areas within or adjacent to turbulent water flows across the Flexicalymene exoskeleton to take advantage of food laden eddies. Regardless, the parameters of the flume study under represent the complexities of the life habit of Flexicalymene as inferred from trace fossils.

Were older adult specimens of Flexicalymene nearing or beyond the terminal molt stage subject to increased fouling as opposed to younger individuals? Kloc (1997) observed that epizoans fouling the trilobite Dicranurus hamatus elegantus were on specimens of different growth stages. Brandt (1996) reported that only large specimens of Flexicalymene, interpreted as older adults nearing the terminal molt stage, were fouled by epizoans and episkeltozoon. Our results indicate that fouling probably occurred throughout most of the holaspis period of Flexicalymene because we observed a range from 6 to 13 mm for the width of the preoccipital lobes of the fouled hosts. Brandt (1996) reported the preoccpital lobe widths to range from 10 to 13 mm among the eight specimens of Flexicalymene that she measured. Together, the results of Brandt (1996) and those reported here indicate that larger, although not necessarily gerontic, trilobites are more likely to be fouled by settling larvae. We interpret this as partly a reflection of the fact that larger trilobites provide larger targets for settling larvae and partly because trilobite size is proportional to molting frequency. Larger, older trilobites probably molted less frequently than smaller, younger trilobites (Hunt, 1967; Chatterton et al., 1994; Clarkson et al., 2003).

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