Substrate specificity in the Devonian tabulate coral *Pleurodictyum*

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The tabulate coral *Pleurodictyum americanum* Roemer has been cited as an example of a host-specific organism occurring exclusively on the shells of gastropods, particularly *Palaeozygopleura hamiltoniae* (Hall). Examination of over 1600 specimens of *P. americanum*, from the Middle Devonian Hamilton Group of western New York, reveals additional complexities which require reinterpretation. While substrate selectivity for *Palaeozygopleura* shells is evident in all 42 subsamples, a variety of other substrates were also utilized by *Pleurodictyum* including corals, brachiopods, other molluscs and pebbles. Recent scleractinian corals inhabiting soft bottoms show similar substrate preference, selecting for the tubes of live serpulids, or gastropod shells (invariably with a secondary sipunculid host), but also occasionally settling on unoccupied shells or pebbles. Shell surfaces of *P. hamiltoniae*, preserved as external molds on the *Pleurodictyum* epitheca, exhibit encrustation by worm tubes and bryozoans as well as borings and mechanical shell damage, suggesting that these were not the shells of live gastropods. However, the invariant aperture-downward orientation and the high degree of selectivity of *P. americanum* strongly suggest that the shells were occupied by secondary hosts. □ *Substrate specificity, commensalism, tabulate coral, gastropod, sipunculid, Devonian, Hamilton Group, New York.*

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Larvae of many marine invertebrates require hard, stable substrates for successful settlement on the sea floor (Thorson 1950; Gray 1974). Many species exhibit nonrandom colonization of particular substrate types, including the skeletons of other living host organisms (Scheltema 1974; Knight-Jones 1951; Crisp & Meadows 1967; and others). Substrate specificity can also be demonstrated among fossil organisms in which the original attachment site is incorporated into the adult skeleton or into the skeleton of another organism (Clarke 1908, 1921; Teichert 1945; Thayer 1974; Brett 1978; MacNamara 1978; Conway Morris 1981). The Devonian tabulate coral *Pleurodictyum* has previously been cited as an ancient organism showing substrate specificity (Ager 1963). As early as 1908, John M. Clarke noted the frequent association of this coral with particular gastropods and inferred the existence of a commensal relationship, in which the coral larvae selected live snail hosts on which to settle. While this suggestion has been much quoted, the relationship has never been thoroughly documented and the hypothesis remains untested. Our detailed study of approximately 1600 specimens of *Pleurodictyum americanum* Roemer from the Hamilton Group of western New York State supports Clarke's suggestion of substrate specificity in *Pleurodictyum;* however, it also reveals additional complexities which require reinterpretation of the relationship.

Materials and methods

Pleurodictyum is a small tabulate coral with a roughly discoidal corallum composed of relatively large, flaring, prismatic corallites and bearing a concentrically wrinkled basal epitheca (Hill & Stumm 1957). The corallum exhibits a high degree of size and morphologic variability, ranging from large hemispherical, flat-based forms, which are generally the most abundant morphotype, to conical and biconical forms, and irregular or aberrant morphotypes (Fig. 1). All forms are intergradational and probably represent ecophenotypic variants of a single species (Ross 1953). *Pleurodictyum americanum* occurs abundantly in the Hamilton Group of New York State, in a wide variety of lithologies. The corals are most abundant and largest in offshore medium to dark gray shales of western New York (e.g. Wanakah and Windom members), but also occur rarely in coarser clastic facies in the Hamilton Group of eastern New York (e.g. King Ferry). *Pleurodictyum* frequently occurs in sparsely

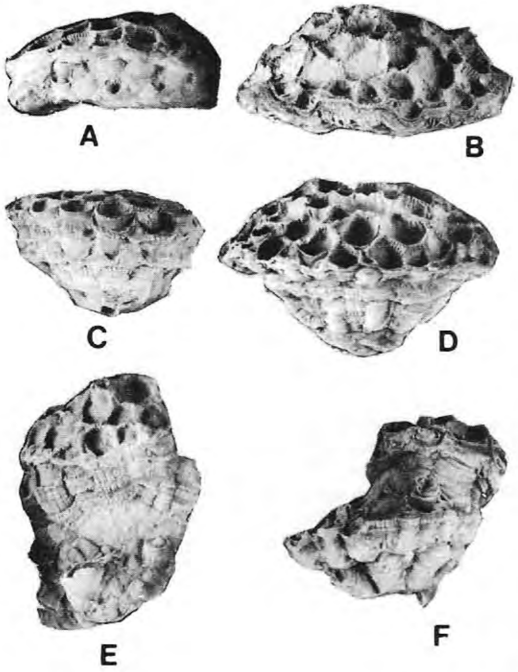

Fig. 1. Morphologic variation in the corallum of *Pleurodictyum* cf. *americanum* Roemer. □A. Morphotype 1: planar base with nearly planar 'upper' corallite surface, BMS E 24955. □B. Morphotype 2: planar base with convex upper surface, BMS E 24954. □C. Morphotype 3: convex base with planar upper surface, BMS E 24956. □D. Morphotype 4: convex base with convex upper surface, BMS E 24957. □E, F. Morphotype 5: specimens exhibiting irregular coralla, BMS E 24958. E 24959. B from Loc. 5A, all others from Loc. 5B. All views × 1.2.

fossiliferous mudstones which lack rugose corals. It evidently was capable of inhabiting relatively soft mud bottoms which otherwise supported only small brachiopods and mollusks. Indeed, *Pleurodictyum* has been cited as an example of an organism adapted for soft substrates (Thayer 1975).

Pleurodictyum is largely confined to several thin but persistent horizons (Fig. 2; Cooper 1930, 1957). The lowest horizon occurs at the base of the Ludlowville Formation in the transition between the Centerfield Limestone and the Ledyard Shale (McCollum 1980). A very widespread unit termed the '*Pleurodictyum* beds' by Grabau (1899) occurs at the base of the Wanakah Shale from Lake Erie to the central Finger Lakes region. Two or three other levels exist in the higher units of the Wanakah and the laterally equivalent King Ferry Shale in the Seneca–Cayuga Lake region (Baird 1981). Scattered specimens of *Pleurodictyum* occur in the Jaycox Member of the Ludlowville Formation and in the Kashong Shale Member of the Moscow Formation (Baird 1979). The highest stratigraphic occurrences of *Pleurodictyum* in western New York are in two richly fossiliferous zones of the Windom Shale in the upper portion of the Moscow Formation (Brett 1974; Baird & Brett, in press).

A total of 42 large samples of *Pleurodictyum* were obtained from various horizons at 31 localities in western and west-central New York State (Fig. 3; Appendix). By far the largest samples were derived from the Wanakah Shale *Pleurodictyum* beds and the basal Windom Shale coral beds, both in Erie County. Specimens were prepared by boiling in Quaternary-O for several hours and then treated with an ultrasonic cleaner. For most specimens in the soft shales of western New York this treatment served to remove the matrix completely from basal surfaces of the corals and their attachment scars. After cleaning, latex casts were prepared of certain samples that showed attachment scars of *Pleurodictyum*. In three sites, where *Pleurodictyum* specimens were particularly common, large blocks of matrix rock were collected and disaggregated in the lab. All contained fossils and their preservations were recorded to determine the bulk composition of the *Pleurodictyum*-bearing fossil assemblages. All corals included in the present study are believed to represent a single species, *Pleurodictyum americanum*; however, further detailed taxonomic studies of the genus *Pleurodictyum* are needed.

Substrates of *Pleurodictyum*

The basal epitheca of *Pleurodictyum* commonly incorporates the remains or impressions of objects which provided initial attachment sites for the corals (Fig. 4). Thus, in the majority of cases, it is possible to identify the initial settlement substrate. A wide variety of hard substrates was utilized by *Pleurodictyum* including both skeletal and inorganic materials such as phosphate pebbles and hiatus concretions (Fig. 4L, M). Over 60 different skeletal substrates have been identified in our study (Tables 1 and 2). These include rugose and auloporid corals (Fig. 4F), brachiopods (Fig. 4C), and a variety of mollusks including cephalopods, bivalves, and gastropods (Figs. 4A, B, E, G–I, K). Thus, statements which imply that *Pleurodictyum americanum* occurs exclu-

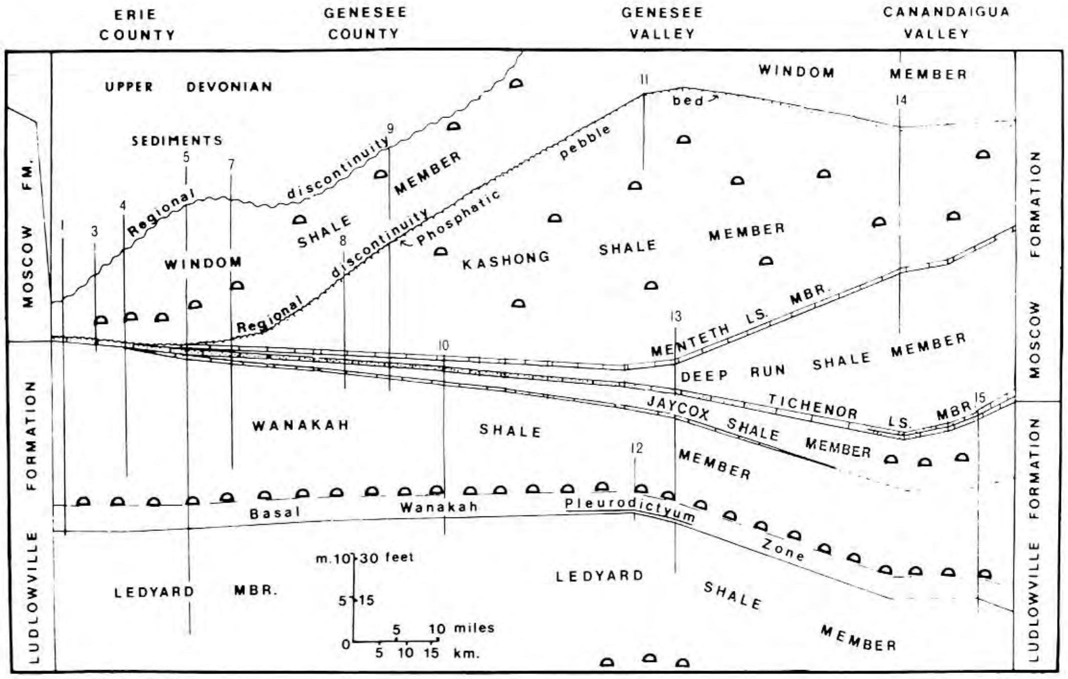

Fig. 2. Diagrammatic cross section of the Upper Hamilton Group (Middle Devonian) in western New York State. Vertical lines represent sections at sampling sites; numbers correspond to localities described in Appendix. *Pleurodictyum*-bearing horizons are denoted by semicircular symbol. Modified from Baird 1979, Fig. 3A.

sively on gastropod shells (Clarke 1908; Ager 1963) are clearly in error. On the other hand, our studies demonstrate that a very large proportion of specimens in all major samples occur on the gastropod *Palaeozygopleura hamiltoniae.* (As a consequence of the present study, the assignment of this species, formerly *Loxonema hamiltoniae,* to the Palaeozygopleuridae by Rollins, Eldredge and Spiller, 1971, is in question. Natural molds on the base of *Pleurodictyum* coralla preserve details of the protoconch which may warrant including this species with the Loxonematidae once again.) In samples of 30 or more *Pleurodictyum* specimens from a single stratigraphic horizon, the percentage of occurrence on *Palaeozygopleura* ranges from 27 % in the Windom Shale of Erie County to 81 % in the Wanakah Shale of the Canandaigua Valley. In most samples, *Palaeozygopleura* is the most common single species of skeletal substrate. In this respect our data suggest substrate specificity. However, the high proportion of *Palaeozygopleura* as substrates might simply reflect an extraordinary abundance of these gastropods within the initial biotic assemblages.

To examine this possibility, proportions of *Pleurodictyum* substrate taxa in particular samples were compared with proportions of taxa in bulk samples from the same horizon and locality; this was done for two samples from the Wanakah Shale *Pleurodictyum* beds and for one from the Windom Shale coral bed. In each case *Palaeozygopleura* accounts for only a minor proportion of the total preserved fossil assemblages at the same localities where it comprises the majority of attachment substrates of *Pleurodictyum* (Table 3). For example, a comparison of the substrate and the matrix data for the *Pleurodictyum* bed of the lower Wanakah Shale at Spring Brook Station, Erie County, shows that whereas *Palaeozygopleura* occurs as an attachment substrate in more than 60 % of the *Pleurodictyum* specimens examined it comprises less than 3 % of the associated biotic assemblage. A χ^2 test of independence was performed on these data for each of the three samples, using a 2×2 contingency table to compare the abundance of *Palaeozygopleura hamiltoniae* against other members of the fossil assemblage in both the substrate and bulk samples. Results of this test support the contention of

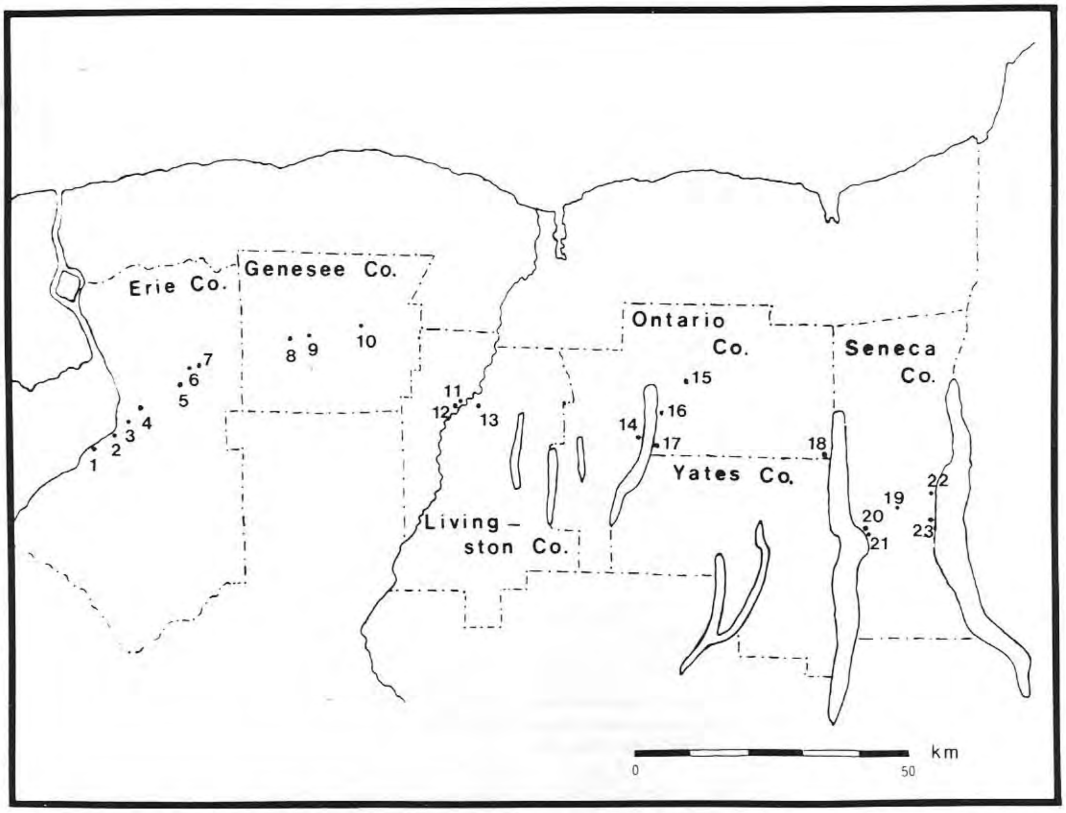

Fig. 3. Index map for sampling localities in western and west central New York State. Numbered localities are described in Appendix. Modified from Baird 1979, Fig. 1B.

substrate selectivity by *Pleurodictyum* for *P. hamiltoniae* in each case (e.g. for Wanakah Shale, sample 1, test statistic = 314; $\chi^2 1,0.01 = 6.64$).

The comparison of substrate and matrix data is complicated by taphonomic processes, in particular, the differential preservability of calcitic vs. aragonitic fossils. Some taphonomic loss of *Palaeozygopleura* and other aragonitic fossils due to dissolution is quite probable (Müller 1979). One might argue that the *Pleurodictyum* substrates provide an unbiased sample of the relative frequencies of various skeletonized taxa in the original community (i.e. random settling of coral larvae onto skeletons on the sea floor). Then, the discrepancy with the matrix data would be due to loss of aragonitic shells. Comparing the ratio of *Palaeozygopleura* to readily preservable calcitic fossils (e.g. brachiopods) in the substrate vs. matrix samples it is evident that more than 99% of the *Palaeozygopleura* shells originally present in the matrix would have had to be lost to account for the difference. Our observations indicate that

Fig. 4. Attachment substrates of *Pleurodictyum americanum* Roemer; A, B, D, E, G, H and K are latex peels from impressions on basal epitheca of *Pleurodictyum* coralla. □A. Gastropod, *Mourlonia capillaria* (Conrad). Loc. 6, BMS E 24960, × 4. □B, E. Bivalve, *Nucula* sp. Coralla attached to articulated shells in two different orientations. In B. attachment is to umbonal region, and in E to the commissural area of gaping valves. Loc. 5B, BMS E 24961, E 24964, × 4, × 2.3. □C. Brachiopod, *Mediospirifer audaculus* (Conrad). Loc. 3, BMS E 24962, × 1.2. □D. Undetermined substrate, possibly lithistid sponge. Loc. 5B, BMS E 24963, × 4. □F. Rugose coral, *Stereolasma rectum* (Hall). Loc. 3, BMS E 24965, × 1.6. □G. Gastropod, bellerophontid. Loc. 5B, BMS E 24966, × 3.7. □H. Mollusc(?) *Coleolus* sp., Loc. 5B, BMS E 24967, × 2.5. □I. External mold of orthoconic nautiloid on *Pleurodictyum* epitheca. Note impression of a septum with siphuncle on broken end of phragmacone. Loc. 5B, BMS E 24968, × 3.1. □J. Crinoid column embedded in base of *Pleurodictyum*. Loc. 10, BMS E 24969, × 1.6. □K. Gastropod, *Palaeozygopleura hamiltoniae* (Hall). Loc. 9, BMS 24970, × 2.2. □L, M. *Pleurodictyum* on bored and epizoan-encrusted hiatus concretions. L is view of corallum from above, M is a cross-section through *Pleurodictyum* and concretion. Loc. 23A, BMS E 24971, E 24972, × 1.0.

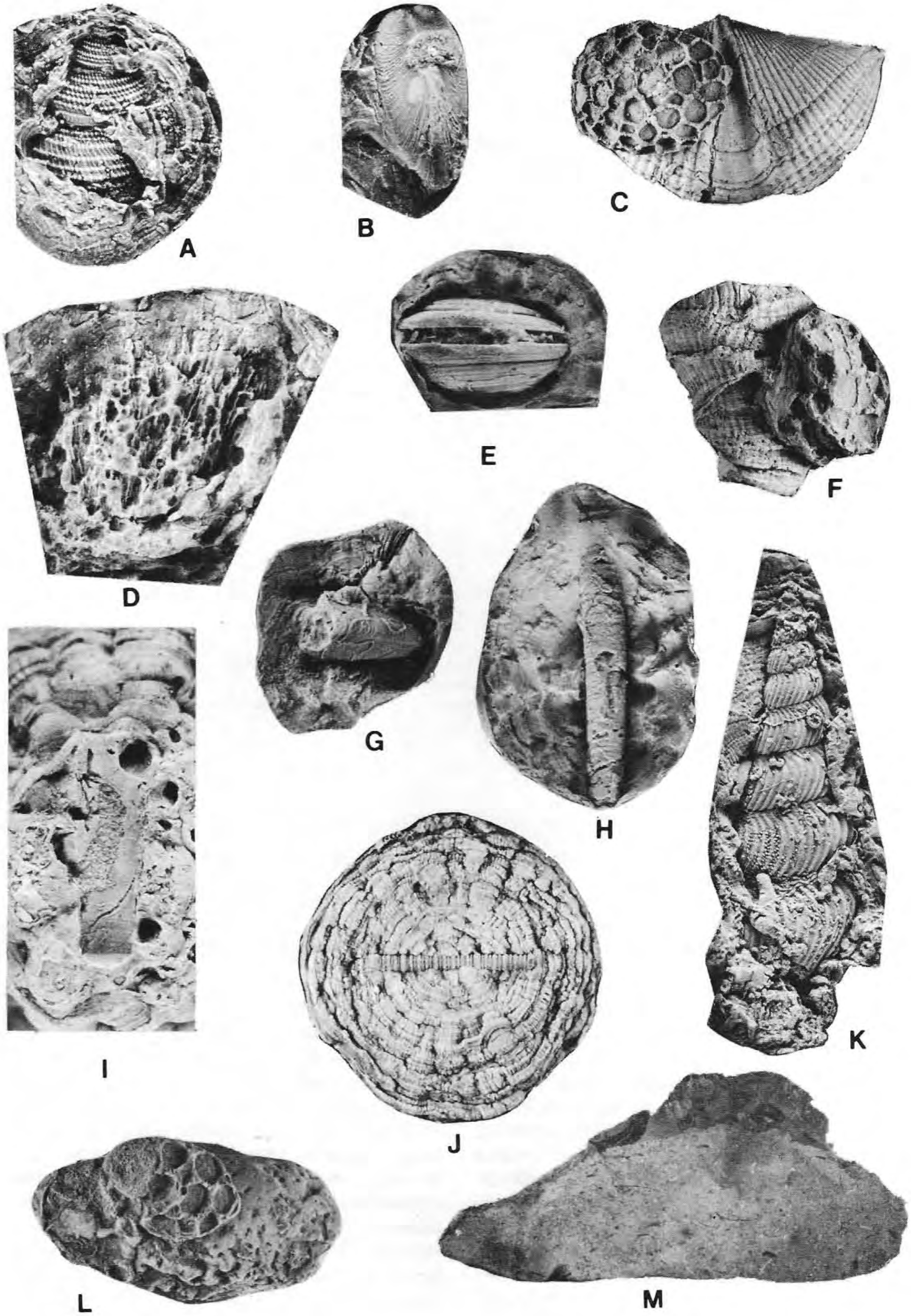
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Table 1. Pleurodictyum substrates. Key to locality numbers in Appendix.

Substrate	Wanakah					Jaycox		King Ferry	Kashong				Windom
Locality numbers:	1–7	8–10	11–13	14–15	16–23	13B	18B	22–23	8B,9	11	14	18C,21	3,5B,7B
Gastropods													
Palaeozygopleura	203	7	17	34	37	1	3	17	6	25	3	–	181
bellerophontids	1	–	1	–	–	–	–	–	–	1	–	–	8
others	5	–	–	1	–	–	–	1	–	1	–	–	8
Bivalves													
Paleoneilo	5	–	–	–	–	–	–	–	–	–	–	–	18
Cypricardella	3	–	–	–	–	–	–	–	–	–	–	–	6
nuculoids	–	–	–	–	–	–	–	4	–	–	–	–	9
others	16	3	1	–	2	–	–	–	–	–	2	–	20
Other molluscs													
Coleolus	18	–	–	–	–	–	–	1	–	–	–	–	12
nautiloid fragments	2	–	2	–	1	1	–	–	–	–	–	–	25
mollusc fragments	19	–	–	–	5	–	2	5	2	–	–	2	49
Corals													
Amplexiphyllum	–	–	–	–	–	–	–	–	–	–	–	–	46
Stereolasma	2	–	–	–	–	–	–	–	–	–	–	–	16
Pleurodictyum	1	–	–	1	–	–	–	2	–	–	–	–	13
auloporids	3	–	–	–	3	–	1	1	–	–	–	–	54
rugose	–	–	–	–	–	–	–	1	–	–	–	–	53
others	2	–	–	–	–	–	–	–	–	–	–	–	–
Brachiopods													
Tropidoleptus	1	–	–	–	–	–	1	–	1	1	8	1	–
Mediospirifer	1	–	–	–	–	–	–	–	–	–	–	–	7
chonetids	3	1	–	–	–	–	–	–	–	–	–	–	4
spiriferids	9	2	–	1	2	–	–	–	–	–	1	1	59
strophomenids	3	–	–	–	–	–	–	–	–	–	–	–	13
others	7	1	–	–	–	–	–	6	1	1	1	1	53
Trilobites	5	–	1	–	1	–	–	–	–	–	–	–	17
Bryozoans	5	1	–	–	–	–	–	–	–	–	1	–	6
Crinoids	4	–	–	1	1	–	–	–	–	–	–	–	7
Other organics	1	–	–	–	–	–	–	2	–	1	–	–	–
Inorganics													
phosphate pebbles	–	–	–	–	–	–	–	4	–	–	–	–	–
hiatus concretions	–	–	–	–	–	–	–	8	–	–	–	–	–
Undetermined													
substrate present	32	1	2	7	12	–	1	19	1	4	4	–	78
no substrate	4	1	–	5	–	–	–	–	–	–	–	–	143
Totals:			510				10	71			70		905

this is an unrealistically high value. In processing bulk samples we were careful to extract all fossils regardless of their preservation. These samples demonstrate that there was not complete loss of aragonitic fossils. Rather, severely compressed, plastically deformed external molds of mollusc shells occur abundantly within the shale matrix. Molds of *Palaeozygopleura* are readily recognizable because of their elongate shape and distinctive ornamentation (Fig. 5). They occur in all sizes, suggesting that taphonomic losses, if present, were not size-selective. Where *Pleurodictyum* specimens were collected with matrix rock, several show the presence of smeared-out molds of *Palaeozygopleura* in the attachment scar (Fig. 5A, B). Evidently, some recognizable molds were preserved, and provide a record of these aragonitic shells. These observations suggest that the demonstrable discrepancy between substrate abundances and matrix abundances is a real phenomenon. In turn, this indicates a high degree of selectivity for *Palaeozygopleura* shells by settling larvae of *Pleurodictyum*. Thus, we characterize *Pleurodictyum* as a semi-specific epizoan organ-

Table 2. Substrates of attachment for *Pleurodictyum americanum* expressed as percentage of total identified substrates.

Substrate	Erie County	Genesee County	Genesee Valley	Canandaigua Valley	Cayuga Valley
Wanakah–King Ferry localities:					
Palaeozygopleura	55.3	46.7	77.3	81.5	71.2
Other molluscs	24.5	20.0	18.1	1.9	15.4
Corals	3.1	–	–	1.9	5.8
Brachiopods	9.2	26.7	–	13.0	3.9
Other organics	4.0	6.7	4.6	1.9	3.9
Kashong localities:					
Palaeozygopleura	–	60.0	83.3	30.0	–
Other molluscs	–	20.0	6.6	20.0	–
Corals	–	–	–	–	–
Brachiopods	–	20.0	6.6	40.0	–
Other organics	–	–	3.3	10.0	–
Windom localities:					
Palaeozygopleura	27.7				
Other molluscs	22.1				
Corals	27.9				
Brachiopods	20.8				
Other organics	4.6				

Table 3. Comparison of taxonomic composition (numbers of specimens and corresponding percentages) of *Pleurodictyum* substrates with that of the total preserved assemblages in the Wanakah Shale (Spring Brook Station, tributary to Buffalo Creek) and the Windom Shale (Cazenovia Creek).

Taxa	Wanakah Shale				Windom Shale			
	Substrate		Total		Substrate		Total	
	n	%	*n*	%	*n*	%	*n*	%
Palaeozygopleura	78	61.4	15	2.4	120	26.7	1	0.3
Other gastropods	2	1.6	9	1.5	13	2.9	1	0.3
Bivalves	11	8.7	14	2.3	27	6.0	15	3.8
Nautiloids	0	0	6	1.0	22	4.9	3	0.8
Other molluscs	20	15.7	4	0.6	42	9.3	0	0
Corals	1	0.7	6	1.0	123	27.3	110	28.1
Brachiopods	10	7.9	487	78.9	84	18.7	131	33.5
Bryozoans	2	1.6	12	1.9	1	0.2	2	0.5
Trilobites	3	2.4	21	3.4	13	2.9	88	22.5
Crinoids	0	0	43	7.0	5	1.1	40	10.2
Undetermined	11				53			
No substrate	4				91			

ism. It could, and frequently did, colonize virtually any hard substrate available, but it shows a nonrandom preference for *Palaeozygopleura*.

Modern marine larvae are known to become decreasingly selective for substrate in later developmental larval stages (Knight-Jones 1953), which provides a probable explanation for semiselectivity of host substrates. We assume that the

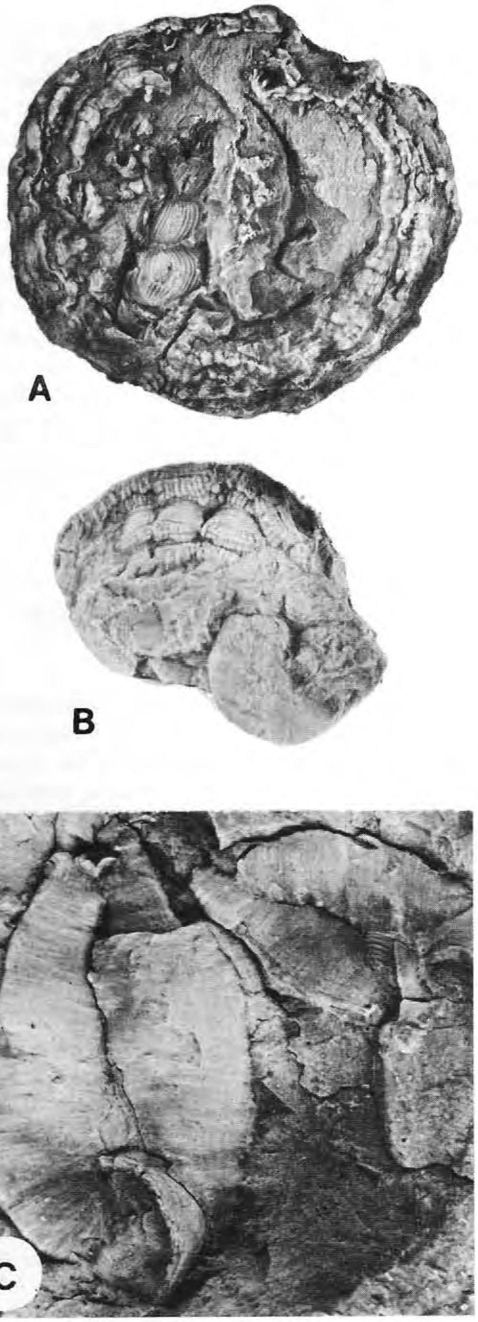


Fig. 5. Preservation modes of *Palaeozygopleura hamiltoniae*. □A. Compressed composite internal/external shale mold remaining intact on undersurface of *Pleurodictyum* specimen. Loc. 17, BMS E 24991, × 1.6. □B. Uncompressed steinkern (calcareous shale) on underside of *Pleurodictyum*. Loc. 22, BMS E 24992, × 3.6. □C. Highly compressed ('smeared') internal/external molds of *Palaeozygopleura*. Note smooth surface with slickensides (arrow points to area of preserved lirae ornamentation). Loc. 16, BMS E 24993, × 1.8.

same may have applied to *Pleurodictyum*. Hence, while the *Pleurodictyum* larvae probably had a preference for *Palaeozygopleura* shells, if such shells were unavailable the larvae did ultimately settle on any other available substrate.

Finally, *P. hamiltoniae* is probably not the only species which was selected as a substrate by *Pleurodictyum*. Certain other shells also occur in greater than expected frequency (based on bulk sample data). Most notable is a smooth, tube-like, annulated shell, tentatively identified as *Coleolus* sp. (Fig. 4H). *Coleolus* is generally quite rare in the matrix rocks. Although this taxon accounts for only a small proportion of *Pleurodictyum* substrates, it is present in many of the samples. This suggests possible selectivity, although insufficient sample sizes are available for statistical testing.

Biostratinomy of substrate fossils

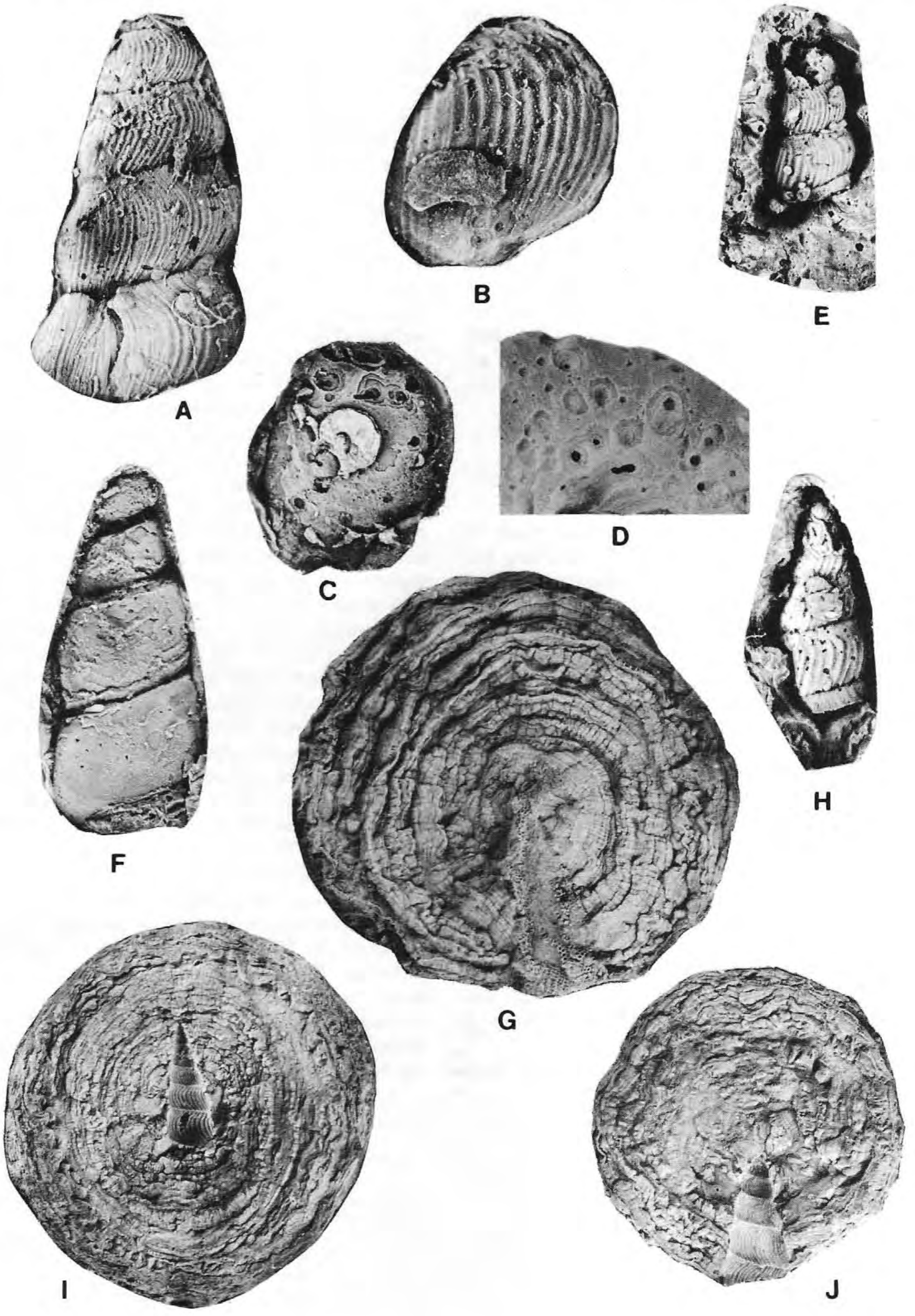
Orientation

The orientation of shells utilized as substrates by *Pleurodictyum* provides additional insights into the relationship between this coral and its substrates. Aside from *Palaeozygopleura,* most skeletal remains were encrusted by *Pleurodictyum* as they lay on the sea floor in a variety of post-mortem orientations (compare Fig. 4B and E). However, in the case of *Palaeozygopleura,* the orientations of the shells at the time of encrustation were remarkably consistent. Wherever the body whorl of the gastropod has been incorporated into the *Pleurodictyum* epitheca, the shell is observed to be oriented in an aperture-downward position. In no case have we noted the aperture of *Palaeozygopleura* preserved as a mold on the base of *Pleurodictyum*.

Observations of Recent empty turreted gastropod shells, although slightly different in morphology from *Palaeozygopleura,* suggest that the most stable orientation is aperture upward. Even in a strictly random distribution, at least some portion of the shells would be expected to occur in this orientation. Indeed, accumulations of *Palaeozygopleura* on bedding planes in the Hamilton Group do show both aperture-upward and aperture-downward orientations. Observations of 56 pyritized steinkerns of *P. hamiltoniae* from bedding planes of the Ledyard Shale at 11 Mile Creek, Genesee County, New York, show an aperture-down/aperture-up ratio of 1:1.95. Similar observations of 53 'smeared' shale molds from the upper Wanakah Shale at Deep Run Gully, Canandaigua Lake, yield a ratio of 1:1.3. Evidently the aperture-upward configuration was, if anything, more common in most accumulations of *Palaeozygopleura* shells. Thus, our data strongly suggest that *Pleurodictyum* did not settle randomly on empty *Palaeozygopleura* shells. Rather, the shells were preferentially oriented aperture downward, i.e. in apparent life orientation.

Observations were also made on the site of attachment of *Pleurodictyum* on the *Palaeozygopleura* shells, to determine whether or not the coral had a preference for a particular region of the shell. Each shell was subdivided into three regions corresponding to the apex, central shell, and the body whorl. That portion of the shell (i.e. apex, body whorl or central region) lying at the approximate center of the epitheca of each *Pleurodictyum* colony was judged to be the position of initial attachment of the founder corallite of that colony (Fig. 6I, J). Counts revealed a relatively high frequency of settlement on the body whorl relative to the center or apex (55.3 % vs. 24.3 % vs. 20.4 %). Initially this suggested a

Fig. 6. Biostratinomy of shells utilized by *Pleurodictyum* as attachment substrates. Specimens A–C, E, F and H are latex peels from external molds of *Palaeozygopleura hamiltoniae* (Hall) on the basal epitheca of *Pleurodictyum* cf. *americanum* Roemer. □A. Pre-mortem breakage and repair in *Palaeozygopleura*. Note crescentic reflection of growth lines in body whorl representing a 'healed' break in the apertural lip which occurred during growth of the gastropod. Note also the encrusting discoid foraminifers (?) and serpulids. Loc. 6, BMS E 24973, × 3.6. □B, C. Solution (?) pitting in *Palaeozygopleura* shells. Pits appear centered on possible sponge borings; note the 'bullseye' pattern due to successive penetration of shell laminae. In B, the shell shows well defined ornament, whereas in C, the exterior of the shell has been destroyed. Loc. 5B, BMS E 24974, E 24975, × 4.1. □D. Analogous 'bullseye' solution pits on shell of Recent freshwater gastropod *Helisoma* sp., × 4.1. □E, H. Post-mortem shell breakage in *Palaeozygopleura,* both specimens show broken margins on the body whorls and E displays a broken apex. Loc. 6, BMS E 24976, E 24977, × 3.6, ×4.1. □F. Shell 'smoothed' by complete removal of ornamented outermost layer (remnants of this layer remain along sutural shoulders). Loc. 3. BMS E 24978, × 4.1. □G. Basal epitheca of *Pleurodictyum* incorporating a shell of *Palaeozygopleura* which has been completely ensheathed with encrusting trepostome bryozoan *(Palaeschara?)* prior to overgrowth by the *Pleurodictyum*. Note the bryozoan sheath has been crushed following dissolution of the gastropod shell. Loc. 11, BMS E 24979, × 2.1. □I, J. Basal surfaces of *Pleurodictyum* coralla showing varying positions of colony center with respect to *Palaeozygopleura* shells. In I, the corallum is centered on the body whorl of the gastropod shell. In J, the colony center is near the apex of the shell. Loc. 8B. BMS E 24980, E 24981, × 1.1.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preference for settlement of the coral onto the body whorl: however, it is also evident that the body whorl presented a considerably larger target area for settlement than did the apical region of the shell. By comparing frequency of attachment in a particular section with the relative proportion of shell surface area represented by that section, it can be shown that *Pleurodictyum* was not, in fact, selective with respect to position on the *Palaeozygopleura* shell. Using a χ^2 test, the null hypothesis – that the proportion of corallite attachments in a given region of the shell is not significantly different from the proportion predicted by the relative surface area of that shell portion – cannot be rejected at all normally accepted levels of probability (test statistic = 4.15; $\chi^{2}2,0.05 = 5.99$, $\chi^{2}2,0.1 = 4.60$).

Condition of PALAEOZYGOPLEURA shells prior to encrustation by PLEURODICTYUM

Latex peels of *Palaeozygopleura* shell molds reveal fine details of shell surface including evidence for encrustation, shell breakage, and corrosion. Both pre-mortem and post-mortem shell damage are in evidence. Pre-mortem shell damage consists of readily discernible shell repairs. These are recognizable as crescentic lines which cut across the vertical shell ornamentation, marking fractures of the former shell apertural margin. The broken apertures were 'healed' by later accretion of shell material, often accompanied by distortion of growth lines and ornamentation (Fig. 6A). Crescentic breaks (repaired and unrepaired) occur frequently in Recent snail apertures and they often result from the action of predators such as crustaceans (Vermeij 1977). Discovery of similar breakage and 'healing' in Devonian gastropod molds represents the oldest record of such breaks (G. J. Vermeij, personal communication, 1980). This also provides evidence for (attempted) predation on gastropods in the Devonian.

Probable post-mortem damage includes unrepaired breaks in the shell, and corrosion or dissolution pitting. In most samples, a significant proportion of the shell casts show breakage. These include broken and chipped apices as well as holes through the shells (Fig. 6E, H). A distinctive type of corrosion pitting, characterized by a concentric or 'bullseye' pattern (Fig. 6C) apparently reflects breaching of successive shell layers around an initial hole through the periostracum. Very similar pitting, of unknown origin, has been found to occur in Recent freshwater gastropods (Fig. 6D). Complete removal of the outer shell layers results in some cases of 'smoothed' shell surfaces (Fig. 6F).

The substrate shells were also typically bored and encrusted by epizoic organisms prior to the final overgrowth by *Pleurodictyum* (Fig. 7). In some cases the gastropod shells were completely ensheathed by a layer of encrusting bryozoan. In Fig. 6G the bryozoan layer has collapsed due to removal, by dissolution, of the aragonitic gastropod shell and subsequent compaction. Most *Palaeozygopleura* and other aragonitic shells were encrusted by serpulid worms (Fig. 7A, D). A few also exhibit *Spirorbis,* ctenostome bryozoans, and possible sponges (Fig. 7G, H, J). Several molds also showed the presence of portions of the articulate brachiopod *Schuchertella,* seemingly attached to the *Palaeozygopleura* shell prior to its encrustation by a *Pleurodictyum;* this supports previous suggestions that these brachiopods were cemented by the interarea region. Many of the *Palaeozygopleura* shells also exhibit minute circular pits, most likely the borings of clionid sponges (Fig. 7D, E).

The abundance of damaged and encrusted *Palaeozygopleura* shells suggests that these were not occupied by living snails at the time of encrustation by *Pleurodictyum.* Most gastropods, including *Palaeozygopleura,* as demonstrated herein, are capable of healing breakage in the apertural region of the shell; yet numerous *Palaeozygopleura* specimens show unhealed breakage. High-spired snails such as *Palaeozygopleura*

Fig. 7. Epifaunal and endolithic organisms on shells utilized as substrates by *Pleurodictyum.* With the exception of H and I, all specimens are latex casts. □A. Basal 'U-tube' of *Hicetes* on *Coleolus* sp., Loc. 5B, BMS E 24982, × 4.1. □B. Minute pits and sinuous channels (sponge borings?) and serpulids on a fragment of mollusc shell. Loc. 5B, BMS E 24983, × 4.1. □C. Encrusting bryozoan (mold of zooecial apertures) on the shell of *Palaeozygopleura.* Loc. 6, BMS E 24984, × 3.8. □D. Serpulid tubes, sponge(?) borings and the brachiopod *Schuchertella* cf. *arctostriata* (Hall), on body whorl of *Palaeozygopleura.* Loc. 5B. BMS E 24985, × 4.1. □E. *Palaeozygopleura* shell 'riddled' with minute sponge(?) pits. Loc. 6, BMS E 24986, × 3.1. □F. Stolons of ctenostome bryozoans on *Palaeozygopleura.* Loc. 5B. BMS E 24987, × 3.6. □G. *Palaeozygopleura* encrusted by several serpulid and *Spirorbis* worm tubes and bryozoans. Loc. 9 BMS E 24970, × 3.1. □H. Base of *Pleurodictyum* on a fragment of brachiopod valve encrusted (on interior of shell) with the ctenostome bryozoan *Ascodictyon.* Loc. 5B, BMS E 24988, × 3.9. □I. Valve of bivalve *Pterinopecten* sp. cut by large channel-like annelid (?) boring. Loc. 2, BMS E 24989, × 2.0. □J. Undetermined encrustation on body whorl of *Palaeozygopleura,* possibly algal or sponge. Loc. 5B, BMS E 24990, × 3.7.

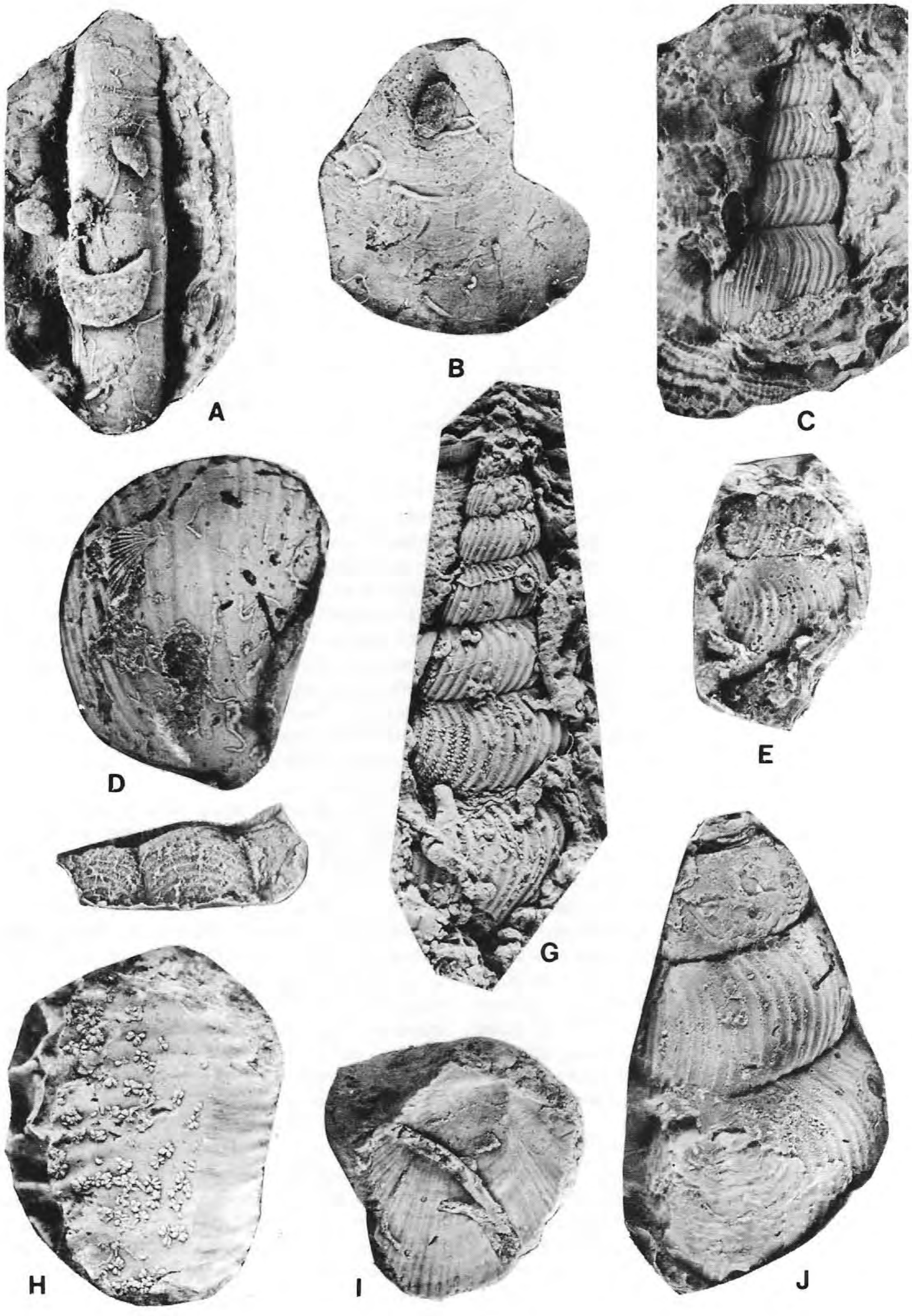
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Table 4. Known associations of encrusting corals and gastropod shells.

Coral	Attachment substrate	Age	Sediment	Remarks
Heteropsammia	gastropod	Recent	muddy sand	Coral settles on gastropod shell occupied by secondary host, *Aspidosiphon* (sipunculid) (Schindewolf 1959)
Heterocyathus	gastropod	Recent	muddy sand	Coral settles on gastropod shell occupied by secondary host, *Aspidosiphon* (sipunculid) (Schindewolf 1959)
Psammoseris	gastropod	Recent		Coral settles on gastropod shell occupied by secondary host, *Aspidosiphon* (sipunculid) (Schindewolf 1959)
Caryophyllia	*Ditrupa* (serpulid)	Recent	fine sand	Although *Ditrupa* appears to be the primary site selected for, the coral also settles on shells of *Aporrhais* and *Dentalium* which are occupied by the secondary host, *Phascolion* (sipunculid) (Wilson 1976)
Symbiangia	*Terebra* (gastropod)	Miocene		Small coral completely encrusts gastropod shell; conspicuous tube indicates possible secondary sipunculid host (Wells 1972)

are almost invariably shell-draggers; i.e. they carry the shell subhorizontally (Linsley 1977, 1979; P. W. Signor, personal communication). This might inhibit the growth of epizoans on the shell. Also, the spiral growth of *Palaeozygopleura* shells would result in epizoan encrusters (including *Pleurodictyum*) being periodically rotated downward into the mud of the sea floor. These lines of evidence suggest that the gastropod shells were not occupied by live snails at the time of attachment by *Pleurodictyum*.

Discussion

Data presented herein suggest a major paradox. On the one hand, the high degree of substrate selectivity by *Pleurodictyum* for *Palaeozygopleura* and the consistent aperture-downward orientations suggest that *Palaeozygopleura* shells were occupied by a living organism. On the other hand, unrepaired shell damage and encrustation argue against occupation of these shells by living snails. Any theory of the relationship involved must explain these facts and also take into account the semiselective nature of the *Pleurodictyum* encrustation.

We sought an answer to this paradox in modern coral analogs. Several living scleractinian corals are known to encrust gastropod shells of a particular species (Bouvier 1895; Schindewolf 1959; Goreau & Yonge 1968; Weisbord 1971; Wells 1972; Gill & Coates 1977). These include both solitary and colonial ahermatypic corals (Table 4). In all known cases, the corals are small forms which live predominantly on mud or muddy sand substrates. All are somewhat selective for particular snail shell types, but as far as known, none settle on living gastropods. Rather, they invariably occur on the shells of dead snails which are secondarily occupied by sipunculid worm hosts. Evidently, such corals are capable of inhabiting muddy areas inhospitable to most other species because of 'towing' by the sipunculids which maintains the polyps above the sediment–water interface during critical early growth stages (Gill & Coates 1977).

The most detailed study of a Recent coral–substrate relationship was that made by J. B. Wilson (1976) for the living coral *Caryophyllia smithii*. This species occurs on both hard rock substrates and on offshore muddy sands where it frequently encrusts the tubes of the polychaete *Ditrupa*. On sands, this coral also selects particular types of gastropod shells; however, again, they are never the shells of live snails, but those occupied by a specific species of sipunculid worm. Like *Pleurodictyum,* this coral is semiselective; whereas it favors *Ditrupa* tubes or secondarily occupied gastropod shells, it may also occur on dead bivalves and pebbles or cobbles. Despite its very distant taxonomic relationship with *Pleurodictyum,* we believe that *Caryophyllia* provides an excellent functional analog for the Devonian coral relationship described herein.

In summary, our studies demonstrate that *Pleurodictyum* was a semiselective epifaunal organism. It could and did inhabit a wide variety of

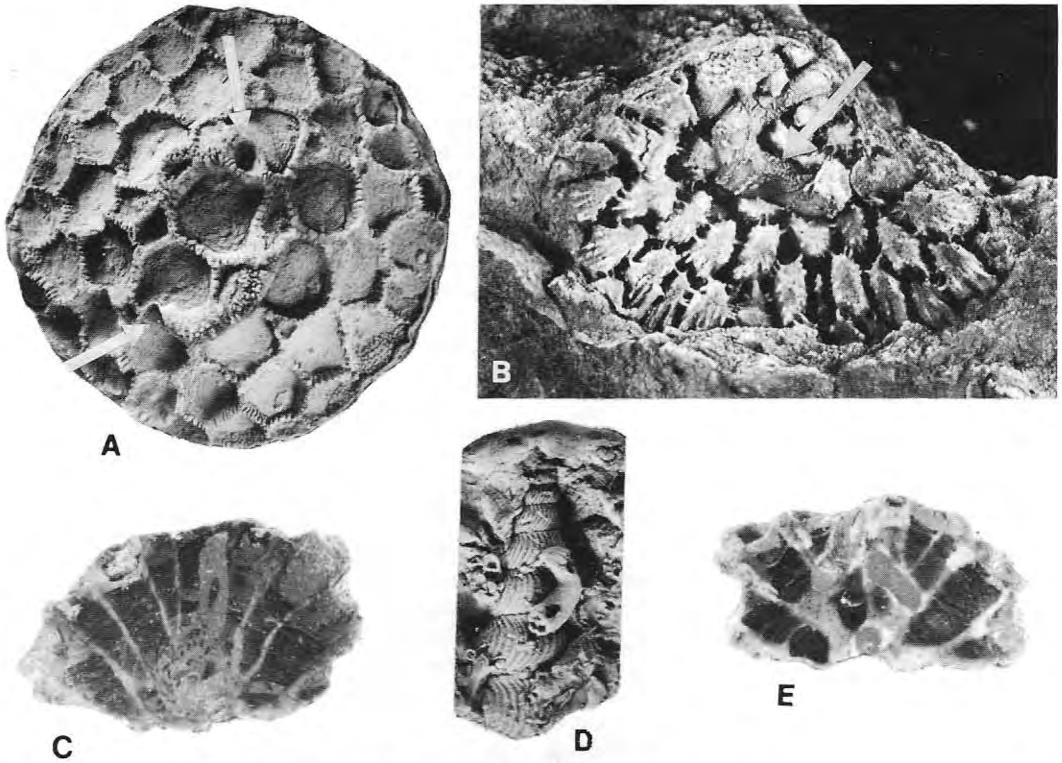

Fig. 8. Hicetes tubes in *Pleurodictyum* coralla. □A. View of upper surface of *Pleurodictyum* corallum showing a portion of the calcified tube of *Hicetes*. Note two circular openings (arrows). Loc. 9, BMS E 24996, × 3.0. □B. Internal mold of *Pleurodictyum* skeleton showing sediment-infilled U-shaped tube of *Hicetes* (arrow). Loc. 24, BMS E 24997, × 2.0. □C, E. Cross-sections through *Pleurodictyum* coralla showing mud and debris-filled, sinuous tubes of *Hicetes*. Locality unknown. BMS E 24999, × 1.5. □D. Basal portion of U-shaped *Hicetes* tube attached to *Palaeozygopleura* shell which served as a substrate for a *Pleurodictyum* colony; specimen is a latex cast of the undersurface of the *Pleurodictyum* corallum. Loc. 6, BMS E 25000, × 3.7.

large stable substrates. On most seafloors, however, settling larvae favored the shells of *Palaeozygopleura hamiltoniae*. We suggest that this selective mechanism was adaptive in assuring settlement of certain larvae on mobile substrates which were maintained above the sediment–water interface (cf. Jackson 1977:755–756). In the course of normal growth, the *Pleurodictyum* colony expanded over the larval substrate and developed secondary adaptations for support on the soft sea floor. These include a broad, flat bearing area ('snow shoe' effect) and a conical base ('iceberg' effect) (Thayer 1975; Seilacher 1978). It is notable that a related Devonian coral genus, *Antholites,* exhibits a similar substrate preference, occurring almost exclusively on the columns of certain large crinoids (McIntosh 1980); again, this allowed the colonies to develop at positions well above the muddy seafloor. Barthel & Barth (1972) also report the selective occurrence of *Michelinia transitoria* on shells of Devonian boring bivalves, which they inferred to have been living at the time of encrustation. These observations suggest that commensal relationships with live hosts were common among members of the Michelinidae.

Finally, data on Recent corals which settle selectively on snail shells provide a reasonable, if still unproven, resolution to the paradox noted above. Evidently, these coral larvae do not respond to chemical stimuli from live gastropods. Instead, it appears that certain empty snail shells are selectively inhabited by species of sipunculid worms (probably because of their shape). It is these reoccupied shells which are, in turn, encrusted by corals. Quite possibly, the coral larvae respond to ectocrine substances of the sipunculids. The 'hermit' sipunculids 'tow' the host shell in an aperture-downward orientation as do the original gastropod occupants (Schindewolf 1959;

Table 5. Co-occurrence of *Hicetes* with *Pleurodictyum* for different substrates at four stratigraphic horizons, expressed as the percentage of *Pleurodictyum* specimens containing *Hicetes*.

Substrate	Wanakah	King Ferry	Kashong	Windom
Palaeozygopleura	81.8	41.2	91.2	89.4
Bivalves	58.1	50.0	50.0	84.6
Other molluscs	83.6	42.8	83.3	84.5
Corals	83.3	–	–	67.6
Brachiopods	43.2	–	54.5	77.5
Bryozoans	66.7	–	–	83.3
Trilobites	71.4	–	–	70.6
Crinoids	66.7	–	–	57.1
Other organics	–	–	–	–
Inorganics	–	33.3	–	–
Undetermined	50.9	26.3	75.0	74.4
No substrate	88.9	–	–	83.9
Total	74.4	31.9	77.8	79.2
Number of specimens	510	71	70	905

Feustel 1965). However, the shell is not moved downward into the substrate nor is it actively growing. Hence, epibionts (including corals) have the advantage of a mobile substrate without the disadvantages associated with live gastropods. Thus, in contrast to the interpretation of Clarke, we do not believe that the interaction between *Pleurodictyum* and *Palaeozygopleura* involved settlement onto a live gastropod, but rather we suggest that *Pleurodictyum* selectively encrusted shells (of *Palaeozygopleura* and perhaps other taxa, e.g., *Coleolus*) which were occupied by secondary hosts, possibly sipunculid worms.

Marek & Galle (1976) discuss the semiselective encrustation of hyolithids, gastropods and nautiloids by the tabulate (alveolitid?) coral *Hyostragulum,* in the Lower Devonian of Bohemia and Moravia. Because of their consistent growth orientations these corals were judged to have settled on living and slightly active hosts; the possibility of secondary occupancy of the shells was not considered.

Pleurodictyum–Hicetes association

The association of *Pleurodictyum* with a spiral tube was first noted by Clarke (1908, 1921) and later studied in detail by Gerth (1952) and Schindewolf (1959). *Hicetes innexus* Clarke is inferred to have been a commensal tubicolous worm which formed an embedment structure (see Bromley 1970) within the corallum of *Pleurodictyum.* The occurrence of *Hicetes* in *P. americanum* is evidenced by two circular tube apertures on the upper surface of the coral colony and/or by a 'U' shaped depression at the site of the attachment scar. *Hicetes* must have settled on the substrate at nearly the same time as the *Pleurodictyum* larvae to produce a scar near the corallum attachment site (Fig. 8). Previous authors (Gerth 1952; Schindewolf 1959) suggested that the *Hicetes* worm occupied empty gastropod shells prior to their encrustation by *Pleurodictyum,* in analogy with a Recent coral–sipunculid association (*Heteropsammia–Aspidosiphon;* Bouvier 1895). However, such an association can be ruled out for *Pleurodictyum* which occur on substrates such as phosphate pebbles yet, nevertheless, have *Hicetes* tubes. We suggest that the *Hicetes* larvae were capable of detecting and settling on *Pleurodictyum* 'spats'. That the 'worms' were also capable of settling on established colonies is evident from specimens in which tubes penetrate only part way into the colony.

In any case, our material proves a very close association of *Hicetes* with *Pleurodictyum* (Table 5). More than 75% of all *Pleurodictyum* specimens examined were found to possess a single centrally located *Hicetes* tube. In certain samples as many as 90% of *Pleurodictyum* specimens were infested. This association does not appear to be related to the type of substrate utilized by *Pleurodictyum.* Slight differences were observed in the proportion of *Hicetes*-infested specimens occurring among *Pleurodictyum* specimens on various substrates, but these are largely artificial. For example, subsamples of *Pleurodictyum* attached to brachiopods and corals tend to exhibit fewer apparent cases of *Hicetes* partly because these calcitic substrates remain intact so that the basal 'scar' can not be examined for traces of the *Hicetes* tube. Thus, we judge the *Pleurodictyum–Hicetes* association to be independent of any *Pleurodictyum*–substrate association.

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Appendix: Locality register

(All quadrangles 1:24,000)

1. Eden Quadrangle – Erie lakeshore bluffs 0.3–0.5 miles south of Wanakah waterworks Wanakah, Erie Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

2. Buffalo Southeast Quadrangle – Shale pit immediately north of unnamed west-flowing creek, and 0.3 miles southwest of WKBW radio towers along Big Tree Road, Blasdell, Erie Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

3. Buffalo Southeast Quadrangle – Large abandoned shale pit of Penn Dixie Cement Co., 0.3 miles northwest of intersection of Big Tree and Bay View roads, Blasdell, Erie Co., N.Y. (Lower Windom Shale, 'coral bed').

4. Buffalo Southeast Quadrangle – Banks of small north-flowing tributary of south branch of Smoke Creek, 0.3 miles north of Mile Strip Road and 0.5 miles west of Abbott Road, Orchard Park, Erie Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

5A. Orchard Park Quadrangle – Bed of Cazenovia Creek 0.5 miles west of Transit Road, West Seneca, Erie Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

5B. Orchard Park Quadrangle – Banks of Cazenovia Creek north and south of Northrup Road, Spring Brook, Erie Co., N.Y. (Windom Shale, 'coral bed').

6. Orchard Park Quadrangle – Bed of north-flowing tributary of Buffalo Creek, immediately north of Bullis Road and 0.7 miles east of intersection with Pound Road, Spring Brook Station, Erie Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

7A. East Aurora Quadrangle – Low banks of Buffalo Creek between Bowen and Girdle Road, Elma, Erie Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

7B. East Aurora Quadrangle – Banks of Buffalo Creek 0.1–0.2 miles south of Bullis Road old bridge, Elma, Erie Co., N.Y. (Windom Shale, 'coral bed').

8A. Alexander Quadrangle – Shale bank along west branch of Murder Creek, 0.6 miles south of Sharrack Road and 0.6 miles north of U.S. 20, Darien, Genesee Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

8B. Alexander Quadrangle – Bed of west branch of Murder Creek, 0.4 miles south of U.S. 20, Darien, Genesee Co., N.Y. (Kashong Shale).

9. Alexander Quadrangle – Banks of west fork of Bowen Creek 0.2 miles south of Walker Road and 0.4 miles west of Gilate Road, Alexander, Genesee Co., N.Y. (Kashong Shale).

10. Batavia South Quadrangle – Railroad cut along Erie–Lackawanna Railroad tracks, just east of Francis Road overpass and 1.7 miles north of U.S. 20, Bethany, Genesee Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

11. Leicester Quadrangle – Shale dumps and railroad cut at International Salt Company mine, 0.35 miles south of N.Y. Route 63, Retsof, Livingston Co., N.Y. (Kashong Shale).

12. Leicester Quadrangle – Shale banks along Bidwell Creek 0.3 miles northwest of Retsof Road, Retsof, Livingston Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

13A. Geneseo Quadrangle – Banks of Jaycox Creek in lower part of Jaycox Run and Wheeler Gully 0.5 miles west of N.Y. Route 39 and 2 miles north northeast of Geneseo, Livingston Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

13B. Geneseo Quadrangle – Jaycox Creek in upper part of Jaycox Run, 0.3 miles east of loc. 13A (Jaycox Shale).

14. Canandaigua Lake Quadrangle – Shale banks upstream from high falls in Menteth Gully 600′ west of West Lake Road, west side of Canandaigua Lake, Ontario Co., N.Y. (Kashong Shale).

15. Rushville Quadrangle – Banks of small unnamed west-flowing creek 0.3 miles north of U.S. Route 20, 3 miles southwest of Hopewell and 2 miles west of Aloquin, Ontario Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

16. Canandaigua Lake Quadrangle – Banks of Deep Run Gully 1.2 miles south of Kipp Road east side of Canandaigua Lake, Gorham, Ontario Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

17. Canandaigua Lake Quadrangle – Banks of Gage Gully 0.3–0.7 miles southeast of East Lake Road, east side of Canandaigua Lake, Gorham, Ontario Co., N.Y. (Kashong Shale).

18A. Geneva South Quadrangle – Shale banks above upper falls in Kashong Creek 4.2 miles west of N.Y. Route 14, south of Geneva, Ontario Co., N.Y. (Kashong Shale).

18B. Geneva South Quadrangle – Lower (high) falls and adjacent shale banks along Kashong Creek about 0.3 miles east of loc. 18A. (Jaycox Shale).

18C. Geneva South Quadrangle – Shale in creek bed and banks of Kashong Creek about 0.3 miles west of N.Y. Route 14 and 0.6 miles east of loc. 18B. (Wanakah Shale, *Pleurodictyum* beds).

19. Romulus Quadrangle – Small roadside quarry along N.Y. Route 336, 3.5 miles east of MacDougall, Seneca Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

20. Dresden Quadrangle – Small man-made cut along lower reaches of stream that marks north border of Sampson Naval Facility, east side Seneca Lake, Seneca Co., N.Y. (Wanakah Shale, *Pleurodictyum* beds).

21. Dresden Quadrangle – Shale banks along Indian Creek between N.Y. Route 96A and the east shore of Seneca Lake near Willard, Ontario Co., N.Y. (Kashong Shale).

22. Ovid Quadrangle – Shale banks along Big Hollow Creek, 0.3 miles north of Swick Road and about 2 miles north of Hayt Corners, Seneca Co., N.Y. (King Ferry Shale; upper hiatus concretion zone).

23A. Ovid Quadrangle – Shale bank along Mack Creek 2 miles east of Hayt Corners and 0.5 miles west of N.Y. Route 89, Seneca Co., N.Y. (King Ferry Shale; upper hiatus concretion zone).

23B. Ovid Quadrangle – Shale banks along Bloomer Creek 0.5 miles south of loc. 23A (King Ferry Shale; upper hiatus concretion zone).

24. Gilboa Quadrangle – Roadcut on unnamed road off Route 30, 3 miles southeast of North Blenheim, Schoharie Co., N.Y. ('Portland Point' equivalent).