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OBSERVATIONS ON THE BIOLOGY OF *LOBIGER SERRADIFALCI*, A SHELLED SACOGLOSSAN OPISTHOBRANCH FROM THE MEDITERRANEAN

by J. J. GONOR (1)

INTRODUCTION

Lobiger serradifalci (Calcara) 1840 was found in considerable numbers in the latter part of September, 1960 in the harbor at Villefranche. Advantage was taken of this opportunity to study some aspects of the biology of this poorly known, but very interesting Opisthobranch. Aside from a few anatomical descriptions and scattered records in taxonomic works, there appears to be no information available on this species. Recently the finding of several new two-valved Sacoglossans (KAWAGUTI and BABA, 1959 and BURN, 1960) has renewed interest in the shelled Sacoglossa which include the previously known genera *Lobiger* and *Oxynoë*. Study of living *Lobiger* provided information for comparison with that recently published findings (KAWAGUTI and BABA, 1959, KAWAGUTI, 1959, and BURN, 1960 a, b,) about the two-valved species.

It is a pleasure to express gratitude for hospitality to Dr. P. BOUGIS, sous-directeur de la Station Zoologique de Villefranche-sur-Mer, who provided laboratory space and facilities for this study. I. should also like to thank Prof. C. M. YONGE, and Dr. P.L. ILLG for critically reading the manuscript. This work was done during tenure of a National Science Foundation pre-doctoral fellowship.

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Lobiger was discovered in a collection of algae from the boat harbor (La Darse) at Villefranche-sur-Mer (Alpes-Maritimes). These algae grow as a mat covering the bottom in shallow water about one and one-half to two meters deep near shore. The principal component of this algal mat is *Caulerpa prolifera* (Siphonales, *Chlorophyaceae*), which grows as a tangled mass of horizontal branching stems from which arise thick, flat spatulate blades of a leathery consistency. These blades are about six centimeters long and of varying width. Mixed in with *Caulerpa* are other, smaller algae, the most abundant of which is a species of *Bryopsis*. It was determined by direct observation that the food plant of *Lobiger* in this mixture was the *Caulerpa*. The animals were fairly abundant at this site; fourteen individuals of various sizes were found in a sample of the algal mat of about one-fourth cubic meter. At that time egg masses of *Lobiger* were even more abundant; about one third of the full-sized *Caulerpa* blades bore one or more.

Caulerpa is apparently not a widely distributed alga in the Mediterranean. In the vicinity of Villefranche, it occurs only in a relatively restricted area of quiet water (la Darse). In view of the definite specificity of feeding habits in the *Sacoglossa* (Gascoigne, 1956, Fretter, 1941, and personal observations) habitat records in the literature listing *Lobiger* from *Posidonia*, etc., should be regarded as approximate only.

This association with *Caulerpa* is of further interest because it reinforces the impression that the shelled *Sacoglossa* are restricted in their habitat and feeding to species of this algal genus. This appears to be true for the two-valved forms of Japan and Australia as well as for more recently discovered forms from Baja California (Keen, 1960 and A. Smith, personal communication). The available records are given in the following table (table I).

This compilation provides strong support for the suggestion of Macnae (1954) that all members of the *Sacoglossa* are restricted to specific algal groups because their feeding habits have become adapted to the structural pecularities of these algae. He further notes that this is usually an association with a section of the order Siphonales, and cites the association of most species of *Elysia* and *Hermaea* with members of the family *Codiaceae* (Siphonales), as an example.

TABLE I

Sacoglossan species	Algal habitat	Author	Location
Oxynoë viridis	*Caulerpa brachypus*	Baba, 1952, 1955	Misaki, Sagami Bay, Japan
	Caulerpa simpliciuscula	Burn, 1960 *b*	Flinders, S. Australia
Oxynoë sp	*Caulerpa sertularioides*	Keen and Smith, 1961	Candeleto Bay, Baja California
Lobiger serradifalci	*Caulerpa prolifera*	Gonor	Villefranche, France
Lobiger souverbiei	*Caulerpa racemosa*	Marcus, 1957	near Santos, Brazil
Lobiger sagamiensis	*Caulerpa brachypus*	Baba, 1955	Misaki, Sagami Bay, Japan
Berthelinia typica	*Caulerpa okamurai*	Kawaguti and Baba, 1959	Bisan Seto, Inland Sea, Japan
	Caulerpa scalpelliformis	Burn, 1960 *b*	Torquay, Victoria State, Australia
	Caulerpa simpliciuscula	Burn, 1960 *b*	Finders, S. Australia
Berthelinia chloris	*Caulerpa racemosa*	Keen and Smith, 1961	Puerto Ballandra Bay, Baja California
	Caulerpa sertularioides		
Midorigai australis	*Caulerpa scalpelliformis*	Burn, 1960 *b*	Torquay, Australia
	Caulerpa simpliciuscula		Flinders, S. Australia
	Caulerpa brownii		Flinders, S. Australia

TAXONOMIC NOTE

For convenience the classification of the order *Sacoglossa* accepted here is that outlined by BABA (1955). The genera *Oxynoë* and *Lobiger* constitute the family *Oxynoidae*, sub-order *Oxynoaceae*. The name *Lobiger serradifalci* has long been used and its synonomy is well known.

KAWAGUTI and BABA (1959) created for their new genus *Tamanovalva* the family *Tamanovalvidae*, sub-order *Tamanovalvacea*. BURN (1960b) demonstrated the synonomy of *Tamanovalva* with *Berthelinia* (prior name) and described the new genus *Midorigai*, which is closely related to *Berthelinia* and therefore would fall in the same sub-order, if not the same family. The sub-ordinal names proposed by KAWAGUTI and BABA are convenient for general reference to the contained genera and are used here.

FEEDING IN *LOBIGER*

Feeding was observed by starving animals for 48 hours and then presenting them with fresh, clean *Caulerpa* blades to feed upon. Feeding begins by the close application of the ventral side of the head against the flat side of the alga. If an individual is removed from the alga at this point a thin stream of thick, opaque white sap can be seen exuding from a minute puncture in the blade. This material is a very viscid and sticky substance immediately upon exudation but in sea water quickly changes to a tough, rubbery consistency. Puncture by a very fine needle causes the quick exudation of the white material from the alga, demonstrating that it is under sufficent pressure to exude on puncture alone. The animals cannot be made to feed on the exuded and coagulated sap.

The *Sacoglossa* usually feed by slitting the thin cell walls of (mostly) filamentous algae such as *Rhizoclonium*, *Vaucheria*, and *Bryopsis* with the blade-like radular teeth while the filament or portion of the thallus is held by the edges of the mouth (MACNAE, 1954, GASCOIGNE, 1956). The fluid cell contents are then sucked out of the cell by the action of the bulbous pharynx. *Caulerpa* is not a filamentous or even cellular alga, but the thick thallus is coenocytic, with fibrous strands of supporting material running across the interior. *Lobiger* cannot grasp the whole blade with the edges of the mouth but rather the mouth area is closely applied against the flat surface. *Lobiger* is thus divergent from many forms in the group by its feeding on a large, tough-bladed alga, but has retained the usual Sacoglossan radula with which it opens a small hole in the blade. Other *Sacoglossa*, notably the *Elysidae*, feed on large algae such as *Ulva*, *Codium* and *Dictyota* (FRETTER, 1941, MACNAE, 1954, MARCUS, 1957) but these are usually forms with a soft, cellular thallus. The enlargement and highly muscular development of the post-pharyngeal crop in *Lobiger* is undoubtedly associated with the problem of handling the thick *Caulerpa* sap.

The small feeding punctures quickly cause the formation of discolored spots on the *Caulerpa* so that the feeding activities of *Lobiger* leave distinct traces, the blades showing rounded, yellowish discolored spots up to a centimeter in diameter which gradually coalese as the animals continue to feed. BURN (1960 b) observed similar discolorations of *Caulerpa scalpelliformis* caused by the feeding activity of *Berthelinia typica*.

REPRODUCTIVE ACTIVITY

Copulation was observed repeatedly in the laboratory. Egg laying also took place in the laboratory but was not directly observed. The egg masses of *Lobiger* are simple in structure and closely resemble those of other *Sacoglossa*, such as *Hermaea* and *Aplysiopsis*. The mass is in the form of a simple coiled ribbon, flat side down, firmly attached to the *Caulerpa* blades. The ribbons vary greatly in size from a small, nearly symmetrical spiral two centimeters in diameter to a greatly elongated spiral five centimeters long. The egg ribbon consists of a central mass of white eggs, each in a thin capsule embedded in and surrounded by clear jelly. There is no regular arrangement of the eggs within the jelly, but they form a layer two or three egg capsules deep.

DESCRIPTION OF THE ANIMAL IN LIFE

Both previously known and newly observed structural features are recorded together here to give a comprehensive picture of the animal in life.

Figures 1, 2, and 3 depict *Lobiger serradifalci* in the position that it assumes normally, when undisturbed on the *Caulerpa* blades. The foot and body are closely applied to the alga while the « parapodial » lobes are held elevated and tilted slightly backward. The jade-green color of this form renders it difficult to see among the green, tangled *Caulerpa* blades. The entire integument is a translucent jade green, but there is a diffuse band of opaque pale lavender pigment on the edges of the parapodial lobes. Each of the many prominent tubercules scattered over the sides of the body, the dorsal surface of the foot and on the outer faces of the lobes is also tipped with this lavender pigment. The mantle under the shell is of the same green color as the rest of the body and this color shows through the thin, translucent shell. The main or sole color of the other well known species of *Lobiger* and *Oxynoë* as well as of the newly found bivalved forms is also green. In *Lobiger serradifalci* there is a narrow black-brown streak (fig. 3) running on the sides of the neck and head from just under the antero-lateral edges of the shell to under and slightly anterior to the black eyes at the base of the rhinophores. The available specimens varied in this feature both among themselves and also from one side of the head to the other in some individuals. The pigment line is occasionally placed so that it is interrupted by the eye rather than passing below the eye. On the right side behind the eye the line passes just below the genital apertures.

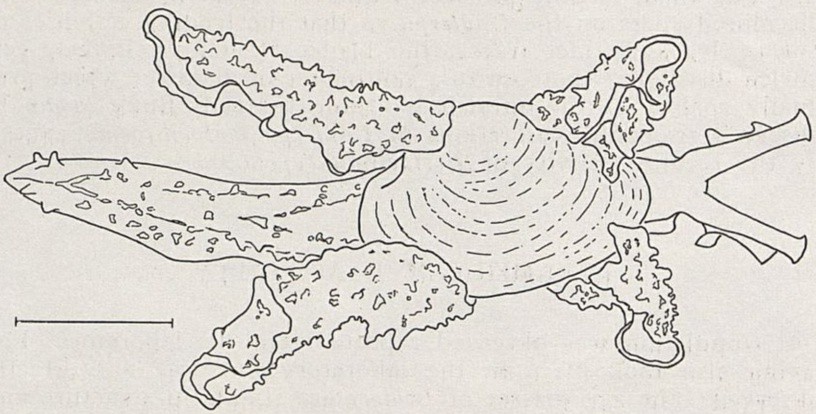

Fig. 1. — *Lobiger serradifalci*, dorsal view of an animal in normal position. Note parapodial lobes recurved over shell. Scale : 5 mm.

HABITUS.

In the normal resting position *Lobiger* (fig. 1, 2, and 3) presents an entirely different appearance from that usually shown in illustrations of the species of this genus. The body is elongate,

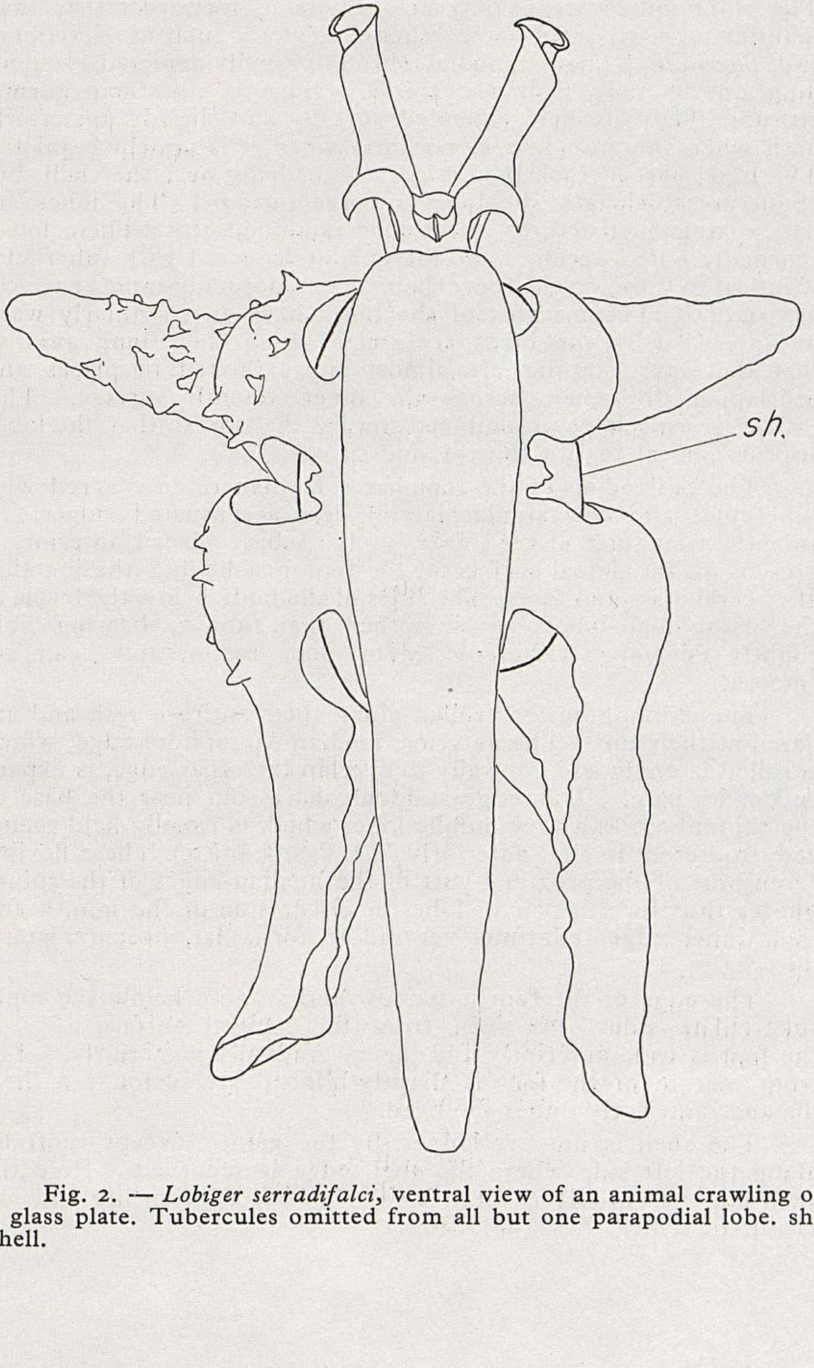

Fig. 2. — *Lobiger serradifalci*, ventral view of an animal crawling on a glass plate. Tubercules omitted from all but one parapodial lobe. sh., shell.

with a prononced « tail » region to the foot which tapers to a point. The rhinophores are usually held extended forward rather than pointing upward as in some other *Sacoglossa* such as *Aplysiopsis* and *Thuridilla*. The parapodial lobes are usually depicted as extending out laterally from the animal. This is not their normal attitude. They are held extended dorsally and slightly posteriorly both when the animal is at rest and when it is crawling quietly. The basal part of each lobe is curved medially over the shell, but about at mid-length the lobes recurve outward. The lobes are flat, spatulate structures with wide, rounded tips. Their lower (normally outer) surfaces and margins are covered with tubercules identical to those on the foot; their upper (normally inner) surfaces are smooth. The margins of the lobes have an irregularly wavy outline. Usually the lobes are rolled along their long axes so that the wavy margins are almost approximated in places and overlapped in other, across the inner smooth surface. This rolling is especially pronounced toward the tips so that the lobes appear conical in life (figs. 1 and 2).

The tail region of the foot has a median ridge covered with tubercules and two similar lateral, less accentuated ridges. A smooth, triangular shaped area, with its base placed anterior, is present on the dorsal surface of the foot just behind the junction of visceral mass and foot. The sides of the body below the levels of the parapodial lobes are smoother than above, bearing only slightly developed tubercules. The neck region and head are smooth.

The rhinophores are rolled along their entire length and are flared at their tips. The anterior, median rhinophore edge, which is rolled laterally and ventrally to overlap the other edge, is expanded at its base. This edge suddenly flares out near the base of the rhinophore as a very mobile lobe, which is usually held recurved, to present its face anteriorly (r. l. figs. 3 and 5). These flexible extensions of the proximal part of the median edges of the rhinophores thus form a pair of lobes at either side of the mouth and their inner edges continue ventrad to form flat, obscure lateral lips (fig. 5, l).

The edge of the foot is narrow and smooth below the high, tuberculate sides. As seen from the ventral surface (fig. 2) the foot is wide anteriorly and tapers gradually posteriorly. The front margin of the foot is slightly bilobed and extends a short distance anteriorly under the head.

The shell is not overlapped by the mantle except ventrally along the left side where the shell edge is recurved. Here the shell edge is entirely covered by the mantle edge in life and not visible in ventral view (fig. 5 m.f.).

DEFENSIVE BEHAVIOR IN *Lobiger*.

The significance of the position in which the parapodial lobes are usually held became apparent when the living animals were touched with a fine probe. If the surface of the head or tail is touched lightly the lobes are quickly swung in the direction of the stimulation and come partially to overhang the stimulated part. Stimulation of the opposite end of the animal will now cause the lobes to be quickly swung in the new direction. This can be repeated many times. Continuons or more intense stimulation causes the wide ends of the lobes to be unrolled and fanned out flat over the stimulated area with the papillate side upwards. Finally continued stimulation will cause glands located on the outer (morphologically ventral) lobe surface and especially on the margin to discharge a copious opalescent white secretion which is thick and sticky. That this secretion was not caused by direct local stimulation of the gland area but rather by that of some remote area was repeatedly demonstrated by carefully stimulating the head surface with a fine probe, taking care not to touch the lobes and withdrawing the probe before the lobes were brought into contact with it. This is clearly a defensive type of reaction in which stimulation brings into action an effector remote from the stimulated site. Similar secretion of a white material upon stimulation of the mantle has been observed in many Gastropods (FRETTER and GRAHAM, 1954, personal observations on

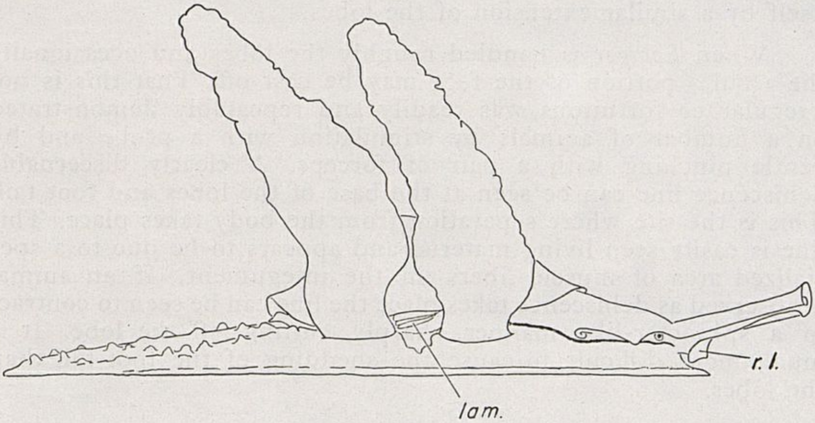

Fig. 3. — *Lobiger serradifalci*, view from right side. lam., lamella of gill; r. l., rhinophore lobe.

Acteon, Haminaea, Oncidiella, Siphonaria). This secretion is usually referred to as a « repugnatory » substance. There appears to be no experimental proof available of the « repugnatory » nature of the substance. The parapodial lobes are occasionally spread out laterally from the body under other conditions. When the animals are disturbed or removed from the alga, the lobes are usually extended and an animal freed from the substrate will often « beat » the parapodia slowly in a dorso-ventral direction. This action resembles a swimming motion, but does not result in lifting the animal above the bottom. If often turns the animal upside down, but an animal placed on its back will often right itself by a similar extension of the lobes.

When *Lobiger* is handled roughly the lobes and occasionally the « tail » portion of the foot may be cast off. That this is not irregular or fortuitous was readily and repeatably demonstrated on a number of animals by stimulation with a probe and by gentle pinching with a pair of forceps. A clearly discernable dehiscence line can be seen at the base of the lobes and foot tail. This is the site where separation from the body takes place. This line is easily seen living material and appears to be due to a specialized area of muscle fibers in the integument. If an animal is observed as dehiscence takes place the line can be seen to contract in a sphincter-like manner, sharply cutting off the lobe. It is much more difficult to cause the shedding of the foot tail than the lobes.

PALLIAL CAVITY, STRUCTURE AND FUNCTION.

Introduction.

Possession of a shell and the associated extensive pallial cavity is important in the understanding of the possible relations of *Lobiger* to other *Opisthobranchia*. The pallial cavity of *Lobiger* is as well developed as that in any bulloid Tectibranch while the gill, consisting of a series of plates dependent from the roof of the pallial cavity superficially resembles the condition found in the pectinibranch *Prosobranchia*.

The extensive studies of YONGE have demonstrated how intimately related are the structural and functional features of the pallial cavity in Gastropods and Lamellibranchs and how these features are in turn closely related to the conditions of life in these groups. Examination in life of the pallial cavities in the *Prosobranchia* enabled YONGE (1947) to explain the probable course of evolution of the pallial cavity complex in this group and relate this to the influence of features of the habitat. It was therefore of interest to study the structure and respiratory currents in the pallial cavity of this form in order to compare conditions here with those in Prosobranchs and in other Opisthobranchs.

Description of the cavity and its contents.

A large chamber, partially divided off from the pallial cavity proper is formed by an anterior extension of the mantle and shell over the neck region. The head can be completely withdrawn into the protection of this chamber when the animal is disturbed. It is irrigated by water brought into the cavity from directly anterior, over the neck. This chamber is almost entirely separated from the more posterior, larger pallial cavity proper by a transverse wall, the anterior mantle commissure, and the weak water current within it does not contribute significantly to the respiratory stream. The roof and floor are weakly ciliated so that a slow current is moved over the epithelium from anterior to posterior, but most of the water leaves on the left side. This currents is continuous with one on the left mantle flap and on the side of the body which leads posteriorly over the ventral surface of the excurrent siphon (described below). The direction of these cleansing currents is indicated by arrows in fig. 5.

The pallial cavity proper is open laterally all along the right side of the animal at the base of the parapodial lobes. The mantle and shell curve down on the right side so that the opening is not evident from a dorsal view but can be seen from the side or from the ventral view in an animal that has lost the parapodial lobes on this side (fig. 5). The opening in ventral view is narrow, slightly wider in the center than at either end. Posteriorly the mantle edge is drawn out on the dorsal, left and ventral sides into an extension which is a short, wide excurrent siphon open laterally only on the right and with its aperture directed posteriorly. Well under the shell, just behind the posterior margin of the gill, the anus (fig. 4, *a*) opens into the broad, slightly trough-like floor of this excurrent area.

The mantle cavity is not deep dorso-ventrally, but is spacious in its horizontal extension, reaching across the full width of the animal. It thus occupies virtually the entire dorsal area covered by the shell, even extending to the left into the apex of the blunt spire. The floor of the pallial cavity, i. e. the upper surface of the visceral mass, is gently convex, roughly matching the curvature of the shell. The epithelium of the inside of the mantle cavity is smooth and clear green dorsally and on the visceral hump at the aperture, but is transparent on the visceral mass deeper in the cavity and the creamy yellow color of the gonad shows through.

The gill, formed of a series of simple, thin triangular plates, extends from the extreme left margin of the roof of the pallial cavity to the free right dorsal mantle edge. The gill lamellae are very pale and translucent. The free edges of a few of the lamellae can occasionally be seen hanging out from under the shell margin (fig. 3, lam.).

WATER CURRENTS IN THE PALLIAL CAVITY.

General description.

Water is drawn into the gill cavity in a respiratory current that enters along the anterior one-half of the mantle cavity aperture in a strong stream, but no water enters the cavity anteriorly from either side or the center. The main incurrent stream is indicated by ic. in fig. 4 and its anterior posterior limits by arrows 1. and 2. Upon entering the cavity, part of the incurrent stream first passes over the osphradium (fig. 4, osp.). The osphradium is a distinct raised yellowish area on the roof of the cavity near the opening, just behind the column-like right margin of the anterior mantle commissure. After entering the cavity from the right anterior to the gill the water is drawn posteriorly across the gill lamellae. Some mucus is produced on the surface of the gill lamellae and some of the particles in the incurrent water become caught in this. Posterior to the lamellae, the water passes over a broad translucent white band of mucus-producing epithelium. This area lies just behind the gill and like it runs transversely the length of the pallial cavity. This mucus gland has a short posterior extension where it overhangs the excurrent area. MARCUS (1957) refers to this structure in *Lobiger souverbiei* as the « Hypobranchial » gland but such use implies homology with the Prosobranch structure, a very dubious point. The gland secretes a thin mucus, further entangling any particulate matter in the water. The excurrent water stream, containing mucus and adherent particles and perhaps feces, then passes out of the excurrent siphon.

Special features.

The siphon is a well-defined structural feature, especially apparent in the living animal, but does not appear to have been previously observed. From the left side, just under the edge of the shell and mantle rim, an extension of the mantle curves

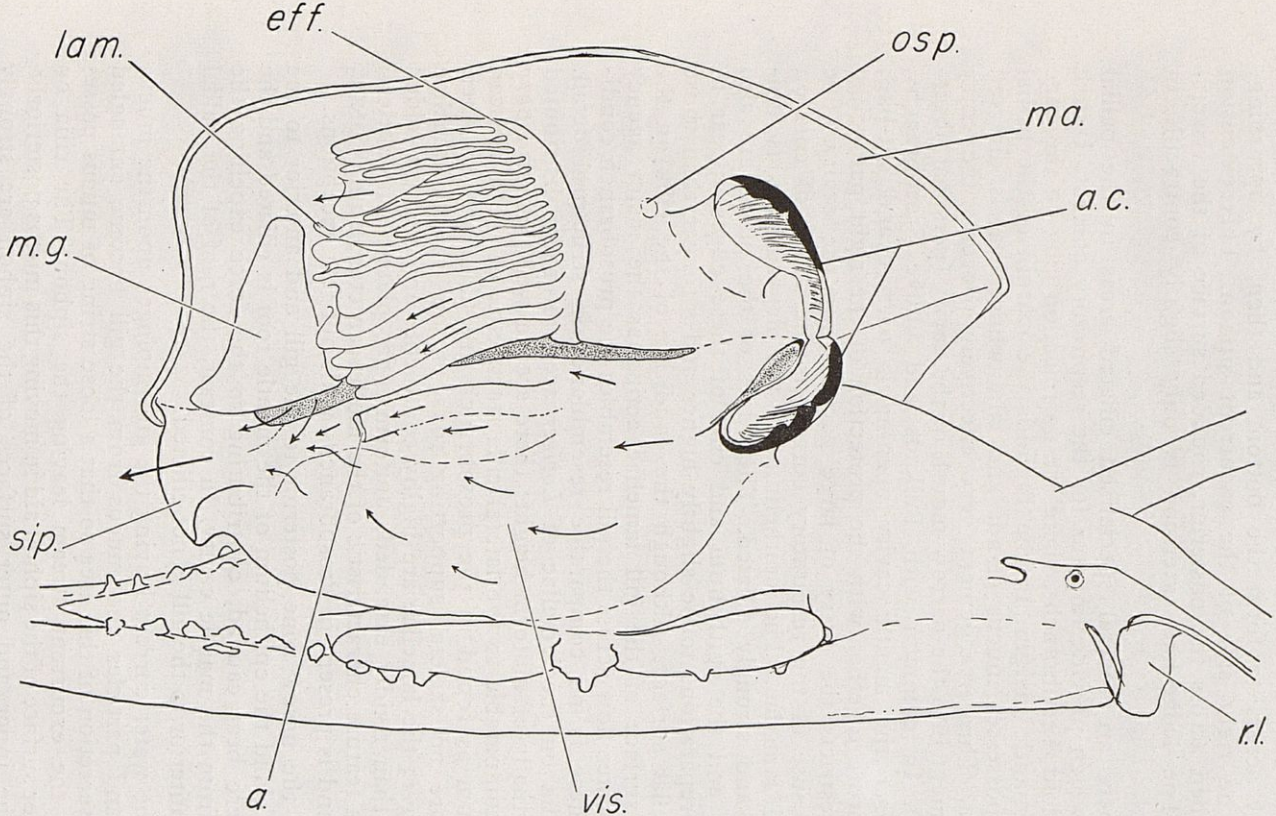

Fig. 4. — *Lobiger serradifalci*, view from right side, from slightly above. Parapodial lobes removed at their bases, anterior mantle commissure cut across and mantle cavity roof reflected to the left. Cut surface of muscle in black, deeper part of cavity and groove behind commissure stippled. Water currents on surfaces indicated by arrows, a., anus; a. c., anterior mantle commissure, bisected; eff., efferent branchial vessel; lam., lamella of gill; ma., mantle, roof of pallial cavity; m. g., mucus gland; osp., osphradium; r. l., rhinosphore lobe; sip., siphon; vis., visceral hump, floor of pallial cavity.

ventrally across to form the bottom and then, by upturning, forms the right side of the excurrent siphon. This extension is attached across the posterior, rounded surface of the visceral mass. The ledge-like extension is only slightly contractile in life.

There are several specialized ciliated areas in the pallial cavity which provide impetus for the respiratory current. Unlike the bulloid Tectibranchs, there are no rejection cilia on the edge of the mantle margin. In the Bulloids the margin of the pallial cavity possesses mucus glands and cilia whose beat is directed outward. This arrangement very effectively prevents the entry of sediment into the narrow mouth of the cavity (personal observations). In common with Bulloids and unlike Prosobranchs, in *Lobiger* the mantle cavity opening is narrow and slit-like; this feature together with the protection of the right parapodial lobes restricts the entry of large particle into the cavity. The major cause of the respiratory current is the action of cilia on the gill lamellae. The epithelium of the flat surfaces is uniformly and strongly ciliated. The edges of the plates are also ciliated and the epithelium and cilia of these edges appear in fresh preparations to be slightly higher and stronger than those of the flat surface. Although the condition of the cilia on the lateral surface of the gill lamellae acting as the major agency of the water flow across the gill resembles the prosobranch condition, there is no comparable resemblance in structural detail. The cilia on the lamellae of *Lobiger* are uniformly distributed and virtually of uniform height; there are no well defined ciliary zones comparable to the lateral cilia tract, etc., of the molluscan ctenidium as found in the prosobranch gill filament. Further, there are no skeletal supporting rods present in the lamellae of *Lobiger*; the lamellae are higlhy contractile and slightly folded rather than rigidly extended, uniformly flat plates. The skeletal rod is a feature characteristic of the molluscan ctenidium (YONGE, 1947) and is present in Prosobranchs with but few exceptions.

In the narow zone posterior to the gill and anterior to the mucus gland the epithelium of the mantle roof is ciliated and the cilia here beat caudad, contributing to the force expelling the water from the mantle cavity. In contrast, the roof of the pallial cavity anterior to the gill is not ciliated.

The water current leaving the gill impinges upon the mucus gland and particles and mucus from the gill become entangled in the secretion of this area so that a loose string of mucus passes out in the excurrent stream leaving the siphon. The cilia on the inner surface of the siphon aid in moving this mucus posteriorly. Both the inner and outer surfaces of the siphon are strongly

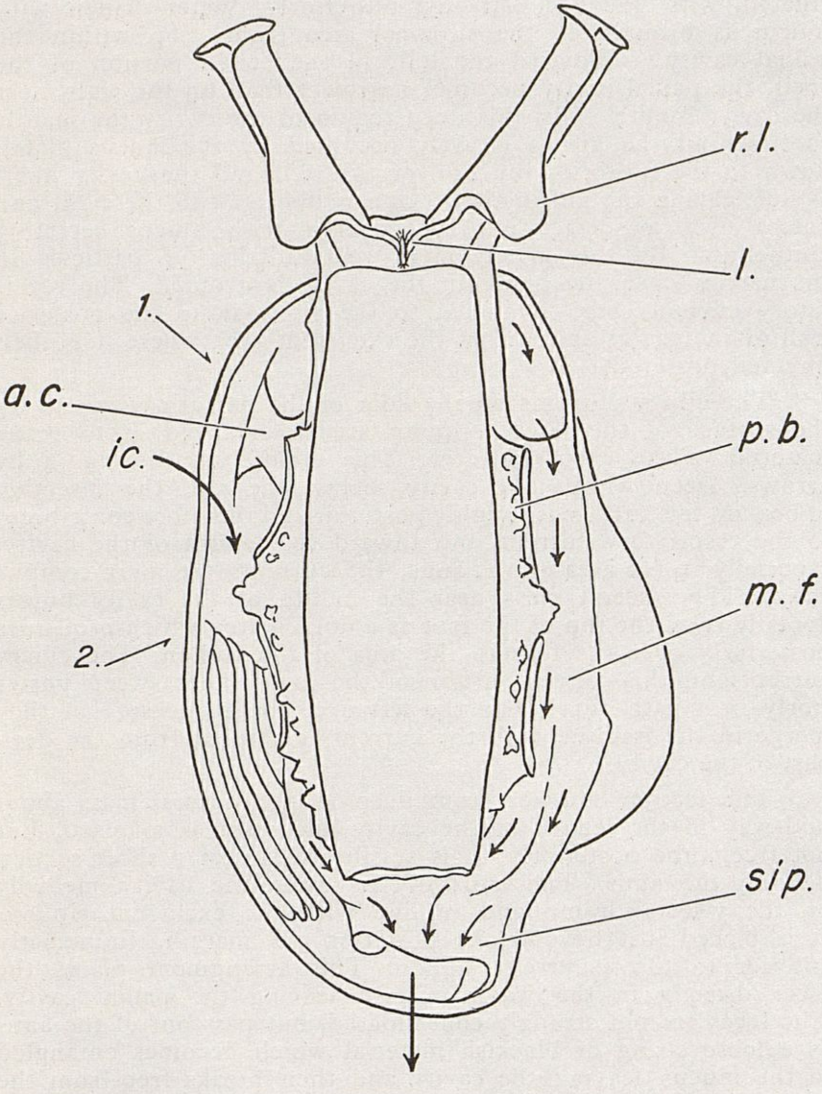

Fig. 5. — *Lobiger serradifalci*, ventral view showing major water currents. Large arrows, incurrent and excurrent streams; small arrows, cleansing currents of ventral surface. All parapodial lobes and tail of foot removed. a.c., anterior mantle commissure; ic. incurrent stream; m. f., mantle flap over recurved shell edge; p.b., parapodial base; r.l., rhinophore lobe; sip., excurrent siphon.

ciliated, with the beat directed posteriorly. Water, laden with mucus is brought to the siphonal area from deep within the pallial cavity. Toward the left, in the coiled portion of the shell, the pallial cavity becomes narrower than on the right near the cavity mouth. In this deep region of the cavity the mantle roof behind the gill is entirely occupied by the mucus gland, down to the posterior junction of the roof and the cavity floor. Water leaving the gill in this region is deflected to the right and passes over a surface entirely covered with mucus secreting epithelium. By this arrangement accumulation of particles in the narrow space deep within the cavity is avoided. The respiratory current thus channeled to the right along the posterior wall of the cavity emerges in the excurrent area where it is then directed posteriad.

The ciliary currents on the floor of the pallial cavity and on the surface of the visceral hump are so arranged as to bring material to the excurrent area. This is indicated in fig. 4 by arrows. Deep within the cavity, below the gill, the direction of beat on this surface is roughly posterior and therefore contributes to the respiratory current, but toward the mouth of the cavity, especially in the area of the anus, the currents are more complicated. The visceral mass near the mouth of the cavity bulges dorsally from the top of the foot as a domed area which protrudes posteriorly over the foot in the area of the siphon. The ciliary currents on this convex portion of the cavity floor sweep posteriorly in a path curving to the left over the bulge so that they merge in the midline with the currents emerging from the deep part of the cavity.

The rectum emerges from deep in the visceral mass about mid-way in the length of the cavity and runs as a raised, but not free, tube posteriorly. It is sessile except for a short section bearing the anus. The anus opens inside the cavity medially on the visceral hump and in line with the excurrent siphon. It is placed just beyond the posterior gill margin, immediatly anterior to the excurrent siphon. This arrangment places the feces directly in the water current leaving the pallial cavity. The feces are not strongly consolidated, but pass out of the anus as a loose string of blackish material which becomes entangled in the mucus leaving the cavity and then breaks free from the anus as it is passed out of the cavity.

Finally, the departing excurrent stream passes over the flat, smooth triangular area of the dorsal surface of the foot. This lies below the protruding posterior end of the visceral hump and the siphon and provides an unobstructed path for material leaving the cavity.

In surface view the gill appears to be composed of uniform, close packed lamellae, but on closer examination there are found many smaller lamellae between larger, more prominent ones. There are about as many smaller irregular lamellae as there are larger ones of more uniform height and length. These do not constitute two sharply defined size classes, but rather there are smaller lamellae of various sizes. These are obscured by the larger partly because they are often of irregular lengths and do not run completely across the gill as do the larger ones. Many of the smaller lamellae are not as high as the larger, so are not easily seen. Both large and small lamellae show some irregular folding either down the length or across the width, but usually the smaller are the more crinkled. A few of the smaller lamellae to arise from the sides of larger lamellae rather than from the roof of the mantle cavity. This gill then does not correspond in structure to the plicate gill of the cephalaspids as has been noted by a number of authors. It also differs fundamentally from the basic structure of the gastropod ctenidium.

The amount of mucus passing out in the respiratory current seems directly related to the amount of sediment present in the water entering the cavity. When large amounts of particulate matter (starch grains) were added to the milieu water of an intact normal animal in order to study the currents entering and leaving the cavity, considerable quantities of mucus with firmly entangled particles emerged from the siphon. By careful pipetting of particles directly into the excurrent stream of a normal animal in clear water the mucus emerging from the pallial cavity could be demonstrated by the particles becoming entangled in it. Under these conditions there was usually less mucus than under conditions with large amounts of particles in the water.

DISCUSSION.

I. — *Pallial cavity; currents and cleansing mechanisms.*

It has been demonstrated that while *Lobiger* has no mechanism to prevent fine particulate matter from entering the pallial cavity, it does have an efficient ciliary and mucus mechanism which prevents particles so entering from accumulating and clogging the respiratory surface. This is effected by entangling entering particles in mucus and removing this material by a posterior excurrent stream leaving through the siphon. Elsewhere, areas of the body such as the sides below the shell edge are kept free of settling material by posteriorly directed ciliary currents.

A consideration of the nature of the pallial cavity and of the habitat reveals features that may have operated in the development of the cleansing mechanism. *Lobiger*, like most of the bulloid Tectibranchs, possesses a pallial cavity that is extensive in horizontal extent but not deep dorso-ventrally. The gill is rather extensive, possessing many closely-spaced lamellae. This type of pallial cavity would be very inefficient without cleansing mechanisms to prevent entrapment of particulate matter deep within the cavity. The habitat in which the *Lobiger* used in this study were found is one in which considerable suspended material is often present. At Villefranche, *Caulerpa prolifera* grows on a sandy-muddy bottom in a quiet embayed area. On the surface lies a thin layer of loose sediment into which the *Caulerpa* holdfasts extend. That the algal mat itself traps considerable amounts of sediment may be readily demonstrated by shaking some of the alga in a container of water. The habitat of *Lobiger* then is just above a soft, silty bottom which, though in a quiet area, is easily stirred up in windy weather. Under these conditions the development of an efficient cavity cleansing mechanism is essential.

The modifications of shell and mantle structures to accommodate the posterior excurrent stream described here for *Lobiger* appear to have their counterpart in *Oxynoë*, judging from the small amount of available information. The shell of *Oxynoë* is distinctly coiled and resembles that of a bulloid Tectibranch; and like the latter, clearly shows a posterior gape and extension to the right side of the coil that would provide an opening for excurrent water. The figure reproduced in PILSBRY (pl. 10, fig. 48, vol. 16) of the opened pallial cavity of *Oxynoë olivacea* clearly shows that the arrangement of pallial structures is identical with that in *Lobiger* and what appears to be a lobe extending from the mantle near the posterior end of the gill on the right, and passing to the left across the posterior end of the visceral mass, behind the anus, may well be the homologue of the excurrent siphon described here. The well developed parapodia in *Oxynoë* may limit the entry of water directly from the side but the water could be brought in under the extended anterior mantle margin to then pass into the pallial cavity from the right. This would be similar to the condition in bulloid Tectibranchs with well developed parapodia.

The relation of the pallial cavity in the *Oxynoidea* to that in the more primitive Opisthobranch groups can be more clearly understood by a consideration of the state of detorsion present in *Lobiger*.

Lobiger shows complete detorsion and almost complete resumption of bilateral symmetry of the visceral mass if the median, posterior position of the anus is used as an orientation point. The pallial cavity, however, is bounded anteriorly by a wall which extends almost completely across the top of the visceral mass, while its opening extends all along the right side and curves to the left posteriorly. This arrangement corresponds to the state approximately 90 degrees of detorsion of the pallial cavity opening in relatively primitive cephalaspid Tectibranchs such as *Acteon* and *Bulla*. Therefore, perhaps detorsion in these Tectibranchs and *Sacoglossa* should be viewed not as a process which has occured synchronously in both the pallial cavity and the visceral organs involved but rather as a process in which these structures have moved somewhat independently to the right toward a more posterior and bilateral position. The pallial cavity opening in Bulloids and the *Oxynoidea* does not seem to have arrived at its present position by simply swinging to the right toward a posterior position but rather by combining detorsion with posterior elongation of the opening of the cavity and by the posterior border receding sufficiently to the left to form a directly posterior exit for the excurrent stream.

This view that the pallial cavity as a whole has elongated posteriorly in Opisthobranchs is simpler than, and somewhat at variance with that expressed by PERRIER and FISCHER (1911) who considered that the present state resulted from backward extension of the original right (sutural) corner of the cavity, with most of the floor of the present cavity being derived from the original right side of the cavity.

II. — *Body form.*

Comparisons of *Lobiger* and *Oxynoë* reveal differences which can be reasonably postulated to be the result of changes during the course of evolution of the line represented by the contemporary genus *Lobiger*.

Oxynoë and *Lobiger* are obviously closely related and it appears that in some respects *Oxynoë* is the more primitive. The shell of *Oxynoë* does not significantly differ from an open bulloid shell. Uncoiling has proceded to the point where only the major whorl of the shell is important, but the coiled portion remains in the position found in involute bulloid shells, and contains the end of the visceral mass. The shel in *Lobiger* is in a reduced and almost uncoiled state with only a remnant of coiling present in the excentrically placed apex. The capshaped shell has a free margin on all sides since there are no overlapping whorls. The shell has undergone changes which bring it into an approximately bilateral condition. This has been achieved by extension of the edges all around. The apex and coiled portion are placed more anteriorly than in the primitive position. The posterior extension of the mantle and shell over the siphonal area appears best explained as an adaptation correlated with improvement in the efficiency of the pallial cavity.

In *Oxynoë* the visceral mass is well separated from the foot on all sides and shows distinct coiling. The attainment of the uncoiled condition in *Lobiger* has been accompanied by changes in the disposition of the visceral mass. These changes have produced a low, rounded mass, almost bilaterally symmetrical. As uncoiling of the shell proceded, the viscera once held in the coiled whorls of the shell were moved to the right dorsally and compacted into the cephalo-pedal mass by dorso-ventral compression. The visceral mass is partially sunk into the foot, but, it is not completely fused with the foot as it is in the non-shelled *Sacoglossa*. Dorsally the visceral mass retains its individuality and even some remnant of coiling. Anteriorly the mass appears sunk into the neck region, but is still partially marked off by a crevice which runs in front of the anterior end of the visceral mass across the dorsal body surface, inside the pallial cavity. Posteriorly, the visceral mass projects free above the foot.

These changes identifiable in *Lobiger* are worthy of attention because they give some clues to the sequence of events by which the more advanced *Sacoglossa* have attained their limaciform body, with its complete external bilateral symmetry. In these forms the visceral mass has disappeared as a separate division of the body, the viscera having completely sunk into the cephalopedal mass. Concomitantly, the shell and associated mantle cavity have disappeared. The conditions represented in *Arthessa* and *Cylindrobulla*, *Oxynoë* and finally *Lobiger* may be used to represent a sequence of steps leading toward this shell-less, bilateral condition. This sequence of progressive detorsion and shell reduction can be deduced because of the existence of extant *Sacoglossa* showing some intermediate conditions between primitive cephalaspid Opisthobranchs and the advanced *Sacoglossa*. It also may indicate what type of changes might have been involved in the attainment of a similar body form in the nudibranch groups, for which we have no comparable series of clearly related forms.

III. — GILL.

The observations made on the gill of *Lobiger* invite comparisons with that in other forms. The question of the homology of the gill of *Lobiger* and *Oxynoë* with that in other Opisthobranchs, especially with that in the cephalaspid Tectibranchs has seldom been discussed. This question must now include the status of the gill of *Arthessa* and *Cylindrobulla* (See EVANS, 1960 and MARCUS and MARCUS, 1956) as well as that in the Tamanovalvidae since it appears that all these Sacoglossa possess an identical gill. HOFFMAN (1940, p. 25) briefly states the conflicting views of PAGENSTECHER and MAZZARELLI on the homology of the gill of *Lobiger*, but does not critically evaluate the evidence or settle the matter. As this question is part of the larger problem of whether or not the gill of all lower Opisthobranchs is a ctenidium (sensu YONGE, 1947), it will not be discussed here. An investigation of the anatomy and function of pallial cavity structures in a number of Tectibranchs and Anaspids has been made recently by me and the report being prepared will include a discussion of the evolution of the pallial cavity in the shelled *Sacoglossa*. The position is here taken that the characteristic gill of the *Sacoglossa* arose in this group and that it and its associated circulatory system do not resemble those in Bulloids sufficiently in either structure or function for homology to be established.

RÉSUMÉ

Lobiger serradifalci (Calcara) 1840 a été récolté sur *Caulerpa prolifera* à Villefranche-sur-Mer (A.-M., France); il se nourrit de cette algue, en perforant la face plane du thalle. L'association constante entre les Mollusques *Sacoglossa* à coquille et le genre *Caulerpa* est étudiée et discutée.

Une description détaillée de l'animal vivant est fournie. L'auteur a observé la réaction de défense provoquée par une excitation, avec désenroulement des lobes parapodiaux et sécrétion d'une substance blanche. Un traitement plus brutal provoque la chute des lobes parapodiaux et de l'extrémité postérieure du pied suivant des lignes de déhiscence préexistantes.

Les caractéristiques structurale et fonctionnelle de la cavité palléale donnent lieu à des considérations détaillées et l'auteur tente d'établir les rapports entre ces caractéristiques et les conditions de vie de cette espèce. L'existence de courants ciliaires et la façon dont sont retenues des substances particulières pénétrant dans la cavité palléale sont spécialement soulignées.

Quelques comparaisons sont faites avec les complexes palléaux des Prosobranches et des Tectibranches *Bulloidea*; l'auteur conclut que la branchie lamelleuse des *Sacoglossa* n'est homologue ni de la branchie plissée des Tectibranches, ni de la cténidie des Prosobranches. La comparaison de la forme du corps chez *Oxynoë* et *Lobiger* permet de mieux comprendre l'apparence limaciforme des *Sacoglossa* nus et l'évolution générale du groupe.

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