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SYMBIOSIS IN SACOGLOSSAN OPISTHOBRANCHS: SYMBIOSIS WITH ALGAL CHLOROPLASTS

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ABSTRACT

The green bodies responsible for the color of 4 species of sacoglossan opisthobranchs (Mollusca: Gastropoda) were investigated and were found to be chloroplasts derived from the animals' algal food. The chloroplasts were invariably restricted to digestive cells of the digestive diverticula in each species.

Chloroplasts in the tissues of *Elysia hedgpethi* and *Placida dendritica* are derived either from *Codium fragile* or *Bryopsis corticulans*. The plastids in the tissues of *Placobranchus ianthobapsus* are derived from an unidentified siphonaceous green alga. In the 3 cases above, the chloroplasts were found to be retained in the animals in a symbiotic condition.

The 4th species investigated, *Hermaeina smithi*, was found to ingest chloroplasts of *Chaetomorpha aerea* and *Cladophora trichotoma*, but the plastids are apparently rapidly degraded.

It is suggested that symbiosis between algal chloroplasts and sea slugs of the Order Sacoglossa may be the rule rather than the exception.

INTRODUCTION

Unicellular algae living in symbiotic associations with a variety of animal hosts have been known since the 19th century. Since that time much work has been done on relationships of algae symbiotic with protozoans, coelenterates and platyhelminths, but comparatively little has been done on molluscs (see reviews by Droop, 1963; McLaughlin & Zahl, 1966; and Yonge, 1957). As early as 1895, it was known through the work of Hecht that opisthobranch molluscs could exist in symbiotic relationships with unicellular algae, specifically zooxanthellae. Naville (1926) showed that the nudibranch *Aeolidiella alderi* contained zooxanthellae intracellularly in its digestive gland. He further showed that the zooxanthellae were derived from the tissues of the actinian, *Heliactis bellis*, upon which the nudibranch fed. It was Naville's belief that the zooxanthellae reproduced within the nudibranch's tissues, but Graham (1938) was unable to observe this.

Buchner (1965) listed 5 species of nudibranchs which reportedly contained zooxanthellae in their tissues. Those species are: *Aeolis glauca*, *Favorinus albus*, *Melibe rangii*, *Phyllirhoe* sp. and *Spurilla neapolitana* which contain zooxanthellae within the cells of the digestive gland in the dorsal appendages, and *Doridoeides gardineri* which apparently contains zoochlorellae, or green algae. It is supposed that in all cases, the algal cells are ingested along with the food.

Yonge & Nicholas (1940) described

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zooxanthellae in the tissues of *Tridachia crispata*, a sacoglossan opisthobranch from Jamaica. This statement was, however, ultimately retracted for lack of evidence (Yonge, 1966).

Kawaguti (1941) reported that another sacoglossan, *Placobranchus ocellatus* from Palao, contained unicellular green algae in its body. He demonstrated that when maintained in the light, the animal/algal association produced more oxygen than it consumed. In 1965, Kawaguti, Yamamoto & Kamishima reported a similar association in *P. ianthobapsus* from Hawaii. On the basis of pigment extracts and observations with the electron microscope, the green bodies were interpreted as unicellular blue-green algae living within the cells of the animal's digestive gland. The present study presents evidence to show that these bodies are not unicellular algae, but algal chloroplasts.

In the same year, Kawaguti & Yamasu (1965) identified the green bodies in the digestive gland cells of *Elysia atroviridis* as chloroplasts of the alga, *Codium fragile*, on the basis of structural similarities revealed with the electron microscope. Taylor (1967) reported finding chloroplasts in the digestive gland cells of five additional sacoglossan slugs: *Elysia viridis*, *Hermaea bifida*, *H. dendritica*, *Acteonia senestra* and *Limapontia capitata*. In a more complete report, Taylor (1968) demonstrated the similarity between the chloroplasts found in the tissues of *Elysia viridis* and those from the alga, *Codium tomentosum*, upon which the animal feeds. The tentative identity of the chloroplasts was established by use of the electron microscope and comparisons of plant pigment extracts. By incubating animals in sea water containing $^{14}CO_2$ and doing radio-autography, he was able to establish that the chloroplasts within the animal's cells fix ^{14}C in the light.

More recently, Trench, Greene & Bystrom (1969) have re-examined *Tridachia crispata* (see also Trench, 1969) and, in addition, have investigated *Tridachiella diomedea* from the Gulf of California and *Placobranchus ianthobapsus* from Hawaii. Chloroplasts have been found in the cells of the digestive diverticula in all 3 species. Exposure of the animals to $^{14}CO_2$ in the light, with subsequent radioautography of the animal tissue has revealed ^{14}C in the chloroplasts.

It is now evident that the occurrence of algal chloroplasts within the tissues of sacoglossan opisthobranchs is a widespread phenomenon.

In the present study, the green bodies in the digestive gland cells of *Placobranchus* have been examined in detail and evidence will be offered to establish their identity not as blue-green algae, but as algal chloroplasts. In addition, chloroplast-animal symbioses are described in two species of sacoglossans from southern California: *Elysia hedgpethi* and *Placida dendritica*. A third sacoglossan from California, *Hermaeina smithi*, was also investigated and was found to lack chloroplast symbionts in its tissues.

MATERIALS AND METHODS

Experimental animals

Four species of animals were used in the present study, and all belong to the Order Sacoglossa (Mollusca: Opisthobranchia).

Elysia hedgpethi Marcus was collected at Flat Rock, Palos Verdes, Los Angeles County, California. *Elysia* was found on fronds of *Codium fragile* Hariot or on filaments of *Bryopsis corticulans* Setchell along with another sacoglossan, *Placida dendritica* Alder & Hancock. Collections were made from low intertidal to about 5 m below low water neaps.

Hermaeina smithi Marcus was collected at Leo Carillo Beach State Park, Los Angeles County, California. This species

was found in the mid-tide region in the rocky tide pools containing either *Cladophora trichotoma* Kützing, or more commonly, *Chaetomorpha aerea* Kützing. *Hermaeina* was not observed on any other algal substrate.

Placobranchus ianthobapsus Gould was collected from reef-flats in Kaneohe Bay, Oahu, Hawaii. The animals were invariably found crawling in the silty white sand which makes up the sediment on the reef-flat. No animal was ever collected from, or observed on, an alga in the field, although the red alga, *Acanthophora* sp., was abundant at the collecting site. Most specimens used in this study were collected from water about 1 m in depth.

Species from California were maintained in large holding tanks in the recirculating sea water system at the Zoology Department of the University of California at Los Angeles. The temperature was maintained at 13°C. The local species were given constant access to their natural algal food.

Placobranchus was maintained in plastic tubs (27 × 32 × 13 cm) at room temperature (about 22°C). Since the algal food of this species is not known, the animals were not fed in the laboratory.

Histology

Whole animals were fixed in Clark's fixative, Bouin's solution made up in sea water, or Fleming's fixatives with and without acetic acid (see Weesner, 1960). Best results were achieved with Clark's and Bouin's fixatives. Fixation times ranged between 1 and 24 hours after which the tissues were transferred directly to 70% ethanol. All animals were dehydrated through serial dilutions of ethanol (1 hour in each solution), cleared in xylene, and embedded in paraffin (56–58°C). Sections were cut at 7 or 10 μ and were stained with Ehrlich's haematoxylin and eosin Y, Mallory triple stain, toluidine blue (Weesner, 1960) or periodic acid-Schiff (PAS) (Lillie, 1965). Materials fixed in Fleming's fixatives were left unstained.

Electron microscopy

Small pieces of tissue (1 mm²) were fixed in 3% glutaraldehyde (with glucose and monosodium phosphate) for 1 hour at 25°C. They were rinsed completely in 3·4% sodium chloride solution and were post-fixed in 1% osmium tetroxide (with glucose and monosodium phosphate) for 1 hour at 25°C (J. Lauritis, pers. comm.). The tissues were then dehydrated through a series of ethanol concentrations and were embedded in Araldite (Luft, 1961).

Sections were cut on a Porter-Blum MT-2 ultra-microtome, then stained with uranyl acetate and lead citrate, and viewed and photographed with an Hitachi 11B electron microscope.

Plant pigment analysis (F.T. Haxo, pers. comm.)

Photosynthetic pigments were extracted from the various plant and animal tissues in the cold (3–4°C) under nitrogen gas with absolute methanol. The pigments in the methanolic extract were transferred to diethyl ether in a separatory funnel and 10% sodium chloride was added to effect phase separation. The diethyl ether phase was further washed with the salt solution to remove any remaining methanol. Petroleum ether (b.p. 60–80°C) was added to the diethyl ether, and was washed with distilled water. The resulting petroleum ether-diethyl ether extract was transferred to a small flask and the remaining traces of water removed by the addition of anhydrous sodium sulfate. The extract was then concentrated by evaporation under nitrogen gas. All extraction procedures were conducted in a darkened room, and the flasks containing

the pigments were wrapped in aluminum foil to shield the extracts from direct light. The dried extracts were taken back into solution in diethyl ether and were spotted on precoated silica-gel sheets (Eastman Chromagram, Type K301R2). The thin layer sheets were then developed in the dark with 15% petroleum ether in diethyl ether.

Comparisons were made between whole extracts from the animals and plants, as well as between separate pigment bands eluted from the thin layer chromatograms. Absorption spectra were read on a Cary 15 Recording Spectrophotometer in diethyl ether unless otherwise specified.

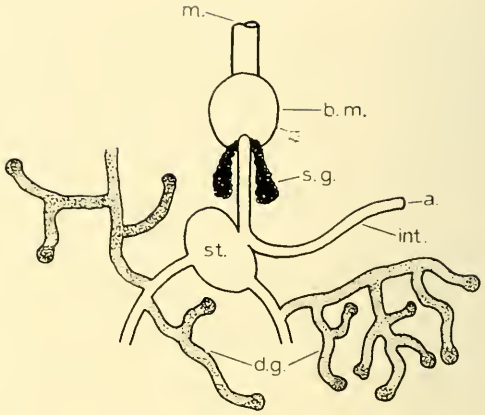

FIG. 1. Diagrammatic representation of a generalized sacoglossan gut. a, anus; b.m., buccal mass; d.g., digestive gland; int., intestine; m., mouth; s.g., salivary gland; st., stomach.

RESULTS

Gross anatomy

A diagrammatic representation of a typical sacoglossan gut appears in Fig. 1. A short oral tube leads from the mouth to the muscular buccal mass which houses the radula. The esophagus runs posteriorly from the buccal mass to the stomach, an outpocketing at the junction of the esophagus and intestine. The stomach receives tubules from the digestive diverticula which branch extensively throughout the body. It is the character of the cells of the digestive diverticula which is of interest in the present study.

Histology of the digestive diverticula

In Elysioid sacoglossans (*Elysia* and *Placobranchus*) the digestive diverticula ramify throughout the entire body of the animal. Sections taken at random through the animals invariably include many sections through digestive tubules (see Fig. 2). In cross-section, the tubules are composed of 5 or 6 cells surrounding a central lumen. These cells, in the living animal, are dark green in color. They stain darkly in tissues fixed in solutions containing osmium tetroxide, indicating the presence of lipid. Such cells appear granular when observed under the light microscope (Fig. 3). The granular bodies, 2–3 μ in diameter and roughly spherical, seem similar to the "Spherules" described in the digestive cells of *Elysia viridis* by Fretter (1941) and Taylor (1968). The spherical bodies are strongly eosinophilic. Evidence presented below will establish these bodies in *Placobranchus* as algal chloroplasts.

Eolidiform sacoglossans (*Placida* and *Hermaeina*) show a slight variation on the pattern described above. The stomach in species of this group is a large, thin-walled sac. The digestive gland sends branches into each of the cerata and is generally less branched than in the elysioid forms. In *Placida*, the digestive diverticula extending into the cerata are very similar in appearance to the digestive tubules in elysioid sacoglossans. The lumen is small compared with the size of the diverticulum. The cells surrounding the lumen are large and rounded. In stained preparations the 2–3 μ spherules are inside the cells. In *Hermaeina*, on the other hand, the

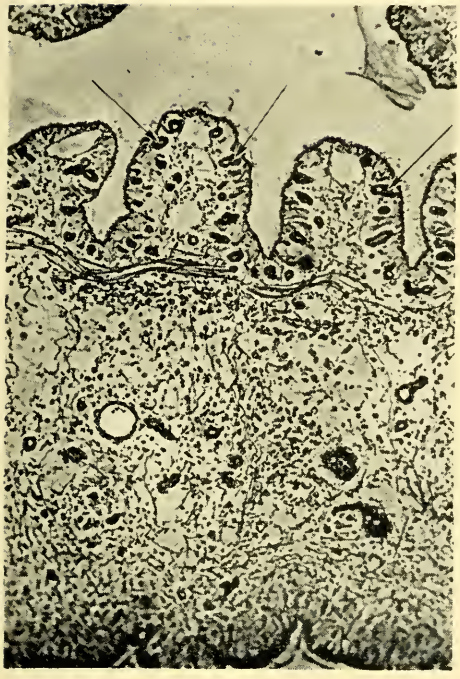

FIG. 2

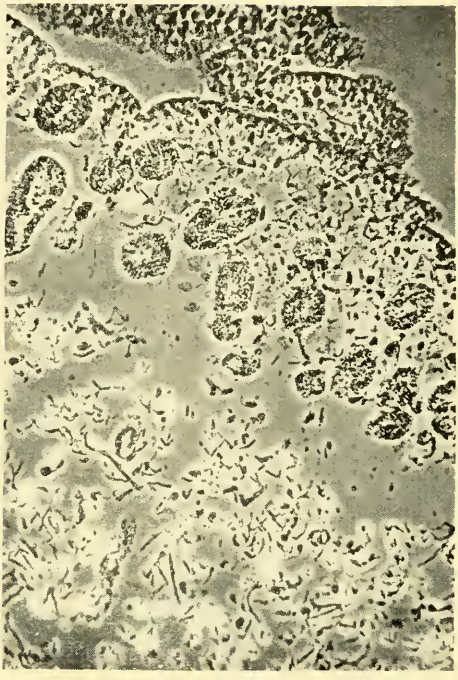

FIG. 3

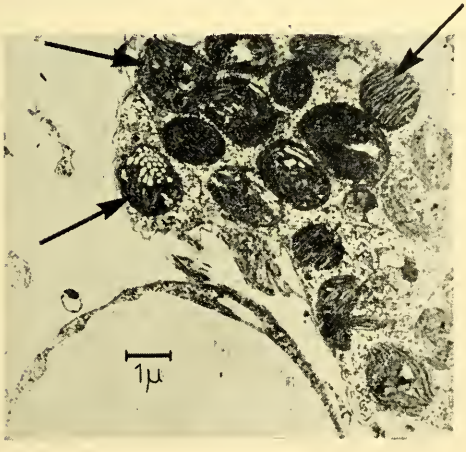

FIG. 4

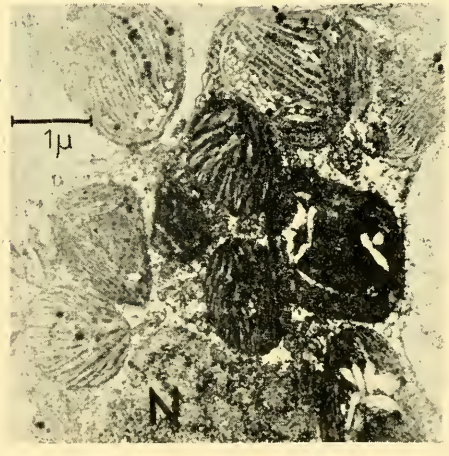

FIG. 5

FIG. 2. Photomicrograph of transverse section through the middle of the body of *Placobranchus*. Clark's fixative, stained with hematoxylin and eosin Y. Arrows indicate digestive gland tubules. 50X.

FIG. 3. Photomicrograph of digestive gland cells of *Placobranchus* showing 2–3 μ granules. Tissue was fixed in Fleming's fixative with acetic acid, and was left unstained. 125X.

FIG. 4. Electron micrograph showing chloroplasts (arrows) within digestive gland cells of *Placobranchus*. 36,500X.

FIG. 5. Electron micrograph showing chloroplasts in cells of *Placobranchus* 75,000X. Animal cell nucleus is designated by " N ".

cells lining the diverticulum are long and narrow. The lumen in this species is large compared with the diameter of the diverticulum, and granules are not visible within the gland cells.

The egg masses and veliger larvae of *Elysia*, *Placida* (= *Hermaea*) and *Hermaeina* have been described elsewhere (Greene, 1968), as have those of *Placobranchus* (Ostergaard, 1950). In no case has it been possible to identify bodies resembling the 2–3 μ plastids described above in the eggs or larvae. This implies that the plastids are not transmitted via eggs or sperm, but are newly acquired by each individual sometime after the late veliger stage.

Electron microscopy

Symbiosis with algal chloroplasts has already been described for species of *Elysia* (Kawaguti & Yamasu, 1965; Taylor, 1967, 1968) and for *Placida* (= *Hermaea*) (Taylor, *loc. cit.*). In the preceding reports, the symbionts have been likened to chloroplasts of species of *Codium*, the alga upon which the animals feed.

The spherical bodies within the digestive cells of *Placobranchus*, however, have been previously identified as unicellular green algae (Kawaguti, 1941) and blue-green algae (Kawaguti *et al.*, 1965). Fig. 4 is an electron micrograph showing lamellar bodies within the cells of the digestive gland of *Placobranchus*. The same bodies appear in Fig. 5 at still higher magnification.

The interior of these bodies is almost completely occupied by lamellae formed of varying numbers of thin membranes. There is no nuclear material in evidence and no cell wall. The bodies are always intracellular and are present only in the digestive cells of the diverticulae. Plastoglobuli are commonly found within the lamellar system of the bodies and are highly osmiophilic.

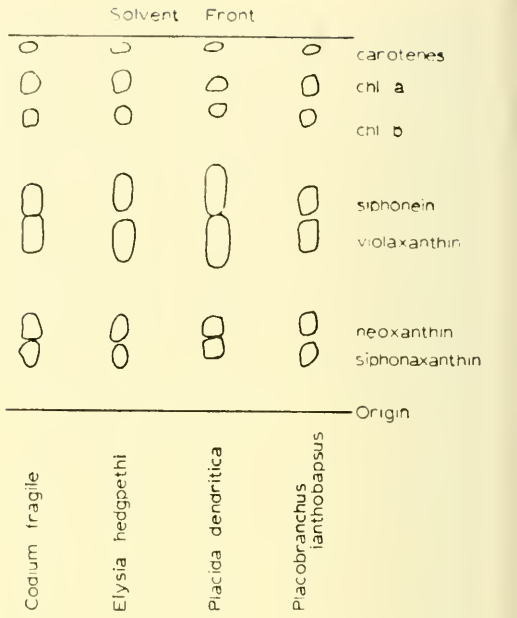

FIG. 6. Thin-layer chromatogram comparing methanolic extracts of *Elysia*, *Placida* and *Placobranchus* with pigments of the alga, *Codium fragile*.

These lamellar bodies are identical with the granular bodies described in the previous section and have now been identified as algal chloroplasts on the basis of the above observations and the following information on pigment extracts.

Pigment analyses

The results of the various pigment analyses appear in Figs. 6 and 7. The animals which normally feed on species of siphonaceous algae (i.e., *Elysia*, *Placida* and *Placobranchus*) are shown together with pigments extracted from *Codium fragile*, the algal substrate of *Elysia* and *Placida*. Each pigment band corresponds to a band in each of the other extracts (Fig. 6). The unique feature of all of these pigment extracts is the presence of siphonein (A_s maxima in petroleum ether, 450 and 475 nm) and siphonaxanthin (A_s maxima in petroleum

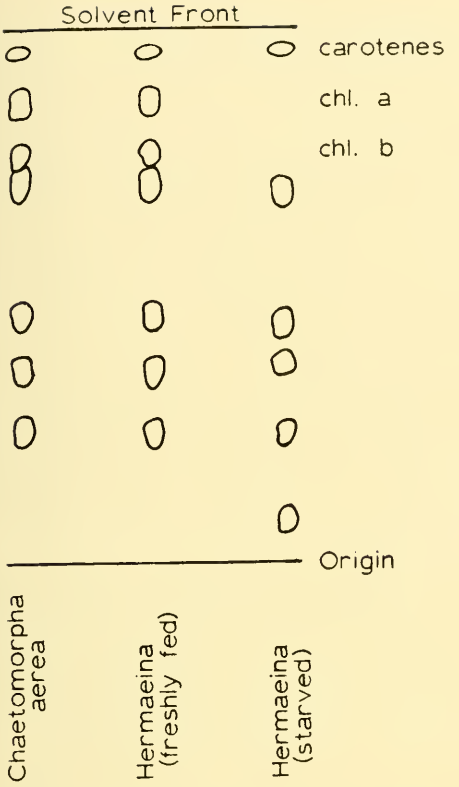

FIG. 7. Thin-layer chromatogram of methanolic extracts of *Hermaeina* (fed and 24 hr.-starved) and its algal food, *Chaetomorpha aerea*.

ether, 450 and 480 nm), 2 pigments characteristic of siphonaceous green algae (Strain, 1965). Although *Placobranchus* has not been observed feeding on algae in the field, the pigment extract conformed to the pattern characteristic of a siphonaceous alga. Thus, on the basis of the pigment analysis, it may be concluded that the chloroplasts in the tissues of *Placobranchus* are derived from an alga belonging to the Order Siphonales. A similar conclusion was drawn from investigations on *Tridachia crispata*, a sacoglossan opisthobranch from Jamaica (Trench, 1969; Trench, Greene & Bystrom, 1969). Pigment extracts from the animal and the siphonaceous alga, *Caulerpa racemosa*, were identical, suggesting that the chloroplasts were originally derived from some species of siphonaceous alga. No attempt has been made in either case to identify the alga.

Pigment extracts of *Hermaeina smithi* were compared with extracts from *Chaetomorpha aerea* (Order Cladophorales), the alga upon which the animal is found. The results are found in Fig. 7. In animals starved one day prior to extraction, the carotenoid pigments show the same mobility as those from the algal food, while the chlorophylls do not. The latter effect may be due to pigment degradation by the animal. In freshly fed animals, extracted pigments were indistinguishable from pigments from *Chaetomorpha*.

DISCUSSION

All of the data presented in the previous section are consistent with the interpretation that the green bodies in the digestive gland cells of *Placobranchus ianthobapsus* are algal chloroplasts. Furthermore, information derived from the separation of the plastid pigments permits the assignment of the chloroplasts to an alga belonging to the Order Siphonales (Chlorophyta). Unfortunately, it is not possible to identify the source of the plastids more completely, since the animals have not been found in close association with any species of alga in the field. Kawaguti *et al.* (1965) identified the bodies in *Placobranchus* as blue-green algae. However, my pigment data (Fig. 6) do not support this interpretation. The presence of chlorophylls *a* and *b* and the xanthophylls, siphonein and siphonaxanthin in the extract establish the symbiont's identity among the siphonaceous green algae (Strain, 1965). If the bodies were blue-green algae, chlorophyll *b* would not be present in the pigment extracts.

Chloroplasts symbiotic with digestive gland cells of species of the genus *Elysia*

have already been described. Kawaguti & Yamasu (1965) found chloroplasts in the tissues of *E. atroviridis* from Japan. In this case the chloroplasts were derived from the green alga, *Codium fragile*. In 1968, Taylor reported finding chloroplasts of *Codium tomentosum* within the digestive cells of *E. viridis* from Great Britain. The present report extends these accounts to include *E. hedgpethi* from California. This species obtains its chloroplasts from either *Codium fragile* or *Bryopsis corticulans*, both siphonaceous green algae.

Another species of sacoglossan which has been discussed in this regard is *Placida dendritica* (Taylor, 1967, 1968). *Placida* from the coast of California has now also been found to contain chloroplasts. Again, the chloroplast source is either *Codium* or *Bryopsis*, whichever happens to be abundant.

A close relative of *Placida*, *Hermaeina smithi*, differs from the other sacoglossans studied. *Hermaeina* shows no sign of chloroplasts within the cells of the digestive gland. Indeed, pigment separations from this species indicate that chloroplasts are ingested, but are rapidly degraded (digested?). In animals starved for very short periods, it can be determined that the chlorophyll pigment from the plastids has been destroyed (Fig. 7). Preliminary studies involving incorporation of $H^{14}CO_3^-$ show that *Hermaeina* is incapable of fixing any more carbon in the light than it can in the dark, inferring that the chloroplasts are no longer photosynthetic. Thus, it must be concluded that a symbiotic association does not exist in the case of *Hermaeina*. Functional aspects of the chloroplasts symbiotic in *Elysia*, *Placida* and *Placobranchus* will be presented elsewhere (Greene, in prep.).

The occurrence of chloroplasts in animal cells raises many questions. Symbiosis between sacoglossan opisthobranchs and algal chloroplasts is an example of an hereditary symbiosis in which the symbiont is not transmitted from one generation to the next through the egg (as in anemones and corals). Each generation must acquire its chloroplasts anew and most hosts must be assured a continuous supply of new chloroplasts to maintain their association (Greene, 1968, and in prep.). In other hosts, the chloroplasts may replicate. The actual mode of primary infection of the animal by the chloroplasts remains unknown, though it seems logical that they are acquired through feeding by the adult and enter the cells of the digestive gland by phagocytosis.

The highly specialized feeding habits exhibited by the Sacoglossa (Fretter, 1941) have generally limited each species within the group to a single species of alga which can be used for food. Some sacoglossans, however, may feed on 2 or 3 species of closely related algae (e.g., *Elysia* on *Codium* or *Bryopsis*). Table 1 shows the results of a food preference survey of 38 sacoglossan species from all over the world. It is significant that 56% of the slugs surveyed fed exclusively on green algae of the Order Siphonales. The question immediately arises as to the nature of the attractant quality of the algae involved in these associations. Evans (1953) and Kay (1968) have mentioned the possible importance of the chemical nature of the food, while MacNae (1954) was more concerned with the structural peculiarities of the algae in question. It is difficult to assess the former possibility since appropriate information on the metabolism of marine algae is unavailable. The idea that the structure of the algal species is an important factor is more easily examined.

First, it is necessary to consider whether or not the animal will be capable of feeding on the alga considering the modified nature of the buccal apparatus.

TABLE 1.* Algae commonly taken as food by sacoglossan opisthobranchs.

Algae**	Per cent of total plant species
Division Clorophyta	
Order Cladophorales	(14·6)
Chaetomorpha	2·1
Cladophora	6·2
Rhizoclonium	2·1
Urospora	2·1
Unspecified Cladophorales	2·1
Order Siphonales	(56·2)
Boodlea	2·1
Bryopsis	2·1
Caulerpa	18·7
Codium	20·8
Halimeda	12·5
Division Xanthophyta	
Order Vaucheriales	(8·3)
Vaucheria	8·3
Division Phaeophyta	
Order Dictyotales	(6·3)
Dictyota	2·1
Padina	4·2
Order Fucales	(2·1)
Sargassum	2·1
Division Rhodophyta	
Order Ceramiales	(8·4)
Delesseria	2·1
Griffithsia	2·1
Laurencia	2·1
Polysiphonia	2·1
Order Gigartinales	(4·2)
Gracilaria	2·1
Gracilariopsis	2·1

* Data compiled from a review of the literature.
** Classification follows the scheme of Dawson (1966).

The algal species best suited for the animals would be those with large cells that could be easily punctured by the radular teeth. Indeed, the algal genera listed in Table 1 reflect this requirement for the most part, and are characterized by having large cells. Algae in the Order Siphonales (Chlorophyta) are coenocytic, or " acellular ", and would, therefore, yield large amounts of cell sap to an animal exerting little energy in feeding.

The other point is the ability of the animals involved to ingest the chloroplasts of the various algal species. Once again

the genera in Table I show a general similarity with regard to their chloroplasts. With the exception of the members of the Order Cladophorales, the algal species fed upon have large numbers of small chloroplasts in their cells. In the Cladophorales each cell contains a single, reticulate chloroplast of large size, which at first would seem impossible for a liquid feeder to ingest. However, under certain conditions this type of chloroplast does fragment into numerous discoid pieces (Smith, 1951), especially after mechanical disruption of the cells. It is these pieces which are ingested by *Hermaeina smithi* (pers. observ.). It was pointed out above that *Hermaeina* did not possess functional chloroplast symbionts since the latter did not fix $^{14}CO_2$. It was assumed that the chloroplasts were degraded shortly after ingestion. My preliminary experiments show that the fragments from disrupted *Chaetomorpha* and *Cladophora* are quite capable of photosynthetic fixation of $^{14}CO_2$ (Greene, unpubl.).

The probability is great that chloroplast-sacoglossan symbiosis is a widespread phenomenon. Of 86 sacoglossan species surveyed for body color, 82% were described as green. Those species that were not green had been collected from non-green algal species, and Taylor (1967) has already shown that at least two of these contain plastids from red algae in their tissues. Thus, it appears that symbiosis with algal chloroplasts may be nearly universal among the Sacoglossa.

In light of information now available, it would seem that Kay's (1968) hypothesis regarding the evolution of feeding habits among sacoglossans must be re-evaluated. The hypothesis, as it stands, states that primitive forms fed on species of *Caulerpa* which supplied a nutrient not available in other algal genera. Then, drawing on the older literature describing symbionts in various sacoglossans as zooxanthellae and zoochlorellae, it is assumed by Kay that the presence of algal symbionts freed the slugs from the *Caulerpa* " habit ". Since, in all cases investigated, the symbionts are now known to be chloroplasts derived from the animal's algal food, the Sacoglossa must now be even more firmly associated with those algal species whose chloroplasts they bear.

ACKNOWLEDGEMENTS

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RÉSUMÉ

SYMBIOSE CHEZ DES OPISTHOBRANCHES SACOGLOSSES SYMBIOSE AVEC DES CHLOROPLASTES D'ALGUES

R. W. Greene

Les corpuscules verts responsables de la couleur de quatre espèces d'Opisthobranches Sacoglosses (Mollusca; Gastropoda) ont été étudiés et l'on a trouvé que les chloroplastes dérivent de l'alimentation en algues de l'animal. Les chloroplastes sont invariablement limités aux cellules des diverticules digestifs dans chaque espèce.

Les chloroplastes des tissus d'*Elysia hedgpethi* et *Placida dendritica* dérivent soit de *Codium fragile* soit de *Bryopsis corticulans*. Les plastes des tissus de *Placobranchus ianthobapsus* dérivent d'une algue verte siphonée non identifiée. Dans les trois cas précédents, on a trouvé que les chloroplastes sont maintenus dans l'animal dans les conditions de symbiose.

La quatrième espèce étudiée, *Hermaeina smithi*, ingère des chloroplastes de *Chaetomorpha aerea* et *Cladophora trichotoma*, mais les plastes sont apparemment vite dégradés.

On pense que la symbiose entre les chloroplastes d'algues et les Opisthobranches de l'ordre des Sacoglosses est peut-être la règle, plutôt que l'exception.

A. L.

RESUMEN

SIMBIOSIS EN OPISTOBRANQUIOS SACOGLOSOS: SIMBIOSIS CON CLOROPLASTOS ALGACEOS

R. W. Greene

Se investigaron los cuerpos verdes causantes de ese color en cuatro especies de opistobranquios sacoglosos, descubriendo que son cloroplastos derivados de la alimentación algácea del molusco, y estan invariablemente restringidos a los divertículos digestivos en cada especie.

Cloroplastos en los tejidos de *Elysia hedgpethi y Placida dendritica*, derivan de *Codium fragile* odde *Bryopsis corticulans*. En los tejidos de *Placobranchus ianthobapsus* derivan de un alga sifonácea verde de especie no identificada. En esos tres casos los cloroplastos estaban retenidos por los animales en condición simbiótica.

La cuarta especie investigada, *Hermaeina smithi*, demostró haber ingerido cloroplastoa de *Chaetomorpha aerea* y *Cladophora trichotoma*, pero aparentemente los plástidos degradaron muy rápido.

Se sugiere que la simbiosis entre cloroplastos algáceos y esas " babosas marinas " del orden Sacoglossa pueda ser la regla en vez de la excepcion.

I. I. D.

АБСТРАКТ

СИМБИОЗ У МОЛЛЮСКОВ SACOGLOSSAN OPISTHOBRANCHS: СИМБИОЗ С ХЛОРОПЛАСТАМИ ВОДОРОСЛЕЙ

Р. ГРИН

Были изучены зеленые тельца, создающие окраску тела у четырех видов Sacoglossa (Mollusca, Gastropoda, Opisthobranchia). Оказалось, что происхождение у них этих хлоропластов связано с питанием моллюсков водорослями. Хлоропласты всегда располагались в пищеварительных клетках пищеварительных дивертикул всех видов моллюсков. Хлоропласты в тканях *Elysia hedgpethi* и *Placida dendritica* происходили или от *Codium fragile* или от *Bryopsis corticulans*. Пластиды в тканях *Placobranchus ianthobapsus* были связаны с неопределенной зеленой водорослью из Siphonacea. В трех случаях, из указанных выше, хлоропласты находились в животных как симбионты. Четвертый из изученных видов- *Hermaeina smithi* получил хлоропласты от заглоченных ею *Chaetomorpha aerea* и *Cladophora trichotoma*, но пластиды, видимо, быстро деградировали.

Предполагается, что симбиоз между хлоропластами водорослей и морскими моллюсками из отряда Sacoglossa может быть скорее правилом, чем исключением.

Z.A.F.