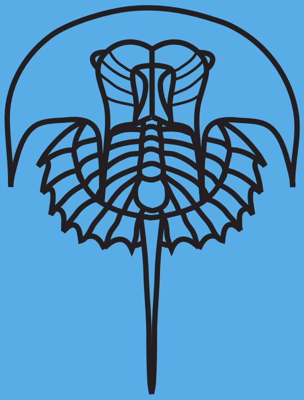

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PART N, REVISED, VOLUME 1, CHAPTER 9: PHOTOSYMBIOSIS IN BIVALVIA

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INTRODUCTION

Animals are involved in a broad range of beneficial trophic symbioses with unicellular symbionts, which facilitate breakdown of otherwise undigestible nutrients or provide fixed carbon through chemo- or autotrophy. Trophic symbioses are well documented in bivalves and characterize several major clades. Xylophagine pholads and teredinids harbor bacteria that facilitate the digestion of cellulose, allowing them to derive nutrition from the wood they bore (DISTEL & others, 2002; WATERBURY, CALLOWAY, & TURNER, 1983). Sulfide-oxidizing and, less commonly, methane-oxidizing bacteria live in the gills of Solemyidae, Nucinellidae, Bathymodiolinae, Lucinidae, Thyasiridae, Montacutidae, Vesicomyidae, Teredinidae, and Saxicavellinae in chemosymbiotic associations that provide their host with fixed carbon (FELBECK, CHILDRESS, & SOMERO, 1981; FISHER, 1990; OLIVER, 2013; OLIVER, SOUTHWARD, & DANDO, 2013; DISTEL & others, 2017). Photosymbiotic associations between unicellular algae and giant clams (YONGE, 1936; TRENCH, WETHEY, & PORTER, 1981; NORTON & others, 1992) and related fragine cockles (summarized in KIRKENDALE, 2009) are well known, whereas more poorly known associations have been documented in pectinids, unionids, and trapezids (NAIDU & SOUTH, 1970; PARDY, 1980; MORTON, 1982).

MARINE INVERTEBRATE PHOTOSYMBIOSES: DIVERSITY AND FUNCTION

Photosymbioses are trophic associations between heterotrophic hosts and autotrophic symbionts (COWEN, 1983; YELLOWLEES, REES, & LEGGAT, 2008). Photosymbiotic associations are widespread among marine invertebrates and protists as hosts, including numerous lineages among the Porifera, Cnidaria, Platyhelminthes, Mollusca, Urochordata, Foraminifera, and Radiolaria (Fig. 1). A diverse suite of autotrophic symbionts participate in these partnerships, including cyanobacteria, chlorophytes, dinoflagellates, diatoms, rhodophytes, chrysophytes, and even free chloroplasts (YONGE, 1975; ZANN, 1980; RUTZLER, 1990; LEE & ANDERSON, 1991). Associations range from facultative to obligate for both host and symbiont, extra- to intracellular, and mutualistic to parasitic for either the host or the symbiont (DIMOND & CARRINGTON, 2008; BANASZAK, GARCÍA RAMOS, & GOULET, 2013; DECELLE, 2013).

The first-discovered and best-studied photosymbiotic association among marine animals is that between stony corals (Scleractinia) and dinoflagellate algae (zooxanthellae, a term for golden algal symbionts) (DANA, 1846 in 1846–1849; YONGE, 1936; LAJEUNESSE & others, 2004; DALY & others, 2007; YELLOWLEES, REES, & LEGGAT, 2008).

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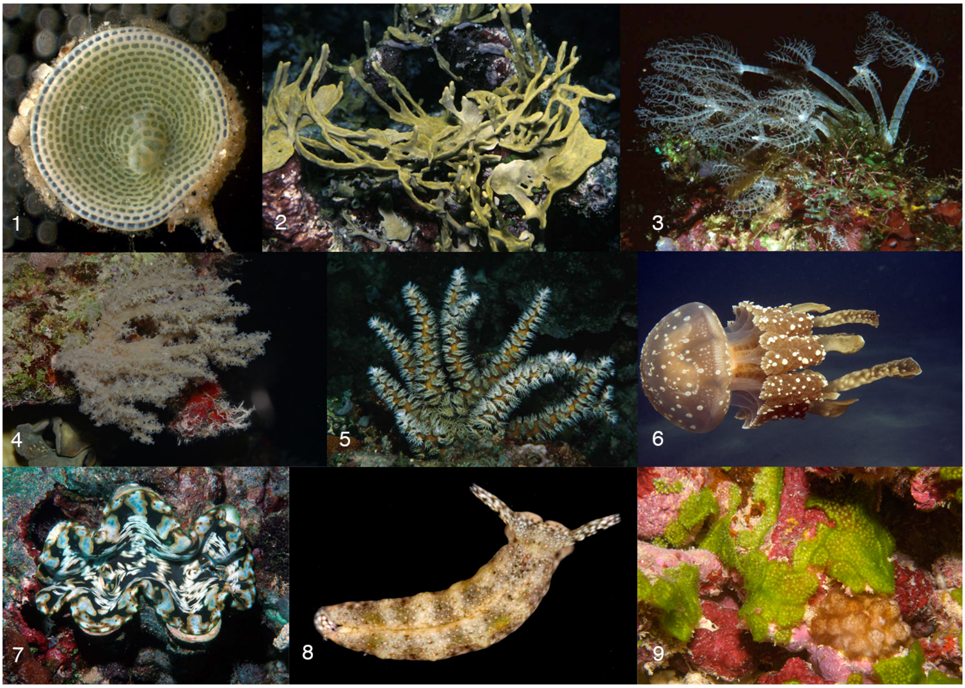

Fig. 1. Tropho-endo-photosymbiotic marine invertebrate hosts occur in diverse phyla. *1,* Foraminifera: Soritidae; *2,* Porifera: *Dysidea* sp.; *3–6,* Cnidaria: *Anthelia* sp. (*3*), octocoral (*4*), *Acrhelia* sp. (*5*), *Mastigias papua* Lesson, 1830 in 1830–1832 (*6*); *7–8,* Mollusca: *Tridacna squamosa* Lamarck, 1819 in 1818–1822 (*7*), *Plakobranchus* sp. (*8*); *9,* Chordata: *Trididemnum* sp. (new).

About half of the more than 1500 species of scleractinians, including most shallow tropical forms, are photosymbiotic with dinoflagellates of the genus *Symbiodinium* Freudenthal, 1962. Genetic evidence indicates that these simple, unicellular algae have radiated extensively across hosts and biogeographic regions (LaJeunesse & others, 2004; Pochon, LaJeunesse, & Pawlowski, 2004; Finney & others, 2010; LaJeunesse & others, 2010; Pochon & Gates, 2010; LaJeunesse & Thornhill, 2011; Pettay & others, 2011). Nine clades (A through I) and an estimated 160 distinct *Symbiodinium* types, each of which may represent distinct species, are now recognized (Yellowlees, Rees, & Leggat, 2008; Pochon & Gates, 2010). There is substantial variation among both symbionts and hosts in the degree of specificity, ranging from highly species specific to very broad associations (Baker, 2003).

Symbiodinium is the dominant photosymbiont on coral reefs today, as it is the alga inhabiting all reefal cnidarians and the bulk of studied molluscs. Forams, sponges, and urochordates on reefs have more diverse symbionts. Pochon and others (2006) proposed that *Symbiodinium* is a relatively young lineage, originating in the Eocene. Evidence for this hypothesis was based on a molecular clock calibrated with the origin of soritid Foraminifera and with divergence between selected soritid-associated *Symbiodinium* on the two sides of the isthmus of Panama. However, both calibration points are based on single dates, and both are conflicted in their data: some *Symbiodinium* that inhabit soritids branched off earlier than the putative origin of soritids (interpreted to have been secondarily invaded), and some soritids show much lower divergence on the two sides of the isthmus than the lineages chosen for calibration

(Pochon, LaJeunesse, & Pawlowski, 2004). If the interpretation of Pochon and others (2006) is correct, then Mesozoic and Paleozoic corals and mollusks were either not photosymbiotic or had other types of algal symbionts (Vermeij, 2013). Alternatively, *Symbiodinium* might be a much older clade.

Vertical transmission of symbionts generates the most specific associations because the host selects, retains, and passes the symbiont to its offspring, leading to potential cospeciation between host and symbiont (Bright & Bulgheresi, 2010; Fig. 2.1). In horizontal transmission, on the other hand, each generation acquires zooxanthellae anew from the environment, and strict coupling is less likely (Fig. 2.2). Recent studies, including one on the chemosymbiotic bivalve *Solemya velum* Say, 1822 (Krueger, Gustafson, & Cavanaugh, 1996), have revealed phylogenetic incongruence in some vertically transmitted systems, implying some horizontal transmission of symbionts as well, resulting in mixed transmission (Fig. 2.3). Although horizontal acquisition is less likely to result in coevolution between host and symbiont than vertical transmission, evidence suggests that cnidarians and giant clams with horizontal acquisition nevertheless are selective in the uptake of zooxanthellae strains from the available pool (LaJeunesse & others, 2004).

Transfer of photosynthate and inorganic nutrients between host and symbiont can make photosymbiotic holobionts competitively superior to autrophs in oligotrophic tropical environments. Photosymbionts can fix and translocate some organic carbon to the host; the provision of photosynthate can be critical for host nutrition (Cowen, 1983; Yellowlees, Rees, & Leggat, 2008). Symbionts in turn are thought to benefit not only from protection within the host, but also from access to a steady supply of normally limiting nutrients (N, P, and Fe) (Cowen, 1983; Douglas, 1994; Rowan, 1998; Richardson, 2001).

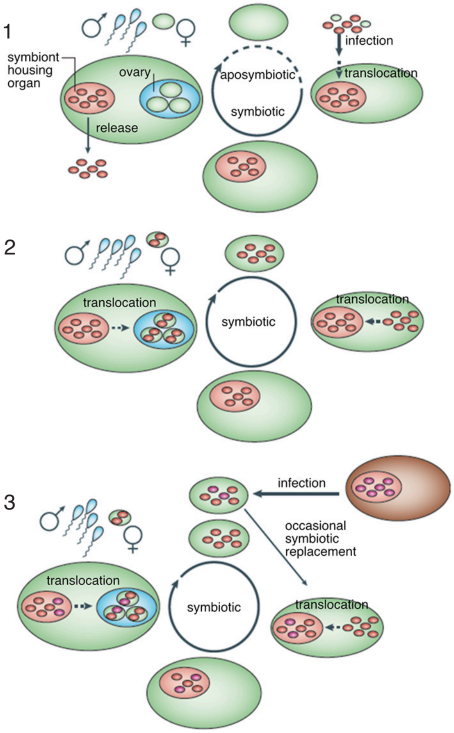

Fig. 2. Modes of symbiont transmission. *1,* Horizontal transmission (from environment); *2,* vertical transmission (from mother); *3,* vertical transmission (from mother) with occasional symbiont switching (Bright & Bulgheresi, 2010; reprinted by permission from Macmillan Publishers Ltd., Nature Reviews Microbiology).

PHOTOSYMBIOSIS AMONG EXTANT BIVALVIA

Most photosymbiotic taxa, including corals and shell-less opisthobranch molluscs, have exposed soft tissues and large surface areas that facilitate light exposure to symbionts (Cowen, 1983). In contrast, the opaque, hard shells of bivalves are clearly not preadapted for photosymbiosis. Nevertheless, shelled molluscs are prone to infestation by zooxanthellae, as recently demonstrated in numerous lineages of prosobranchs that harbor healthy zooxanthellae (Berner, Wishkovsky, & Dubinsky, 1986; Banaszak, García Ramos, & Goulet, 2013). Banaszak, García Ramos, and Goulet (2013) argued that such associations in shelled gastropods

FIG. 3. *1–2,* Live collected specimens of *Fluviolanatus subtorta* (DUNKER, 1857) from Western Australia, showing brown coloration of siphons (possibly due to presence of pigments not zooxanthellae), white coloration of gills, and brown particles in mantle. *3,* Posterior mantle area around siphons of *Clinocardium nuttallii* (CONRAD, 1837); note clumped colonies of green zoochlorellae (new).

are mutualistic during larval life, but they turn parasitic in mature animals. A parasitic origin of photosymbiosis is an attractive hypothesis that needs to be evaluated in facultatively symbiotic bivalves. Seven photosymbiotic lineages are currently known in the Bivalvia, but obligate associations are limited to tropical representatives of the Cardiidae, which also exhibit a suite of behavioral, anatomical and microstructural adaptations.

The freshwater unionids *Anodonta cygnea* (LINNAEUS, 1758) and *Unio pictorum* (LINNAEUS, 1758) harbor green algal symbionts (zoochlorellae) in tissues that receive maximum illumination; these symbionts may translocate fixed carbon to their host (PARDY, 1980). *Fluviolanatus subtortus* (DUNKER, 1857), a bizarre putative trapezid clam that inhabits estuaries in tropical and temperate Australia, was described as harboring presumed zooxanthellae in its ventral mantle margin (MORTON, 1982). Recent observations suggest that the brown coloration may be due to pigmentation and not zooxanthellae (Fig. 3.1), and genetic and histological testing is underway to confirm this new interpretation. The temperate scallop *Placopecten magellanicus* (GMELIN, 1791 in 1791–1793) has also been noted to harbor zoochlorellae in its mantle (NAIDU & SOUTH, 1970).

In addition to the two tropical photosymbiotic lineages among cardiids, the relatively large, temperate cockle *Clinocardium nuttallii* (CONRAD, 1837) harbors zoochlorellae in mantle, siphon, and foot tissues (HARTMAN & PRATT, 1976; Fig. 3.2). These algae, provisionally identified as a *Chlorella* species, inhabit only older clams that have become epifaunal, and live both intra- and intercellularly (JONES & JACOBS, 1992). Algal cells are aggregated in colonies, suggesting opportunistic proliferation rather than a well-regulated symbiotic association. At present, there is evidence for neither benefit nor harm to the host from this association (HARTMAN & PRATT, 1976). The four known zoochlorellal associations—*Anodonta* LAMARCK, 1799; *Unio* PHILIPSSON, 1788; *Placopecten* VERRILL, 1897; and *Clinocardium* KEEN, 1936—are all temperate, opportunistic, and may represent invasion of the host by algal cells. They require further study to ascertain the details of association, especially to evaluate the potential transfer of nutrients. It is plausible that these partnerships represent early forays, trials, or intermediate stepping stones in the evolution of bivalve photosymbiosis (JONES & JACOBS, 1992).

All giant clams (Cardiidae: Tridacninae) possess zooxanthellae; the added nutrition provided by photosymbionts (FITT & TRENCH, 1981; TRENCH, WETHEY, & PORTER, 1981; FITT, FISHER, & TRENCH, 1986), coupled with a fully functional gut, has allowed them to attain great sizes: adults of all species reach at least 15 cm in length, with the largest, *Tridacna gigas* (LINNAEUS, 1758), attaining lengths of more than 1

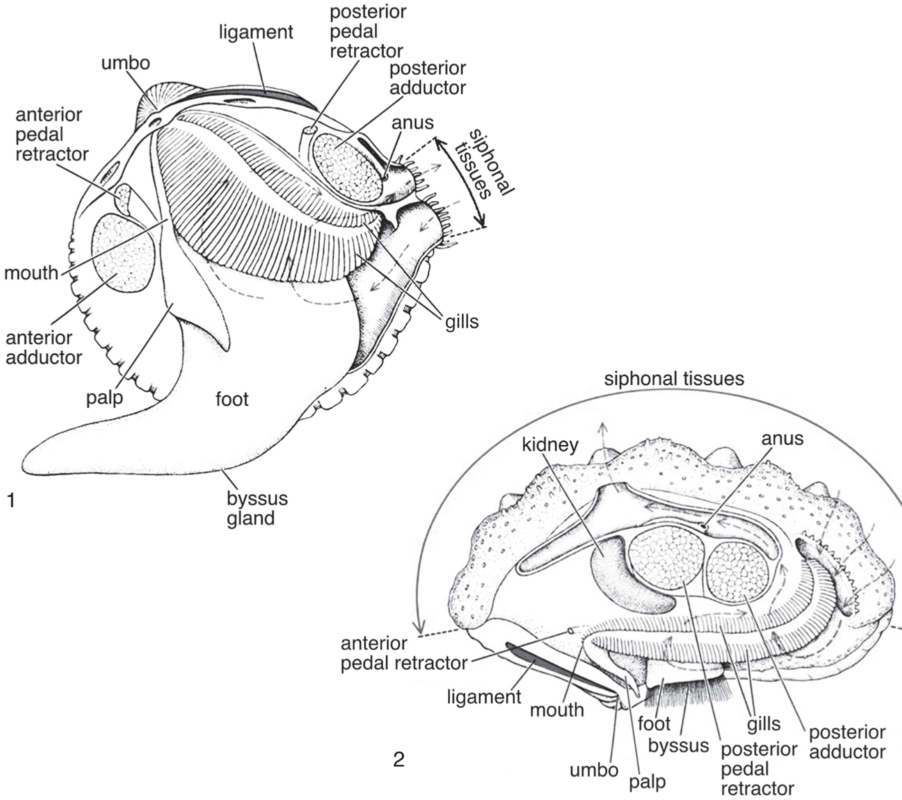

FIG. 4. Typical cardiid (*1*) contrasted with *Tridacna* BRUGUIÈRE, 1797 in BRUGUIÈRE & others, 1791–1827 (*2*), highlighting the expansion of the posterior mantle in the latter (Yonge, 1975; reproduced with permission, copyright ©1979 Scientific American, Inc., all rights reserved).

meter. They were the first photosymbiotic association documented among bivalves (YONGE, 1936), roughly a century after the discovery of photosymbiotic partnership in corals (DANA, 1846 in 1846–1849). Unlike most cardiids or heterodonts, tridacnines are epibenthic and, thus, have moved out from the sediment into the sunshine. This transition in habit was accompanied by a reorganization of the body that involved a great expansion of the posterior, siphonal region at the expense of the anterior anatomy, including the loss of the anterior adductor. The mantle of this posterior region is greatly hypertrophied and is exposed upward to the light between widely gaping valves; in *Tridacna* BRUGUIÈRE, 1797 in BRUGUIÈRE & others, 1791–1827 (but not *Hippopus* LAMARCK, 1799), the mantle also extends beyond the shell margins (Fig. 4).

Because of their apomorphic morphology, giant clams were long placed in a separate family, but they are now recognized as highly modified cardiids (SCHNEIDER, 1998; HERRERA & others, 2015). The number of giant clam species is growing, with two new species recently recognized (SU & others, 2014; MONSECOUR, 2016; Table 1), and others under study. Aside from corals, these are the best-characterized marine photosymbiotic taxa, with studies on their phylogenetic relationships, both morphological (SCHNEIDER, 1998) and molecular (SCHNEIDER & Ó FOIGHIL, 1999);

TABLE 1. Photosymbiosis in extant Bivalvia; the host-symbiont relationship is defined as obligate, if mortality followed bleaching or no specimens observed without symbionts, or facultative if specimen observed both with and without symbionts; host species listed under family and subfamily headings (in boldfaced type); taxonomy based mostly on WoRMS, 2014 (new).

Host species	Photosymbiosis evidence	Symbiont type	Nature of relationship
Cardiidae, Tridacninae			
Hippopus hippopus (Linnaeus, 1758)	well established	*Symbiodinium* Freudenthal, 1962 expected (strain unknown); Jameson, 1976	obligate
H. porcellanus Rosewater, 1982	Baillie, Belda-Baillie, & Maruyama, 2000	*Symbiodinium* expected (strain unknown)	obligate
Tridacna sp. Bruguière, 1797 in Bruguière & others, 1797–1827	Baillie, Belda-Baillie, & Maruyama, 2000; LaJeunesse & others, 2004, Japan	*Symbiodinium* A6 specific to tridacnid clams	unknown
T. crocea Lamarck, 1819 in 1818–1822	DeBoer & others, 2012, table 3	*Symbiodinium:* C>D, also A	obligate
T. derasa (Röding, 1798)	Klump & Lucas, 1994	*Symbiodinium* (strain unknown)	obligate
T. gigas (Linnaeus, 1758)	Norton & Jones, 1992	*Symbiodinium* (strain unknown)	obligate
T. lorenzi Monsecour, 2016	well established	*Symbiodinium* expected (strain unknown)	obligate
T. maxima (Röding, 1798)	DeBoer & others, 2012, table 3	*Symbiodinium:* A, C, D	obligate
T. mbalavuana Ladd, 1934	Klump & Lucas, 1994, as *T. tevoroa*	*Symbiodinium* expected (strain unknown)	obligate
T. noae (Röding, 1798)	Su & others, 2014	*Symbiodinium* expected (strain unknown)	obligate
T. rosewateri Sirenko & Scarlato, 1991	well established	*Symbiodinium* expected	obligate
T. squamosa Lamarck, 1819 in 1818–1822	DeBoer & others, 2012, table 3	*Symbiodinium:* D>C	obligate
T. squamosina Sturany, 1899	Richter & others, 2008, as *T. costata*	*Symbiodinium* expected (strain unknown)	obligate
Cardiidae, Fraginae			
Corculum aequale (Deshayes, 1855)	unknown	unknown	unknown
C. aselae Bartsch, 1947	unknown	unknown	unknown
C. cardissa (Linnaeus, 1758)	Kawaguti 1941, 1950, 1968; Farmer, Fitt, & Trench, 2001; Kirkendale, 2009	*S. corculorum* Trench in Farmer, Fitt, & Trench, 2001	obligate
C. impressum (Lightfoot, 1786)	unknown	unknown	unknown
C. lorenzi Huber, 2013	unknown	unknown	unknown
C. monstrosum (Gmelin, 1791 in 1791–1793)	unknown	unknown	unknown
C. roseum (Gmelin, 1791 in 1791–1793)	unknown	unknown	unknown
Fragum fragum (Linnaeus, 1758)	Kawaguti, 1983; Kirkendale, 2009	zooxanthellae	obligate
F. erugatum (Tate, 1889)	Morton, 2000; Kirkendale, 2009	zooxanthellae	obligate
F. grasi Poorten, 2009	unknown	unknown	unknown
F. mundum (Reeve, 1845 in 1844–1845)	Persselin, 1998; Kirkendale, 2009	zooxanthellae	obligate
F. aff. *mundum* (Reeve, 1845 in 1844–1845)	Persselin, 1998; Kirkendale, 2009	zooxanthellae	obligate
F. nivale (Reeve, 1845 in 1844–1845)	Persselin, 1998	zooxanthellae	obligate
F. scruposum (Deshayes, 1855)	Ohno, Katoh, & Yamasu, 1995; Kirkendale, 2009	zooxanthellae	obligate

Continued on facing page.

Table 1. *Continued from facing page.*

F. sueziense (Issel, 1869)	Persselin 1998; Kirkendale, 2009	zooxanthellae	obligate
F. unedo (Linnaeus, 1758)	Umeshita & Yamasu, 1985; Kirkendale, 2009	zooxanthellae	obligate
F. vanuatuense Poorten, 2015	Poorten, 2015	zooxanthellae	unknown
F. whitleyi Iredale, 1929	Kirkendale 2009, as *F. scruposum*	zooxanthellae	obligate
Lunulicardia auricula (Niebuhr, 1775)	unknown	unknown	unknown
L. hemicardium (Linnaeus, 1758)	Kirkendale, 2009	zooxanthellae	unknown
L. orlini Mienis, 2009	unknown	unknown	unknown
L. retusa auricula (Niebuhr, 1775)	unknown	unknown	unknown
Cardiidae, Clinocardiinae			
Clinocardium nuttallii (Conrad, 1837)	Hartman & Pratt, 1976; Jones & Jacobs, 1992	zoochlorellae	facultative
Trapezidae			
Fluviolanatus subtortus (Dunker, 1857)	Morton, 1982	zooxanthellae?	unknown
Pectinidae, Palliolinae			
Placopecten magellanicus (Gmelin, 1791 in 1791–1793)	Naidu & South, 1970	zoochlorellae	facultative
Unioniidae			
Anodonta cygnea (Linnaeus, 1758)	Pardy, 1980	zoochlorellae	facultative
Unio pictorum (Linnaeus, 1758)	Pardy, 1980	zoochlorellae	facultative

morphology (Norton & Jones, 1992); distribution and phylogeography (DeBoer & others, 2008; Kochzius & Nuryanto, 2008; Nuryanto & Kochzius, 2009; Huelsken & others, 2013; Hui & others, 2016); feeding (Morton, 1978); behavior (Todd, Lee, & Chou, 2009; Neo & Todd, 2011a, 2011b); aquaculture (Lucas & others, 1989; Klumpp & Lucas, 1994; Boglio & Lucas, 1997); physiology, symbiosis, and paleontology (see references in later sections); and, increasingly, conservation (Richter & others, 2008).

Just five years following the discovery of photosymbiosis in giant clams, Kawaguti (1941) noted zooxanthellae in the much smaller *Corculum cardissa* (Linnaeus, 1758) (Cardiidae: Fraginae). Surveys of fragine species for zooxanthellae have shown that all examined species of *Fragum* Röding, 1798; *Lunulicardia* Gray, 1853; and *Corculum* Röding, 1798, possess them, whereas no examined species in other fragine genera do (Tables 1–2) (Kawaguti, 1950, 1983; Ohno, Katoh, & Yamasu, 1995; Persslein, 1998; Morton, 2000; Schneider & Carter, 2001; Kirkendale, 2009). In contrast to tridacnines, fragines display substantial morphological variation that is presumably related to different modes of exposing algae to light (Kirkendale, 2009; Fig. 5). Some species are little modified, appearing morphologically similar to non-photosymbiotic species in shell shape and size—e.g., *Fragum erugatum* (Tate, 1889) and *F. fragum* (Linnaeus, 1758) (Fig. 5). Others exhibit putative adaptions for light capture, including mantle hypertrophy and exposure as in tridacnines and *F. unedo* (Linnaeus, 1758), and varied alternative morphologies that facilitate light capture, such as microstructural translucencies, shell thinning, and shell flattening of the posterior shell surface in *Lunulicardia* and *Corculum* (Fig. 5).

PHOTOSYMBIONT ACQUISITION AND PLACEMENT

Tridacnines and fragines both harbor symbiotic algae extracellularly in a finely ramified digestive tube system (Mansour, 1946; Norton & others, 1992; Farmer,

Table 2. Photosymbiotic status of extant Fraginae; presence of photosymbionts is based on previously published studies (*1*) or microscopic examination of live (*2*), formalin-fixed (*3*), or ethanol-fixed (*4*) animals (adapted from Kirkendale, 2009; nomenclature updated).

Species	Number of specimens	Presence of photosymbionts
Americardia biangulata (Broderip & Sowerby, 1829)	2	absent[2]
A. media (Linnaeus, 1758)	3	absent[2]
Apiocardia obovalis (Sowerby, 1833)		absent[4]
Corculum cardissa (Linnaeus, 1758)	3	present[1]
Ctenocardia fornicata (Sowerby, 1841)		absent[1]
C. gustavi Vidal & Kirkendale, 2007	1	absent[3]
Fragum sp. (Persselin, 1998)	11	present[1]
F. carinatum (Lynge, 1909)	13	present[3]
F. fragum (Linnaeus, 1758)	50	present[2]
F. loochoanum Kira, 1959	20	present[2]
F. mundum (Reeve, 1845 in 1844–1845)	3	present[3]
F. aff. *mundum* (Reeve, 1845 in 1844–1845)	3	present[3]
F. nivale (Reeve, 1845 in 1844–1845)		present[1]
F. scruposum (Deshayes, 1855)	20	present[2]
F. sueziense (Issel, 1869)	6	present[2]
F. unedo (Linnaeus, 1758)	5	present[2]
Freneixicardia victor (Angas, 1872)		absent[1]
Lunulicardia sp. (Persselin, 1998)	1	present[3]
L. hemicardium (Linnaeus, 1758)	2	present[1]
L. retusa (Linnaeus, 1767 in 1766–1768)		present[3]
Microfragum erugatum (Tate, 1889)	20	present[3]
M. festivum (Deshayes, 1855)	10	absent[3]
M. subfestivum (Vidal & Kirkendale, 2007)	3	absent[3]
Papillicardium papillosum (Poli, 1791)	8	absent[2]
Parvicardium exiguum (Gmelin, 1791 in 1791–1792)		absent[4]
P. scriptum (Bucquoy, Dautzenberg, & Dollfus, 1892 in 1887–1898)	10	absent[2]
P. vroomi van Aartsen, Menkhorst, & Gittenberger, 1984	10	absent[2]
Trigoniocardia granifera (Broderip & Sowerby, 1829)	10	absent[2]

Fitt, & Trench, 2011). Algae are packed in the lumen of thin, tertiary tubules, separated from the surrounding haemocoel by the tubule's epithelium (Farmer, Fitt, & Trench, 2011). The zooxanthellal tube system of giant clams arises from one of the digestive diverticular ducts of the stomach and divides into right and left tubes above the digestive organs (Fig. 6). Secondary zooxanthellal tubes branch in the upper levels of the inner fold of the siphonal mantle, where they terminate in thin, convoluted, blind-ending tertiary tubes. Primary, secondary, and tertiary tubes are histologically differentiated, with the more robust, ciliated, primary tubes giving rise to thin-walled, ciliated, secondary tubes and similarly thin-walled tertiary tubes that lack cilia. Tertiary zooxanthellal tubes atrophy following bleaching, suggesting that they may be ephemeral and possibly regenerative following bleaching incidents (Norton & others, 1992). Tubules develop only in the presence of zooxanthellae in juvenile clams (Fitt & Trench, 1981; Fitt, Fisher, & Trench, 1986). More research is needed to understand how this inducible tubular system functions and is maintained at the molecular and cellular levels.

Remarkably, given that fragines appear to have evolved photosymbiosis independently from giant clams, a similar, complex zooxanthellal tubular system has been found in *Corculum;* this system extends not only into the mantle, but also to the ctenidia and foot, harboring zooxanthellae throughout (Farmer, Fitt, & Trench, 2001; Kirkendale, 2009; Fig. 7). Early work by Kawaguti (1983) and TEM images by Kempf (in Farmer, Fitt, & Trench, 2001) have also revealed evidence for a comparable tubular system in *Fragum*

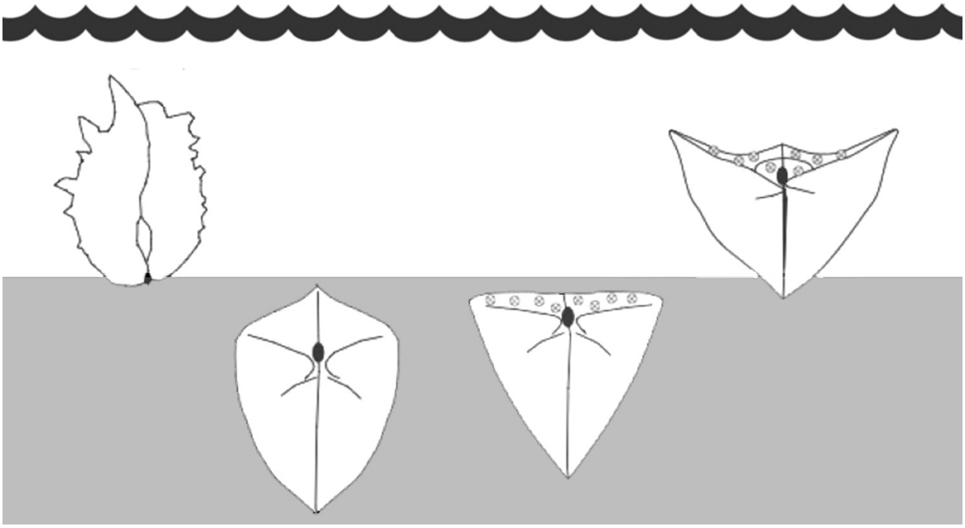

FIG. 5. Photosymbiotic lifestyle in extant Cardiidae; from left to right: *Tridacna squamosa* LAMARCK, 1819 in 1818–1822, *Fragum fragum* (LINNAEUS, 1758), *Lunulicardia hemicardium* (LINNAEUS, 1758), and *Corculum cardissa* (LINNAEUS, 1758) (new).

fragum. The broad distribution of zooxanthellae through the body may be a consequence of the relatively small body size of fragines, permitting much broader transmittance of light (i.e, irradiance) across the body than in giant clams. Whereas FARMER, FITT, & TRENCH (2001) stated that tubule extensions of the digestive system likely typify photosymbiosis across molluscs, *Clinocardium* does not appear to have such a system (Fig. 4; HARTMAN & PRATT, 1976). No aposymbiotic (non-photosymbiotic) bivalves have been reported with a comparable, digestive, tubular system (FARMER, FITT, & TRENCH, 2001).

Oocytes and embryos of giant clams do not possess zooxanthellae; giant clams acquire zooxanthellae in veliger and juvenile stages through ingestion (LABARBERA, 1974; JAMESON, 1976; FITT & TRENCH, 1981; NORTON & others, 1992; FARMER, FITT, & TRENCH, 2001; HIROSE, IWAI, & MARUYAMA, 2006). Juvenile giant clams develop the zooxanthellal tubular network that elongates from stomach to mantle, several days following metamorphosis, triggered by the presence of zooxanthellae (NORTON & others, 1992; HIROSE, IWAI, & MARUYAMA, 2006). The appearance of a line of zooxanthellae indicates the development of the tubule system, and is the first conspicuous sign of the establishment of symbiosis in giant clams (Fig. 8). Zooxanthellae proliferate by cell division within the tubular system as well as through ingestion of algae from the environment (HIROSE, IWAI, & MARUYAMA, 2006).

ORIGIN OF PHOTOSYMBIOSIS IN CARDIIDS

Photosymbiosis appears to have a diphyletic origin in the Cardiidae, arising separately in the Tridacninae and Fraginae. The relationship of Fraginae and Tridacninae is as yet unresolved (SCHNEIDER, 1998; HERRERA & others, 2015). However, photosymbiosis is restricted to one clade within the Fraginae (KIRKENDALE, 2009; Fig. 9), suggesting either independent origin in Tridacninae and *Fragum-Lunulicarida-Corculum,* or loss of photosymbiosis in at least the *Ctenocardia*-complex of genera and potentially in additional clades, depending on the relationship of Fraginae and Tridacninae. The greatest challenge to the diphyletic hypothesis is the

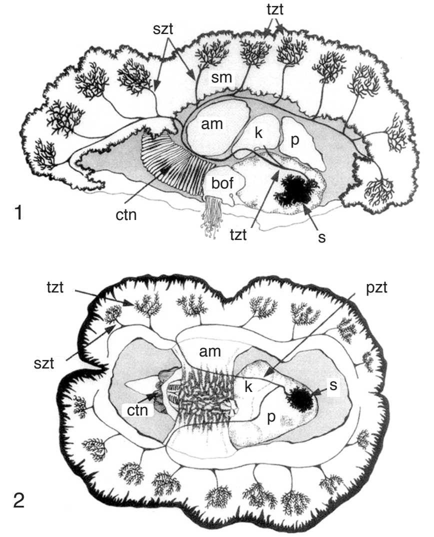

Fig. 6. Diagram of the path followed by zooxanthellal tube through a giant clam. *1,* Medial view of a bisected clam; *2,* dorsal view of a bisected clam; *am,* adductor muscle; *bof,* byssal organ (foot); *ctn,* ctenidia; *k,* kidney; *p,* pericardium; *pzt,* primary zooxanthellal tube; *s,* stomach; *sm,* siphonal muscle; *szt,* secondary zooxanthellal tube; *tzt,* tertiary zooxanthellal tube (Norton & others, 1992; fig. 1 from Norton & others, 1992, Biol. Bull. 183:503–506, reprinted with permission from the Marine Biological Laboratory, Woods Hole, Massachusetts).

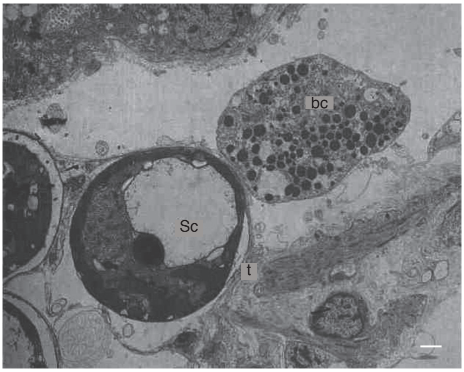

Fig. 7. TEM photograph showing proximity of tertiary tubule of zooxanthellae to blood cell in the gill of *Corculum cardissa* (Linnaeus, 1758), scale bar, 1 µm; *bc,* blood cell; *Sc, Symbiodinium corculorum* (photosymbiont); *t,* tertiary tubule (adapted from Norton & others, 1992; fig.3 from Biol. Bull. 200:336–343, reprinted with permission from the Marine Biological Laboratory, Woods Hole, Massachusetts).

presence of remarkably similar and complex tubule systems to house zooxanthellae in both subfamilies (Norton & others, 1992; Farmer, Fitt, & Trench, 2001). Either this tubule system evolved convergently or photosymbiosis was lost in multiple lineages between tridacnines and the *Fragum-Lunulicardia-Corculum* clade. The former hypothesis gains support from the general association of zooxanthellae with the digestive system, especially the digestive gland, in many mollusks (Berner, Wishkovsky, & Dubinsky, 1986; Banaszak, García Ramos, & Goulet, 2013). An especially illuminating example is the cooption of digestive diverticula, which pervade ceratal extensions, to farm chloroplasts acquired by kleptoplasty in sacoglossans (Jensen, 1997). Other evidence consistent with dual origin is that the tubular system is a dynamic entity, able to spontaneously form in response to presence of zooxanthellae early in ontogeny (Hirose, Iwai, & Maruyama, 2006) and to regrow following bleaching (Norton & others, 1995). A monophyletic origin of photosymbiosis would gain support if fragines and tridacnines were found to be sister lineages (Herrera, 2013) and an early acquisition of photosymbiosis in a suitable ancestor was supported.

ADAPTATIONS FOR PHOTOSYMBIOTIC LIFESTYLE: FUNCTIONAL MORPHOLOGY

BACKGROUND

No photosymbiotic metazoans are known that rely entirely on symbiont-derived nutrition (i.e., are autotrophic). In contrast, sole reliance on symbiont-derived nutrition is prevalent among chemosymbiotic metazoans and internal parasites. Although some chemosymbiotic bivalves (Reid & Bernard, 1980) and worms (Jones, 1981) have lost a functional gut, internal parasites can degenerate so far as to lose most organ systems (including the nervous system), as in dicyemid mesozoans, a phylum of highly derived parasitic lophotrochozoans (Suzuki

& others, 2010), or in myxozoans, a group of highly degenerate cnidarians that have been misclassified as protists in the past (EVANS & others, 2010).

ANATOMICAL MODIFICATIONS INCLUDING SOFT PARTS, BEHAVIOR AND STORAGE

Photosymbiotic animals retain a full complement of functional organ systems, including a well-developed gut, and are mixotrophic. SCHNEIDER (1993) commented on several anatomical simplifications observed in fragine stomachs and suggested these might be related to photosymbiosis. However, aposymbiotic fragines also have simplified stomachs (e.g., type IV *sensu* PURCHON, 1987, in *Plagiocardium*), suggesting that other selective forces, perhaps paedomorphosis, are involved. Indeed, fragines show other evidence for juvenilization, including small size and lack of mantle suture around the incurrent siphon.

Important modifications of the body plan of the host are related to (1) light acquisition, (2) housing the symbionts (the tubule system discussed above), and (3) material exchange between host and symbiont. Light obviously limits photosymbioses to shallow to moderate depths in relatively clear waters. Light, as well as competitive advantage against both autotrophs and heterotrophs, give photosymbiotic mixotrophs an advantage in oligotrophic waters (HALLOCK & SCHLAGER, 1986).

Light acquisition imposes limits on life styles. Infaunal, endolithic, or cryptic habits, which limit access to light, are pervasive among bivalves because of the protection they provide against predation. Access to light and protection from predators are generally opposing selective forces for bivalves. An exposed, epifaunal mode of life would seem necessary for a photosymbiotic existence and

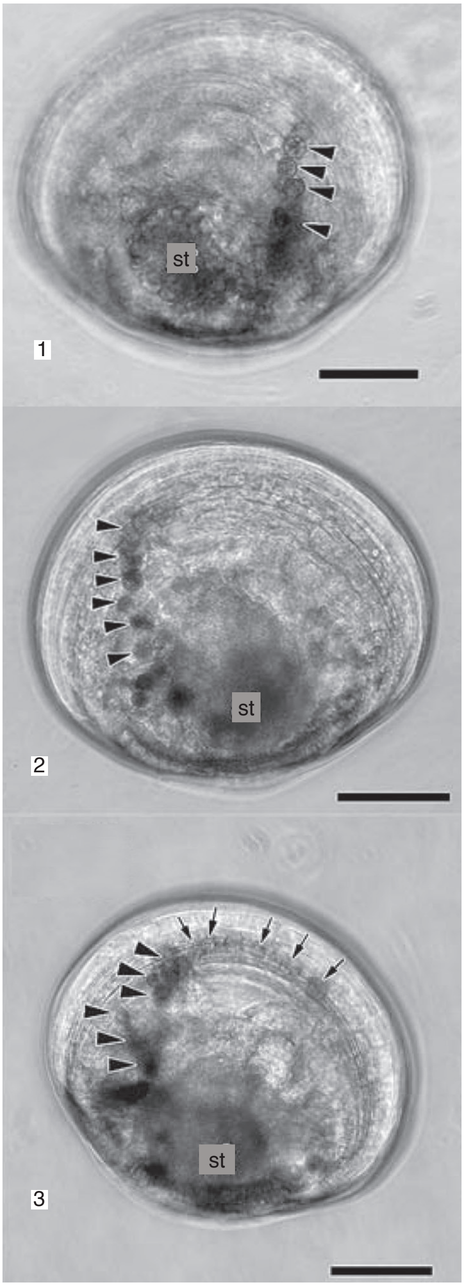

FIG. 8. Juvenile *Tridacna* BRUGUIÉRE in BRUGUIÉRE, & others, 1791–1827, showing appearance of zooxanthellae in tubular system of clams. *1, T. crocea* LAMARCK, 1819 in 1818–1822; *2–3, T. squamosa* LAMARCK, 1819 in 1818–1822; *arrowheads,* zooaxonthellal tubes; *arrows,* zooxanthellae lined along mantle edge; *st,* stomach; scale bar, 50 µm (adapted from Hirose, Iwai, & Maruyama, 2006; Springer & Marine Biology 148(2006), p. 551–558, *Continued on adjacent column.*

FIG. 8. *Continued from adjacent column.*
Hirose, Iwai, & Maruyama, Establishment of the photosymbiosis in the early ontogeny of three giant clams, fig. 3, ©Springer-Verlag 2005, reprinted with kind permission from Springer Science+Business Media B.V.).

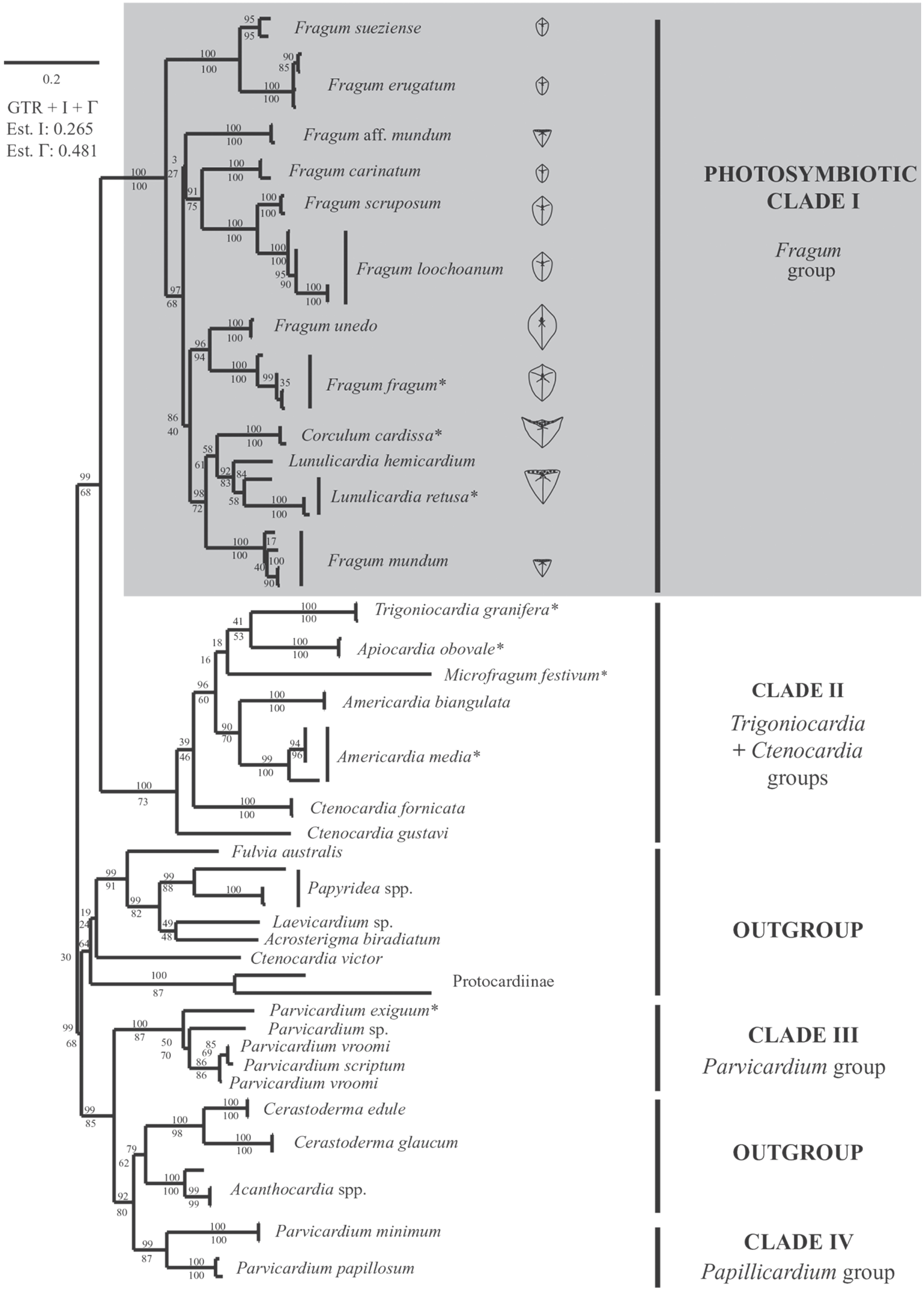

FIG. 9. Origin of photosymbiosis in the Fraginae (adapted from Kirkendale, 2009).

is the mode of life of tridacnines, *Corculum,* and some *Fragum* species, including *F. mundum* (REEVE, 1845 in 1844–1845) and *F. erugatum.* JONES and JACOBS (1992) demonstrated that algae are acquired by the cardiid *Clinocardium nuttallii* only when the clams change from an infaunal to an epifaunal habit during ontogeny. However other photosym-

FIG. 10. Mucus-bound mat of living photosymbiotic bivalve *Fragum erugatum* (TATE, 1889), Nanga Station, Shark Bay, Western Australia (Hickman, 2003; reproduced with permission).

biotic cardiids (most *Fragum* and *Lunulicardia* species) are infaunal, but shallowly buried. The intense sunlight in shallow, tropical, reef habitats clearly reaches a modest distance into the sediment, allowing these animals to be photosymbiotic. A preadaptation of cardiids to photosymbiosis is their relatively simple, short siphons that limit depth of burial, keeping the animal near the better-lit sediment surface. All three lineages of cardiids with photosymbionts have moved from an infaunal to an epifaunal life style, supporting the hypothesis that the benefits of photosymbiosis have selected them to abandon the safety of infaunal existence (SEILACHER, 1984; JONES & JACOBS, 1992).

Epibiotic and shallowly infaunal habits pose high predation risk, which extant photosymbiotic bivalves often minimize through escape to safe places, crypsis, or gigantism. Thus, fragines are abundant in places that are difficult for predators to access, such as exposed, intertidal reef flats and reef crests, and hypersaline waters. The epifaunal *Fragum mundum* and small-bodied species of *Corculum* may be so locally abundant in some atolls of the Tuamotu Archipelago that they constitute a large fraction of the beach sediment behind shallow, exposed outer reef flats (Gustav Paulay, personal observation). *Fragum erugatum* similarly thrives in the hypersaline portions of Australia's Shark Bay, reaching densities of 4000/m^2 (HICKMAN, 2003; Fig. 10). *Fragum fragum* is among the last bivalves to thrive in the drying, detached lagoonal ponds on the mildly emergent Kiritimati atoll (PAULAY, 1991), and it is also a dominant species in some closed lagoons of the Tuamotu Archipelago, as *Tridacna maxima* (RÖDING, 1798) is in others (RICHARD, 1985). In less extreme marine habitats, photosymbiotic fragines typically have much lower population densities and are often challenging to find alive. Crypsis, through encrustation of the upper surface (posterior slope) of fragines that live epifaunally, also provides protection. The complex mantle color patterns in tridacnines may also aid in crypsis and lead to reduced rates of predation (Ozog, 2009; Todd, Lee, & Chou, 2009). Tridacnines escape predation through gigantism, with smaller species gaining further protection through extremely strong byssal attachment and, in some instances, a fully endolithic habit. The attached, endolithic giant clams *Tridacna crocea* Lamarck, 1819 in 1818–1822, and to a lesser extent *T. maxima* can form very dense populations, especially on the intertidal tops of patch reefs (Hamner & Jones, 1976; Richard, 1985; Sirenko, 1991).

Symbionts can be exposed to light when tissue is exposed through shell gape, mantle extension, or reorganization or reduction of the shell. Gape is an effective method for exposing symbionts to light and can be associated with hypertrophy of mantle tissue, as in tridacnines (Yonge, 1936), fragines (Ohno, Katoh, & Yamasu, 1995), and *Clinocardium nuttallii* (Jones & Jacobs, 1992). Tridacnine evolution has focused on increasing the amount of mantle surface that can be exposed by (1) habitually opening the valves broadly, (2) extending the mantle laterally beyond the valve margin (in *Tridacna*), (3) lengthening the commissure by large marginal folds in the shell, and (4) substantial reorganization of the body. The initially small, posterior siphonal area has become greatly expanded and positioned on the upper surface of the animal that remains attached by ventral byssus (Fig. 5). *Fragum* species also show a limited extension of the mantle beyond the shell margin (Ohno, Katoh, & Yamasu, 1995). Mantle extension over the shell (as evidenced by inductural deposits) has been used as potential evidence for photosymbiosis in fossil *Protocardia (Pachycardium) stantoni* (Wade, 1926) (Schneider & Carter, 2001). However, the extension of the mantle over the shell is not, in itself, sufficient evidence for photosymbiosis, as it is prevalent in some aposymbiotic lineages. For example, many species of the diverse galeommatoid bivalves have extensive, reflected mantles, often combined with shells that are reduced in size and thickness, yet none have been observed (or suggested) to possess algal symbionts. Light capture is thought to be further enhanced by abundant light-scattering iridophores situated in the mantle of tridacnines (Griffiths, Winsor, & Luongvan, 1992).

SHELL AND SHELL MICROSTRUCTURAL ADAPTATIONS FOR PHOTOSYMBIOSIS

Light can also pass through the shell and be captured by zooxanthellae in internal tissues, a path taken by members of the Fraginae. Fragines expose symbionts by gaping and through shell translucency, with the former more important in basal members of the family and the latter more prevalent in apomorphic *Fragum; Lunulicardia;* and *Corculum.* The capacity for gaping is reduced in light-transmissive shells, especially in *Corculum.* Light penetration through the shell is facilitated by (1) small sizes, (2) thin shells, (3) a reduction in shell pigmentation, and (4) the development of the window and condensing-lens microstructure; all of these are apparent in fragines. Several species have adult sizes of about 5 mm, with commensurately thin shells, but lack other apparent adaptations to light capture, suggesting that paedomorphosis might have facilitated the evolution of photosymbiosis (Kirkendale, 2009). Moreover, small animals live closer to the sediment surface, further enhancing light availability in infaunal bivalves. *Corculum,* the genus most specialized for through-the-shell illumination of zooxanthellae, is characterized by especially thin shells. Shell transparency can vary substantially with (Carter & Schneider, 1997) or without obvious gross correlates in microstructure. Windows, or more transparent shell areas, resulting solely from low pigmentation are apparent in some species, such as *Fragum fragum.* The incursion of the fibrous, prismatic microstructure of the outer-shell layer in patches within the shell can make the windows more transparent, as demonstrated in *Corculum* (Watson & Signor, 1986); this can be coupled with changes to the inner-shell surface shape to form small light-condensing lenses (Carter & Schneider, 1997). Shell thinness and transparency are also common in aposymbiotic bivalves (e.g., *Limaria* Link, 1807 in 1806–1808), many galeommatoids, pectinids, anomiids, and several lineages of small bivalves in reef caves (Hayami & Kase, 1996), so caution is needed when using these features as sole evidence of photosymbiosis in fossils.

Increasing the surface area of the shell is another adaptation seen in lineages relying on shell transparency for light capture. In this adaptation the posterior slope of the shell is flattened so that it lies parallel to the sediment surface and is substantially widened to serve as a kind of solar panel. Although significant widening of the posterior slope and corresponding antero-posterior foreshortening of the shell is unique to *Corculum,* other fragines display limited flattening and slight elongation of the posterior slope, but such shapes are also encountered in aposymbiotic relatives as *Ctenocardia* Adams & Adams, 1857 in 1853–1858, and *Americardia* Stewart, 1930.

An interesting twist to the relevance of shell transparency was the recent discovery that numerous large, thick-shelled gastropods also harbor healthy zooxanthellae in their digestive system. These algae, however, may rely on fixed carbon from the host, rather than contributing it (Berner, Wishkovsky, & Dubinsky, 1986; Banaszak, García Ramos, & Goulet, 2013).

EVIDENCE FOR PHOTOSYMBIOSIS IN EXTINCT TAXA

THE CHALLENGE OF INFERENCE

Photosymbiosis has been inferred for numerous extinct lineages based on morphological, paleoecological, and isotopic evidence (e.g., Cowen, 1983; Seilacher, 1990; Jones & Jacobs, 1992; Vermeij, 2013). Such inferences, however, are questionable because virtually none of the attributes used as evidence are unique to photosymbiotic bivalves—they are present or even common in extant aposymbiotic taxa. Furthermore, a large proportion of the living photosymbiotic bivalves (unionids, *Clinocardium,* and most *Fragum*) lack any evidence of photosymbiosis in their hard parts and, thus, would not be suspected to be photosymbiotic as fossils.

Specialized morphologies that enhance surface area for light capture are seen in extant tridacnines and *Corculum* (Fig. 11), and have been used as evidence to infer photosymbiosis in fossils. The proposed morphologies include hinges that permit a broad gape, undulating shell margins, mantles extended over the shells (indicated by inductural deposits), thin shells, and microstructures conducive to light penetration (Seilacher, 1990; Vermeij, 2013). Inferring photosymbiosis from these morphologies is problematic, however, because most of these features are not diagnostic of photosymbiosis, as is apparent from consideration of extant aposymbiotic bivalves. Examples include the broad gape in *Limaria;* undulating shell margin in *Hyotissa* Stenzel, 1971; reflected mantles in *Scintilla* Deshayes, 1856; thin, translucent shells in *Placuna* Lightfoot, 1786; and thin, transparent shells with thick, prismatic microstructure in *Streptopinna* Martens, 1880. The only putative adaptive feature currently known to occur only in photosymbiotic bivalves is the localized shell-window microstructure and associated convex lenses on the inner shell surface in *Corculum;* however, similar features have not yet been encountered in fossil taxa.

Rapid shell mineralization, rapid growth rates, and gigantism have been used to infer photosymbiosis in fossil taxa, based on enhanced growth rates from mixotrophic nutrition and the potential facilitation of calcification by algal symbionts seen in

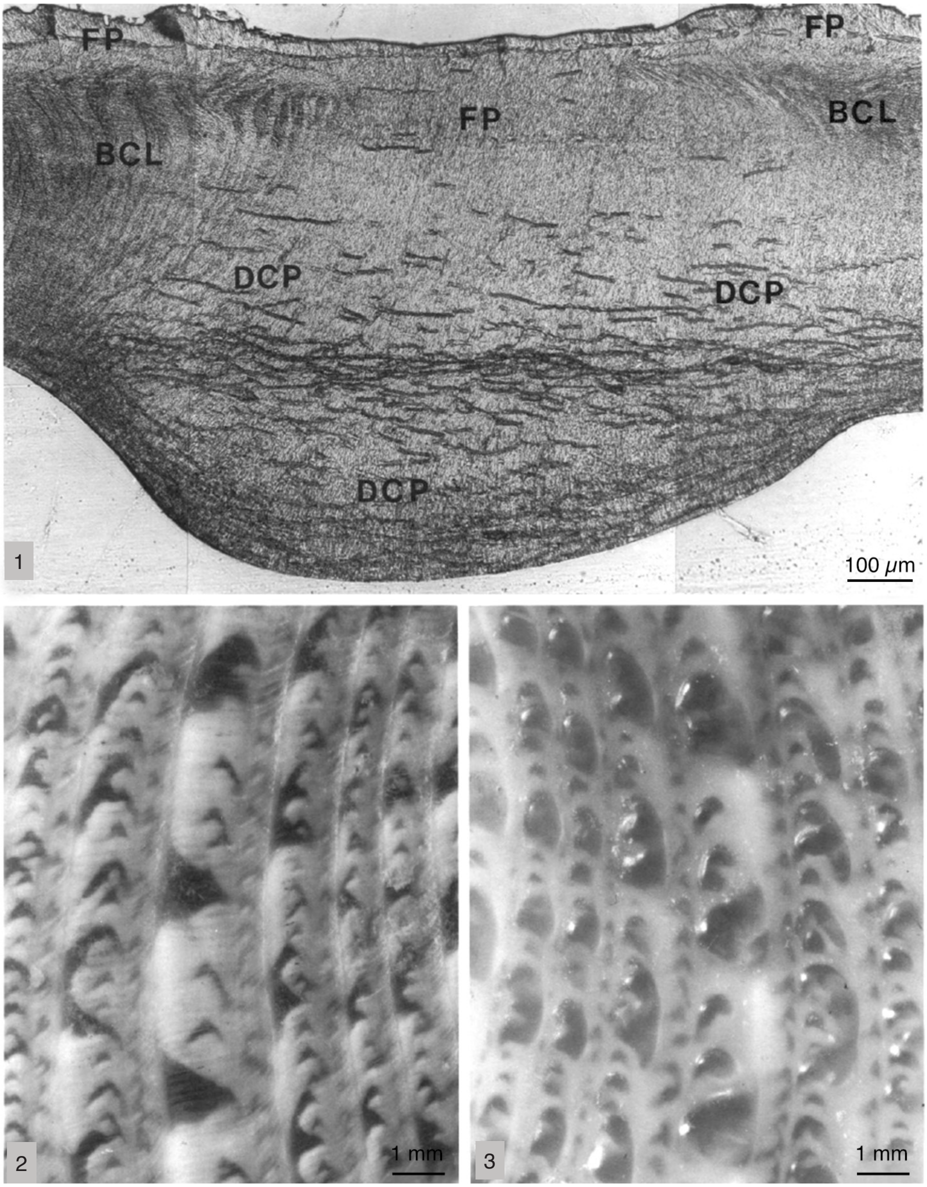

Fig. 11. *Corculum cardissa* (Linnaeus, 1758), illustrating condensing lens (*1*) and posterior shell translucencies (*2–3*) in the Fraginae; *BCL,* branched cross-lamellar; *DCP,* dissected cross-prismatic; *FP,* fibrous prismatic (adapted from Carter & Schneider, 1997).

tridacnines (Seilacher, 1990; Vermeij, 2013). However, other living photosymbiotic and chemosymbiotic bivalves are not larger than their aposymbiotic counterparts, and aposymbiotic species commonly have large, heavily calcified shells, comparable to those of small to medium-sized tridacnines (e.g., *Hyotissa; Empressostrea* Huber & Lorenz, 2007; *Spondylus* Linnaeus, 1758; *Mercenaria* Schumacher, 1817).

An exposed habit in shallow, clear, tropical waters is typical for most photosymbioses, a mode of life best developed today in tropical coral reefs. Photosymbioses are competitively advantageous in oligotrophic waters because of the nutrient recycling offered by mixotrophy (HALLOCK & SCHLAGER, 1986). The restriction to shallow, well-lit waters is necessary for and suggestive of, but again not unique to, photosymbioses. *Hyotissa; Isognomon* LIGHTFOOT, 1786; *Malleus* LAMARCK, 1799; *Spondylus; Chama* LINNAEUS, 1758; several ostreids; pteriids; and pinnids also form large, exposed populations on (and often limited to) shallow, reef-associated habitats. Indeed, these taxa are commonly more conspicuous and abundant than tridacnines and fragines on Indo-Pacific reefs.

Bivalve lineages that move from infaunal to epifaunal habits have been regarded as "primary suspects because photosymbiosis appears as the only feasible trade-off that could have lured a bivalve out of a more protected life within the sediment" (SEILACHER, 1990, p. 294). Tridacnines, fragines, and *Clinocardium nuttallii* show this transition and, when combined with other lines of evidence (e.g., restriction to well-lit waters, suggestive morphology), this transition provides strong evidence for photosymbiosis. Again, though, aposymbiotic counterexamples are not uncommon, as exemplified by the nestling pinnid *Streptopinna saccata* (LINNAEUS, 1758) and the venerid *Periglypta reticulata* (LINNAEUS, 1758) on reefs.

JONES, WILLIAMS, and ROMANEK (1986) proposed that depleted C^{13}:C^{12} ratios were indicative of photosymbiosis. However, more thorough sampling demonstrated substantial variation and complete overlap between photosymbiotic and aposymbiotic bivalves (JONES, WILLIAMS, & SPERO, 1988; ROMANEK & GROSSMAN, 1989; JONES & JACOBS, 1992).

The difficulty of inferring photosymbiosis in fossils is also demonstrated in extant taxa. For example, based on living habits, habitat, and morphology, SEILACHER (1990) predicted that the pectinid *Pedum* BRUGUIÈRE, 1792 in BRUGUIÈRE, LAMARCK, & others, 1791–1827, and the pinnid *Streptopinna* would be found to host zooxanthellae, but both taxa are aposymbiotic (Kirkendale, personal observation). Similarly, SCHNEIDER (1993) predicted that all fragines would be found to be photosymbiotic, based on their simplified stomachs, and we also expected the fragines *Ctenocardia* and *Americardia* would be photosymbiotic, based on their marked keels and broad, flat posterior slopes. However, as noted above, photosymbiosis in fragines is restricted to the *Fragum-Lunulicardia-Corculum* clade.

FOSSIL TRIDACNINES

Both main clades of living photosymbiotic cardiids have a fossil record and represent the only definitively photosymbiotic fossil bivalves. The fossil record of photosymbiotic fragines (*Fragum, Lunulicardia*, and *Corculum*) is limited, extending only to the Miocene (SCHNEIDER, 1998).

The living tridacnines *Tridacna* and *Hippopus* are preceded by a series of fossil genera that well illustrate the transformation from typical cardiid to tridacnine body plan (SCHNEIDER, 1998; Fig. 12). Three early genera differentiated rapidly and are represented in the Lutetian (SCHNEIDER, 1993). *Goniocardium* VASSEUR, 1880, resembles ancestral cockles, except for the reduction of the anterior hinge and almost complete loss of lateral hinge teeth. The anterior adductor muscle is then greatly reduced in *Avicularium* GRAY, 1853; it is lost in *Byssocardium* MUNIER-CHALMAS in TOURNOUËR, 1882, and in the related *Omanidacna* HARZHAUSER & others, 2008, while the posterior adductor muscle migrates to a central position. The anterior hinge is similarly reduced with the loss of an anterior, lateral tooth remnant and reduction and loss of the anterior cardinal teeth (SCHNEIDER, 1998). As the anterior region of the shell and body are reduced, the posterior region is correspondingly enlarged (STASEK, 1962). A byssal gape is lacking in the presumably infaunal *Goniocardium,* slightly developed in *Avicularium,* and

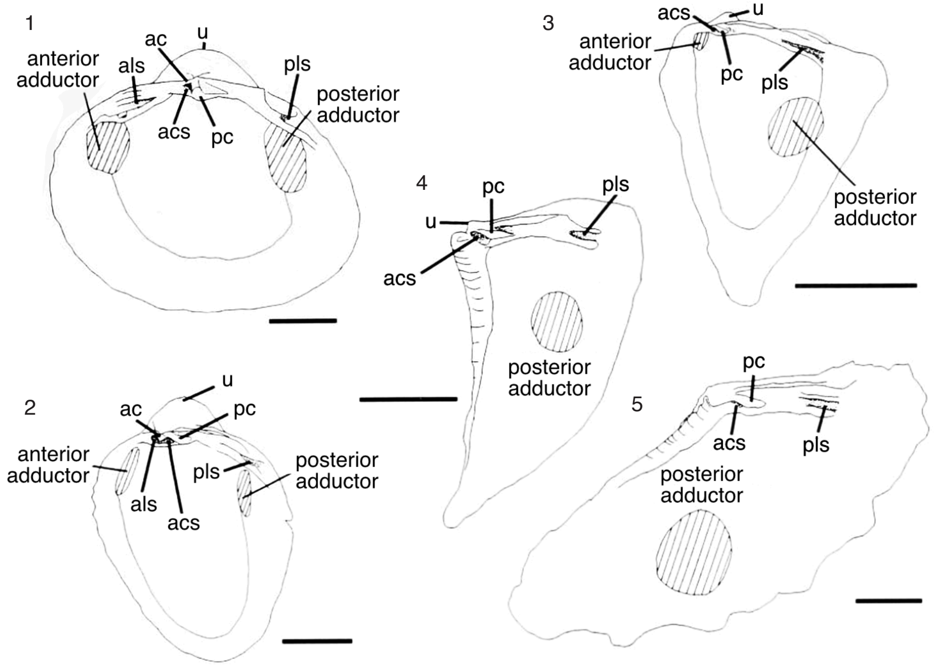

Fig. 12. Evolution of tridacnine body plan from that of a typical cockle, exemplified by *Cerastoderma edule* (Linnaeus, 1758) (*1*), to extinct *Goniocardium* Vasseur, 1880 (*2*), fossil *Avicularium* Gray, 1853 (*3*), fossil *Byssocardium* Munier-Chalmas in Tournouër, 1882 (*4*), and extant *Tridacna* Bruguière, 1797 in Bruguière, Lamarck, & others, 1791–1827 (*5*); *ac,* anterior cardinal; *acs,* anterior cardinal socket; *als,* anterior lateral socket; *pc,* posterior cardinal tooth; *pls,* posterior lateral socket; *u,* umbo; scale bars, 10 mm (*1–3, 5*) and 15 mm (*4*) (Schneider, 1998).

well developed in *Byssocardium,* marking the transition to an epibenthic mode of life. These morphological transformations are recapitulated in the ontogeny of giant clams, wherein anterior lateral and cardinal teeth and adductor muscles are present in early ontogeny but lost in subsequent development (LaBarbera, 1974; Rosewater, 1981; Schneider, 1998; Fig. 13).

SUGGESTED FOSSIL PHOTOSYMBIOTIC BIVALVES

Although several extinct bivalve clades were proposed to have been photosymbiotic based on the types of evidence reviewed above, the evidence is equivocal. Rudists are the most frequently cited likely photosymbiotic clades, as they exhibit epifaunal habits and paleoecological and morphological attributes suggestive of photosymbiosis (e.g., Kauffman & Sohl, 1974; Vogel, 1975; Skelton & Wright, 1987; Kauffman & Johnson, 1988; Seilacher, 1990, 1998). As such, they are large, abundant, sessile or epibenthic recliners with thick shells and rapid growth rates that indicate high rates of calcification, and they are restricted to low latitudes and mostly shallow waters (Skelton, 1978; Kauffman & Johnson, 1988; Lewy, 1995; Steuber, 2000). Rudist bioherms largely displaced tropical coral reefs through the middle and late Cretaceous, further suggesting ecological equivalency, although this replacement was possibly facilitated or driven by the superheated, hypersaline waters of the equatorial Supertethys being inimical to reef coral growth (Kauffman & Johnson, 1988).

Comparisons with living bivalves reveal numerous aposymbiotic clades that share these attributes with rudists. The commonness of epibenthic and sessile habits and large size in aposymbiotic bivalves on the shallow reef (and other habitats) was discussed above. The rapid growth rate and mineralization of rudists is not greater than that of present mussel or oyster beds (Steuber, 2000). Chamids are frequently considered modern analogs of rudists; their morphology and life habits are quite similar to such basal rudists as diceratids. Both chamids and the ecologically similar spondylids are large, heavily mineralized, sessile, mostly cemented bivalves that are restricted to warm, shallow waters, and both are abundant on coral reefs. None are known to harbor zooxanthellae, based on hundreds of specimens of dozens of species in both groups that have been examined and that lacked macroscopic evidence of algal symbionts (bright white indicating lack of substantial chlorophyll in tissues).

Morphological evidence suggesting photosymbiosis in rudists includes mantle exposure or upper valves that are likely translucent (Vogel, 1975; Seilacher, 1990, 1998; Vermeij, 2013). Tissues may have been exposed to light (1) around the periphery of the upper valve, as in *Torreites* Palmer, 1933 (Skelton & Wright, 1987) and *Durania* Douvillé, 1908 (Seilacher, 1990); (2) through a porous upper valve, as in *Osculigera* (Vogel, 1970); or (3) by elaboration in a canal system and overlap of mantle onto the upper valve, as in *Vaccinites* Fischer, 1887 in 1880–1887 (Schumann, 2010). Figure 14 illustrates the upper part of the shell with thick extensions of mantle margin projecting out between the valve rims, in the manner of the living giant clam *Tridacna.* It may be surmised that, as in the latter, these mantle extensions were vividly and variably colored (Skelton & Wright, 1987). However, these specializations, some lacking modern counterparts, have also been interpreted as adaptations for food entrapment (Skelton, 1978; Schumann, 2010) or respiration (Vogel, 1970), as well as photosymbiosis (Vogel, 1975; Seilacher, 1990, 1998; Vermeij, 2013).

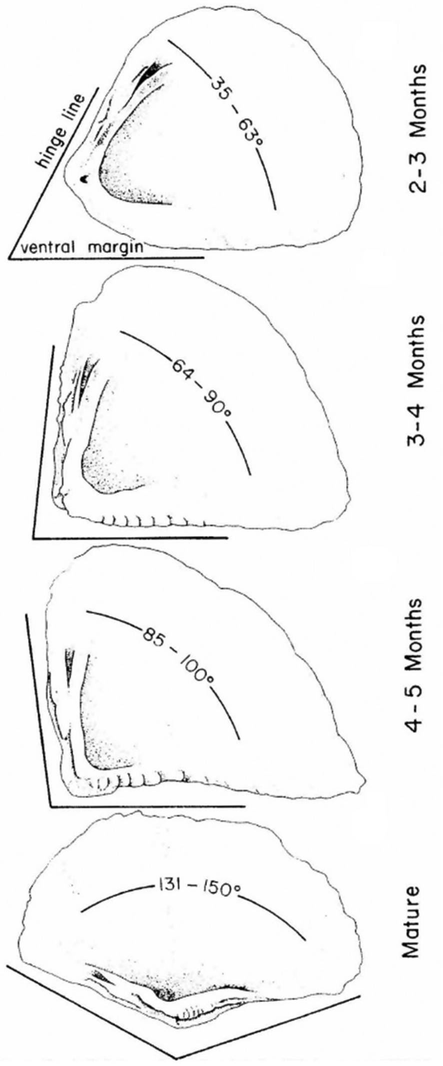

Fig. 13. Morphological transformation observed in giant clam ontogeny closely mirrors evolution of tridacnine body plan (see Fig. 12) (Rosewater, 1981; reproduced with permission of Bulletin of the American Malacological Union).

The weight of evidence from morphology, ecology, and domination of reef-like habitats for rudists is highly suggestive that at least some lineages were photosymbiotic. Photosymbiosis has also been proposed for

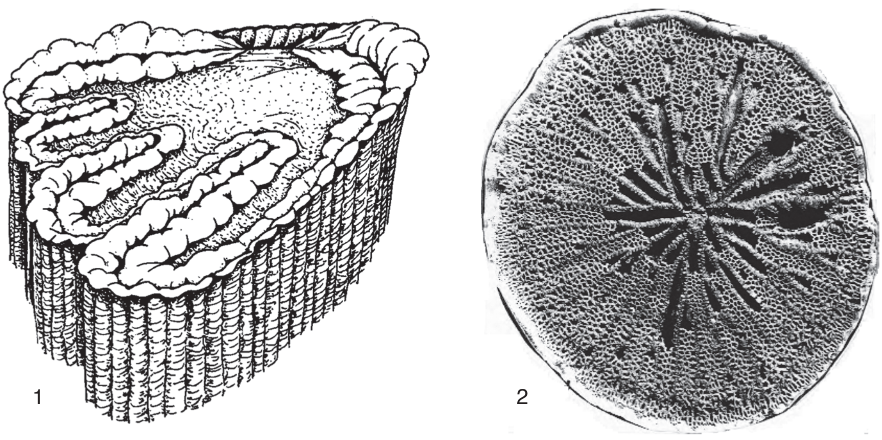

FIG. 14. *1,* Reconstruction of *Torreites sanchezi milovanovici* GRUBIC, 1980, as it appeared in life, showing upper part of shell with mantle margin projecting out between valve rims; *2,* upper surface of upper valve in *Vaccinites vesiculosus* WOODWARD, 1855 (Schumann, 2010; reprinted with permission of TÜBİTAK, Turkish Journal of Earth Sciences).

their ancestors, the megalodontids (VÉGH-NEUBRANDT, 1982; KAUFMANN & JOHNSON, 1988; VERMEIJ, 2013), albeit with more-limited evidence. Suggestive evidence includes their massive, heavily calcified shells, evolutionary transition from infaunal to epifaunal habit, proposed wide gape, and occurrence in shallow, well-lit, tropical waters.

The Upper Triassic megalodontoids *Dicerocardium* STOPPANI, 1857, and *Wallowaconcha* YANCEY & STANLEY, 1999, have similarly been suspected of being photosymbiotic (SEILACHER, 1990; YANCEY & STANLEY, 1999; VERMEIJ, 2013). These reclining, epibenthic clams expanded their valves laterally around a sharp keel, in a

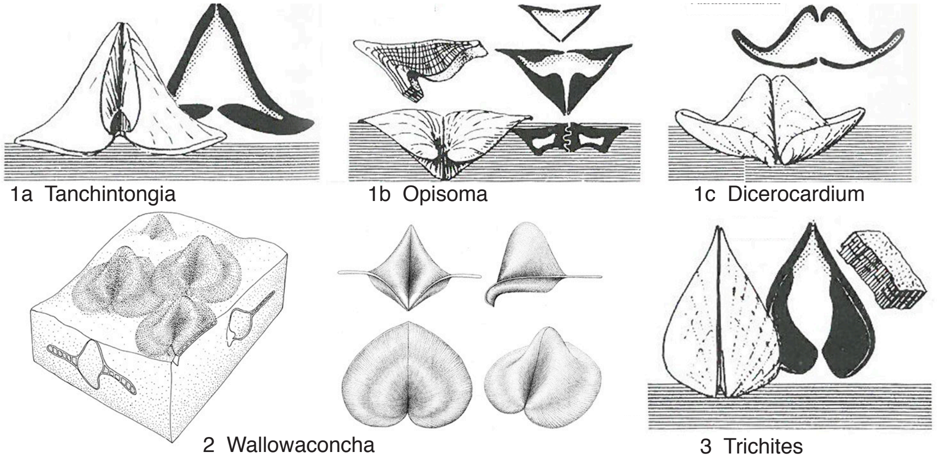

FIG. 15. Putative photosymbiotic fossil bivalves. *1a–c,* Fossil analogs of extant *Corculum,* highlighting repeated evolution of similar forms *Tanchintongia* OZAKI, 1968; *Opisoma* STOLICZKA, 1871 in 1870–1871; and *Dicerocardium* STOPPANI, 1857 (adapted from Seilacher, 1990; reproduced with permission, Historical Biology, Taylor & Francis Ltd.); *2, Wallowaconcha raylenea* YANCEY & STANLEY, 1999, block diagram of ecological grouping on seafloor (*left*) and views of fossil specimen (*right*) (adapted from Yancey & Stanley, 1999; reproduced with permission, Palaeontology, John Wiley and Sons, Publisher); *3,* fossil *Trichites* LHUYD, 1760 (adapted from Seilacher, 1990; reproduced with permission, Historical Biology, Taylor & Francis Ltd.).

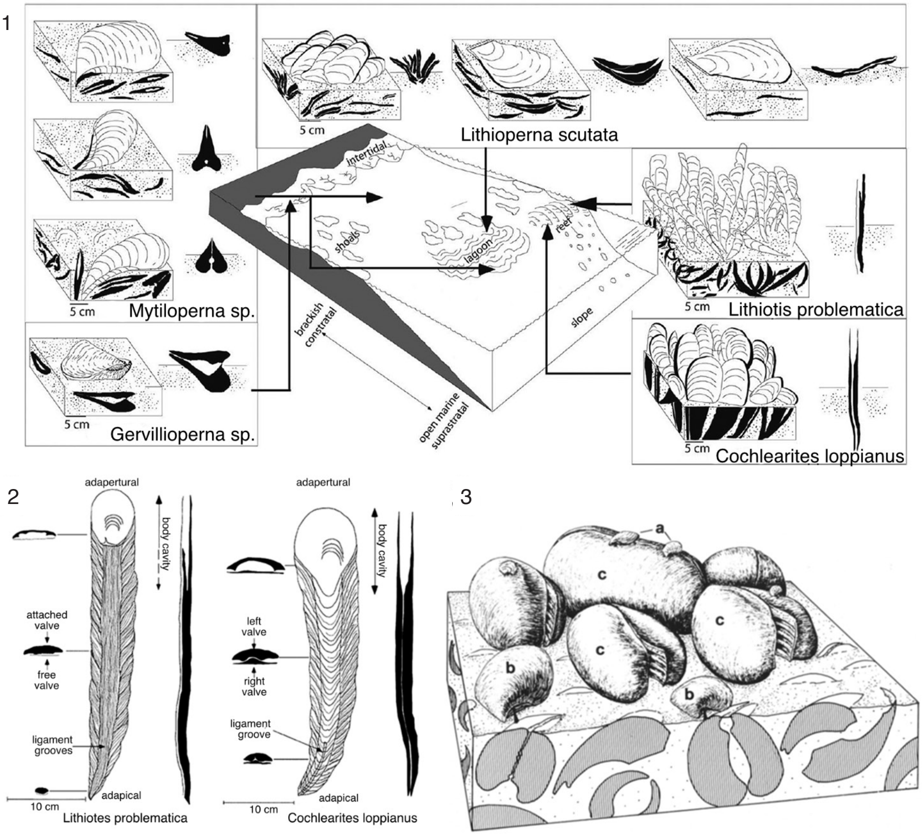

FIG. 16. Habit, zonation, and morphology of putative photosymbiotic fossil bivalves. *1–2,* Habit and zonation (*1*) and morphology (*2*) of *Gervilleioperna* sp. KRUMBECK, 1923; *Mytilioperna* sp. IHERING, 1903; *Lithioperna scutata* (DUBAR, 1948); *Lithiotis problematica* GÜMBEL, 1871; and *Cochlearites loppianus* (TAUSCH, 1890); *3, Pachyperna laverdana* OPPENHEIM, 1900, habit through ontogeny; juvenile (*a*), epibyssate (*b*) stages as hard-bottom dwellers; *c,* adult, edgewise recliners, likely soft-bottom dwellers (adapted from Fraser, Bottjer, & Fischer, 2004).

broad, *Corculum*-like manner suggestive of a solar-panel function (Fig. 15). Such a shell form works well only if light can pass through the shell, as the shell morphology limits gaping. That both were large animals with fairly thick shells challenges a hypothesis of photosymbiosis (YANCEY & STANLEY, 1999). A similar reclining, broad, solar-panel morphology developed in other tropical, shallow-water bivalve groups, including three lineages of pteriomorphians (Permian alatoconchids and *Tanchintongia* OZAKI, 1968, as well as Triassic ramonalinids) and the Jurassic astartid *Opisoma* STOLICZKA, 1871 in 1870–1871(Fig. 15.1). All of these groups have been suggested to have been photosymbiotic based on their morphology, life habit, and occurrence in shallow, tropical settings (SEILACHER, 1990; ISOZAKI, 2006; YANCEY, WILSON, & MIONE, 2009; VERMEIJ, 2013). Although alatoconchids were also very large animals, their outer prismatic shell layer has been proposed to have been potentially fairly transparent to light; they thrived in shallow, tropical environments, in association with presumably photosymbiotic rugose corals and fusulinid forams (ISOZAKI, 2006).

SEILACHER (1990) and VERMEIJ (2013) also proposed photosymbiosis for the Jurassic and Cretaceous pinnids *Trichites* LHUYD, 1760 (Fig. 15.3) and *Stegoconcha* BÖHM, 1907. As with the megalodontoids and

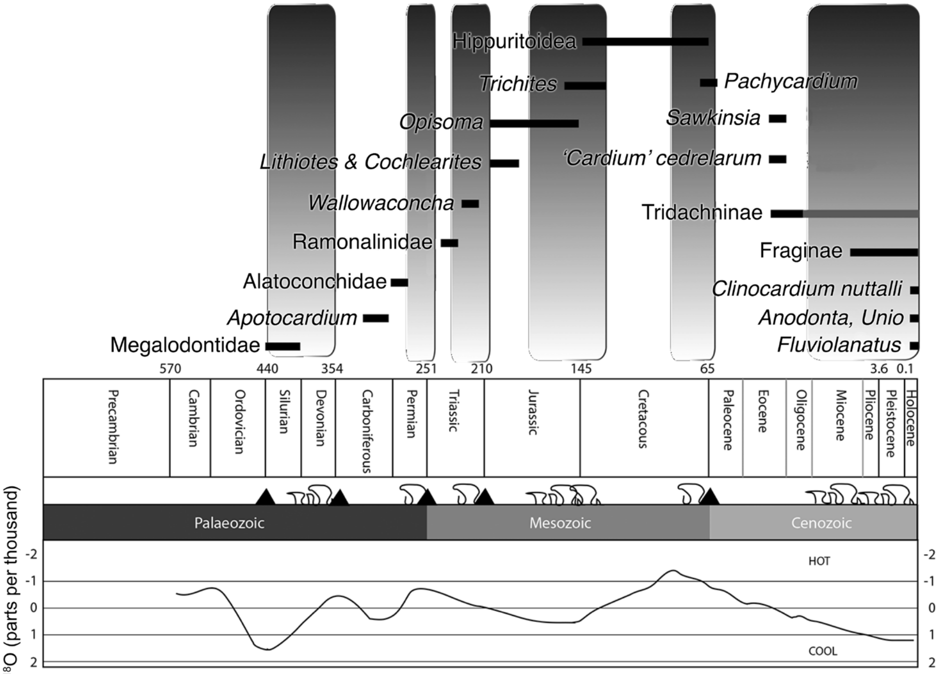

FIG. 17. Geological ages with climate change through Phanerozoic (*line* is long-term average, based on VEIZER & others, 1999), mass extinctions (*black triangles*), and major episodes of coral reef building (denoted by *corals;* VERON, 2008); occurrence and/or duration of paleophotosymbiotic bivalves and extant photosymbiotic bivalves are plotted; note that early Eocene appearance of *Symbiodinium* FREUDENTHAL, 1962, has been proposed (VERMEIJ, 2013) (new).

pteriomorphians just discussed, they are epibenthic recliners, but not so laterally expanded; however, they possess a translucent shell microstructure of especially long prisms. FRASER, BOTTJER, and FISCHER (2004, p. 64) proposed possible photosymbiotic life styles for the reef-building Jurassic pterioids *Lithiotis* GÜMBEL, 1871, and *Cochlearites* REIS, 1903, because of "their growth habit, extensive calcification, presumed oligotrophic environment, and pseudocoloniality" (Fig. 16.1–16.2). POSENATO (1994, 1995) proposed that the Eocene isognomonid *Pachyperna* OPPENHEIM, 1900, may have been photosymbiotic, based on its large size, heavy skeleton, and reclining habit (Fig. 16.3). In all these aspects this species is similar to the related *Malleus malleus* (LINNAEUS, 1758), a large, aposymbiotic recliner common on the shallow reefs of the Palau islands.

Finally, several extinct cardiid lineages have been proposed to have harbored photosymbionts. The Late Cretaceous *Protocardia (Pachycardium) stantoni* is characterized by extensive inductural deposits, indicating the extension of the mantle over the shell that is suggestive of exposing algal symbionts (SCHNEIDER & CARTER, 2001). VERMEIJ (2013) proposed potential photosymbiosis in *'Cardium' cedrelarum* COX, 1941, and *Sawkinsia,* two large, epibenthic cardiids from shallow, tropical, late Eocene limestones in Jamaica (Fig. 17).

SUMMARY AND A LOOK TO THE FUTURE

Cardiids are the only extant bivalves known to be involved in obligate photosymbiosis. Tridacnines have locked into a specialized body plan and show limited variation among species in adaptations for photosymbiosis. In contrast, photosymbiotic fragines show a range of intermediate strategies for light capture. Photosymbiotic relationships reported outside cardiids are uncommon, facultative, and poorly understood. That algal symbionts may be parasitic, rather than beneficial to their host, has recently been suggested in plankton (Decelle, 2013) and gastropod (Banaszak, García Ramos, & Goulet, 2013) symbioses. New analytical tools, such as nano-scale secondary ion mass spectrometry (NanoSIMS), that enable quantification of small amounts of nutrient exchange between partners will be instrumental in understanding these photosymbioses. However, additional basic research such as identifying photosymbiont lineages in bivalves beyond giant clams is also required.

Convincing evidence for photosymbiosis in extinct bivalves is limited. Window-shell microstructure underlain by convexities, the only character restricted to extant photosymbiotic bivalves, is the best character for identifying extinct photosymbiosis. To date, no fossil bivalves have been found with this feature. Other lines of evidence for inferring photosymbiosis in fossils are equivocal, as demonstrated by living aposymbiotic clades that possess them. Moreover, the fact that the majority of clades with the most suggestive morphologies and distributions are deep and highly specialized lineages with no modern analogs makes inferences challenging.

Photosymbiotic associations shape past and present coral reef biodiversity. Although these associations are more fragile than aposymbiotic partnerships, research has indicated that they are potentially more dynamic and responsive to climate change than previously assumed (Buddemeier & Fautin, 1993). The evolution of new forms and strategies for photosymbiosis in the Bivalvia will undoubtedly persist, as life finds a way.

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