

THE ORIGIN OF ALGAL-BIVALVE PHOTO-SYMBIOSIS

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ABSTRACT. The photo-symbiotic bivalves *Fragum fragum* and *Fragum loochooanum* burrow in sediments and supply light through a posterior shell gape to zooxanthellae within their internal soft parts. This newly discovered mode of photo-symbiosis in bivalves can be termed *sciaphilous* (shade-loving), and the hitherto known one, in which bivalves expose mantles or transparent shells out of the sediment to harvest light, as *heliophilous* (sun-loving). *Fragum unedo*, also examined here, is heliophilous. Sciaphilous photo-symbiosis in *F. fragum* is enabled by the zooxanthellae's low compensation point of photosynthesis ($50 \mu\text{Einstein m}^{-2} \text{s}^{-1}$), a point far lower than the ambient light intensity of their habitat. The zooxanthellae's pre-adaptation to low light intensity might have played an important role in originating the zooxanthella-bivalve symbiosis. Sciaphilous photo-symbiosis allows bivalves to profit from photo-symbiosis without risking predation or epibiont attachment, and thus may have been common among fossil photo-symbiotic bivalves. The disproportionately rapid increase in the length of the posterior shell gape and the very rapid decrease of the angle between the posterior and ventral valve margins during the growth of two sciaphilous *Fragum* species, which ensure effective light harvesting by the zooxanthellae, can be used as criteria in searching for fossil sciaphilous microbial-bivalve photo-symbiosis.

SYMBIOSIS between bivalves and contained photosynthetic zooxanthellae has been known since the detailed study by Yonge (1936). This occurs in the genera *Tridacna* (Yonge 1936), *Hippopus* (Yonge 1936) and *Corculum* (Kawaguti 1941), all of which are Indo-Pacific tropical shallow-water dwellers. Symbiosis between non-photosynthetic organisms and photosynthetic microbes will be termed photo-symbiosis hereafter. The symbiotic unicellular, brown-coloured algae, traditionally called zooxanthellae, are currently placed in the dinoflagellate genus *Symbiodinium* (Blank and Trench 1986). This same genus is harboured within all the modern hermatypic corals. Although Yonge (1936) observed zooxanthellae contained within cells (phagocytic blood-cells) of the animals, the zooxanthellae are more commonly located intercellularly in the host bivalve's soft tissues (Trench *et al.* 1981).

With the exception of *Tridacna crocea* Lamarck, which bores in reef coral, all the taxa above are epifaunal. The hitherto known living photo-symbiotic bivalves, both epifaunal and infaunal, place their hypertrophied mantle edges (*Hippopus* and *Tridacna*, including *T. crocea*) or transparent windows on extremely flat posterior valve surfaces (*Corculum cardissa* (Linnaeus); Vogel 1975; Watson and Signor 1986) above the sediment surface in order to expose part of the animal to sunlight. This life habit can be termed *heliophilous* (sun-loving).

All the known photo-symbiotic bivalves belong to the superfamilies Cardiacea and Tridacnacea, which are closely related to each other. The majority of the bivalves of the superfamily Cardiacea adopt an infaunal mode of life. Thus the ancestors of the photo-symbiotic bivalves mentioned above were most probably infaunal bivalves. This raises the question of how the symbiotic relationship originated between the infaunal ancestors of these bivalves and the light-demanding photosynthetic zooxanthellae.

Photo-symbiosis has been inferred in fossil bivalves (Philip 1972; Vogel 1975; Loriga and Benini 1977; Skelton 1979; Thiele and Tichy 1980; Yancey and Boyd 1983; Skelton and Wright 1987; Seilacher 1990) as well as among fossil brachiopods (Cowen 1970, 1982). This inference is based on

features of their shell morphology, shell microstructures and their palaeoecology, which are similar to those of living photo-symbiotic bivalves or hermatypic corals.

Recently, Kawaguti (1983) and Yamasu (1988*a, b*) have reported new examples of zooxanthella-bivalve symbiosis in *Fragum fragum* (Linnaeus) and *Fragum unedo* (Linnaeus). Umeshita and Yamasu (1985) found another example in a third species, *Fragum mundum* (Reeve). In contrast with the highly specialized shell forms of other known photo-symbiotic bivalves, the shell shape of the *Fragum* species is similar to other non-symbiotic cardiid bivalves, except for their long and straight posterior margin as well as the angular corner formed where the posterior and ventral valve margins meet. This suggested that a detailed investigation of bivalves belonging to the genus *Fragum* could provide us with information about the initial stage of zooxanthella-bivalve symbiosis. Further, information on the zooxanthella-symbiosis of the genus would also contribute to a safer basis for inferring the existence of photo-symbiosis among fossil bivalves. For these reasons, three living specimens of strawberry cockles, *F. fragum*, *F. unedo* and *F. loochooanum* Kira, were examined on the basis of their ecology, anatomy, distribution of zooxanthellae within their soft tissues, shell form and shell microstructure. For *F. fragum*, shell transparency and photosynthetic activity of symbiotic zooxanthellae were also examined.

The present investigation reports the finding of the new life mode for photo-symbiotic bivalves, in *F. fragum* and *F. loochooanum*, which may be termed *sciaphilous* (shade loving). The adaptive significance and origin of photo-symbiosis in bivalves, as well as the criteria for inferring sciaphilous photo-symbiosis in fossil bivalves, are discussed.

MATERIALS AND METHODS

Habitats of the examined bivalves

The majority of the observations of the life habits of the three species of *Fragum*, as well as the collection of materials for the further studies, were carried out by numerous scuba dives on the shallow sand flat of Amitori Bay in front of the Okinawa Regional Research Centre, Tokai University, Iriomote Island, Okinawa Prefecture, Japan, between November 1988 and November 1991. The substratum consists of light grey silty coarse sand. The sand grains are mainly calcareous bioclasts. The flat is exposed during the low tides of Spring and late Autumn, when the tidal range is largest. At average high tides, it is covered with about 2 m sea water. The mean monthly temperature fluctuates between 22 °C in February and 29 °C in July (from data for the period May 1977 to December 1989; Okinawa Regional Research Centre 1990).

On test-dives to the deeper part of the bay, a few living individuals with zooxanthellae were also found at a depth of 20 m in muddy sand substrata. They were not incorporated into the material of the present study.

Additional samples of living *F. unedo* were collected from the adjacent sandy flats within the bay and from the sandy flat at the mouth of Sakiyama Bay, which is located about 1.5 km south of the centre and separated from Amitori Bay by a small peninsula. For the study of shell allometry, *F. unedo* specimens collected from the Kabira Bay on Ishigaki Island, which is located about 50 km from Amitori Bay, were incorporated.

The specimen for Plate 1, figures 5 and 8 was collected at Bise, Okinawa Island, Okinawa Prefecture.

All the examined specimens, except for those photographically documented in the field study, are stored in the Museum of the Department of Geology and Mineralogy, Faculty of Science, Kyoto University (JCTO0014-JCTO0019).

Burrowing rate index

The collected samples were kept in a laboratory aquarium filled with a sufficient thickness of silty coarse sand from their natural habitats before measurement of burrowing rate indexes. The samples were provided with running sea water and received ambient light from windows. The burrowing of

the cockles was recorded by a video-camera. Burrowing periods (time between erection of shells and complete burrowing of the posterior shell margin), and number of rocking motions during burrowing were determined from video-images. Mass (wet weight) and shell length of the samples were also measured. For each individual, burrowing rate index (BRI), defined by Stanley (1970), was calculated according to the following equation:

$$\text{BRI} = \frac{[\text{mass (g)}]^{1/3}}{\text{burrowing period (s)}} \times 100.$$

Shell transparency of Fragam fragum

Measurements were carried out using a spectro-photometer (Hitachi Type 3400). The shell surface is exposed to a light source. Behind it is a hole 3 mm in diameter in an opaque board. The light transmitted through the shell and the hole is then gathered and measured using a photo-multiplier equipped with an integrating sphere.

Measurements of the photosynthesis-irradiance profile of the zooxanthellae of Fragam fragum

The cockles were collected on the sandy flat in Amitori Bay in October, 1990 and kept in an aquarium for several days under the same conditions as the samples for the measurement of the burrowing index, and then examined for the photosynthetic activity of the zooxanthellae.

Zooxanthellae in the cockles were isolated from the mantle tissues by squeezing them in sterilized and filtered sea water. The sea water with liberated zooxanthellae was then passed through a nylon mesh (50 μm) to remove tissue fragments, and then centrifuged at 1200 g for 10 min to separate bacteria and various small particles which were left in the supernatant. The red precipitate of zooxanthellae was then suspended in filtered sea water and placed in a 3.0 ml vessel with a rotating platinum electrode, fitted with a circulating water-jacket to keep a constant temperature of 20 °C. The light beam from a 350 W incandescent lamp was passed through two infrared-absorbing filters (Hoya, HA-30) and a diaphragm, to attenuate the light intensity in a step-wise fashion, and then focused on the vessel. Light intensity at the surface of the vessel was monitored with a Licor Quantum Sensor. Both O₂ concentration in the vessel, as monitored by the platinum electrode, and the light intensity were automatically recorded.

SCIAPHILOUS LIFE MODE AND POSTERIOR MANTLE EDGES

More than two hundred living *F. fragum* were observed on the tidal flat in front of the Okinawa Regional Research Centre. Their population density here seldom exceeds one or two individuals per square metre, although an exact determination was not carried out.

On burrowing, the valves become completely immersed in the sediment, with the flattened posterior valve slopes just beneath the thin sediment cover (Pl. 1, fig. 3; Text-fig. 1B). The posterior shell gape is covered by partly fused mantle edges (Pl. 1, figs 1 and 2; Text-figs 1A and 2). From both posterior valve margins, mantle edges extend laterally. They are furnished with numerous tentacles, and are moderately hypertrophied, especially ventral to the inhalant siphon. The tentacles secrete mucus and sand grains adhere around them. Consequently, the extended mantle edges and tentacles are covered by sand grains (Pl. 1, fig. 9). Therefore in the natural life position of *F. fragum*, it is only the exhalant and inhalant siphons and a part of the posterior mantle edges covering the shell gape that are continuously exposed through the sediment (Pl. 1, fig. 3; Text-fig. 1B). These exposed soft parts covering the posterior shell gape are spotted with transparent and non-transparent patches and are as a whole semitransparent (Pl. 1, fig. 2). Large transparent patches commonly occur around the exhalant and inhalant siphons.

More than eighty living *F. loochooanum* were observed. They have a life habit rather similar to *F. fragum*, and burrow completely into the sediment. Their very weakly hypertrophied lateral

expansions of posterior mantle edges, together with numerous tentacles (Text-fig. 1A), are covered by the sediment (Pl. 1, fig. 6; Text-fig. 1B). Therefore, only the posterior mantle edges covering the posterior shell gape, including the inhalant and exhalant siphons, are continuously exposed through the sediment. Transparent and non-transparent patches spot these exposed soft parts and make them semitransparent. Large transparent patches occur on the mantle edges covering the notches of the marginal crenulations along the posterior valve margins in addition to those around the exhalant and inhalant siphons. This species does not fix sand grains around its tentacles.

Five living *F. unedo* were available for observation. They bury their valves completely in the sediment. Their posterior mantle edges are furnished with tentacles and are strongly hypertrophied, especially ventral to the inhalant siphon. Here, they form fan-shaped lobes (Pl. 1, fig. 7; Text-figs 1A–B). The lobes continue as broad fleshy stripes along the rest of the posterior margin. These hypertrophied mantle edges are spread over the surface of the substratum (Pl. 1, fig. 7; Text-fig. 1B). The mantle edges covering the posterior gape, including inhalant and exhalant siphons, are thick and less transparent. Most of the individuals show a negative reaction to shade and draw back their posterior mantle edges when a shadow crosses over them.

All the examined samples of these three species contain zooxanthellae within their soft tissues. Therefore, their coexistence with zooxanthellae is not purely fortuitous but very probably symbiotic.

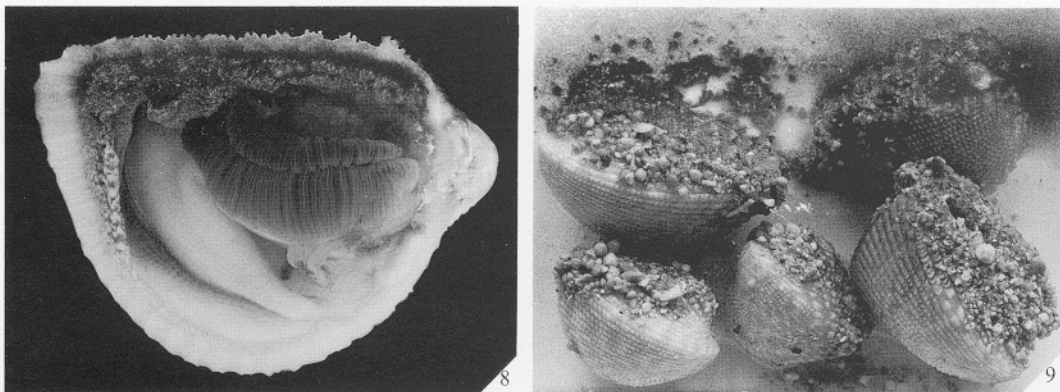
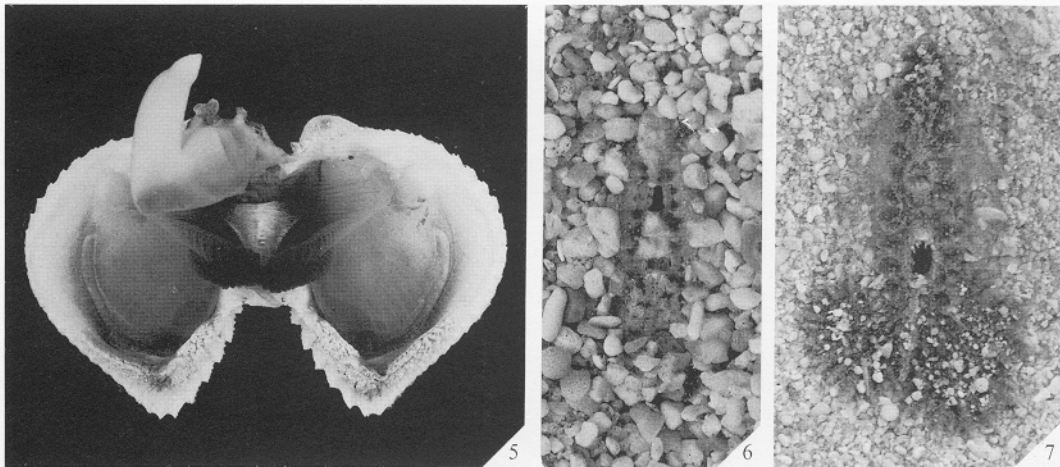
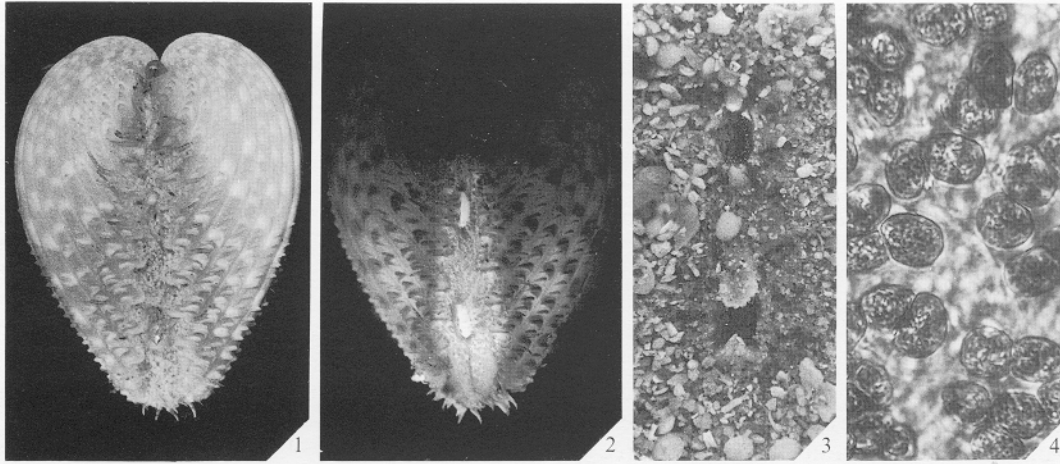
F. fragum and *F. lochooanum* adopt infaunal life habits and do not extend their mantle margins and valves out of the sediment, except for the regions around the inhalant and exhalant siphons. Furthermore, *F. fragum* apparently deliberately minimizes the exposure on sediment by mucus secretion from the tentacles and adhesion of sediment grains around them. This previously unrecognized photo-symbiotic life mode, in which the host bivalves do not expose their mantle edges to the light, except for small areas stretched between the posterior shell gape, can be called *sciaphilous* (shade loving; Text-fig. 7). In contrast, all the hitherto known living photo-symbiotic bivalves, both epifaunal and infaunal, can be termed *heliophilous* (sun loving), because they put their hypertrophied mantle margins or transparent shells out of the sediment to expose them directly to the light. *F. unedo*, which is infaunal and extends its hypertrophied mantle margins and tentacles out of the sediment, belongs to this latter category.

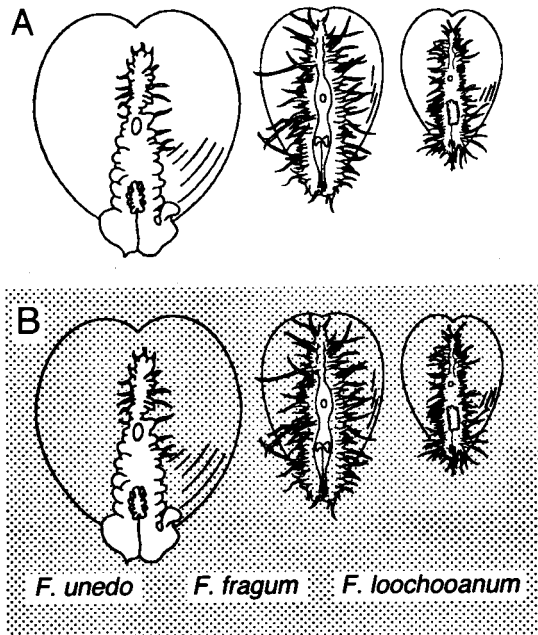
EXPLANATION OF PLATE 1

Figs. 1–5, 8–9. *Fragum fragum*. 1–2, with moderately expanded mantle edges and tentacles. 1, illuminated from above. 2, illuminated from below in dark room. Mantle edges covering the shell posterior gape are more transparent than the semi-transparent valves. Non-fused part of the mantle edges meet together along the dark line running along the middle of the shell gape from the inhalant siphon to the ventral margin. Both $\times 1.7$. 3, in natural life position, posterior part of the shell covered with foraminiferal sand, $\times 3.3$. 4, zooxanthellae in the mantle tissue, $\times c. 600$. 5, soft parts: gills and mantle covering the inner shell surface, especially near the posterior gape, containing abundant zooxanthellae, are dark coloured. Condensation of zooxanthellae, partly caused by the contraction of muscles, has darkened the pallial lines. The bottom wall of the supra-branchial chamber (triangular white area in the middle of the photograph) contains fewer zooxanthellae than the area of the foot surface (upper left of the bottom wall of the supra-branchial chamber), which faces the bottom wall in life, $\times 1.4$. 8, soft parts: abundant zooxanthellae darken both the outer and the inner gill demibranchs. In contrast, the posterior mantle edges are spotted with transparent flecks (dark in the photo) and white flecks, and contain very few zooxanthellae. The distal half of the L-shaped foot, and the mantle covering the anterior part of the shell interior, both located rather distant from the posterior shell gape from which light penetrates into the shell interior, are white and contain very few zooxanthellae, $\times 1.9$. 9, the posterior slopes of shells are covered with sand grains, adhering to them because of the presence of mucus secreted by the tentacles.

Fig. 6. *Fragum lochooanum* in natural life position. Only the posterior gape is visible through the sediment, $\times 4.3$.

Fig. 7. *Fragum unedo* in natural life position with strongly expanded mantle edges lying on the sediment, $\times 1.7$.





TEXT-FIG. 1. Sketch of three *Fragum* species. A, Mantle edges fully expanded. B, Exposure of mantle edges through sediment cover (sediment is stippled).

ACTIVE BURROWING ABILITY

As a measure of locomotion ability, the burrowing time and burrowing rate index (BRI) were determined for ten individuals of *F. fragum*, six individuals of *F. loochooanum* and one individual of *F. unedo* (Table 1).

For the Cardiacea, to which *Fragum* also belongs, Stanley (1970) reported BRI values for seven species. Following Stanley's statement that temperature has a minor effect on BRI value within the range 20–30 °C, a comparison of BRI values between the present species and Stanley's six species was made, all measured within this temperature range. Stanley's seventh species, *Dinocardium robustum* shows an exceptionally large BRI value of 5 (measured at 18 °C) in comparison with his other six species.

Three of Stanley's (1970) species have a BRI value of 1, and of the other three, one species has a value of 0.9, another 0.5, and the last 0.4. Thus *F. fragum* (mean BRI = 0.7) burrows as effectively as Stanley's six cardiacean species without symbiotic zooxanthellae. For *F. unedo* only one measurement is available (BRI = 0.4) which does not allow us to draw any conclusion, although it is comparable to the BRI values of Stanley's six cardiaceans.

F. loochooanum has a very low BRI value (mean BRI = 0.075) in comparison with the above discussed species. Perhaps the BRI value underestimates locomotive activity of small sized animals, which cannot use weight, for example, to help in cutting themselves into the sediment. If locomotive activity is measured in terms of burrowing period, *F. loochooanum* (114 s) burrows far faster than *F. fragum*.

BIVALVE ANATOMY

Mantle edges

When the three examined strawberry cockle species open their valves, the mantle edges cover the shell gape along its whole length (Text-fig. 2). They are fused between the beak and the inhalant siphon. Along the rest of the gape, they are not fused, yet meet tightly together. The ventral mantle edges as well as the anterior mantle edges are thin, except for the rather thick ventral mantle edges near the angular postero-ventral shell corner.

TABLE 1. Burrowing index of three *Fragum* species. Abbreviations: M, mass; L, length; BP, burrowing period; R, number of rocking motions; BRI, burrowing rate index; std., standard deviation. The centre referred to is the Okinawa Regional Research Centre.

	M (g)	L (mm)	BP (s)	R (times)	BRI
<i>Fragum fragum</i> *					
(n = 10)					
	1.86	14.4	891	3	0.14
	3.24	17.0	129	4	1.15
	3.44	17.4	231	3	0.65
	3.89	17.9	115	3	1.37
	4.48	19.2	316	4	0.52
	4.54	18.9	305	4	0.54
	4.89	19.0	1347	4	0.13
	6.36	20.3	543	6	0.34
	6.49	22.7	824	6	0.23
	10.99	24.5	103	4	2.16
Mean	5.02	19.13	480.4	4.1	0.72
SD	2.39	2.73	395.1	1.0	0.62
<i>Fragum loochooanum</i> †					
(n = 6)					
	0.16	7.1	50	4	0.076
	0.24	8.6	129	4	0.073
	0.25	8.5	122	5	0.074
	0.27	8.5	124	5	0.076
	0.29	8.6	160	4	0.077
	0.39	9.7	100	4	0.075
Mean	0.27	8.5	114.2	4.3	0.075
SD	0.07	0.75	33.7	0.5	0.001
<i>Fragum unedo</i> ‡					
(n = 1)					
	6.86	25.1	484	11	0.40

* Samples from the sandy bottom in front of the centre; collected between 26 and 29 Oct. 1990; measured on 30 Oct. 1990 at water temperature of 26.8 °C.

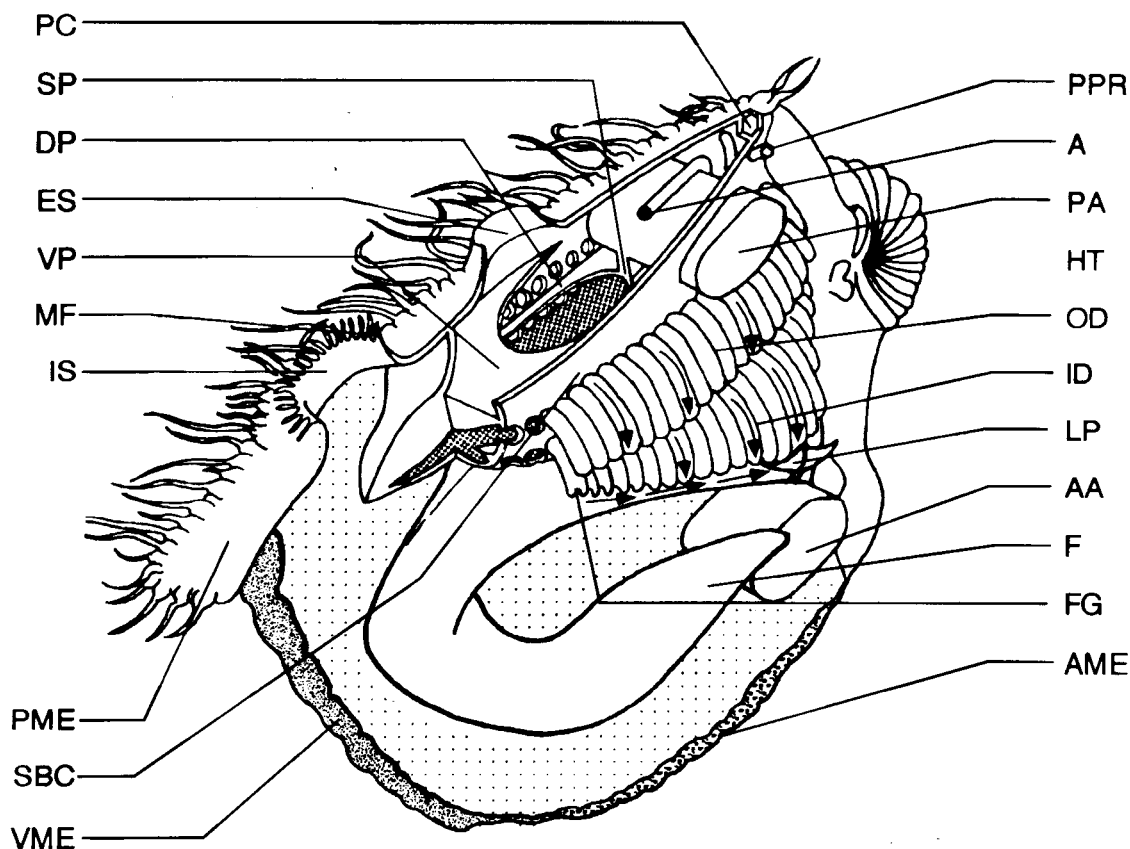
† Samples from the sandy bottom in front of the centre; collected between 26 and 31 Oct. 1990; measured on 5 Nov. 1990 at water temperature of 26.2 °C.

‡ Sample from sandy flat at the mouth of Sakiyama Bay; collected on 31 May 1989; measured on 2 June, 1989 at water temperature of 25.9 °C.

As already described, the mantle edges along the posterior valve margins show considerable variation between the sciaphilous and the heliophilous species. In brief, the sciaphilous *F. fragum* and *F. loochooanum* have less hypertrophied, less extensively laterally expanded, and more transparent posterior mantle edges than the heliophilous *F. unedo*. It is difficult to estimate quantitatively the proportion of the incident light that is transmitted through the mantle edges covering the posterior gape of the sciaphilous *F. fragum* and *F. loochooanum*. In *F. fragum*, however, they are more transparent than the semitransparent posterior slope of their valves (Pl. 1, fig. 2).

Soft parts within the shell interior

The anatomy of the soft parts within the shell interior is quite similar in all three *Fragum* species. The description below is mainly based on *F. fragum* (Pl. 1, figs 5 and 8; Text-fig. 2).



TEXT-FIG. 2. Anatomy of *Fragum fragum*. Inner surface of the bottom (anterior side) of the supra-branchial chamber is densely stippled. Mantle covering the inner surface of the shell is weakly, but regularly, stippled. Ventral and anterior mantle edges are irregularly stippled. Arrows on inner and outer demibranchs indicate the direction of ciliary grain transportation. Abbreviations: A, anus; AA, anterior adductor muscle; AME, anterior mantle edge; DP, dorsal partition of supra-branchial chamber; ES, exhalant siphon; F, foot; FG, food groove (inner marginal food groove of ctenidium); ID, inner demibranch; IS, inhalant siphon; LP, labial palp; MF, ventral end of mantle fusion; OD, outer demibranch; PA, posterior adductor muscle; PC, pericardium; PME, posterior mantle edge; PPR, posterior pedal retractor muscle; SBC, supra-branchial chamber; SP, sagittal partition connecting posterior adductor muscle and dorsal partition of supra-branchial chamber; VME, ventral mantle edge; VP, ventral partition of supra-branchial chamber.

Just under the posterior shell gape there is an elongated tube separated off by a thin membrane (supra-branchial chamber; Purchon 1955) running parallel to the posterior valve margins. Its dorsal end reaches to the foot, yet the membrane is not fused with the latter but is separated by a very narrow slit. The tube is bipartite ventral to the exhalant siphon, where a thin membrane divides a lower (anterior) chamber, with attachment of demibranchs, from the upper chamber. Dorsal to the exhalant siphon it is tripartite. Here, there is a hollow between the mantle edge and the posterior adductor muscle. The anus opens in this hollow. Below it, a thin membrane separates two chambers, each with attachment areas for outer and inner demibranchs, respectively. The upper of the two chambers has a sagittal partition. The three examined species have inner and outer gill demibranchs which hang from the lateral wall of the supra-branchial chamber. The inner demibranchs are considerably larger than the outer demibranchs and have food grooves along their free edges (inner marginal food grooves of ctenidium). The inner demibranchs are connected by a

pair of labial palps to the mouth on the ventral side of the foot. The palps, considerably smaller than those illustrated in *Clinocardium nuttali* (Stasek 1961), are located at about one-third of the length of the inner demibranchs from their dorsal ends. Each of the labial palps is composed of two small triangular lobes. The adductor muscles are located near the beak. The foot is large and L-shaped.

DISTRIBUTION OF ZOOXANTHELLAE

Zooxanthellae (Pl. 1, fig. 4) are contained intercellularly among the tissues of the strawberry cockles. Their brown colour makes it easy to determine their occurrence and relative abundance within the cockle tissues.

In the two sciaphilous species, *F. fragum* and *F. loochooanum*, the zooxanthellae are contained in the innermost part of the hypertrophied lateral expansions of the posterior mantle edges, but in only small quantities. Their tentacles, as well as the mantle covering the posterior margins, both of which are more or less transparent, do not contain abundant zooxanthellae. The ventral mantle edges contain abundant zooxanthellae just near the corner where the posterior and ventral margins meet. The zooxanthellae content of the mantle edges gradually decreases towards the anterior mantle edges.

In the shell interior of these sciaphilous species, the thin membranes of the supra-branchial chamber contain zooxanthellae, but not very abundantly. The surfaces of the gill demibranchs are strongly dark brown coloured (Pl. 1, figs 5 and 8). On the outer surfaces of the demibranchs, the brown colour fades gradually towards the beak. The inner sides of the demibranchs are brown coloured, especially strongly along the line of their attachment to the supra-branchial chamber wall. Weak brown coloration is also observed on the foot facing the floor of the supra-branchial chamber. The membrane covering the posterior adductor muscle is strongly brown coloured. Abundant zooxanthellae also exist within the mantle lining the shell interior: in the smallest species, *F. loochooanum*, the whole surface is coloured dark brown; in *F. fragum* the coloration is more vivid along the posterior valve margins and posterior part of the ventral margin.

The hypertrophied and laterally expanded mantle edges of the heliophilous *F. unedo*, which are exposed to light on the sediment surface, harbour a large number of zooxanthellae under their thick, almost non-transparent tissue. Zooxanthellae are also abundant in the ventral mantle edge just near the corner where it meets with the posterior mantle edge. Their abundance gradually decreases towards the anterior mantle edges. In the shell interior, the thin membrane of the walls and floor of the supra-branchial chamber contains a large number of zooxanthellae. The coloration of the gills and the mantle lining the shell interior is much weaker than the two sciaphilous species. In particular, the anterior part of the mantle lining the shell interior is almost white and contains very few zooxanthellae.

In summary, the sciaphilous *F. fragum* and *F. loochooanum* farm the zooxanthellae mainly within their internal soft tissues, whereas the heliophilous *F. unedo* farms them chiefly in its exposed and hypertrophied posterior mantle edges. In the two sciaphilous species, the mantle edges covering the posterior shell gape and supra-branchial chamber, which aligns the gills just beneath and parallel with the posterior shell gape, are semi-transparent. They ensure the penetration of light to the gills and other internal soft tissues with abundant zooxanthellae. The heliophilous *F. unedo* also has a long supra-branchial chamber. This species, however, uses it as an area for farming the zooxanthellae rather than as a device for ensuring light supply to the gills. The light for the zooxanthellae within the tissues of the supra-branchial chamber is supplied from the inhalant and exhalant siphons.

ACTIVE GRAIN TRANSPORTATION ON THE GILL SURFACE

Transportation of grains by ciliary action (Text-fig. 2) was monitored by sprinkling fine grinding powder over the gill surfaces of *F. fragum*. On each outer demibranch grains are transported from the ascending branch to its free edge, and then on, over the descending branch on to and along the

ctenidial axis. On the inner demibranch, grains are transported on both the descending and ascending branches to the food groove along its free edge. The action of cilia in the food groove then transports fine particles, via the labial palps, to the mouth. In one specimen it takes about a minute for the grains to cross the brightest part of the descending lamella of the inner demibranch from the ctenidial axis to the food groove, even after three hours have elapsed since the beginning of dissection. Excess grains are sorted by the labial palps, mixed with mucus to form small round balls and then expelled from its pointed end. The above construction of the gill as well as the manner of fine grain transportation on it closely resembles that of *Clinocardium nuttali* described by Stasek (1961).

The similar construction of the gills and the labial palps of the three examined *Fragum* species suggests that these species actively transport and sort grains on the gills and labial palps, as observed in *F. fragum*, which in turn indicates that the three examined *Fragum* species retain active filter feeding.

SHELL FORM AND ALLOMETRIC GROWTH

Shell form

In accordance with the diagnosis of the genus *Fragum* (Keen 1980), the three examined *Fragum* species have fairly inflated valves, flattened posterior valve slopes, well defined umbonal ridges along the intersection of the posterior and ventral valve slopes, as well as an angular postero-ventral corner of the valve margins. The posterior valve margin is very long and almost straight except near the beak. It meets with a more or less straight ventral margin and forms an angular corner. In the present study the angle of this corner is referred to as the PV-angle. In some specimens the umbonal ridge protrudes weakly at the shell margin postero-ventrally. In this case the margin ventral to it is weakly concave near the angular corner.

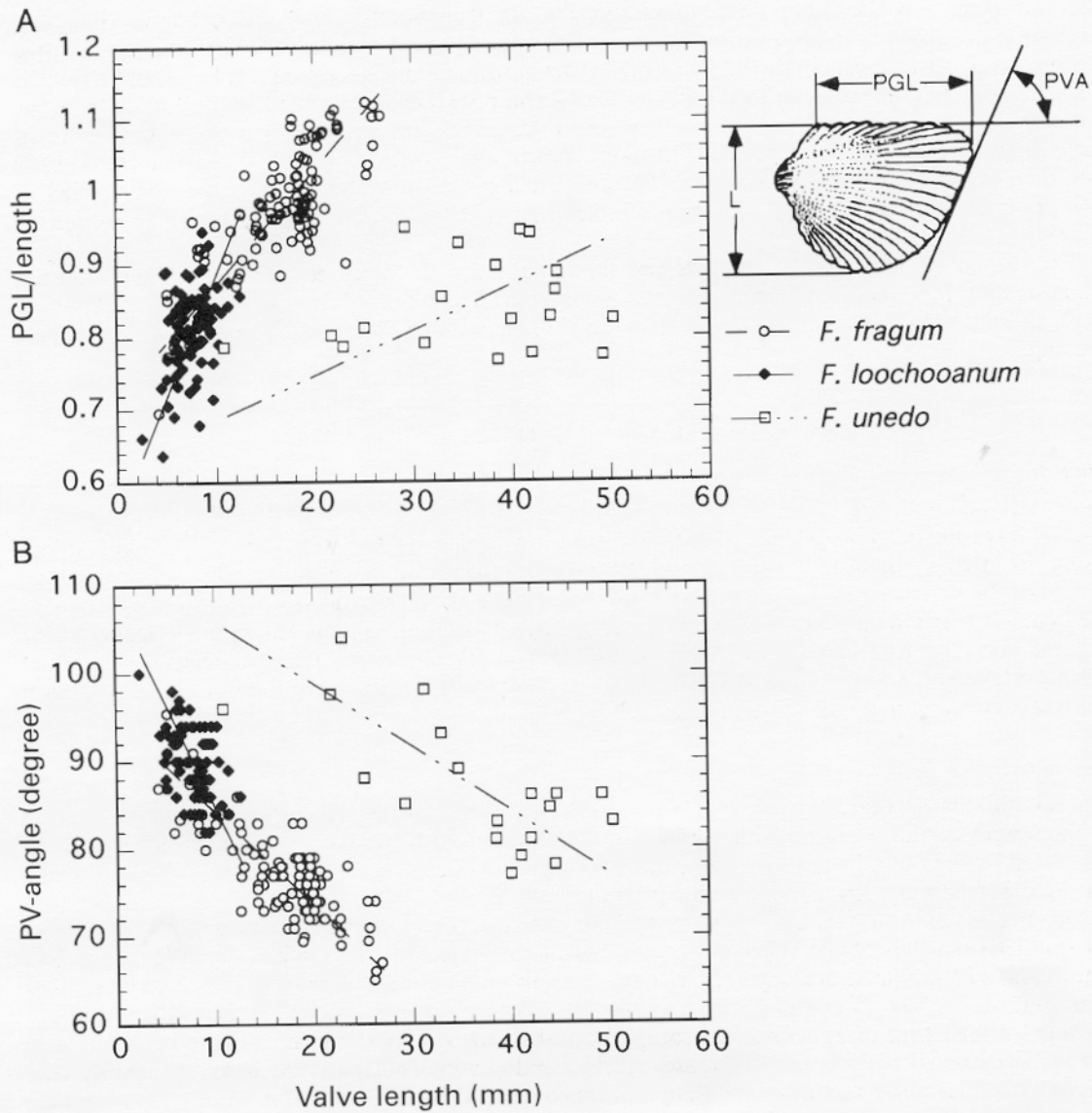
Allometric growth

The sciaphilous *F. fragum* and *F. loochooanum* show a very conspicuous disproportionate increase in the length of the posterior gape (PGL) in comparison with the increase in shell length (L) as expressed by the rapid increase in PGL/L ratio (Text-fig. 3A; Table 2). In the heliophilous *F. unedo*, on the other hand, this tendency is not present.

The angles between posterior and ventral margins (PV-angle) of the two sciaphilous species are far smaller than that of the heliophilous one, when compared for the same L value (Text-fig. 3B). The average PV-angle of the largest specimens (L = about 25 mm) of *F. fragum* is 20 degrees smaller than that of *F. unedo* of comparative L value. The average for *F. loochooanum* is smaller by about 10 degrees than that of *F. unedo*, for comparable shell sizes (L = 10 mm).

Furthermore, the PV-angle decreases very rapidly with increased shell length (L) in the sciaphilous *F. fragum* and *F. loochooanum* (Text-fig. 3B; Table 2). The heliophilous *F. unedo* also shows this tendency, but weakly.

The strongly disproportionate increase in the length of the posterior shell gape (PGL) during the growth of *F. fragum* and *F. loochooanum* leads to a rapid enlargement of the area of the posterior shell gape through which light penetrates into the shell interior. The rapid decrease in the PV-angle during shell growth keeps an increasingly larger area of the ventral mantle edges near the angular postero-ventral corner in a short distance from the posterior shell gape. Thus the allometric growth of these two shell characters ensures a light supply to the areas rich in zooxanthellae in the soft tissues of the shell interior and along the shell margins of the two sciaphilous species. The heliophilous *F. unedo* farms its zooxanthellae mainly in its hypertrophied mantle edges exposed above the sediment. Therefore, for this species the above mentioned two shell characters are not so important and allometry is weakly developed.



TEXT-FIG. 3. Allometric shell growth of *Fragum* species. A, Posterior gape length (PGL)/length (L) ratio plotted against length (L). B, Angle between posterior and ventral valve margins (PV-angle) plotted against length (L). (Registration numbers of samples: *Fragum fragum* = CTO0014; *F. loochooanum* = CTO0015; *F. unedo* = CTO0016). Parameters of reduced major axes are listed in Table 2.

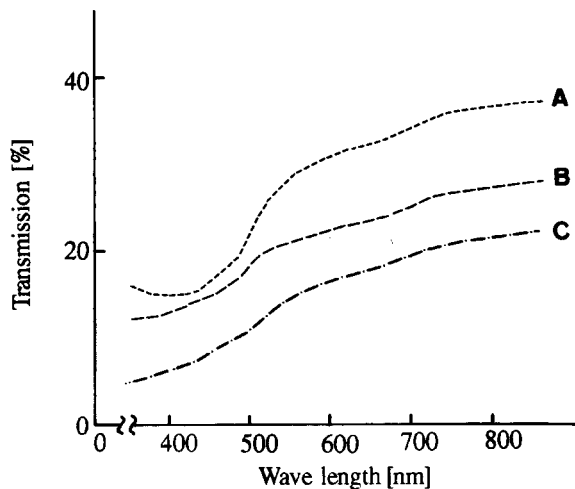
TRANSMISSION OF LIGHT THROUGH THE SHELL

The shell of *F. unedo* is thick and non-transparent. In contrast, *F. fragum* and *F. loochooanum* have rather thin and semi-transparent shells. The shell of *F. fragum* transmits more light than that of *F. loochooanum*. The shell structure and the transmission of light through the shell was examined for *F. fragum*.

The shell of *F. fragum* is composed of a mosaic of transparent and non-transparent domains of mm order. The shell consists of an outer layer of needle-shaped crystallites radiating in a fan-shape

TABLE 2. Reduced major axis ($Y = aX + b$) related to allometric shell growth of *Fragum* species. Abbreviations: L, shell length (mm); n , number of samples; PGL, posterior gape length (mm); PVA, angle between posterior and ventral valve margins (PV-angle) (degrees); r , correlation coefficient; n.s., not significant. For the definition of the reduced major axis, see Agterberg (1974, p. 122).

	Y	X	a	b	r	Level of significance
<i>F. fragum</i> ($n = 109$; CTO0014)	PGL/L	L	0.0157	0.7169	0.78813	$P < 0.001$
	PVA	L	-1.0707	95.0033	0.80577	$P < 0.001$
<i>F. loochooanum</i> ($n = 80$; CTO0015)	PGL/L	L	0.0331	0.5551	0.38645	$P < 0.001$
	PVA	L	-2.4040	108.4430	0.41084	$P < 0.001$
<i>F. unedo</i> ($n = 19$; CTO0016)	PGL/L	L	0.0061	0.6233	0.18729	n.s.
	PVA	L	-0.7236	113.1170	0.70156	$P < 0.01$



TEXT-FIG. 4. Transmission of light through the posterior slopes of *Fragum fragum* shells. A, the smallest specimen (shell length = 22.1 mm; CTO0017); B, the largest specimen (shell length = 31.5 mm; CTO0018); C, a medium-sized specimen (shell length = 15.8 mm; CTO0019).

towards the growth margin and an inner layer of crossed-lamellar structure. These two shell layers show no microstructural modifications producing different transparency, thus the transparency must be achieved by factors other than microstructure.

The posterior slope is the most transparent part of the shell of *F. fragum*. In Text-figure 4, the transmission/wavelength curves of this part are shown for three specimens of different sizes. The most transparent sample is the smallest one, but the least transparent sample is a medium sized specimen. Therefore the shell transparency of *F. fragum* may have considerable individual variability. The transparency of the posterior slope is between 13 and 18 per cent. for the least transparent specimen and between 14 and 22 per cent. in the most transparent one for light with wavelengths in the range 400–500 nm. As the wavelength increases to 800 nm this value increases to 27 per cent. in the least transparent specimen and 36 per cent. in the most transparent one.

The needle-shaped crystallites of the outer shell layer radiate and those of the crossed lamellae in the inner shell layer are differently orientated from one lamella subunit to another. Therefore the light penetrating into the shell of this species will be scattered by these variously orientated crystallites and illuminates the shell interior uniformly. This is in contrast with the transparent windows of the photo-symbiotic bivalve *Corculum cardissa*. In the latter, bundles of fine needle-like

crystallites radiate inwards from the shell external surface to form windows (Watson and Signor 1986), which transmit light effectively, with minimum dispersion, into the shell interior where there are abundant zooxanthellae.

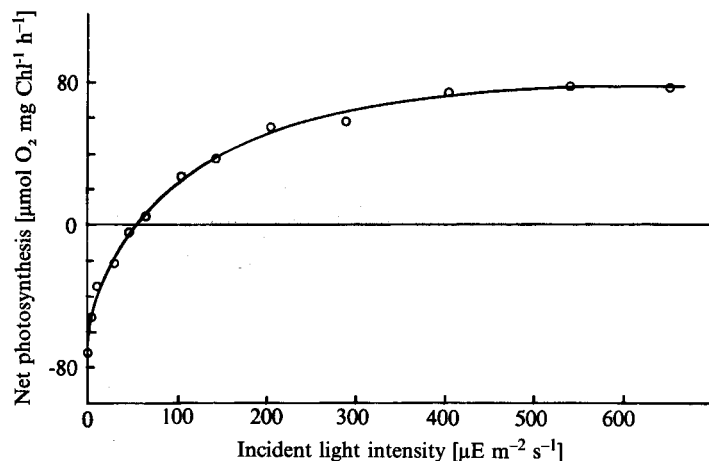
A direct comparison of the shell transparency of *Corculum cardissa* and *F. fragum* is not possible because Watson and Signor (1986) do not give the size of their measured shells. However, the lower transmission values of the present three specimens compared with the samples studied by Watson and Signor (maximum light transmission value of 40 per cent. at 620 nm) does not contradict our impression that the transparency of the shell in *Corculum cardissa* is higher.

The shell transparency of *F. fragum*, as well as of *Corculum cardissa*, is relatively low up to a wavelength of 500 nm, where the photosynthetic pigments (peridinin) of zooxanthellae have a strong absorption peak (Jeffrey and Haxo 1968). *Corculum cardissa* additionally exhibits a relatively low transparency around 675 nm (Watson and Signor 1986), close to where a second peak of the zooxanthellae's action spectrum exists (at 672 nm; Scott and Jitts 1977; Dustan 1982). Therefore the shells of these two bivalves are not perfectly adapted to transmit light in the optimal wavelengths for the zooxanthellae's photosynthesis.

PHOTOSYNTHESIS-IRRADIANCE PROFILE OF ZOOXANTHELLAE

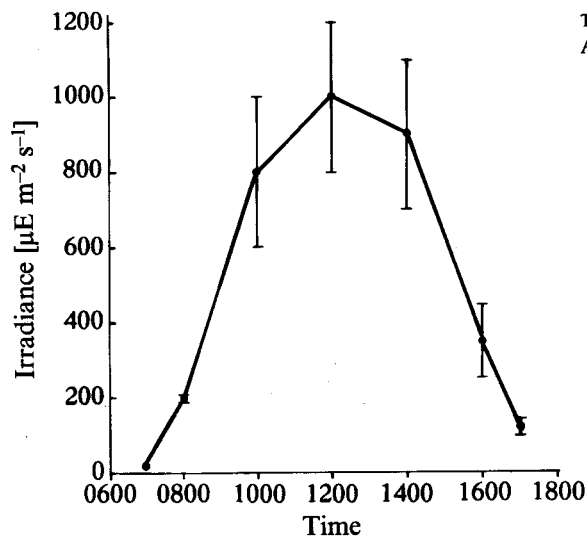
The photosynthesis versus irradiance curve was measured for the zooxanthellae extracted from *F. fragum* (Text-fig. 5). This curve indicates that the compensation light level of photosynthesis of

TEXT-FIG. 5. Photosynthesis-irradiance profile of zooxanthellae extracted from *Fragum fragum*.



the zooxanthellae is $50 \mu\text{Einstein m}^{-2} \text{s}^{-1}$ (an Einstein equals Avogadro's number $- 6.02 \times 10^{23}$ of quanta). Above this light level, zooxanthellae can produce organic matter in excess of their respiration. With increasing irradiance intensity, the rate of photosynthesis gradually increases until it attains a maximum value of about $80 \mu\text{mol O}_2 \text{ mgChl}^{-1} \text{ h}^{-1}$ at an intensity of 400–500 $\mu\text{Einstein m}^{-2} \text{s}^{-1}$.

The daily variation in light intensity at a depth of 2 m on a sunny day is shown in Text-fig. 6. The measurement was carried out in front of the Okinawa Research Centre at Amitori, the habitat of the three examined *Fragum* species, on 6 Nov. 1991. Even during late Autumn, the light intensity greatly exceeds the compensation point of the zooxanthellae of *F. fragum* ($50 \mu\text{Einstein m}^{-2} \text{s}^{-1}$) for at least 9 hours each day (08.00 to 17.00 hours). Because of the tide, the sandy flats where the three *Fragum* species live are submerged to a water depth of about two m only during spring high tides. At other times the water depth is less. The light intensity at the sea bottom will therefore, in general, be greater than that shown by the curve of Text-figure 6.



TEXT-FIG. 6. Light intensity at 2 m water depth in Amitori Bay measured on an Autumn sunny day (6 Nov. 1991).

DISCUSSION

Sciaphilous photo-symbiosis in Fragum and its advantages

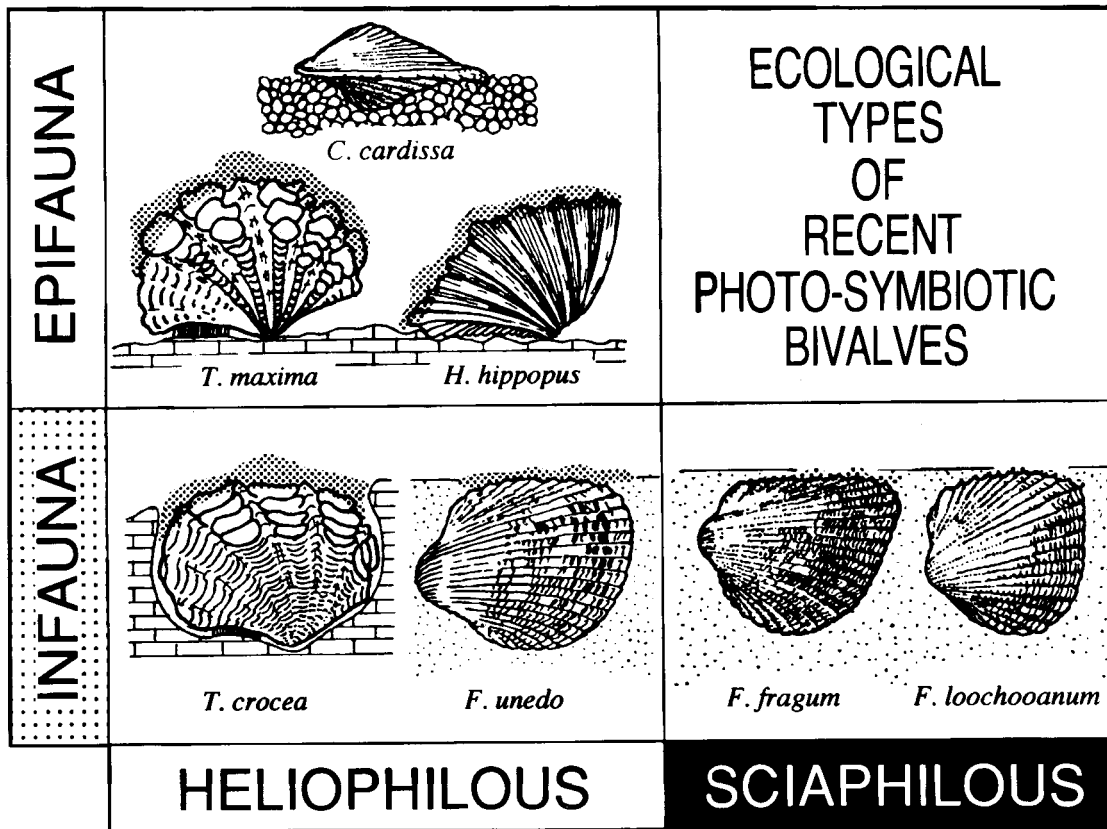
Fragum loochooanum adds a new fourth example of symbiosis with zooxanthellae (*Symbiodinium*) in the genus *Fragum*. The present study also reveals that *F. fragum* and *F. loochooanum* have adopted a new and previously unrecognized life mode among photo-symbiotic bivalves, i.e., sciaphilous (shade loving) photo-symbiosis, in which they do not expose their soft tissues and shells out of the sediment (Text-fig. 7). *F. fragum* even seems to hide itself actively by adhering sand grains to its posterior shell slope by extensively secreting mucus (Pl. 1, fig. 9). The mucus is probably derived from the zooxanthellae's photosynthetic product, as in the two slugs studied by Trench *et al.* (1972).

In the warm shallow seas of the present day, epifaunal bivalves are susceptible to bivalve-eating predators (Vermeij 1977, 1987, p. 167), or suffer from uncomfortable epibiont growth (Stanley 1970, pl. 116, figs 10 and 11; Dörjes 1978, p. 130). *F. fragum* and *F. loochooanum* are well protected from predation and epibiont attachment. Their active locomotion ability (Table 1) also allows them to escape from these disadvantages. Therefore these two sciaphilous bivalves enjoy the benefit of photo-symbiosis without trading their security.

Symbiodinium

To enable photosynthesis in a wide range of daily and seasonal as well as depth-dependent fluctuations of light intensity, marine algae can evolve molecular level adaptations. Shade adaptation is one such, and has been observed in a wide range of marine algae (Falkowski and Owens 1980). It is achieved by increase in number and/or size of photosynthetic units per algal cell (Falkowski and Owens 1980; Falkowski and Dubinsky 1981). Some dinoflagellates also increase the amount of their light-harvesting pigment-protein complex (peridinin-chlorophyll-*a* proteins) when cultured under low light (Prézelin 1976).

It is this shade adaptation which enables the zooxanthellae within *F. fragum* to photosynthesize with the limited amount of light coming through the host's narrow shell gape. In fact, the compensation point of photosynthesis of the zooxanthellae of *F. fragum* (Table 3) is about one-quarter of that of the zooxanthellae of epifaunal and heliophilous *Tridacna maxima* (Roeding) (Scott and Jitts 1977), and about one-twentieth of the maximum intensity of the ambient light of the cockle's habitat measured on a sunny Autumn day (Text-fig. 6). The photosynthesis irradiance



TEXT-FIG. 7. Life habits of photo-symbiotic bivalves.

TABLE 3. List of reported I_c (= compensation point) values (in $\mu\text{Einstein m}^{-2} \text{s}^{-1}$).

Host species	Remarks	I_c	Authors
Measured on hosts			
Hermatypic coral			
<i>Stylophora pistillata</i>	Light adapted	<i>c</i> 250	Falkowski and Dubinsky (1981)
	Shade adapted	<i>c</i> 30	(estimated from their fig. 2)
<i>Stylophora pistillata</i>	Light adapted	127	Porter <i>et al.</i> (1984)
	Shade adapted	26	<i>ibid.</i>
<i>Anthopleura elegantissima</i>	Starved	<i>c</i> 30	Fitt and Pardy (1981) (estimated from their fig. 1)
Bivalve			
<i>Tridacna maxima</i>		<i>c</i> 160–240	Trench <i>et al.</i> (1981) (estimated from their fig. 17)
Measured on zooxanthellae extracted from host bivalve			
<i>Tridacna maxima</i>		<i>c</i> 230	Scott and Jitts (1977) (estimated from their fig. 6)
<i>Fragum fragum</i>		50	Present study

curve for the zooxanthellae of *F. loochooanum* is not available. However, we suggest that the same behaviour of zooxanthellae is essential for the sciaphilous photo-symbiosis of this species.

Symbiodinium belongs to the 'naked' dinoflagellate order Gymnodiniales, which has a very sparse fossil record (Sarjeant and Downie 1974; Norris 1978; Williams 1978). Circumstantial evidence, however, suggests that it has a long symbiotic history. The changes in the relative importance of sponges and corals during the Middle Triassic–Late Jurassic interval probably coincided with the development of a symbiotic relationship between zooxanthellae (= *Symbiodinium*) and corals (Fagerstrom 1987, p. 292). Since then, some of the *Symbiodinium* may have become successfully shade adapted, either as they accompanied hosts exploiting deeper and darker habitats, or because their built-in flexibility enabled them to photosynthesize in very low light intensity allowing corals to exploit darker habitats. In fact the present day shade-adapted *Symbiodinium* of the hermatypic coral *Stylophora pistillata* shows a compensation point of about $30 \mu\text{Einstein m}^{-2} \text{s}^{-1}$ (Falkowski and Dubinsky 1981) which is even lower than that of the zooxanthellae living in *F. fragum* (Table 3).

Besides bivalves, *Symbiodinium* is present in a wide range of hosts such as the jellyfish *Cassiopea*, and numerous species of hermatypic corals (Trench and Blank 1987). The genus's ability to overcome the self-defence system of a wide variety of invertebrate host taxa may also be related to its long symbiotic history.

Scarcity of photo-symbiosis

The zooxanthellae's shade adaptation makes all shallow sea bivalves potential hosts. Yet, among living bivalves, symbiosis with zooxanthellae is confined to the genera *Tridacna*, *Hippopus*, *Corculum* and *Fragum*. *Microfragum festivum* (Deshayes), belonging to the subfamily Fraginae and closely related to *Fragum* and *Corculum*, or *Pinna* sp., which exposes a considerable part of its transparent shell out of the sediment, do not harbour zooxanthellae in their soft tissues (personal observation), although they are living in the same sand flats as the three examined *Fragum* species. These observations suggest that the scarcity of zooxanthella–bivalve photo-symbiosis may not be the result of insufficient observation but is reality.

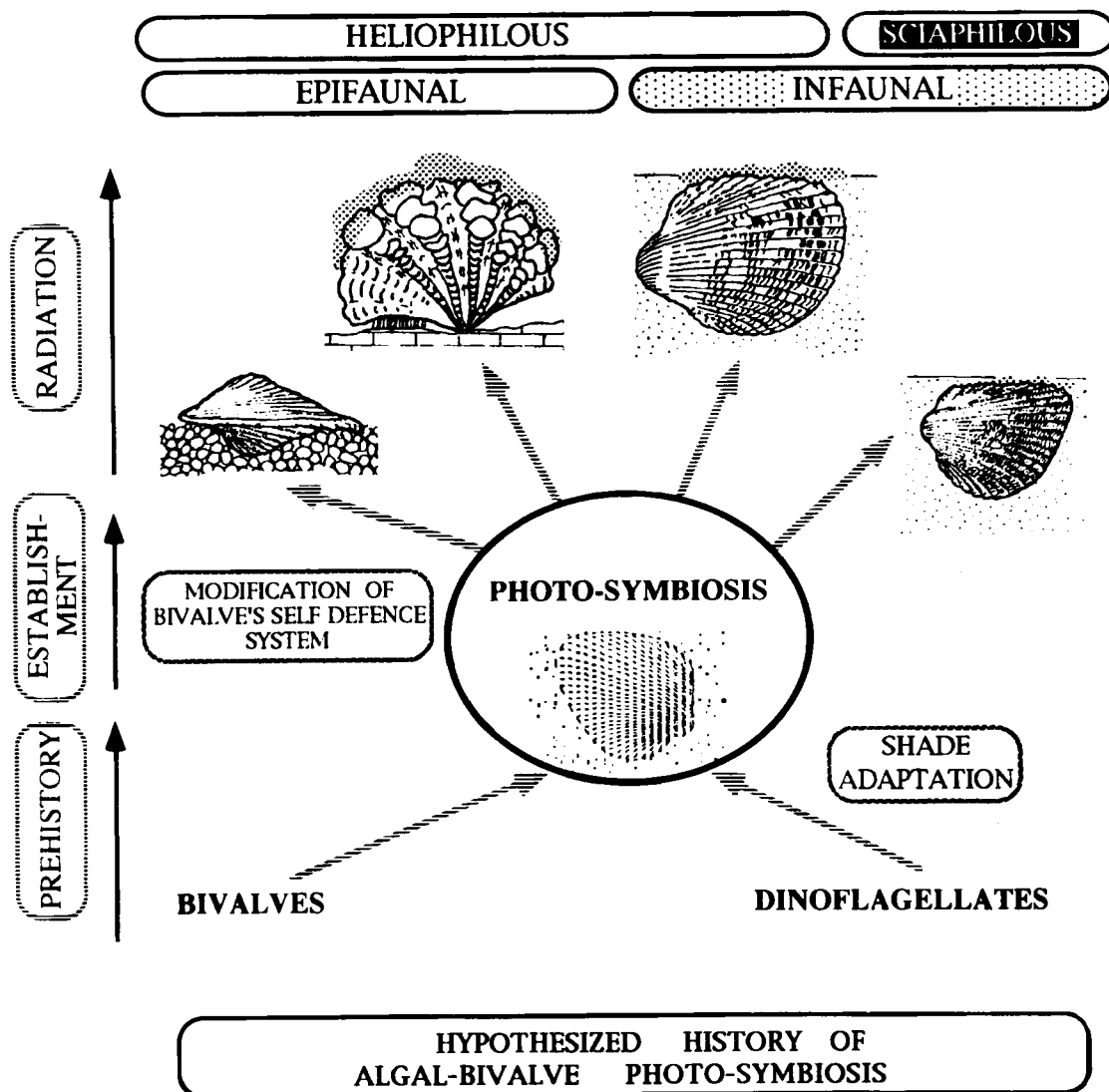
Smith (1991) also pointed out that very few animals are involved in symbiosis with photosynthetic microbes. He considered that costs imposed upon the animal hosts, including those of mechanisms for control of symbiont cell division and regulation of symbiont population size and location, might make photo-symbiosis less economic than the greatly prevalent herbivory for gaining access to photosynthetically-fixed carbon.

Palaeontological implications

The recognition of sciaphilous photo-symbiosis in *F. fragum* and *F. loochooanum* with shade adapted zooxanthellae has several palaeontological implications. Firstly, the photo-symbiosis in this genus and other extant photo-symbiotic bivalves seems to have initiated as a sciaphilous one. Secondly, a sciaphilous origin of photo-symbiosis seems applicable also to some fossil photo-symbiotic bivalves. Finally, several fossil bivalve taxa are now becoming candidates for being (sciaphilous) photo-symbiotic bivalves. In the following we discuss these points in some detail.

Sciaphilous origin of extant photo-symbiotic bivalves. The sciaphilous *F. fragum* and *F. loochooanum* do not show any indication that they once had mantle edges similarly expanded like those of *F. unedo*. Thus they seem to retain a more ancestral form than the latter. Yet they harbour zooxanthellae in their inner soft tissues. Therefore it seems that the photo-symbiosis in the genus *Fragum* was initiated by the association of shade (pre-)adapted *Symbiodinium* and an ancestral infaunal bivalve which was not pre-adapted for light harvesting for symbionts.

As mentioned earlier, the symbiotic relationship between *Symbiodinium* and hermatypic corals was initiated between the Middle Triassic and Late Jurassic, which predates the known range of the genus *Fragum* (Miocene–Recent) by at least about 80 My. It is probable that some *Symbiodinium*



TEXT-FIG. 8. Highly simplified hypothesized history of zooxanthella-bivalve photo-symbiosis (figure of bivalve in ellipse after Stasek 1961).

TABLE 4. Features related to the sciaphilous life mode of *Fragum fragum* and *Fragum loochooanum*.

1. More or less transparent mantle edges covering the posterior shell gape allows light penetration into the shell interior.
2. Long and rather transparent supra-branchial chamber aligns the gills with abundant zooxanthellae just beneath and along the posterior shell gape, through which light penetrates.
3. The rapid increase in the length of the straight shell posterior gape during shell growth increases the area of light penetration.
4. The rapid decrease in the angle between the posterior and ventral valve margins (PV-angle) during shell growth keeps soft parts with abundant zooxanthellae near the shell gape.

species might have successfully shade adapted prior to the initiation of the photo-symbiosis with *Fragum*.

Like *Fragum*, other extant photo-symbiotic bivalves (*Tridacna*, *Hippopus* and *Corculum*) either belong to, or are closely related to, the superfamily Cardiacea, the majority of the members of which are infaunal. Thus the ancestors of these photo-symbiotic bivalves were also most probably infaunal. If so, the above stated scenario may also be applied to the origination of photo-symbiosis of these bivalves. The varied geological ranges of these photo-symbiotic bivalves (*Tridacna* since Miocene; Stasek 1961; *Hippopus* since ?Miocene, but with certainty in Recent; Stasek 1961; and *Corculum* in Recent; Keen 1980) suggests that the establishment of zooxanthella-bivalve photo-symbiosis took place several times.

Once photo-symbiosis is established in a sciaphilous form, the selection pressure would favour the tendency to optimize the benefits of the symbiosis. There is not a unique solution in optimizing (Text-fig. 8). *F. fragum* and *F. loochooanum* sustained their sciaphilous life mode, which would minimize the danger of predation. Infaunal *F. unedo* evolved hypertrophied mantle edges and exposes them widely on the sediment surface to collect more light. *Tridacna*, *Hippopus* and *Corculum* shifted to epifaunal life. The former two expose their mantle tissues out of the shell to collect light, whereas *Corculum* makes its shell transparent to illuminate algae nesting in their soft parts which are protected within the host's valves. Indeed the acquisition of photo-symbiosis with zooxanthellae led to a strong radiation in bivalve morphology and ecology.

Sciaphilous origin of fossil photo-symbiotic bivalves. When considering the origin of photo-symbiosis in bivalves, earlier studies have emphasized the bivalve's adaptations for supplying light to the photosynthetic microbial symbionts. Yonge (1936) suggested infection of zooxanthellae in the siphonal area of tridacnids as the starting point for the photo-symbiosis. Cowen (1982) postulated that symbiosis can only develop in a host that is pre-adapted by tissue exposure to light. Skelton (1979) also suggested pre-adaptation of bivalves for the establishment of the inferred photo-symbiosis in an extinct radiolitid rudist bivalve, *Radiolites* cf. *angeoides* (De Lapeirouse). The latter's extremely narrow valve gape and its small body/mantle cavity ratio were interpreted as indicating atrophy of the gills and the loss of effective filter feeding. Skelton further suggested that the species developed expanded and tentacled mantle margins to make up for its ineffective filter feeding. These tentacled mantle margins, which were expanded out of the shell for collecting food particles, were later infected by the zooxanthellae.

An alternative interpretation of the evolution of photo-symbiosis in this species may be a sciaphilous origin, i.e. the infection of shade adapted microbes within the internal soft tissues of the ancestor of this species. Then the expanded mantle margins of this rudist can be interpreted simply as the result of optimizing light harvesting, followed by the loss of efficient filter feeding. Because this scenario ensures nutrition of the bivalve by photosynthetic products, we can further curtail an evolutionary stage of food collection with expanded and tentacled mantle margins (Skelton 1979). For such a feeding method, it is necessary to conceive a probably very complicated mechanism for smooth transportation of the collected food particles through a very narrow gape and for passing over then to the labial palps or mouth. In future, the initiation of photo-symbiosis in this rudist bivalve and other inferred fossil photo-symbiotic bivalves should not be viewed only as the result of the bivalve's pre-adaptation, but the possibility of their origination in a sciaphilous form should also be considered.

New candidates of fossil photo-symbiotic bivalves. Because sciaphilous photo-symbiosis allows host bivalves to enjoy the benefit of symbiosis without the dangers of predation or epibiont attachment, many fossil photo-symbiotic bivalves, if they ever existed, are likely to have adopted, or even clung to, this option of symbiosis.

F. fragum and *F. loochooanum* show certain morphological features related to their sciaphilous photo-symbiosis with zooxanthellae (Table 4). Among them, rapid increase in the PGL/L ratio as well as a rapid decrease in PV-angle during shell growth (Text-fig. 3; Table 2) can be preserved in

fossil shells. These two features together with the occurrence of fossils from shallow sea sediments would be helpful criteria in the search for sciaphilous photo-symbiosis among fossil bivalves.

Some promising fossil candidates may be expected among the trigoniid bivalves which adopted a life mode similar to the present day cardiids, in warm shallow marine sandy habitats during the Mesozoic (Stanley 1978). Indeed, a specimen of the Bajocian *Trigonia denticulata* Ag. in our possession has an overall shell form quite similar to that of *F. fragum* and *F. loochooanum*. Furthermore, it would be interesting to see if the ancestors of *Opisoma* Stoliczka (Chavan 1969, N572 and fig. E72, 4) have a similar form to *F. fragum* or *F. loochooanum*. The shell morphology of this Lower Jurassic astartid bivalve has an overall resemblance to that of the living photo-symbiotic bivalve *Corculum cardissa*. These fossil bivalves tempt us to examine them and related species in detail, although their geological age suggests that their symbiotic photosynthetic microbes are not necessarily identical or related to the present day *Symbiodinium*.

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