

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

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ABSTRACT—Commensal epizoozoans 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 epizoozoans 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 weathers 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.

Epizoozoans 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, foraminiferans, hydrozoans, 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 Biodiversification 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 epizoozoan, 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 episkeletozoan-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 epizoozoans.

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 Šaric, 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 Šaric'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 nonbiomineralized 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 *Arctinurus boltoni* (Bigsby, 1825) supported *Cornulites* sp. Schlothheim, 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 *Arctinurus* 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 epizoozoans.

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 epizoozoans 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 epizoozoan biotic interactions; 4) document preferred larval settling and alignment of epizoozoans; 5) discuss the feeding habits of epizoozoans 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 epizoozoans 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 epizoozoans. 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 (Ferree, 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 Cincinnati 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 1p 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 cephalae; displaced, disarticulated,

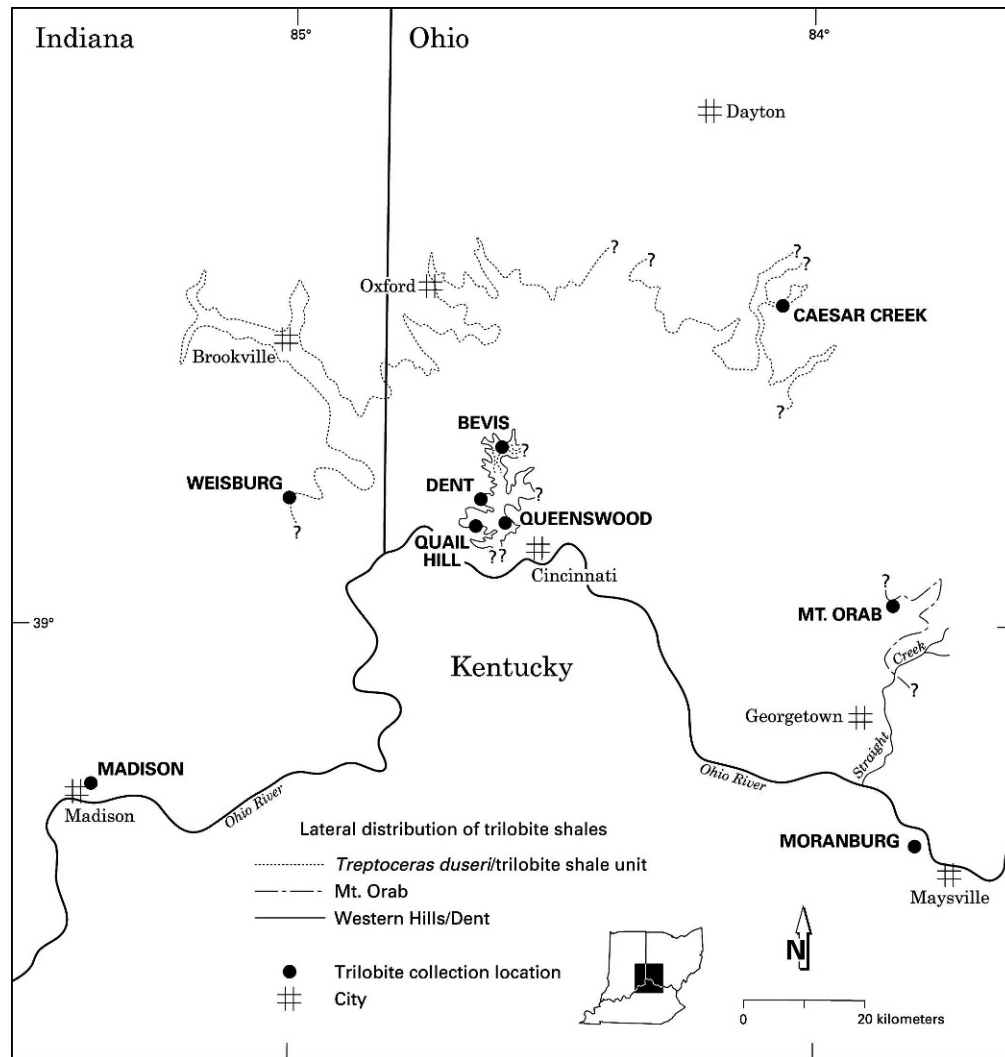


FIGURE 1—Locations of studied *Flexicalymene* Shirley, 1936 trilobites and outcrop pattern of trilobite shale beds from Upper Ordovician rocks of southwestern Ohio, southeastern Indiana, and northern Kentucky. The lateral distribution of the Madison trilobite shale bed is unknown. The Moranburg trilobite shale bed has been traced for 0.5 km.

telescoped, or unevenly spaced thoracic segments; or rotated pygidia or cephalae.

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 repositied 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 Cincinnati 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 Cincinnati 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 Cincinnati shales and limestones. However, the frequency of articulated *Flexicalymene* specimens is generally low in most stratigraphic intervals. So called

SERIES	STAGE	SEQUENCE	LITHOSTRATIGRAPHY				TRILOBITE SHALES (Number of <i>Flexicalymene</i> specimens with episkeletozoans collected from each shale)
			INDIANA Brown and Lineback (1966)	OHIO modified from Schumacher et al. (1991)		KENTUCKY Peck (1966)	
				Cincinnati/Oxford Region	Georgetown/ Maysville Region		
CINCIANNATIAN	RICHMONDIAN	C6	Whitewater Fm Saluda Fm	Drakes Fm	Drakes Fm	Bull Fork Fm	← <i>Treptoceras duseri</i> and trilobite shale unit (8) ← Madison (1) ← Mt. Orab (3) ← Dent (1) ← Western Hills (2) ← Moranburg (1)
		C5		Whitewater Fm	White- water Fm		
				Liberty Fm	Liberty Fm		
				Waynesville Fm	Waynesville Fm		
		C4		Dillsboro Fm	Arnheim fm		
	C3	Grant Lake Fm	Mount Auburn Mbr		Straight Creek Mbr	Grant Lake Ls	
			Corryville Mbr				
		Miami- town Sh	Bellevue Mbr				
	C2	Fairview Fm	Fairview Fm		Fairview Fm		
	EDENIAN	C1	Kope Fm	Kope Fm	Kope Fm	Kope Fm	

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.

“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, butterflyed 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 Cincinnati trilobite shale beds.

Number of <i>Flexicalymene</i> specimens examined	Number of fouled <i>Flexicalymene</i> specimens	Prevalence (%)	Trilobite shale bed	Location	Reference
2,030	8	0.39	Multiple beds	Cincinnati, OH region	Brandt (1996)
~14,500	3	0.02	Mt. Orab	Georgetown, OH	This study
383	5	1.3	<i>Treptoceras duseri</i>	Bevis, OH	This study
37	2	5.4	<i>Treptoceras duseri</i>	Caesar Creek, OH	This study
12	1	8.3	Madison	Madison, IN	This study
11	1	9.1	Western Hills	Queenswood Road, OH	This study
6	1	17	Western Hills	Quail Hill Road, OH	This study
4	1	25	Dent	Dent, OH	This study
3	1	33	Moranburg	Maysville, KY	This study
2	1	50	<i>Treptoceras duseri</i>	Weisburg, IN	This study
~14,958	16	0.11		Total this study	

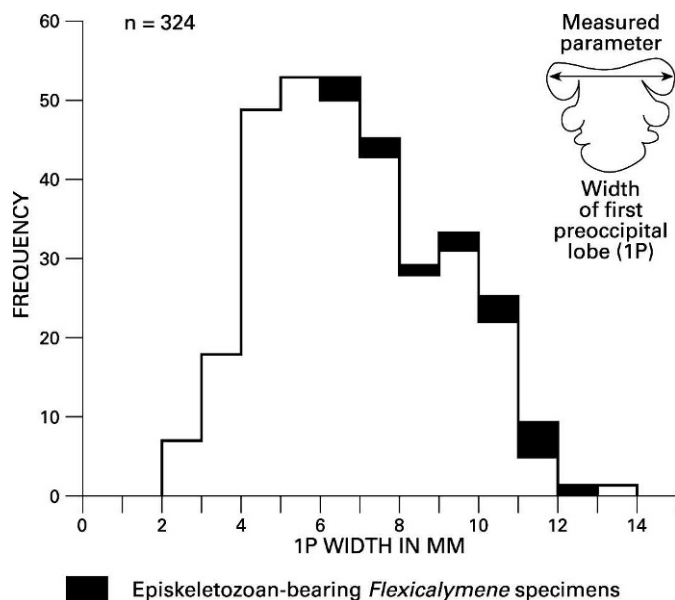


FIGURE 3—Size-frequency histogram of the *Flexicalymene* Shirley, 1936 population collected from the *Treptoceras duseri* shale exposed at Bevis, Ohio, compared to the size-frequency of the 16 fouled *Flexicalymene* specimens.

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 Cincinnati (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 cephalae ranging from 6.61 to 12.90 mm (mean = 9.50 mm) across the width of the 1p preoccipital 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

TABLE 2—Enrollment attitude, fossil type, and size information for the 16 fouled specimens of *Flexicalymene* and their episkeletozoans.

<i>Flexicalymene</i> specimen number	Enrollment attitude	Fossil type	1p width (mm)	Projected or measured dorsal surface area of host carapace (mm ²)	Number of bryozoan colonies	Total surface area of all bryozoan colonies (mm ²)	Maximum bryozoan colony height (mm) above host carapace
OSU 53684	enrolled	carcass	9.10	491	10	82.47	4
OSU 53685	prone	carcass	9.93	607	0		
OSU 53686	semi-enrolled	exuvia	11.34	612	0		
OSU 53687	enrolled	carcass	11.50	621	3	109.61	2
OSU 53688	prone	carcass	7.50	405	1	158.42	7
OSU 53689	prone	carcass	8.35	460	0		
OSU 53690	prone	exuvia	6.61	309	0		
OSU 53691	enrolled	carcass	6.76	365	0		
OSU 53692	enrolled	carcass	6.64	359	0		
OSU 53693	enrolled	carcass	10.44	564	0		
OSU 53694	enrolled	carcass	7.50	405	2	19.48	1
OSU 53695	enrolled	carcass	10.95	591	1	47.47	2
OSU 53696	enrolled	carcass	9.90	535	1	7.54	1
OSU 53697	semi-enrolled	exuvia	11.11	600	1	18.93	1
OSU 53698	enrolled	carcass	12.90	697	1	23.07	1
OSU 53699	prone	carcass	11.50	621	30	55.35	2
Mean:			9.50	515	3.1	58.0	
Sum:				8242	50	522	
Minimum:			6.61	309	0	7.54	
Maximum:			12.90	697	30	158.42	
Standard deviation:			2.04	117	7.6	50.30	

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 *Cornulites 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 mm²) than worm tubes (mean = 1.24 mm²) or brachiopods (mean = 0.92 mm²). 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 simply 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 epizoozoans 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. epizoozoans 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 bioclastration (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 sectioning 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.

Epizoozoans and episkeletozoans are not randomly distributed on the 16 fouled *Flexicalymene* specimens, but

TABLE 2—Extended.

Bryozoan genus	Number of brachiopods	Total surface area of all brachiopods (mm ²)	Number of <i>Cornulites</i>	Total surface area of all <i>Cornulites</i> (mm ²)	Total number of episkeletozoans	Total surface area of all episkeletozoans (mm ²)	% of dorsal surface area of host carapace covered by episkeletozoans
<i>Parvohallopore</i>	0		0		10	82.47	16.8
	0		1	2.46	1	2.46	0.4
	1	29.65	0		1	29.65	4.8
<i>Heterotrypa</i>	0		0		3	109.61	17.7
<i>Heterotrypa</i>	0		0		1	158.42	39.1
	0		11	9.55	11	9.55	2.1
	124	34.23	0		124	34.23	11.1
	5	11.93	0		5	11.93	3.3
	0		1	0.26	1	0.26	0.1
	0		8	0.72	8	0.72	0.1
<i>Amplexopora</i>	0		0		2	19.48	4.8
<i>Amplexopora</i>	0		0		1	47.47	8.0
<i>Amplexopora?</i>	0		0		1	7.54	1.4
<i>Amplexopora</i>	0		0		1	18.93	3.2
<i>Amplexopora</i>	0		1	1.94	2	25.01	3.6
<i>Parvohallopore</i>	0		0		30	55.35	8.9
	8.1	25.27	1.4	2.99	12.6	38.32	7.8
	130	75.81	22	14.9	202	613	
	0	11.93	0	0.26	1	0.26	0.1
	124	34.23	11	9.55	124	158.42	39.1
	30.9	11.8	3.2	3.78	30.6	44.3	10.0

preferentially encrust the elevated regions of the exoskeleton. On the 13 carcasses, 55 (65%) of the epizoozoans 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%) epizoozoans were attached to the anterior margin of the cephalon and doublure. The remaining 13 (15%) epizoozoans 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).

Parvohallopore 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 *Parvohallopore* 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 *Parvohallopore* 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 investigation adds 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 epizoozoans 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 epizoozoans, 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).

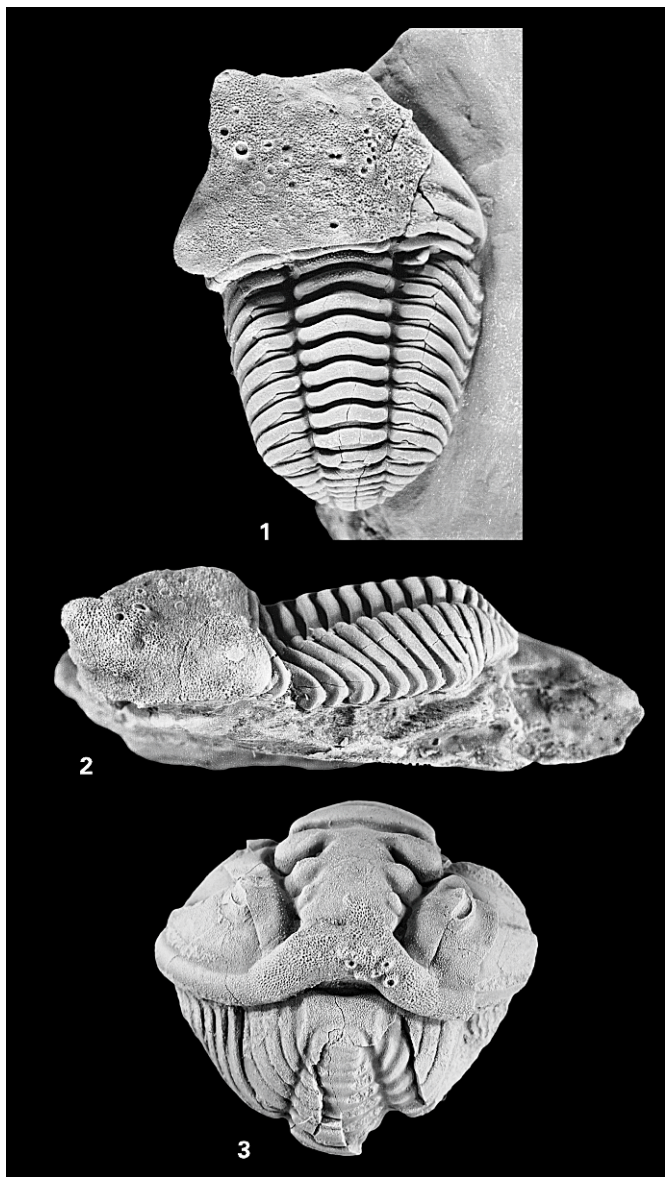


FIGURE 4—1–3, *Flexicalymene retrorsa retrorsa* (Foerste, 1910) fouled by *Heterotrypa* sp. Nicholson, 1879 and *Amplexopora* sp. Ulrich, 1882 bryozoan colonies containing tube-dwelling/boring nonbiomineralized organisms including *Sanctum* sp. Erickson and Bouchard, 2003; 1, *F. retrorsa retrorsa*, OSU 53688 from Mt. Orab trilobite shale bed exposed near Georgetown, Ohio, fouled with *Heterotrypa* sp. bryozoan colony covering ~80% of the cephalon and containing 25 vertical tubes/borings, dorsal view, 1p width: 7.50 mm; 2, OSU 53688, tube-dwelling/boring organisms are restricted to the elevated portions of the colony, lateral view, 1p width: 7.50 mm; 3, *F. retrorsa retrorsa*, OSU 53695 from the *Treptoceras dusevi* shale exposed at Bevis, Ohio, encrusted along the anterior margin by an *Amplexopora* sp. bryozoan colony and five, anteriorly directed, horizontally oriented tubes/borings, anterior view, 1p width: 10.95 mm.

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.

Episkeletozoan	<i>Flexicalymene</i> specimen number	Topographically elevated regions of carapace						Topographically depressed regions of carapace														
		Cephalon	Thorax	Pygidium	Anterior margin	Cephalon	Thorax	Pygidium	Anterior margin	Cephalon	Thorax	Pygidium										
		Occipital ring	Eye ridges	Axial rings	Pleura fulcra	Axial rings	Librigena	Doubleure	Axial furrows	Pleura	Pleura field	Occipital ring	Eye ridges	Axial rings	Pleura fulcra	Axial rings	Librigena	Doubleure	Axial furrows	Pleura	Pleura field	
<i>Amplexopora, Heterotrypa, and Parvothalporea</i>	OSU 53684	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
	OSU 53687	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53688	1 ^a	0	0	0	0	0	1 ^a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53694	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53695	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53696	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53697	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53698	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53699	3	1	1	8	9	3	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	Sum:	10	3	5	8	9	3	4	0	6	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coronulites corrugatus</i>	OSU 53685	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53689	3 ^d	3 ^d	0	1 ^e	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53692	1 ^d	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53693	2 ^d , 1 ^c	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53698	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sum:	9	1	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Schizocerania filiosa and Petrocrania scabiosa</i>	OSU 53686	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	OSU 53691	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sum:	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Zygospira modesta</i>	OSU 53690	13	0	27	44	0	7	0	0	0	0	0	0	0	0	0	0	0	25	3	0	0
	Grand total:	33	8	35	54	3	11	2	28	4	3	0	0	0	0	0	0	0	28	4	3	0

^a colony covers most of cephalon. ^b colony extends onto doubleure. ^c aperture facing anterior. ^d aperture facing posterior. ^e aperture facing perpendicular to host's sagittal axis.

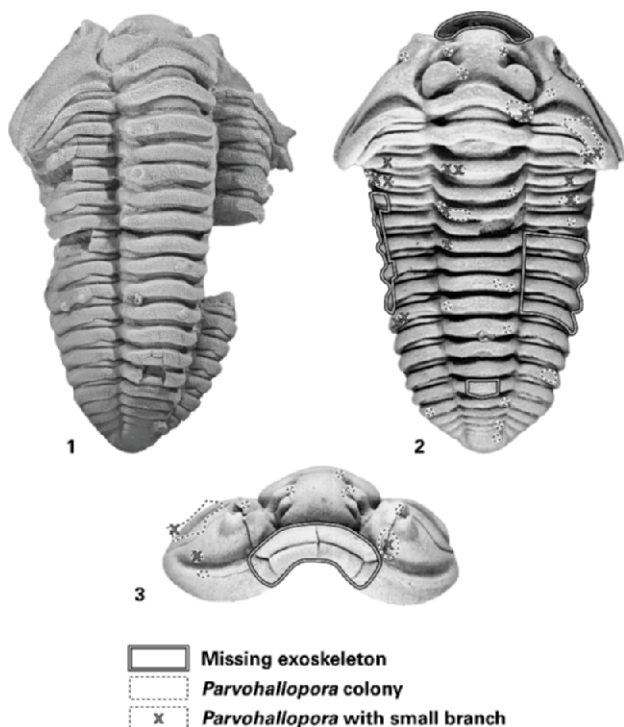


FIGURE 5—1–3, *Flexicalymene meeki* (Foerste, 1910), OSU 53699 from the Moranburg trilobite shale bed exposed at Maysville, Kentucky fouled with juvenile *Parvohallopora* sp. Singh, 1979 bryozoan colonies; 1, *Parvohallopora* sp. bryozoan colonies preferentially fouling the cranidium, eye ridges, axial rings, and pleural fulcra adjacent to the axial furrows; Lateral deformation and attitude of the cephalon obscures some of the *Parvohallopora* sp. bryozoan colonies on the right librigena and pleura, dorsal view, 1p width: 11.50 mm; 2, Locations of 28 of 30 *Parvohallopora* sp. bryozoan colonies on the elevated portions of the exoskeleton of OSU 53699 mapped onto a dorsal view of an unfouled specimen of *Flexicalymene* sp. modified from Babcock (2005, fig. 8–1.10); 3, Locations of *Parvohallopora* sp. bryozoan colonies adjacent to the axial furrows of the cephalon of OSU 53699 mapped onto an anterior view of an unfouled specimen of *Flexicalymene* sp. modified from Babcock (2005, fig. 8–1.8).

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 Cincinnati, 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 holaspis 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 episkeletozoans 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 episkeletozoans can go unreported in taxonomic studies because the presence of episkeletozoans seems irrelevant to those studying the hosts. Observational bias may have

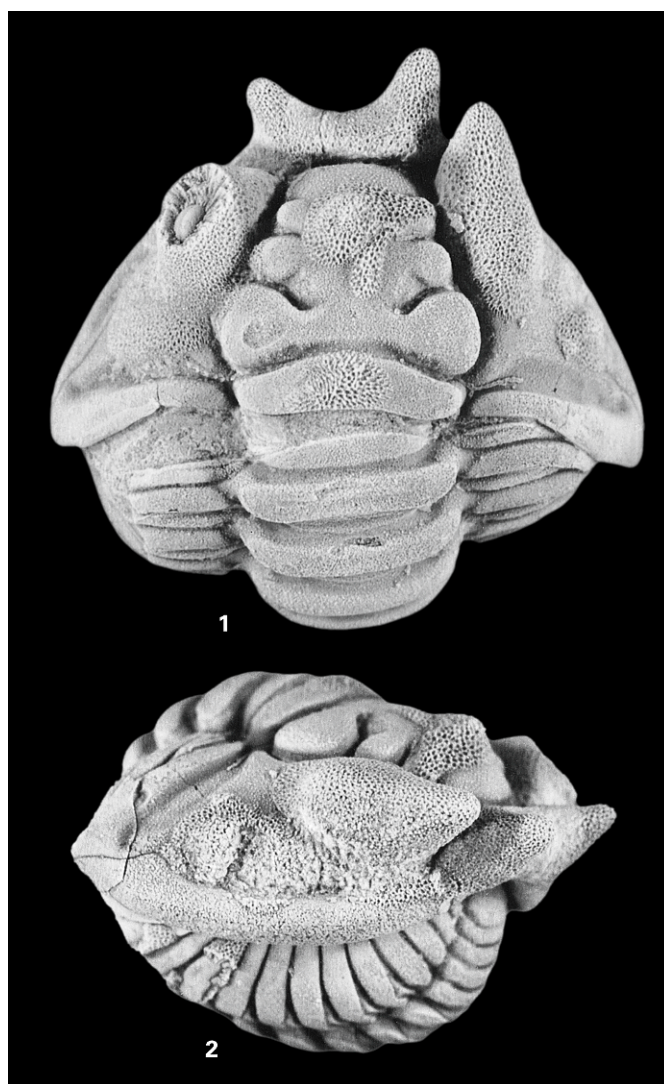


FIGURE 6—1–2, Preferred alignment of *Parvohallopora* sp. Singh, 1979 bryozoan colonies on *Flexicalymene retrorsa retrorsa* (Foerste, 1910), OSU 53684 from the *Treptoceras duseri* shale exposed at Caesar Creek, Ohio, 1p width: 9.10 mm; 1, alignment of *Parvohallopora* sp. bryozoan colonies originating from the glabella, occipital ring, eye ridges, anterior margin and paralleling the axial furrows, dorsal view; 2, anterior growth of *Parvohallopora* sp. bryozoan branches extending beyond anterior margin and parallel one another, lateral view.

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 episkeletozoans were undoubtedly overlooked.

Preservational bias is another possible cause of the apparent low prevalence of fouling. Some episkeletozoans were almost certainly lost from *Flexicalymene* specimens as they weathered from the soft Cincinnati shales. Further taphonomic bias could result from the degradation of *Flexicalymene* epicuticle, 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 epicuticle similar to that of decapods. Low prevalence of fouling observed in *Flexicalymene* may reflect the loss of the epicuticle along with its episkeletozoans before fossilization.

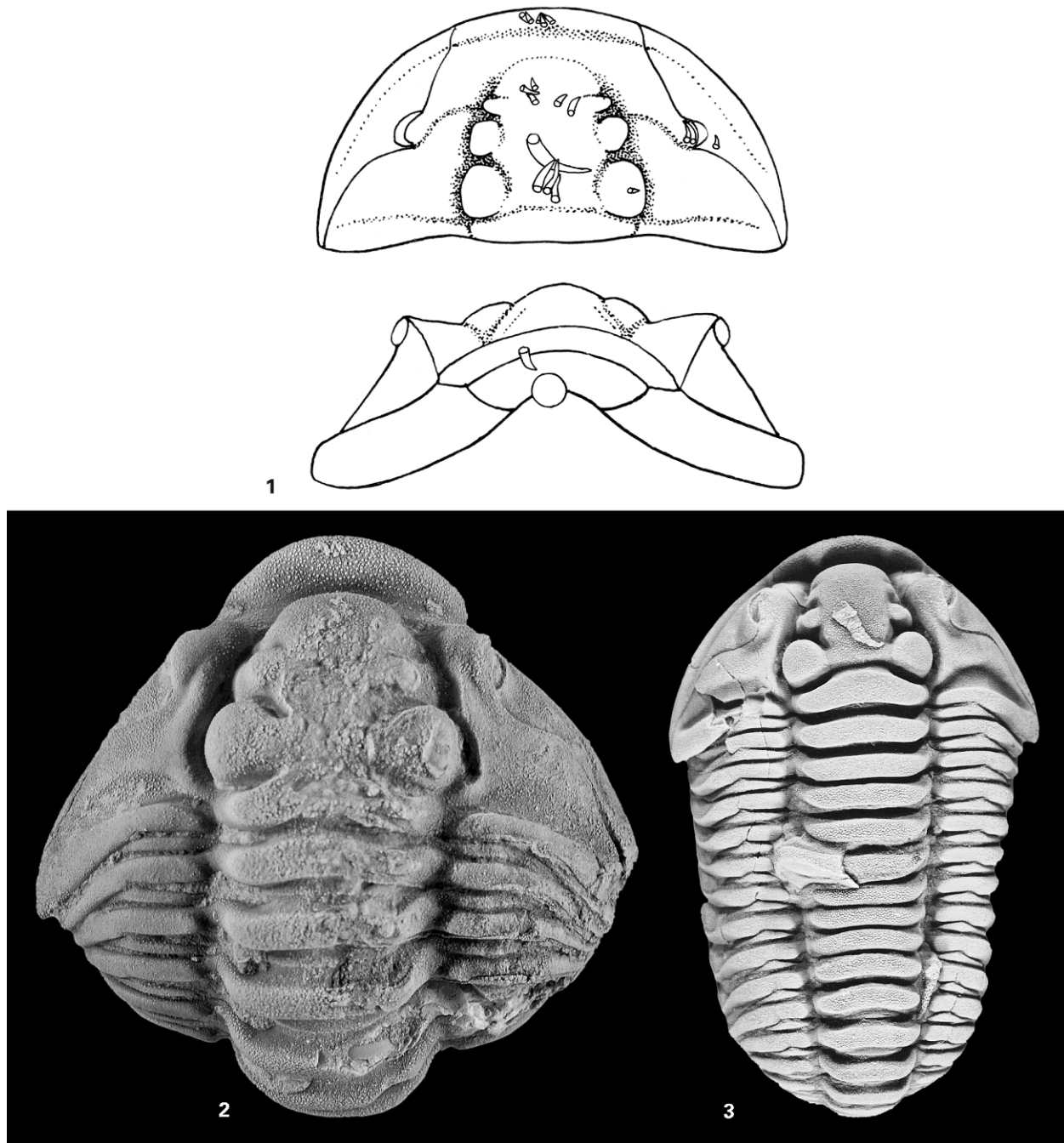


FIGURE 7—1–3, *Cornulites corrugatus* (Hall, 1888) annelid tubes encrusting the cephalon of *Flexicalymene retrorsa retrorsa* (Foerste, 1910). 1, A composite sketch from OSU 53685, OSU 53692, OSU 53693, and OSU 53698 from the Madison trilobite shale bed exposed at Madison, Indiana, and the *Treptoceras duseri* shale exposed at Caesar Creek, Ohio, illustrating a posterior preferred orientation of the apertures of 14 specimens of *C. corrugatus* mapped onto a dorsal and anterior view of an unfouled cephalon of *Flexicalymene* sp. modified from Harrington et al. (1959, fig. 354, 1a and 1c); 2, five smaller *C. corrugatus* with four displaying posteriorly oriented apertures and the fifth an anterior orientation, fouling the anterior margin of an enrolled *F. retrorsa retrorsa*, OSU 53693 from the Dent trilobite shale bed, dorsal view, 1p width: 10.44 mm; 3, larger *C. corrugatus* with anterior aperture fouling *F. retrorsa retrorsa*, OSU 53685, dorsal view, 1p width: 9.93 mm.

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

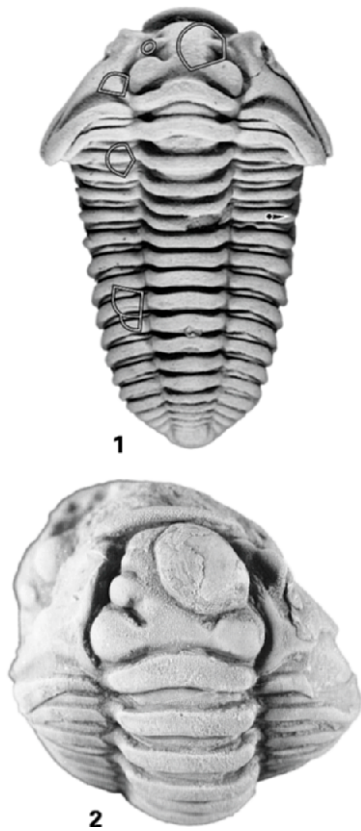


FIGURE 8—1–2, *Schizocrania filosa* Hall, 1847 brachiopods encrusting *Flexicalymene* sp. (Foerste, 1910). 1, A composite sketch from OSU 53686 and OSU 53691 from the *Treptoceras duseri* shale and the Western Hills trilobite shale bed illustrating six *S. filosa* and one *Cornulites corrugatus* (Hall, 1888) encrusting *Flexicalymene* sp. mapped onto a dorsal view of an unfouled specimen of *Flexicalymene* sp. modified from Babcock (2005, fig. 8-1.10), apices of each *S. filosa* specimen are oriented within the axial furrows of *Flexicalymene* sp. and the anterior margin of each valve aligns with the elevated portions of the exoskeleton (i.e., glabella, pleural fulcra, and fixigenae); 2, anterior margin of *S. filosa* oriented along the preglabellar furrow and the central area of the glabella of a semi-enrolled *F. retrorsa retrorsa*, OSU 53686 from the *T. duseri* shale exposed at Caesar Creek, Ohio, dorsal view, 1p width: 11.34 mm.

Flexicalymene preferred the elevated portions of the exoskeleton or the anterior cephalic margin. On *Flexicalymene* carcasses, 81% of the epizoozoans 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 epizoozoans 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 epizoozoans preserved on motile cephalopods, tergomyans, gastropods, and hyolithids displayed preferential orientation to take advantage of the movement or feeding currents generated by the hosts.

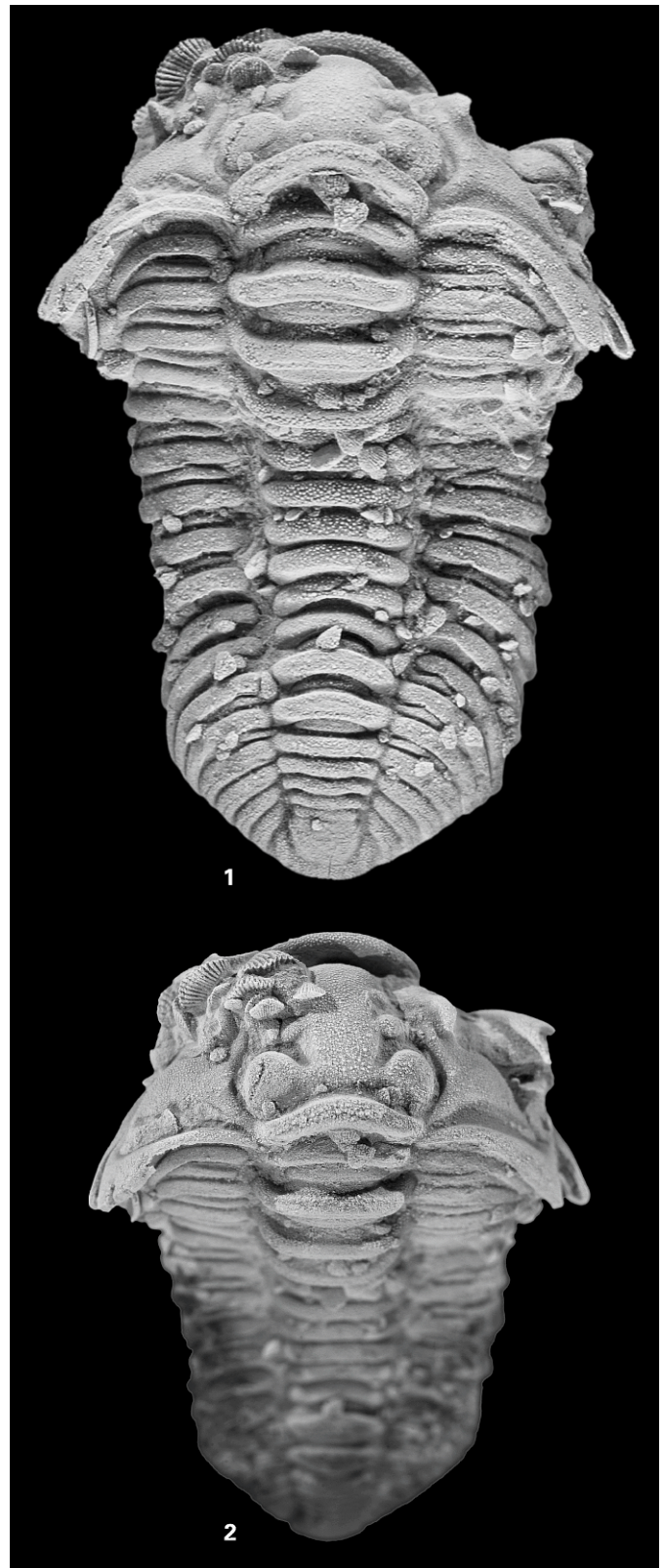


FIGURE 9—1–2, *Zygospira modesta* (Say in Hall, 1847) brachiopods fouling the dorsal exoskeleton of a *Flexicalymene meeki* (Foerste, 1910) exuvium, OSU 53690 from the Western Hills trilobite shale bed exposed at the Queenswood Road location, Ohio, dorsal view, 1p width: 6.61 mm; 1, *Z. modesta* juveniles preserved in life position with pedicle openings adjacent to the *F. meeki* exoskeleton and concentrated along the elevated axial rings and pleura fulcra; 2, cluster of adult *Z. modesta* in life position fouling the anterior margin and adjacent glabellar furrow.

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 epizoozoans on *Flexicalymene* were possibly oriented to take advantage of feeding currents generated by the trilobite (Brandt, 1996). Examination of *Rusophycus 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 carnivore (English and Babcock, 2007), at least in part. An interpretation of a carnivorous life habit, including hunting of infauna, is consistent with phylogenetic evidence, which suggests an affinity of the trilobites among the largely carnivorous arachnomorph arthropods (Fortey and Owens, 1999; Babcock, 2003; English and Babcock, 2007). Not all *Rusophycus pudicum* traces were necessarily hunting or suspension feeding traces, but the abundance of such traces in Cincinnatian strata indicates that *Flexicalymene* was an active nekto-benthic swimmer and burrower. Preferential disposition of epizoozoans therefore likely reflects sites on the trilobite exoskeleton that were inflexible or weakly flexible. This same pattern is seen among epizoozoans on a variety of extant hosts (Key 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 *Calymene celebra* 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 epizoozoans 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 epizoozoans 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 epizoozoans 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 epizoozoans and episkeletozoans. Our results indicate that fouling probably occurred throughout most of the holaspid 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 preoccipital 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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