

Significance of the occurrence of chemoautotrophic bacterial endosymbionts in lucinid clams from Bermuda

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ABSTRACT: Five species of lucinid clams from Bermuda (*Codakia costata*, *Ctena orbiculata*, *Parvilucina multilineata*, *Lucina radians*, *Anodontia philippiana*) had ribulose-1,5-bisphosphate carboxylase activity in the gills. Presence of this enzyme of the Calvin-Benson cycle along with dark coloration of gills and morphologically simplified digestive tract strongly suggests presence of chemoautotrophic bacteria living symbiotically with the clams. Natural history is described for these 5 lucinids and several others not studied biochemically. All inhabit reduced sediments rich in organic matter, where hydrogen sulfide is detectable. Results, along with previously published studies, indicate that most clams of the family Lucinidae live symbiotically with chemoautotrophic bacteria in their gills and inhabit sulfide-rich environments.

INTRODUCTION

Since the original discovery of a symbiosis between invertebrates and intracellular chemoautotrophic bacteria in animals from hydrothermal vents (Cavanaugh et al. 1981, Felbeck 1981), this type of symbiosis has been discovered in molluscs (Cavanaugh 1983, Felbeck et al. 1983), pogonophorans (Southward et al. 1981, Southward 1982), and annelids (Giere 1981). A relatively large number of bivalves have been determined by optical and enzymatic methods to contain symbiotic bacteria inside the gill cells. Among these are phylogenetically diverse molluscs including representatives of the protobranchs, *Solemya reidi* (Felbeck 1983) and *S. velum* (Cavanaugh 1983), and diverse eulamellibranchs (see Felbeck et al. 1983 for review). So far, all eulamellibranchs known to contain endosymbiotic bacteria are predominantly of the family Lucinidae and, to a lesser extent, of the family Vesicomidae. Typically, clams with symbionts lack a digestive tract (*S. reidi*: Reid 1980), or have it greatly reduced (*S. velum*: Cavanaugh 1983). The symbionts may provide the host bivalves with reduced organic matter, facilitate their digestion or synthesize vitamins necessary for the host (Felbeck et al. 1983). Energy the bacteria need for these tasks is derived mainly from

oxidation of sulfide from the environment. This sulfide can originate either from geothermal sources as at the hydrothermal vents or from decaying organic matter as, for example, in the habitat of the clam *S. reidi*, which lives close to sewage outfalls (Felbeck 1983) or near pulp mills (Reid 1980). Similarly, sulfide is produced by decaying seagrass leaves in the habitats of *S. velum* (Cavanaugh 1983) and *Lucina floridana* (Fisher & Hand 1984).

In this study we searched for more mollusc species with autotrophic symbiotic bacteria. The survey was conducted in Bermuda in similar habitats to those described for other symbiont-containing bivalves, primarily members of the family Lucinidae. We also addressed the question whether the presence of symbiotic bacteria is characteristic for a given genus or whether it may be an adaptation of individual species or even individual animals.

MATERIAL AND METHODS

Most ecological studies were conducted during 2 stays on Bermuda, in 1978 and 1980 to 1981. Species for enzyme analysis were collected in Bermuda in July 1984. Specimens were identified using Abbott (1974)

and Britton (1972). The most common clams *Codakia orbicularis*, *C. costata*, *Ctena orbiculata*, and *Parvilucina multilineata* were sampled quantitatively by SCUBA diving using an air-suction sampler manually controlled by the diver (frame size of sampled area was 400 cm²; mesh size 500 µm). Collection site for these animals was the inshore lagoon, Harrington Sound, south of Trunk Island where 6 or 7 samples were taken from each of 3 stations (3 m, 9 m, and 13 m depth) at monthly intervals. In 1978 samples from 2 transects, from shallow water down into the basin, were used for estimates of animal distribution. Sediments were taken and analyzed for grain size as described by Neumann (1965).

The redox potential discontinuity layer (RPD-layer) was identified by the sulfide dependent change of color in carbonate sediments as described by Adshead (1964).

Since the other 2 species collected, *Anodontia philippiana* and *Lucina radians*, are uncommon or rare on Bermuda a quantitative analysis of their life habits could not be performed. *A. philippiana* was found in Mangrove Bay, Ferry Reach, using the method described by Obrochta & Paisley (1970). *L. radians* could be detected offshore of Windsor Beach, north of North Rock in 17 m depth, and off the North East Breakers in 18 m depth in canyons.

Results from Harrington Sound were analyzed using the U-test of Mann and Whitney (95 % confidence) for the comparison of populations of species in different habitats. Thus the favorite biotopes of species were emphasized and compared to records of molluscan associations on the Bermuda platform and descriptions of their habitats (Gould 1968, Aurelia 1969, Waller 1973, Barnes & v. Bodungen 1978, v. Bodungen et al. 1982).

The method described by Felbeck (1981) was used for testing the enzyme indicative of the presence of autotrophic bacteria in the gills, the characteristic enzyme of the Calvin-Benson cycle, ribulose-1,5-bisphosphate carboxylase. Gills were dissected from freshly collected animals and the activity assayed in

the supernatant of a centrifuged (10 min, 27,000 g) homogenate.

RESULTS

Occurrence and habitat of lucinid species in Bermuda

Eight species of lucinids are known to live in Bermuda (Table 1), 5 of which we investigated; the other 3 species could not be found. The main collection site was in Harrington Sound where their habitat could be described by sediment analyses.

Grain size analyses of 2 transects in Harrington Sound are shown in Table 2. The grain size shifts to smaller fractions with increasing depth. In Harrington Sound lucinid species range from shallow water (sea-grass beds or close vicinity) down to the upper part of the *Oculina* zone (10 to 13 m) (Fig. 1). In other lagoons, e.g. St. George's Harbour and Castle Harbour, lucinid species favor habitats with grain sizes similar to those found in Harrington Sound (Morris et al. 1977, v. Bodungen et al. 1982).

Codakia orbicularis predominantly occurs in sea-grass beds ($p < 0.05$, Fig. 1) (*Thalassia testudium*, *Syringodium filiforme*) in 5 to 12 cm depth, a few cm below the RPD-layer, although juveniles also settle in sandy and muddy sediments (Fig. 2). There, however, *C. orbicularis* does not reach the size possible in sea-grass beds (no more than 16 mm compared to > 9 cm).

Codakia costata and *Ctena orbiculata* are less abundant and show a very patchy distribution. Specimens of 1 cm diameter were found in the *Oculina* zone in about 4 cm depth. According to Aurelia (1969) they can be very abundant in *Thalassia* beds (26 ind m⁻²) but he did not separate the 2 species. Larval settlement is very low since the size classes of 1 to 2 mm were very rare throughout the year. *C. orbiculata* is not restricted to shallow water sediments but also favors muddy sediments (St. George's Harbour) or deeper water (Jackson 1973, Treece 1980). *C. orbiculata* has been described as a conspicuous infaunal element in Great Sound (v. Bodungen et al. 1982).

Table 1. Species of bivalves collected in Bermuda with locations (shown in Fig. 1) and range of distribution

Species	Locality	Range of distribution
<i>Linga pensylvanica</i> (Linne 1758)	1, 2	Cape Hatteras-West Indies
<i>Parvilucina multilineata</i> (Tuomey & Holmes 1857)	3, 4, 5, 6, 8, 9	Cape Hatteras-West Indies-Brazil
<i>Codakia orbicularis</i> (Linne 1758)	3, 4, 5, 6, 7, 8	Florida-West Indies-Brazil
<i>Codakia costata</i> (Orbigny 1842)	5, 8	Cape Hatteras-West Indies-Brazil
<i>Ctena orbiculata</i> (Montagu 1808)	3, 5, 8, 9	Cape Hatteras-West Indies-Brazil
<i>Ctena pectinella</i> (Adams 1852)	3, 6, 9	Florida-West Indies-Brazil
<i>Lucina radians</i> (Conrad 1841)	10, 11, 12	Cape Hatteras-West Indies
<i>Anodontia philippiana</i> (Reeve 1850)	4, 8	Cape Hatteras-Florida-Cuba

Table 2. Grain size distribution (1 exemplary sample per depth) of various surface sediments from 2 transects in Harrington Sound. Fractions expressed as % of total dry weight. S: medium sand; SS: medium sand with fine sand and silt; M + S: silt with fine sand; M: silt; Sh: shell fragments; Oc: *Oculina*

Depth (m)	> 2000 μm	> 500 μm	> 200 μm	> 63 μm	> 20 μm	< 20 μm	Sediment
Transect A							
10	30.6	11.4	9.2	27.2	17.4	2.2	M + S, Sh, Oc
11	4.7	15.9	13.7	20.6	40.9	3.6	M + S, Sh, Oc
16	1.5	5.1	4.8	25.2	58.1	4.9	M, Sh
19	0.5	4.8	5.9	15.1	65.7	7.9	M, Sh
22	0.4	0.2	0.9	10.2	76.8	10.7	M
24	0.7	0.3	0.9	5.7	78.6	11.6	M
Transect B							
2.5	6.2	37.1	50.0	5.6	0.9	0.2	S
7	13.3	31.3	39.7	7.8	5.1	2.9	SS, Sh
12	9.8	6.8	7.9	25.9	48.1	3.8	M + S, Sh, Oc
15	1.4	2.9	3.7	22.0	55.9	4.5	M, Sh
16	17.2	4.9	3.9	10.1	58.0	5.0	M, Sh
18	14.3	8.9	7.9	10.2	53.2	4.7	M, Sh
20	3.5	5.0	10.2	12.0	63.6	4.7	M, Sh

Ctena pectinella prefers rather fine sandy sediments in protected shallow inshore bays (e.g. northeast of Smith's Island in St. George's Harbour and Tucker Town Cove in Castle Harbour) which are influenced by weak tidal currents.

Parvilucina multilinea is found predominantly in sheltered inshore bays with high sedimentation rates of fine particles due to reduced water movement (Fig. 3). It is very abundant and part of the dominant

infauna. Harrington Sound which was investigated more closely has a variety of sediments ranging from very little silt content to silt with shell fragments (Table 1; Neumann 1965). The population density of *P. multilinea* ranges from 2 to 20 ind 0.1 m^{-2} in shallow sand, 3 to 46 ind 0.1 m^{-2} in sand with higher silt components, and 9 to 63 ind 0.1 m^{-2} in the upper part of the *Oculina* zone (Fig. 3), a belt ranging from 10 to 13 m depth with high sedimentation rates of fine

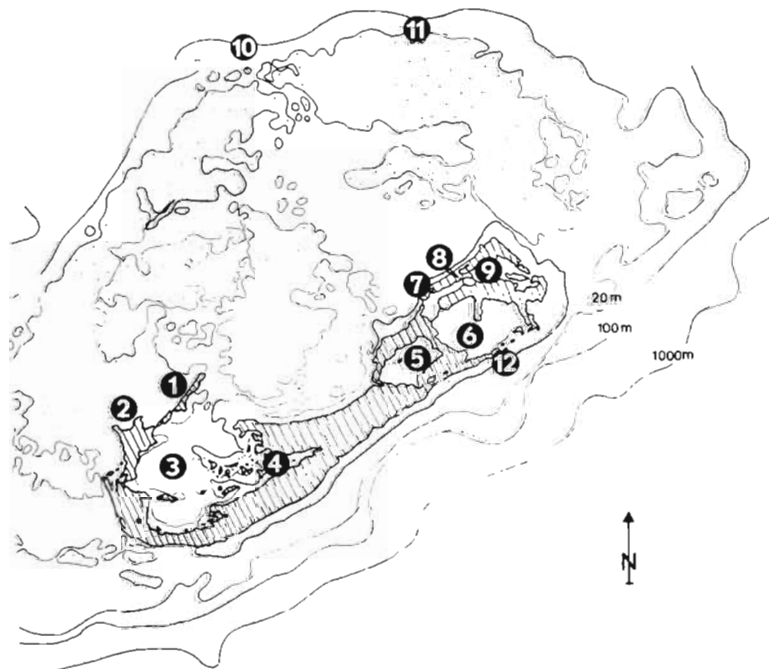


Fig. 1. Map of Bermuda with sampling locations: (1) Ireland Island, (2) Somerset Island, (3) Great Sound, (4) Hamilton Harbour, (5) Harrington Sound, (6) Castle Harbour, (7) Whalebone Bay, (8) Mangrove Bay, (9) St. George's Harbour, (10) North Rock, (11) North-eastern Breakers, (12) Southshore

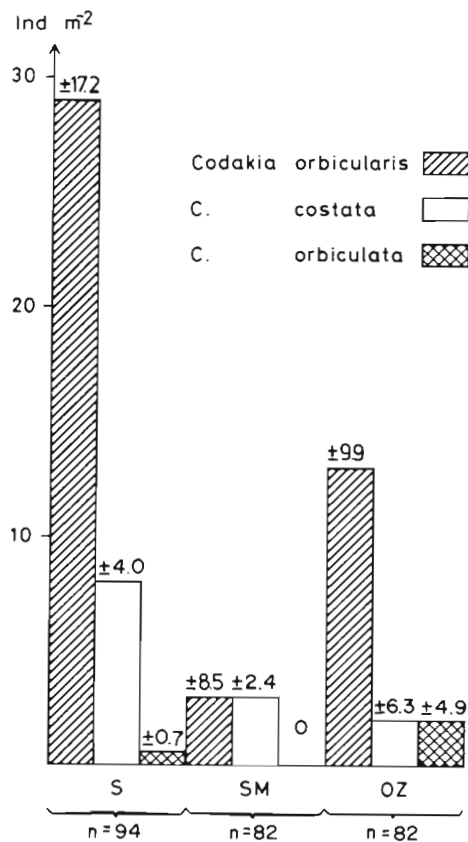


Fig. 2. *Codakia orbicularis*, *C. costata*, *C. orbiculata*. Abundance in various sediments. Means \pm SD. S: shallow sand (1 to 3 m depth) (n = 94); SM: sand with higher silt content (5 to 9 m depth) (n = 82); OZ: *Oculina* zone, shell and coral fragments, predominantly silt with a small fraction of fine sand

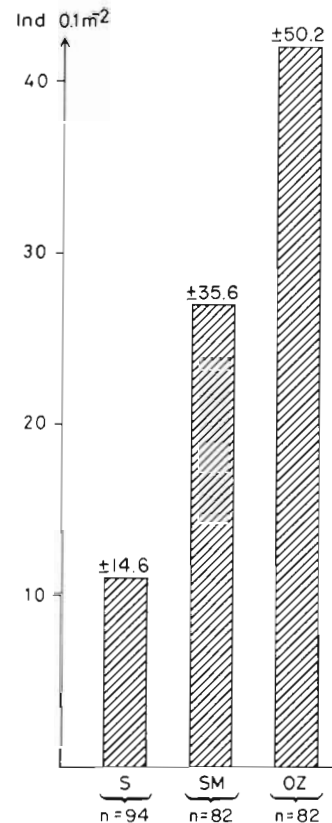


Fig. 3. *Parvilucina multilineata*. Abundance in various sediments. Means \pm SD. See Fig. 2 for explanation of abbreviations

particles. From October to February *P. multilineata* was present in 43 to 71 % of the samples taken at shallow sand stations while from March to September this ratio was between 86 and 100 %. Presence at other stations ranges between 83 and 100 % throughout the year. The RPD-layer in this environment is at a few mm depth. Dwarf forms of 1 to 4 mm diameter lived down to 1 cm in the sediment, below the RPD-layer, and contained males (3.5 mm size) with ripe gonads and females (4.4 mm size) with fully developed eggs.

Lucina radians occurs in canyons along the reef fringe (North Rock, 15 m depth; N. E. Breakers, 17 m depth; sheltered canyons along South Shore). It is common in its habitat (2 ind m⁻²) but the distribution pattern is patchy. Although still offering quite sheltered conditions the sediments inhabited by *L. radians* are more frequently disturbed by wave action or wind-induced currents than inshore sediments. Sediment fractions are ~ 10 % debris (corals, shells) > 2 mm, ~ 50 % very coarse to coarse sand with fine gravel 500 to 2,000 μ m, ~ 38 % fine sand 125 to 500 μ m, the rest contains silt plus organic components.

Linga pensylvanica was only found at 2 sites (Ireland Island, Somerset Island) in shallow water *Thalassia* beds. It is considered to be very rare in Bermuda. Fossil records, however, are common in the vicinity of Mangrove Bay, Somerset Island and the southern part of Ireland Island (pers. obs. and collections).

Anodontia philippiana inhabits very sheltered bays often close to mangrove stands, e.g. Mangrove Bay, Ferry Reach (Obrochta & Paisley 1970), and Hamilton Harbour (v. Bodungen et al. 1982). This species was widely distributed in inshore shallow waters in the past but possibly due to anthropogenic reduction of mangroves, populations are now very small and almost exclusively only fossil records are left (e.g. Millhouse Bay, Gibbet Island). Reminders of peat layers consisting of leaf and branch material were observed close to the fossils in these shallow bays. Specimens of 7 cm diameter were collected in Mangrove Bay, Ferry Reach, 60 to 70 cm deep in the sediment at the edge of a mangrove stand. The undisturbed sediments consist of silt to clay with thin intervening layers of fine sand. No juveniles were found. In Hamilton Harbour *A. philippiana* lives in muddy sediments in a passage with an abundance up to 319 \pm 256 ind m⁻² (v. Bodungen et al. 1982 p. 77, Sta. 20).

Table 3. Activities of ribulose-1,5-bisphosphate carboxylase in the gills of some bivalve species from Bermuda

Species	Activity $\mu\text{mol min}^{-1} (\text{g fresh wt})^{-1}$
<i>Codakia orbiculata</i>	0.14
<i>Codakia costata</i>	0.32
<i>Anodontia philippiana</i>	0.1
<i>Lucina radians</i> ¹	0.03
<i>Parvilucina multilineata</i> ¹	0.03

¹ Due to the small size of the animals no clean preparation of gills was possible i.e. gill tissue was probably contaminated with mantle or foot tissue

Indication for autotrophic symbiotic bacteria in gills of Lucinidae

Gills were dissected from 5 bivalve species (listed in Table 3) and the activity of ribulose-1,5-bisphosphate carboxylase tested. The tests were positive indicating the presence of autotrophic bacteria. All gills were unusually thick, the color ranging from light brown to dark purple.

DISCUSSION

Five species of lucinid clams were shown to contain the enzyme ribulose-1,5-bisphosphate carboxylase in extracts of gill tissue. This enzyme is characteristic for

the presence of the Calvin-Benson cycle of autotrophic CO₂ fixation in microorganisms and plants, but not in animals. The presence of this enzyme in non-digestive (to avoid contamination by food or gut bacteria) and non-green (to avoid symbiotic algae or chloroplasts as source) animal tissues has been used in the past to indicate the existence of a symbiosis of autotrophic bacteria with an invertebrate host (Felbeck 1981, Felbeck et al. 1981). In all cases where a closer examination of the bacterial symbionts with electron microscopy was performed, its existence could be proven (Cavanaugh et al. 1981, Cavanaugh 1983, Felbeck 1983, Berg & Alatalo 1984, Fischer & Hand 1984, Giere et al. 1984, Giere 1985). It is therefore assumed that also in these newly described cases the enzyme is an indicator for bacteria in the gill cells. All the clams from Bermuda investigated in this paper live in a common environment which may be typical for lucinid bivalves containing bacterial symbionts. It is characterized by the availability of undisturbed sediments and input of organic material as has been summarized by Morris et al. (1977).

Lucinid clams containing bacterial symbionts are listed in Table 4. One group (*Codakia orbicularis*, *Ctena orbiculata*) prefers shallow inshore sediments in seagrass beds which are known to stabilize sediments, reduce water movements, and trap detritus and organic debris from the phytal zone of rocky shorelines (Fenchel 1970, Jackson 1972). This preference is also observed in the Caribbean (Stanley 1970, Jackson 1972, 1973, Turney & Perkins 1972, Young & Young

Table 4. List of lucinid clams proven or suspected to contain bacterial symbionts. Where no + is listed no information is available

Subfamily and species	Dark gills	RuBPCase	Reference
Lucininae			
<i>Linga (Lucina) pensylvanica</i>	+	+	Berg & Alatalo 1984
<i>Parvilucina tenuisculpta</i>	+	+	Felbeck et al. 1981
<i>P. multilineata</i>	+	+	*
<i>Codakia orbicularis</i>	+	+	Berg & Alatalo 1984
<i>C. costata</i>	+	+	*
<i>Ctena orbiculata</i>	+	+	*
<i>Ct. pectinella</i>	+		Jackson 1973
<i>Lucina pectinata</i>	+		Read 1966, Jackson 1973
<i>L. radians</i>	+	+	*
<i>L. nassula</i>	+	+	Berg & Alatalo 1984
Myrteinae			
<i>Myrtea spinifera</i>	+		Schweinemanns unpubl.
<i>Lucinoma annulata</i>	+	+	Felbeck et al. 1981
Milthinae			
<i>Anodontia alba</i>	+		Jackson 1973
<i>A. philippiana</i>	+	+	*
<i>Pseudomiltha (Lucina) floridana</i>	+	+	Fischer & Hand 1984

* Species investigated in this study

1982). The same habitat is preferred by *Lucina pectinata* and *Linga pensylvanica* (Stanley 1970, Young & Young 1982). *C. orbiculata* dominates in sea water ponds (e.g. Walsingham Pond) with slow water exchange in 'muddy' sediments (Gould 1968). *Parvilucina multilineata* prefers biotopes with high organic sedimentation and resuspension. A similar distribution pattern is shown by the Pacific relative *P. tenuisculpta*, which favors either a biotope with coarse carbonate sediments and high organic content or a habitat influenced by highly organic sewage wastewater (Jones & Thompson 1984).

Several adaptations to the habitat can be found in the lucinids on Bermuda and generally in other relatives, e.g. embryo protection by egg capsules (Miyazaki 1938, Blacknell & Ansell 1974), and a reduction of the digestive tract which is expressed in loss of sorting areas and reduction of palps and ducts connecting digestive diverticula and stomach (Allen 1958). In the past, this has been interpreted as a simplification to enable species which live in an environment poor in suspended small food to consume large food particles such as decomposed organic material (Purchon 1960). The presence of symbiotic bacteria in the clam gills suggests another explanation for the reduced digestive tract, i.e. the animals do not need much, if any, particulate food, because all or part of their nutritional requirements are satisfied by using organic material released by the bacteria. In some other bivalves (*Solemya reidi*) or worms (e.g. all pogonophorans, the oligochaete *Phallodrilus leukodermatus*) containing bacterial symbionts the reduction of the digestive tract is complete, i.e. no digestive tract is formed (Reid 1980, Giere 1981, Ott et al. 1982). This finding suggests that these animals are able to survive entirely on the supply of reduced organic matter produced by the bacteria and uptake of dissolved organic material from the environment. It has been proposed that the symbiotic bacteria are supported by the presence of environmental hydrogen sulfide which they oxidize to gain energy for CO₂ fixation (Felbeck et al. 1983). In the environment of the lucinid species in Bermuda conditions are comparable to the biotopes where other animals with reduced or absent guts are found. Sediments are rich in particulate and dissolved organic material (Erlenkeuser et al. 1981, Giere et al. 1982), and microbially produced sulfide is present in the immediate environment since all clams in Bermuda ascertained to have symbionts live beneath the RPD-layer (pers. obs.). Many other lucinid clams described live in similar environments to those on Bermuda (Stanley 1970, Moore & Lopez 1972, Poore & Rainer 1974, Tanaka & Kikuchi 1979, Morton 1983). It has been shown that other animal/bacteria symbioses from sulfide rich habitats not only survive high sulfide concentrations,

but also metabolize sulfide efficiently (Arp & Childress 1983, Felbeck 1983, Powell & Somero 1983). This ability has been attributed to either a sulfide detoxification system or the hemoglobin present in the gills of these animals (Doeller 1984). This dark color (ranging from light brown to deep purple), probably due to hemoglobin, has been found in gills of all bivalves containing bacteria. Unfortunately, only a few morphological descriptions of bivalves in the literature describe the color of the gill. Only Jackson (1973) mentions that *Anodontia alba* and *Ctena pectinella* from Jamaica have 'dark colored' gills with granules interpreted as respiratory pigments (Jackson 1973, Read 1966). The color of the gills is not characteristic for a given species but depends on the nutritional status of the clam. The gills of freshly collected clams are usually light brown and turn darker to dark purple during holding (Vetter 1985).

In summary, all lucinid species we have investigated contain symbiotic bacteria and live in environments with similar characteristics. In addition, all species have colored gills, which is a common feature of all bivalves with bacterial symbionts so far identified. Based on our results and information from the literature the conclusion is obvious that the presence of symbiotic bacteria may be a family characteristic of the Lucinidae. It could explain the reduced digestive tracts and the observation that lucinids are found in environments considered hostile to animals because of their high concentrations of sulfide.

Whether all members of the superfamily Lucinoidea form symbiotic associations still has to be evaluated. The Thyasiridae are certainly probable candidates to contain bacteria since they have so many characteristics in common with the Lucinidae, including dark colored gills with granules (Allen 1958, Jackson 1973), deep burrows in sediments (Stanley 1970), and egg capsules and lecithrophic development with short pelagic stage (Blacknell & Ansell 1974).

How widely spread this phenomenon of a symbiosis between autotrophic bacteria and molluscs really is will be shown in the future. The number of associations known has increased dramatically since the original discovery in 1981 (Cavanaugh et al. 1981, Felbeck 1981). This occurrence of symbioses in pogonophorans, oligochaetes, and molluscs of the families Vesicommyidae, Solemyidae, and Lucinidae although polyphyletically acquired may have important evolutionary and systematical significance. An example could be the occurrence of endosymbionts in the Lucinidae which could provide another clue to possible relationships with other families, e.g. Thyasiridae.

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