SUBSTRATE SPECIFIC ASSOCIATIONS OF EPIBIONTS ON MIDDLE DEVONIAN BRACHIOPODS: IMPLICATIONS FOR PALEOECOLOGY

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A detailed study of over 2500 host brachiopods, from the Middle Devonian Hamilton Group of New York State, revealed distinct patterns of epibiont encrustation, that provide insight into taphonomy and paleoautecology of the host brachiopod shells and depositional environments. The concavo-convex orthid, *Tropidoleptus carinatus* (Conrad), as well as strophomenid, and smooth athyrid brachiopods are among the most heavily encrusted. However, terebratulids of nearly identical size and shape are relatively clean of epibionts. This selective distribution strongly suggests that epibionts were discouraged from settling on punctate brachiopods. Brachiopods with small spines and frills were also nearly clean of epibionts, possibly because of entrapment of a mud layer, which made the outer layer of the host inhospitable for larval settling. Concavo-convex taxa reveal high percent coverage and diversity of epibionts on the convex valve, which probably rested on the substrate during the life of brachiopod. This pattern is observed even on brachiopods that were buried with the convex valve downward. This implies complex post-mortem histories involving multiple episodes of reorientation and colonization.

KEY WORDS: Articulate brachiopods, encrusting epibionts, Middle Devonian.

INTRODUCTION

Encrusting epibionts provide extremely valuable tools in paleoecological research (Ager, 1963; Boucot, 1981). Not only are epibionts themselves a significant, if often overlooked, component of marine communites, but also these organisms frequently interact in varied ways with both live and dead host substrates. In the process, they "perform" natural experiments that provide insights about the life habits and/or post-mortem histories of their hosts. Ecological study of recent marine hard substrate communities shows that some epibiontic organisms are extremely sensitive gauges of environmental stresses, such as turbidity and pollution (Osman, 1975). Thus, preserved distribution patterns may permit refinement of paleoenvironmental indicators.

Host specificity by encrusters has been demonstrated in many instances in the fossil record (Spjeldnaes, 1972, 1984; Richards, 1972; Thayer, 1974; Hurst, 1974; Brett, 1978; McNamara, 1978; Sparks *et al.*, 1980; Watkins, 1981; Brett and Cottrell, 1982). Besides studies of substrate specificity of particular epibiont species, numerous epibiont studies have centered on the autecology of host brachiopods (see Ager, 1963; Rudwick, 1970). The types and positions of

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epibionts have been used to determine the life orientation of the hosts. In one study, cryptic bryozoans and *Cornulites* were used to infer the life positions of several species of brachiopods, in some cases corroborating what other workers had inferred to be the life positions of these hosts, and in others suggesting alternative interpretations (Spjeldnaes, 1984).

Middle Devonian marine mudstones and carbonates of the Hamilton Group of New York State are a rich source of extremely well preserved invertebrate fossils, including many epibionts. The Hamilton Group is characterized by black and gray shales, mudstones and siltstones, as well as by widespread, thin carbonate and sandstone units. These facies represent poorly oxygenated to fully aerobic settings in the northern end of the Appalachian Basin, after the early phases of the Acadian Orogeny (see Brett, 1986, and references therein). This sequence was laid down in shallow, euphotic to dysphotic epeiric seas, with a water depth range believed to be between about 10 m and 100 m (Brett, Baird, and Miller, 1986; Vogel, Golubic, and Brett, 1987).

Brachiopods harbored diverse epibiont subcommunities, allowing for detailed study. The present study concentrates on host specimens from the Kashong Shale Member of the Moscow Formation (for further details see Baird *et al.*, this volume), a light, blue-gray, bioturbated, blocky mudstone. The Kashong Member is characterized by a moderately diverse fauna ranging from 30 to 50 invertebrate species and dominated by brachiopods, especially *Tropidoleptus carinatus* (Conrad), *Devonochonetes coronatus* (Conrad), and *Mucrospirifer mucronatus* (Conrad). The bottom sediment consisted of water-rich muds. Aerobic bottom waters promoted a fairly diverse but patchy benthic fauna to dominate; patch communities with diverse epifaunal organisms occur scattered in nearly barren mudstone (Baird, 1978).

Large samples of exceptionally well preserved brachiopods, with abundant encrusting epibionts, have been obtained from the Kashong beds at several localities. The present paper stems particularly from study of a large suite of specimens gathered from weathered Kashong Shale in western New York. Casual observations suggested interesting and nonrandom patterns of epibiont distribution and detailed study was undertaken to document patterns and test initial hypotheses.

MATERIALS AND METHODS

More than 2500 specimens, representing 17 different species of brachiopods (see Table 1), were collected from the Middle Devonian Kashong Shale at Retsof, Livingston County, New York (see locality register in Baird *et al.*, this volume for details). All of the specimens were taken from a single stratigraphic interval, about 2 m thick, and are considered to represent a single community of organisms.

Preparation of specimens included boiling them in Quaternary O to remove the surrounding matrix from a fossil specimen. After boiling for 2–4 hours, the specimens were placed in an ultrasonic cleaner to remove any remaining loose material. This allowed detailed examination of the shell surfaces. Each specimen was then examined under a binocular microscope to determine the types and numbers of encrusting epibionts.

The surface area for a single valve of each brachiopod species was calculated to determine if the amount of surface area available to the epibiont affected the degree of encrustation of certain host species. The area was determined by placing

50–100 random specimens of a particular brachiopod species on graph paper. The area covered by these specimens was then divided by the number of specimens on the graph paper to find the average size of that species of brachiopod. The resulting number represents an approximation of the surface area of a single valve of each species (Table 1). A frequency index was then calculated by dividing the total potentially exposed area for brachiopod species (the average size of one valve multiplied by the total number of specimens collected of that species) by the total number of epibionts found on that species (Table 1).

Table 1 : Summary of Kashong brachiopods collected and epibiont frequencies. N = total number of brachiopods examined; area = calculated exposed surface area for these brachiopods; see text for explanations of frequency and deviation from average

Brachiopod	N	Area (cm²)	Frequency Epibionts	Deviation from Average
Ambocoelia spinosa Clarke	153	68.36	1.9	0.0
Athyris spiriferoides (Eaton)	281	2174.32	0.3	− 1.6*
Camarotoechia horsfordi Hall	200	211.18	4.0	2.1**
Camarotoechia spp.	96	101.37	2.2	0.3
Cryptonella rectirostra (Hall)	182	360.36	0.6	− 1.3*
Cryptonella planirostra (Hall)	161	369.31	0.2	− 1.7*
Cyrtina hamiltonensis Hall	66	42.24	0.7	− 1.2*
Elita fimbriata (Conrad)	63	143.31	0.2	− 1.7*
Devonochonetes coronatus (Conrad)	128	424.95	1.7	− 0.2
Mediospirifer audaculus (Conrad)	48	193.96	2.0	0.1
Megakoslowskiella spp.	101	87.87	2.1	0.2
Meristella haskinsi Hall	60	103.40	4.5	2.6**
Mucrospirifer mucronatus (Conrad)	140	615.13	0.8	− 1.1*
Nucleospira concinna (Hall)	449	806.85	0.2	− 1.7*
Pustulatia pustulosa (Hall)	133	107.88	6.5	4.6**
Trematospira gibbosa Hall	54	67.77	0.8	− 1.1*
Tropidoleptus carinatus (Conrad)	197	894.20	2.8	0.9
		Average =	1.9	0.5

*Indicates slight deviation from the average.
**Indicates strong deviation from the average.

Each host brachiopod shell was divided into nine subequal sections, which were then examined for: (1) the location of the epibionts; (2) evidence of epibiont interactions; and (3) general preservation of each host specimen. Colonial epibionts, such as *Hederella* and other bryozoans, were counted as one specimen for each section that they were found in. Therefore, when *Hederella* completely encrusted a valve of *Tropidoleptus carinatus* it was counted as nine units because it was found in all nine sections of the brachiopod. Thus, the numbers of colonial epibionts in the data represent relative abundances, rather than actual numbers of zooids or colonies. An average frequency of occurrence of all epibionts was computed for each of the 17 brachiopod species. As an indication of host preference the deviation of coverage was computed for each species by subtracting the overall average coverage index for all brachiopods from the average coverage index for each species. High positive values indicate a strongly preferred host species; negative values suggest an avoided species (Table 1).

Comparisons between brachiopods of different species were made to ascertain if types and numbers of encrusters occur non-randomly on any brachiopods. To examine for patterns of selective encrustation of pedicle versus brachial valves, the two valves of each articulated specimen were examined separately and epibiont abundances were recorded. A binomial test was used to determine whether significant deviations existed in the frequency of various encrusters on the two valves.

In order to learn more about the occurrence of post-mortem encrustation of reoriented brachiopods, oriented samples were taken from the Kashong Shale. In these samples, *Tropidoleptus carinatus* specimens were marked in the field to show their orientation, as preserved in the shale (i.e., convex up, down, or inclined). Then, frequencies of epibionts on pedicle versus brachial valves were tabulated, to determine if there was any significant relationship between encrustation frequency and the position in which they were found in-situ.
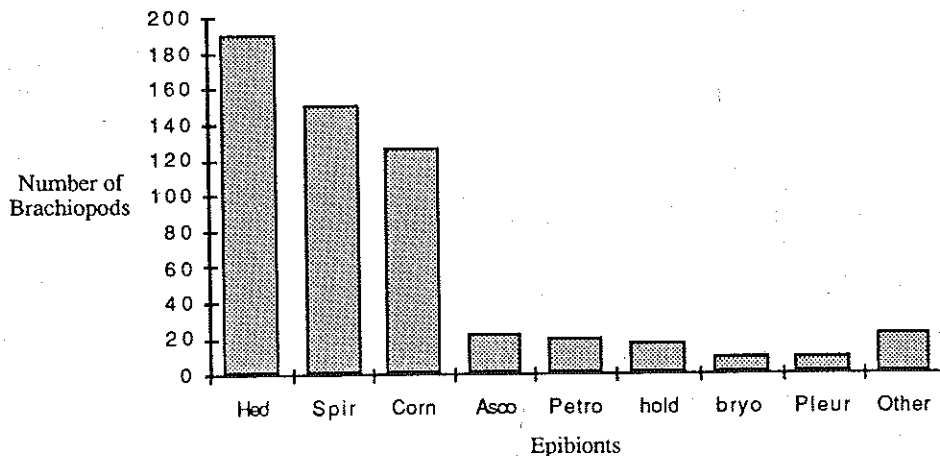

Figure 1 Distribution of various epibiont taxa on shells of *Tropidoleptus carinatus* (Conrad) from the Kashong Shale Member at Retsof, Livingston Co., New York. Histogram shows number of brachiopod shells bearing at least one specimen of each particular epibiont. Abbreviations for epibionts: Hed = *Hederella* spp; Spri = *Spirorbis angulatus*; Corn = *Cornulites* cf. *C. hamiltoniae*; Asco. = *Ascodictyon* spp.; Petro = *Petrocrania hamiltoniae*; hold = pelmatozoan holdfast; bryo = encrusting trepostome bryozoan; Pleur = *Pleurodictyum americanum*; other = auloporids, *Eliasopora, Lieoclema,* bryozoan holdfast, and tolypaminid foraminifera.

COMMON EPIBIONTS

Over a dozen species of epibionts were found commonly on brachiopod specimens from the Kashong Shale (Figures 1 and 2). Of these epibionts, the three most common were the worm tubes *Cornulites* and *Spirorbis,* and the tubuliporate bryozoan *Hederella*: other common epibionts included ctenostome bryozoans, encrusting sheet-like trepostomes, holdfasts, and inarticulate brachiopods. These are discussed briefly in the following sections.

Cornulites. Cornulites cf. *C. hamiltoniae* Grabau is a cone shaped, annulated, shell ranging from 0.2 to over 10 mm in length belonging to an extinct organism (Figure 2A).
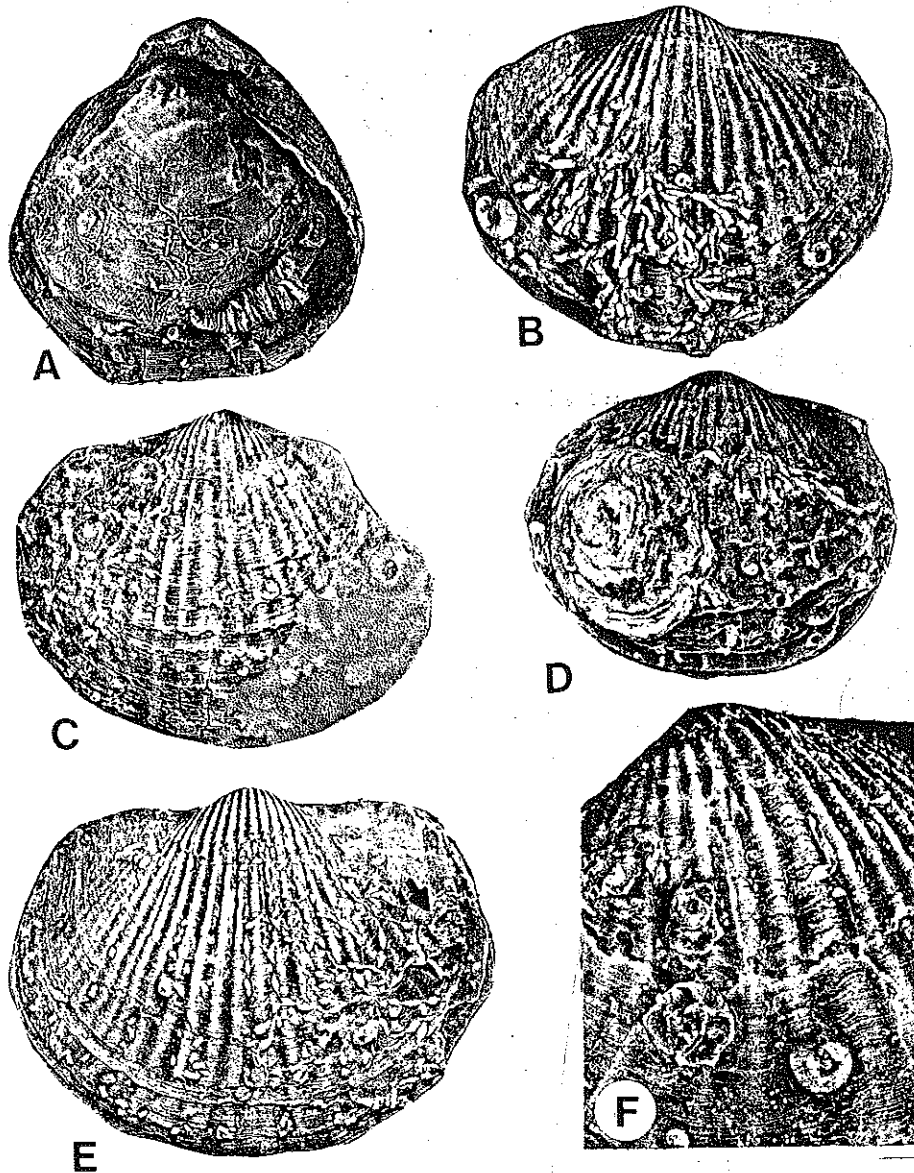
Figure 2 Epibionts on Devonian brachiopods. All specimens from Middle Devonian, Hamilton Group, Kashong Shale; Retsof, Livingston County, New York; all figures except for F, ×1.5. (A) *Meristella* cf. *M. haskinsi* Hall. Specimen showing small holdfasts of pelmatozoans, vine-like growths of *Hederella* and large conical tube of *Cornulites* cf *C. hamiltoniae* Grabau, on brachial valve; RMSC 89.30.1. B-F. Epibionts on pedicle (convex) valve of *Tropidoleptus carinatus* (Conrad). (B) Specimen showing encrustation by the bryozoan *Hederella* sp. note aperatures aligned toward commissure of brachiopod shell; also note small *Cornulites* and *Spirorbis* worm tubes near commissure of shell; RMSC 89.30.3. (C) Note encrustation by fistuliporoid bryozoan in lower right and some *Hederella* zooecia; RMSC 89.30.4. (D) Specimen with large inarticulate brachiopod *Petrocrania hamiltoniae* (Hall) on lower left of valve; RMSC 89.30.5. (E) Specimen with heavy encrustation by ctenostome bryozoan *Ascodictyon*; also note small node-like objects scattered across shell, and incipient colony of the tabulate coral *Pleurodictyum americanum* (Hall) with three corallites (arrow); RMSC 89.30.6. (F) Enlargement of shell surface showing three specimens of the worm tube *Spirorbis angulatus* Hall; note two at left of center are broken away showing internal details of coiled shell; also note small tolypamanid foraminifera and small *Cornulites* as well as stolons of ctenostome bryozoans; ×4; RMSC 89.30.7.

Classification of cornulitids is uncertain; they have been placed in either the Phylum Mollusca or the Phylum Annelida by various workers. Cornulitids are most commonly considered to represent a group of annelid worms. The ecology of the Cornulitidae was studied in detail by Richards (1974), who concluded that most Ordovician species were solitary commensals, that attached to hard shelled invertebrates on muddy sea floors. It is believed that the organisms were filter feeders, often deriving their food from the feeding currents of their host (Richards, 1974).

Hurst (1974) determined that *Cornulites* preferred brachiopods with angular ribs to those with spinose or smooth shells. In the Kashong sample, small *Cornulites* were found generally between the ribs of the host specimen. In situations where *Cornulites* had grown across the ribs, the original larvae had evidently settled between the ribs and grown for a short time between them, before turning and growing over them. Most specimens were clustered along the commissure or with their apertures pointed in the direction of the commissure.

Spirorbis. The spiral annelid (?) worm tube, *Spirorbis angulatus* (Hall) (Figure 2B, F), is also abundant on Kashong brachiopods. This long-ranging genus (Ordovician-Recent) apparently preferred shallow ribbed hosts or the lateral surfaces of angular ribs on brachiopods, at least in the Silurian (Hurst, 1974). *Spirorbis* larvae typically did not settle between the ribs of the host, but on top of them. In the Kashong sample, certain brachiopods hosted a large individual of *Spirorbis* (1–2 mm) which was surrounded by several tiny *Spirorbis* (<0.5 mm). This may indicate that suitable substrate was limited, forcing larvae to settle close to the parent; or it may suggest a gregarious settlement behavior, which has been reported in Recent *Spirorbis* (Crisp, 1974).

Bryozoans. In general, encrusting bryozoans did not completely cover a host shell. Most bryozoan mats found were tiny colonies of <1 cm in diameter; this contrasts with some other Hamilton samples in which bryozoans may cover large areas of many brachiopods (Figure 2C). In the few Kashong examples where mats of trepostome bryozoans did cover the majority or entirety of the shell of the host, they also encrusted over other epibionts, such as *Cornulites* and *Spirorbis.*

The tubuliporate bryozoan *Hederella* is one of the most abundant epizoans in the Kashong (Figure 2A, B). Over a dozen species of *Hederella* have been described (Bassler, 1939). At least three species are represented in the Kashong material; others may well be present, but were not differentiated in this study. This reptant bryozoan commonly encrusted much of the brachiopod valve to the exclusion of other epibionts. In a few instances, *Hederella* grew over *Spirorbis* or *Cornulites,* but this was clearly the exception rather than the rule. Where it was possible to identify the ancestrula, it was noted that most of the colonies started growing between the ribs of the host. In these instances the rest of the colony seemed to grow and expand over the ribs, with little regard to the host shell topography. The ctenostome bryozoans *Ascodictyon* and *Eliaspora* are vesicular and vine-like. They are not abundant, but when they do occur, they may occupy much of the surface (Figure 2E).

Pleurodictyum. These tabulate corals occur mainly as small incipient colonies of one to four corallites (Figure 2E). They rarely appeared to be any larger than a few cm in diameter. However, collections of large *Pleurodictyum americanum* (Hall) from the Kashong beds commonly revealed brachiopod shells, especially *Tropidoleptus carinatus* (Conrad) embedded in the corallum.

Brachiopods. The inarticulate brachiopod, *Petrocrania hamiltoniae* (Hall), encrusted several species of larger brachiopods (Figure 2D). These encrusting brachiopods often demonstrated xenomorphism of the host shell structure.

Pelmatozoan holdfasts. Five or six different types of discoidal crinoid or blastoid holdfasts occur (Figure 2A). Some are simple disks while others display digitate outgrowths. They commonly occur in clusters on a single brachiopod specimen.

HOST PREFERENCES

Over 17 species of brachiopods present in the Kashong Shale represent potential hosts for epibionts (Figure 3). However, the occurrence of epibionts was non-random among brachiopod host shells. The frequency of epibionts per area is listed in Table 1. The average frequency of occurrence was 1.9 epibionts/cm^2. The computed index for each brachiopod species and its deviation from the mean are also shown in Table 1.

The relative amounts of encrustation of different brachiopod host species clearly differ greatly, but did not follow size or taxonomic lines. Comparison of three small spiriferids of about the same size demonstrates this point (Figure 3A–F). *Cyrtina hamiltonensis* Hall (Figure 3C, D) had one of the lowest encrustation frequencies, with an epibiont frequency of only 0.7; *Ambocoelia spinosa* Clarke (Figure 3E, F) had an average amount at 1.9 epibionts/cm^2; and *Pustulatia pustulosa* (Hall) (Figure 3A, B), the most highly encrusted species in the Kashong material had a frequency of 6.5 epibionts/cm^2. Conversely, several large brachiopod species have relatively low degrees of encrustation; for example, *Athyris spiriferoides* (Eaton) (Figure 6A), with the largest surface area, has an encrustation frequency of only 0.3. Taxonomic lines were also crossed, as can be seen by comparison of *Mediospirifer audaculus* (Conrad) and *Mucrospirifer mucronatus* (Conrad) (Figure 3G–I). These brachiopods are similar in size, shape, and coarseness of ribbing, as well as belonging to relatively closely related families. Yet, they had very different frequencies of epibionts, with *Mediospirifer audaculus* (Conrad) having one of the largest frequencies at 2.0 epibionts/cm^2 and *Mucrospirifer mucronatus* (Conrad) having one of the lower encrustation frequencies at 0.8. The encrustation patterns were quite different, as well. Epibionts were clustered along the hinge on specimens of *Mucrospirifer mucronatus* (Conrad), whereas they tended to cluster along the commissure of *Mediospirifer audaculus* (Conrad) specimens.

General morphology of shells also does not appear to be a major factor controlling encrustation. *Cryptonella planirostra* (Hall), *Cryptonella rectirostra* (Hall), and *Meristella haskinsi* Hall, are brachiopods of nearly the same average size, shape, and general shell structure (Figure 4). Despite their similarities, however, these hosts differ markedly in degree of encrustation by the three most common epibionts (Table 2). The epibiont frequency per area for *Cryptonella planirostra* is only 0.14, and that of *Cryptonella rectirostra* is 0.46, whereas that of *Meristella haskinsi* is an extremely high 4.11. The low frequencies of encrustation may be caused by the presence of punctae in the shell of the terebratulids, *C. rectirostra* and *C. planirostra*; on the other hand *Meristella haskinsi* is an impunctate spiriferid. The punctae presumably contained fingers of mantle tissue or caecae (Thayer, 1986). Curry (1983) claimed terebratulids secrete mucopolysacharides via their caecae to repel microborers. These toxic or repellent substances may have deterred epibiont larvae from settling on the shell. In fact, all
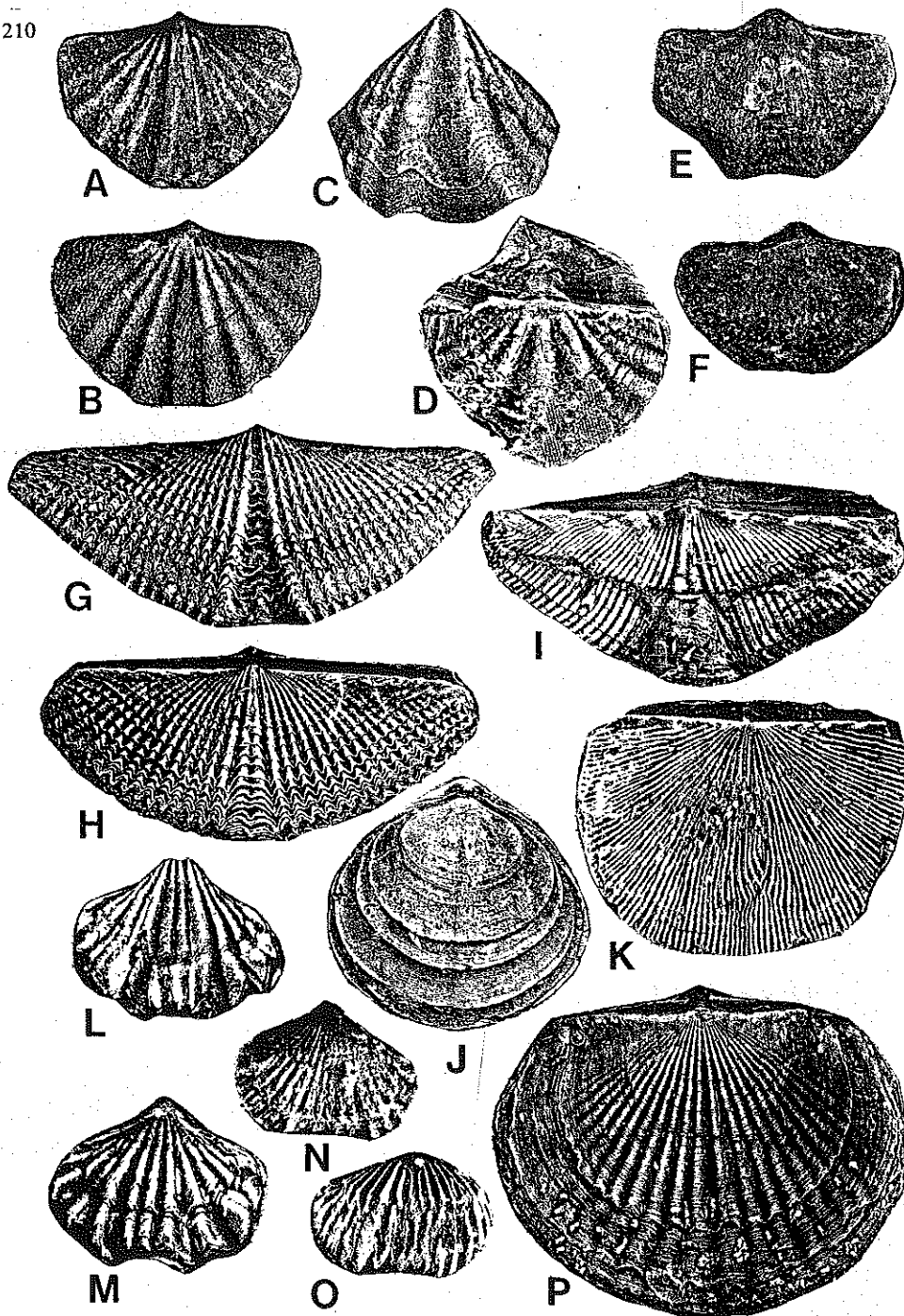
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Figure 3 Common brachiopods from the Kashong Shale at Retsof, New York, which served as substrates for epibionts. (A, B) *Pustulatia pustulosa* (Hall); pedicle and brachial views; ×2; RMSC 89.30.8. (C, D) *Cyrtina hamiltonensis* Hall; pedicle and brachial valve views; ×2; 89.30.9. (E, F) *Ambocoelia* cf. *A. spinosa* Clarke; pedicle and brachial views; ×2; RMSC 89.30.10. (G, H) *Mucrospirifer mucronatus* (Conrad); pedicle and brachial views of typical specimen with alae broken off; ×15; RMSC 89.30.11. (I) *Mediospirifer audaculus* (Conrad); brachial valve view; RMSC 89.30.12. (J) *Nucleospira concinna* (Hall); pedicle valve view; ×2; RMSC 89.30.13. (K) *Devonochonetes coronatus* (Conrad); brachial valve view; ×2; RMSC 89.30.14. (L, M) *Trematospira gibbosa* Hall; pedicle and brachial valve views; ×2; RMSC 89.30.15. (N, O) *Camarotoechia* cf. *C. horsfordi* Hall, pedicle valve and commissural views; ×2; (O) RMSC 89.30.16. (P) *Tropidoleptus carinatus* (Conrad); brachial valve view; ×2; RMSC 89.30.17.

punctate brachiopods in the sample, with the exception of the orthid *Tropidoleptus carinatus* (Figures 2B–F, 3P), showed low frequencies of epibiont encrustation. The relatively small percentage of epibionts that did grow on these punctate shells may have done so after the death of the host brachiopod.
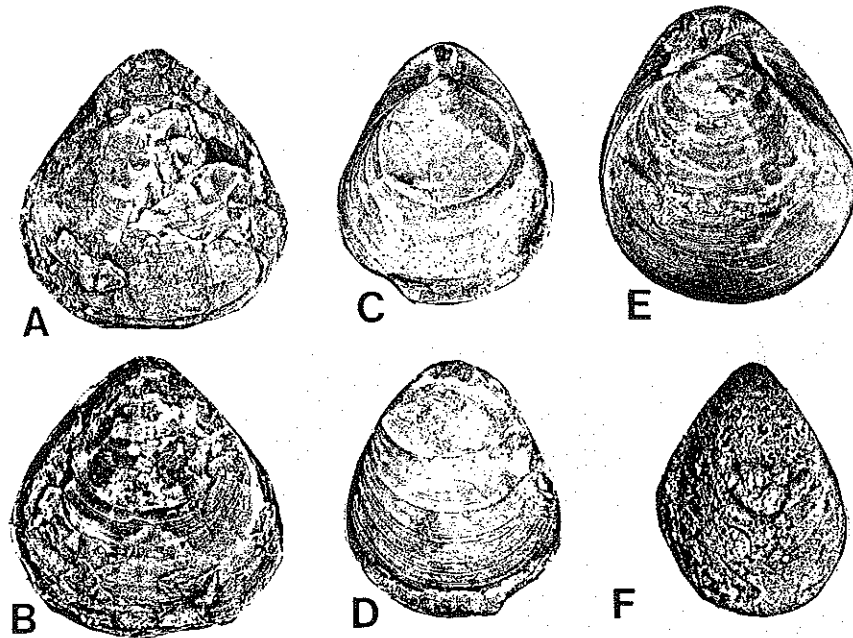

Figure 4 Comparison of various taxa of smooth oblate shaped brachiopods. (A, B) *Meristella* cf. *M. haskinsi* Hall; pedicle and brachial valve views of single specimen; note encrusting *Hederella* sp. and *Cornulites* near commissure of brachial valve; RMSC 89.30.18. (C, D) *Cryptonella* cf. *C. planirostra* (Hall); pedicle and brachial valve views; note shell is free of epibionts; both specimens × 2; RMSC 89.30.19. (E) *Cryptonella* sp., brachial valve view of robust terebratulid specimen free of epibionts; × 2; RMSC 89.30.20. (F) *Cryptonella rectirostra* (Hall); pedicle view; × 2; RMSC 89.30.21.

Table 2 Comparisons of epibiont frequencies on *Meristella haskinsi* (Hall) versus two terebratulids

	Meristella haskinsi (Hall)		*Cryptonella planirostra* (Hall)		*Cryptonella rectirostra* (Hall)	
	Number	Number/ cm^2	Number	Number/ cm^2	Number	Number/ cm^2
Cornulites cf. *C. hamiltoniae*	107	1.01	20	0.08	115	0.32
Spirorbis angulatus	31	0.30	5	0.01	6	0.02
Hederella spp.	207	2.00	20	0.05	43	0.12
Total =	425	4.11	53	0.14	164	0.46

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The low encrustation rate on *Nucleospira concinna* (Hall) and *Elita fimbriata* (Conrad) (Figure 5) may be related to the presence of spines on these shells. Although the spines apparently did not deter predatory gastropods from attacking these favored "prey" species (Smith *et al.*, 1985), they evidently trapped and held mud on the shell, which might have made the shell surface unsuitable for settling epibiont larvae (L. M. Gray, pers. comm. 1984). The frilled growth lines of *Athyris spiriferoides* (Eaton) (Figure 6) may have had a similar mud-trapping effect; this brachiopod also displays very low epibiont coverage.
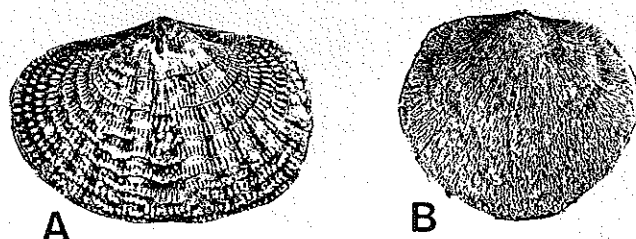

Figure 5 Two spinose brachiopods from the Middle Devonian, Kashong Shale, which have very low coverages by epibionts: (A) *Elita fimbriata* (Conrad); pedicle valve view; note small spines which have been partially broken away; ×2; RMSC 89.30.22. (B) *Nucleospira concinna* (Hall); pedicle valve view; note mat of hair-like spines over the entire surface of the shell and absence of epibionts; ×2; RMSC 89.30.23.
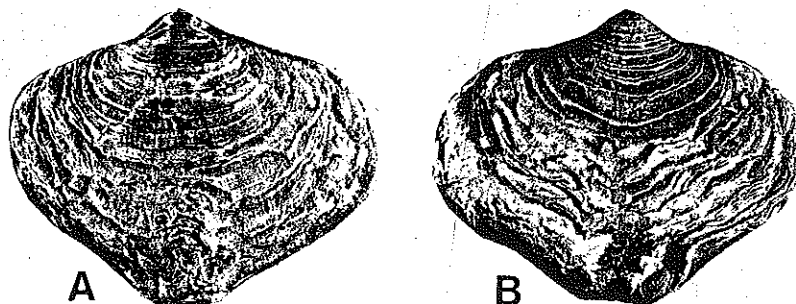

Figure 6 *Athyris* cf. *A. spiriferoides* (Eaton) (A) brachial and (B) pedicle valve views of typical specimen; note frilly growth lamellae; Kashong Shale, Retsof, New York. ×1.5 RMSC 89.30.24.

The Kashong material displayed definite trends in the percentage of certain types of epizoans (Figures 7 and 8). *Cornulites* cf. *C. hamiltoniae* was more frequent than *Spirorbis angulatus* on all brachiopod species except *Tropidoleptus carinatus* (Figure 8), which had nearly twice as many *Spirorbis* as *Cornulites*. *Nucleospira concinna* possessed equal numbers of *Spirorbis* and *Cornulites*. *Pustulatia pustulosa*, the genus with the greatest number of *Cornulites* per area, had one of the lowest concentrations of *Spirorbis*. Despite these observations, there was no direct correlation between the concentrations of *Cornulites* and *Spirorbis*.
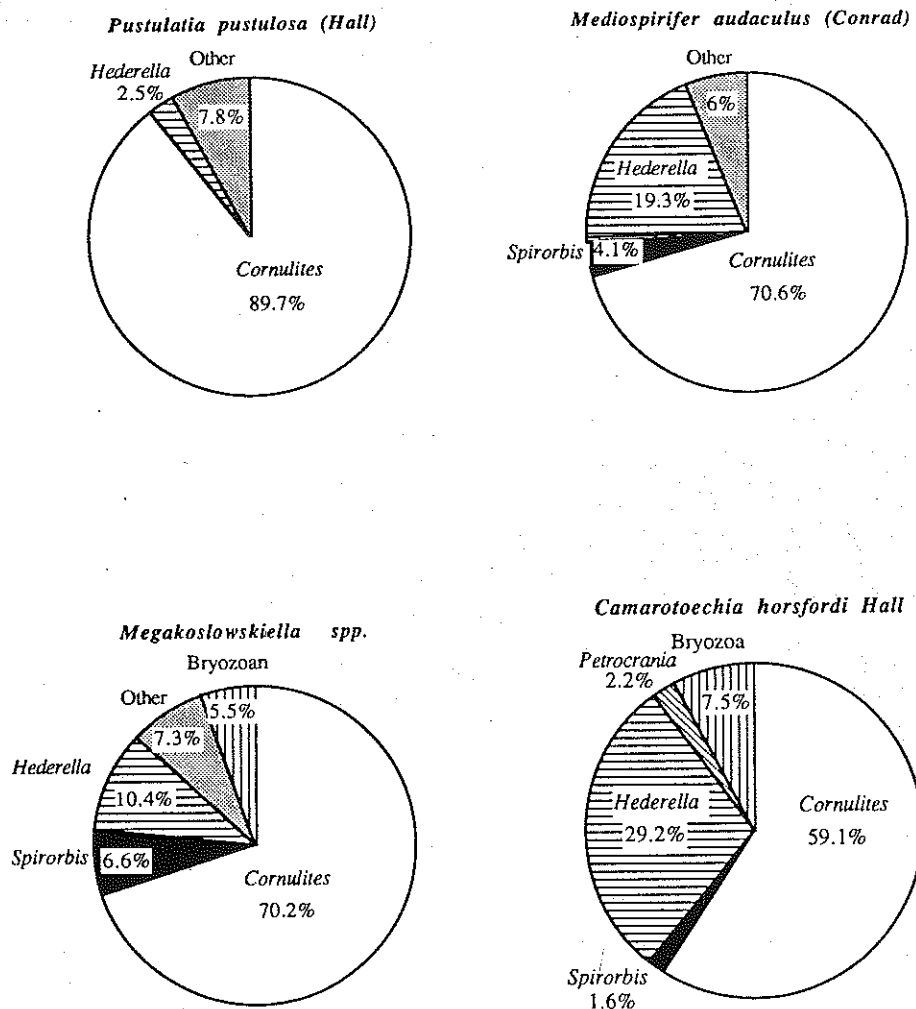
Pustulatia pustulosa (Hall)

Hederella
2.5%

Other
7.8%

Cornulites
89.7%

Mediospirifer audaculus (Conrad)

Other
6%

Hederella
19.3%

Spirorbis 4.1%

Cornulites
70.6%

Megakoslowskiella spp.

Bryozoan

Other
5.5%

7.3%

Hederella
10.4%

Spirorbis 6.6%

Cornulites
70.2%

Camarotoechia horsfordi Hall

Bryozoa

Petrocrania
2.2%

7.5%

Hederella
29.2%

Cornulites
59.1%

Spirorbis
1.6%

Figure 7 Pie diagram illustrating proportions of various epibiont taxa; the other category includes pelmatozoan holdfasts, *Ascodictyon*, foraminifera, *Petrocrania*, trepostome bryozoans, and *Pleurodictyum*. This diagram illustrates four brachiopods on which *Cornulites* occur as > 50% of all epibionts.

All brachiopod species in which *Cornulites* were clearly dominant, making up more than 50% of the epibionts, had deep ribs (Figure 7). This sugggests that *Cornulites* larvae were rugophilic and would naturally seek the protection of the deep grooves between ribs of the host, as previously noted by Hurst (1972). Note, however, that Alexander and Scharpf (this volume) and Powers and Ausich (this volume) observe *Cornulites* mainly on smooth brachiopods from the Ordovician and Mississippian, respectively.

Brachiopod hosts dominated by *Spirorbis* were not as easily characterized. *Spirorbis* was present on concavo-convex forms, elongate spiriferids, and small

biconvex hosts (Figure 8). *Spirorbis* was also common on the otherwise sparsely encrusted *Nucleospira concinna.* A common factor uniting these forms can be inferred from field observations of their associations. All of these brachiopods were part of the "background" fauna characterizing mudstones between diverse bryozoan patches. These brachiopods were probably turbidity and sediment tolerant, as must have been true for the *Spirorbis* which encrusted them.
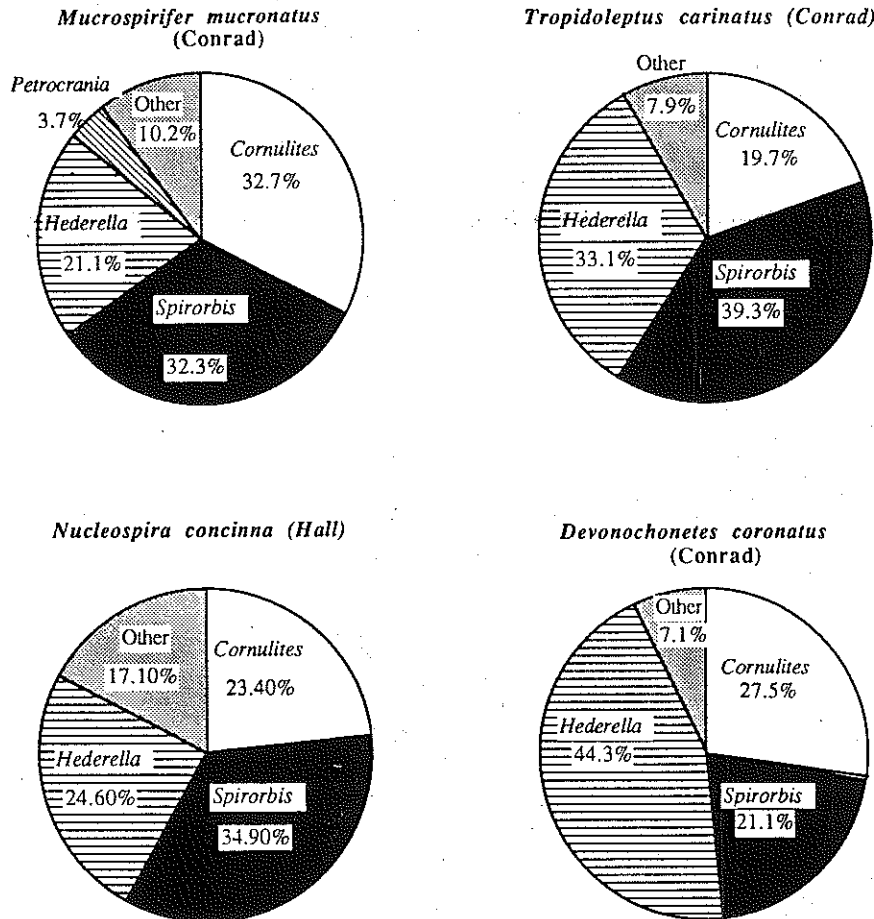

Figure 8   Pie diagram illustrating proportions of various epibiont taxa; other category same as Figure 7. This diagram illustrates four brachiopods on which *Spirorbis* is a dominant epizoan.

PEDICLE/BRACHIAL COMPARISONS

Biconvex Brachiopods

The number of epibionts per area on the pedicle versus the brachial valve, was nearly a 1:1 ratio for most species (Figure 9, Table 3), although, there were a few exceptions. Equal concentrations of epibionts on both valves of the host indicates

equal exposure. These hosts were pedically attached with their commissures oriented perpendicular to the sea floor or were pendant from crinoid stems or the branches of bryozoans well above the substrate. In these instances both valves would be equally exposed to settling larvae.

A 1:1 epibiont ratio is present on most biconvex forms such as *Cryptonella rectirostra* and *Meristella haskinsi* (Figure 4F, A, Table 4). Independent evidence supports the view that these brachiopods were attached by pedicles, commonly on upright bryozoan zoaria (G. Kloc, pers. comm.). Thus, both valves were available for epibiont colonization. However, a 1:1 ratio is not found on the equibiconvex *N. concinna*. The pedicle valve of this species was encrusted much more commonly than the brachial valve (3:1). Thus, *N. concinna* may have been oriented with its brachial valve against the substrate, unlike many other biconvex brachiopods.

Concavo-convex Brachiopods and Post-mortem Encrustation

Concavo-convex species, such as *Tropidoleptus carinatus* (Figure 10), might be expected to have epibiont preferences for the brachial valve, as this valve was probably oriented upward during the life of the brachiopod. However, most previous studies point to a greater frequency of encrustation of the convex valves (see particularly Richards, 1972; Spjeldnaes, 1984). Richards (1972) interpreted this as mainly a post-mortem encrustation. This interpretation is consistent with the total numbers of epibionts on the pedicle versus the brachial valve in *T. carinatus* from the Kashong sample. Epibionts are scattered fairly evenly across the convex valve. The concave, brachial valve, which faced upward during the life of the brachiopod, had the majority of the epibionts concentrated along the commissure of the valve, as might be expected of pre-mortal encrusters.

The low level of encrustation on the brachial valve might best be explained by a quasi-infauna mode of life. With the pedicle valve against the substrate, the dish-shaped brachial valve may have been filled with sediment. Therefore, the only available substrate on a living *T. carinatus* was a reduced area along the commissure, which was held above the substrate. In contrast, the greatest concentration of epibionts on the convex, pedicle valve, is on the highest point of the valve. Many of the epibionts show growth vectors away from the commissure. These observations seem to require encrustation while shells lay in a convex-upward position. In these instances, post-mortem flipping of the shell to a more hydrodynamically stable pedicle (convex) up position is probably what resulted in the high rate of encrustation on the pedicle valve. Thus, specimens of *T. carinatus* that were buried in convex up orientations, had dissimilar frequencies of encrustation on the brachial and pedicle valves, with generally lower frequencies on the concave, brachial, valve (Figure 9). Surprisingly, some *T. carinatus* specimens preserved concave upward, in the assumed life position, showed higher overall percent coverage and were more equally covered on both valves. Apparently, these specimens were not in life position, as had been assumed, but had been inverted and reinverted possibly more than once, despite the fact that the brachiopod shells showed no sign of wear. This indicates that the brachiopods had complex post-mortem histories that were not indicated by surrounding sediments or any other paleoenvironmental indicators.

Evidently, many *T. carinatus* shells from Kashong mudstones suffered multiple episodes of post-mortem movement, including flipping to unstable concave upward positions. Such inversions may take place if shells are lifted off the bottom and then resettle, as might occur during storms when waves reached the muddy seafloor.

Table 3 Summary of epibiont coverage on the pedicle versus the brachial valves

Brachiopod	N	Pedicle/brachial ratio	Preferred valve
Ambocoelia spinosa Clarke	153	1.68	Pedicle
Athyris spiriferoides (Eaton)	281	0.98	None
Camarotoechia horsfordi Hall	200	1.82	Pedicle
Camarotoechia spp.	96	2.29	Pedicle
Cryptonella rectirostra (Hall)	182	1.07	None
Cryptonella planirostra (Hall)	161	0.80	Pedicle (slight)
Cyrtina hamiltonensis Hall	66	0.82	Pedicle (slight)
Elita fimbriata (Conrad)	63	1.90	Pedicle (slight)
Devonochonetes coronatus (Conrad)	128	0.94	None
Mediospirifer andaculus (Conrad)	48	0.92	None
Megakoslowskiella spp.	101	1.06	None
Merisiella haskinsi Hall	60	0.81	Brachial (slight)
Mucrospirifer mucronatus (Conrad)	140	1.02	None
Nucleospira concinna (Hall)	449	3.06	Pedicle
Pustulatia pustulosa (Hall)	133	4.70	Pedicle
Trematospira gibbosa Hall	54	1.80	Pedicle
Tropidoleptus carinatus (Conrad)	197	2.31	Pedicle

Table 4 Epibiont frequency on pedicle versus brachial valves of biconvex genera

Epibiont	Brachial	Pedicle	Pedicle/ brachial ratio	Binomial test $(p = 0.01)$ BIAS?
Cryptonella rectirostra (Hall)			$N = 182$	
Cornulites cf.				
C. hamiltoniae	59	56	0.95	NO
Spirorbis angulatus	3	3	1.00	NO
Hederella spp.	20	23	1.15	NO
TOTAL=	82	82	1.00	NO
Meristella haskinsi (Hall)			$N = 60$	
Cornulites cf.				
C. hamiltoniae	118	69	0.58	YES
Spirorbis angulatus	16	15	0.94	NO
Hederella spp.	105	102	0.97	NO
TOTAL=	239	186	0.78	NO
Nucleospira concinna (Hall)			$N = 449$	
Cornulites cf.				
C. hamiltoniae	1	40	40.00	YES
Spirorbis angulatus	14	47	3.36	YES
Hederella spp.	6	37	6.17	YES
TOTAL=	21	124	5.90	YES

Alternatively, the supporting sediment may have been scoured out from around the brachiopod causing the shell to slump over into a depression (Alexander, 1984). The fact that concave upward shells display approximately equal coverage of both valves, suggests that, in the inversion process, the concave brachial valve was temporarily cleaned of sediment, enabling colonization of the dish-shaped area, which did not commonly occur with living brachiopods. The complex post-mortem histories must have involved exposure of the shells on the seafloor for periods of months up to several years after death to allow the fairly rapid colonization and growth of epibiont communities. Nonetheless, the shells show little or no sign of wear and are, in fact, still articulated.
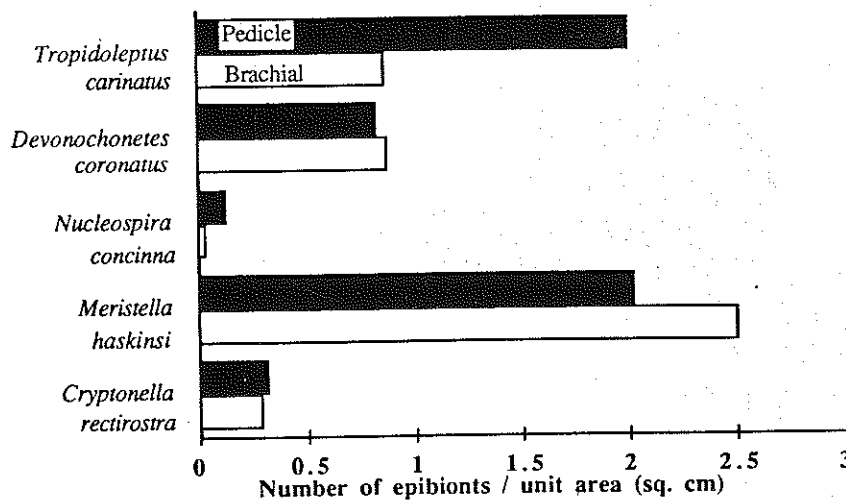
Figure 9 Proportion of epibionts (measured in number of epibionts per square centimeter of shell surface) on pedicle versus brachial valves for five common host brachiopods in the Kashong Shale at Retsof, New York.

The plano-convex genus *Pustalatia pustulosa* displays a pattern similar to *T. carinatus*. The high encrustation rate of the pedicle valve either indicates that in life the flat brachial valve rested against the sediment and its pedicle valve was exposed, or, more probably, that most encrustation is post-mortem.

The same encrustation pattern might be expected for the associated concavo-convex species, *Devonochonetes coronatus* (Conrad) (Figure 10). However, this was not the case. Instead, *D. coronatus* showed a nearly 1:1 ratio of encrustation on both valves. The best explanation may be the lower convexity of *D. coronatus* as compared to *T. carinatus*. This shape may have made the brachiopod relatively stable in either pedicle or brachial upward positions and less susceptible to post-mortem flipping. This tendency has been experimentally documented with *Chonetes* in flume experiments (Alexander, 1984). *D. coronatus* apparently displays more pre-mortem colonization, while *T. carinatus* displays more post-mortem encrustation. Thus, *D. coronatus* may have been less frequently flipped to the convex up position. Alternatively, these two brachiopods may have had separate modes of life, which exposed them to varying amounts of encrustation.
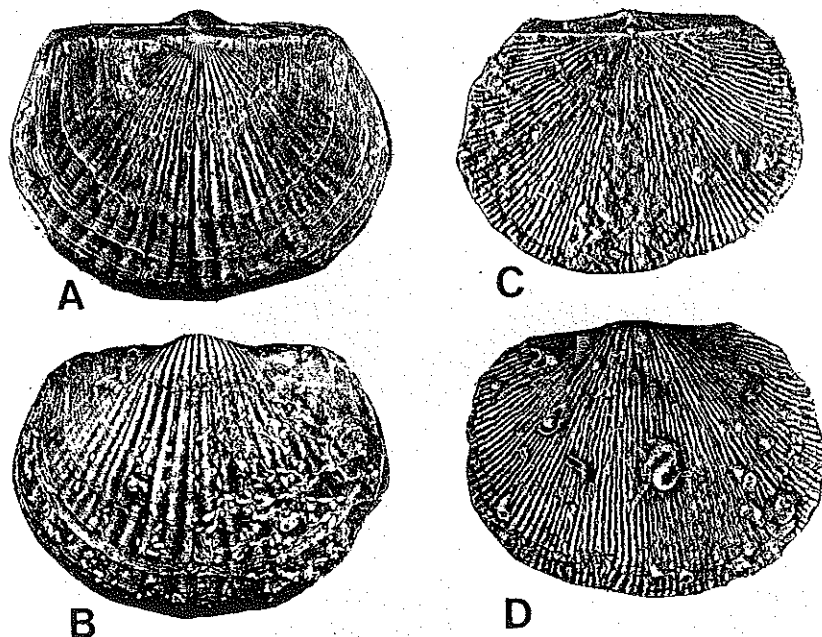
Figure 10 Comparison of two common concavo-convex brachiopods from the Kashong Shale at Retsof, New York. (A, B) *Tropidoleptus carinatus* (Conrad); orthid; concave (brachial) and convex (pedicle) views; × 1.5; RMSC 89.30.6. (C, D) *Devonochonetes coronatus* (Conrad); strophomenid; concave (brachial) and convex (pedicle) views; × 1.5; RMSC 89.30.25.

SUMMARY

Detailed examination of epibionts on over 2500 Middle Devonian brachiopods leads to the following conclusions:

1) Over 16 species of epibionts occur on 17 species of brachiopods, of which the most common are the worm tubes *Spirorbis* and *Cornulites*, and the bryozoan *Hederella*.

2) Epibionts display distinct preference for certain taxa of brachiopod hosts, when frequencies are adjusted for surface area.

3) Heavily ribbed taxa (e.g. spiriferids) were favored hosts of *Cornulites*. *Spirorbis* appears to have avoided angulate ribs but was tolerant of muddy substrates.

4) Punctate brachiopods and those with frills or small spines, that trapped mud on their surfaces, were avoided by most epibionts.

5) Distribution of epibionts on the pedicle versus brachial valves of hosts varies among the brachiopods examined. Some biconvex forms display approximately 1:1 ratios, indicating equal exposure of both valves to encrustation; others, including concavo- to plano-convex forms and biconvex *Nucleospira concinna* (Hall), show much higher frequencies of encrustation on the pedicle valve. This pattern may reflect pedicle-upward life orientation or more likely post-mortem inversion.

6) Detailed study of epibiont frequencies on the pedicle versus brachial valves of *Tropidoleptus carinatus* (Conrad) indicate complex post-mortem inversion histories, prolonged exposure (up to several years), and colonization on the seafloor after death.

7) Close examination of epibionts on Devonian brachiopod shells gives many clues to the hosts' life histories. In addition, epibionts may be the only record of complex sedimentological and reworking histories that might not be indicated by other fossil invertebrates in the strata.

Acknowledgements

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