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# The Habits and Habitats of the Opisthobranch Molluscs of the British Solomon Islands

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# The habits and habitats of the opisthobranch molluscs of the British Solomon Islands

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## Introduction

Often bizarre in shape and gaudily coloured, the opisthobranchs of the tropical Indo-Pacific have always been attractive subjects for the specialist worker and for writers of popular natural history. There is certainly no lack of papers describing their anatomy and systematics (Marcus & Burch (1965) give a fairly full bibliography), but only in those by Risbec (1928*a*, *b*, 1951, 1953) are there descriptions of where or how they live and his statements are brief and rather vague. I collected opisthobranchs so as to record them for the British Solomon Islands for the first time and, whenever possible, I noted their habits and habitats. My observations on gut contents are rather scanty as I did not wish to damage any of the few specimens of each species collected.

From an examination of ten different types of reef formation I discovered that opisthobranchs are common in only two places; (1) the crest of a semi-exposed reef where algae occur in pools, and (2) the flat of a sheltered or semi-sheltered reef. At each of these sites several distinct habitats can be distinguished. Unfortunately my recognition of these habitats is not supported by strong numerical evidence as none of the 55 species occurred in large numbers.

Before presenting the results of the field work it would be helpful to summarize our knowledge of the food and feeding habits of this group of molluscs. Altogether there are eight orders of opisthobranchs, but this study is only concerned with members of five of them. The most primitive opisthobranchs, the bubble-shells (order Cephalaspidea), feed on green algae, polychaete worms, other opisthobranchs or bivalves which they swallow whole. Two groups are exclusively herbivorous, feeding on delicate green and red algae; the sea hares (order Anaspidea) bite off large pieces from thalli, whereas the sacoglossan sea slugs (order Sacoglossa) pierce the cell walls and suck out the protoplasm. The remaining two orders are carnivorous; the side-gilled sea slugs (order Notaspidea) eat ascidians and the true sea slugs (order Nudibranchia) feed, by scraping, sucking or cutting and tearing, on a wide variety of sedentary invertebrates, though one or two specialized kinds eat fish eggs. Within these five orders there are varying degrees of food choice, at one extreme there are species which feed on several organisms (belonging to one or two systematic groups, plant or animal, but never both) and at the other there are the specialists which eat only one kind of prey.

## Reef (algal) crest

A few opisthobranchs inhabit the reef (algal) crest where it is well developed and emergent at low tide, as on the 'weather coast' (at Banika Island in the Russells) or at fairly exposed places where reef front and beach rock are contiguous and form a very

narrow platform (at Matui Island, Marovo Lagoon). Altogether five species were collected, all herbivores. Four of these species are, at low tide, pool dwellers; they are *Oxynoë viridis* (Pease), *Elysia* sp. and *Placida* sp. (order Sacoglossa) and *Dolabrifera dolabrifera* (Rang) (order Anaspidea). The three sacoglossans live together amongst, and feed suctorially on, the green alga *Caulerpa*. They are fairly common at Banika where *C. racemosa* and *C. sertularioides* grow profusely in shallow pools on the reef crest immediately behind the narrow zone of *Sargassum binderi*. These pools are continually and heavily splashed with spray from the breakers when the tide is out and completely flooded at high water. *C. racemosa* and three other species, *C. serrulata*, *C. urvilliana* and *C. webbiana*, are common at New Munda (Gizo), where the reef is fairly similar in profile but more exposed. A great quantity of *Caulerpa* was searched but no sacoglossans were found. *Dolabrifera dolabrifera*, a small warty sea hare, lives in deeper pools where it crops the sparse algal carpet. This sea hare is ideally adapted for life in turbulent water with its compressed body, reduced mantle cavity and parapodia, and very broad foot by which it clings limpet-like to the rock. The fifth species is *Smaragdinella calyculata* (Broderip & Sowerby), a small squat bubble-shell (order Cephalaspidea); it was found in crevices in the heavily pitted yellowish green zone on the outer (northern) side of Matui Island (Marovo Lagoon). This was the only opisthobranch found uncovered at low water, though its habitat is kept moist by spray from the breaking waves.

## Reef flat

Almost all of the opisthobranchs of the reef flat were collected on sheltered or semi-sheltered sections of the broad fringing reefs of mainland and cay, particularly where a moat is, at low tide, joined to the sea through surge channels. None was seen on the reef flat of a 'weather coast' and only a small number were found on the heavily silted reefs of extreme shelter.

### *Boulder zone*

Most of the opisthobranchs of the reef flat were found in the region just behind the crest where the base rock is scoured clear of all but the coarsest particles by currents and small waves generated by the breakers at the reef front. This part of the flat is a mosaic of base rock encrusted with coralline algae and patches of coarse coral fragments; it is littered with upturned dead *Acropora* tables, loose dead *Porites* micro-atolls and smaller lumps of coral rock such as dead *Goniastrea* mounds and for this reason is often called the boulder zone. Carnivorous opisthobranchs were found either beneath these coral rocks and boulders feeding on certain of the encrusting sponges, sea mats and sea squirts, or nearby crawling across the floor of the moat or pool. No one species was especially abundant, but prominent were the sponge-eating dorids *Platydoris flammulata* Bergh and *P. cruenta* (Quoy & Gaimard), *Casella atromarginata* (Guvier), *Chromodoris inornata* (Pease), *C. quadricolor* (Ruppell & Leukart), *C. alderi* (Collingwood) and *C. geometrica* (Risbec), all of which rasp their food, and *Dendodoris rubra* (Kelaart) and *D. nigra* (Stimpson) which are sucking forms. *Gymnodoris citrina* (Bergh), a polyzoan feeder, was also fairly common. Several specimens of *Hexabranchus marginatus* (Quoy & Gaimard), a large and very handsome dorid, were found. This species is perhaps the best known of all tropical nudibranchs

because of its spectacular swimming movements and flashy colouring. Risbec (1928*a*), briefly, and Morton (1964) have described the sequence of movements.* *Hexabranchus* swims by alternate dorsal and ventral bending of the body synchronized with waves of contraction passing backwards along the expansive and extended lateral flaps of the mantle. Of the vertical flexions, the ventral are the strongest and most acute. This ventral

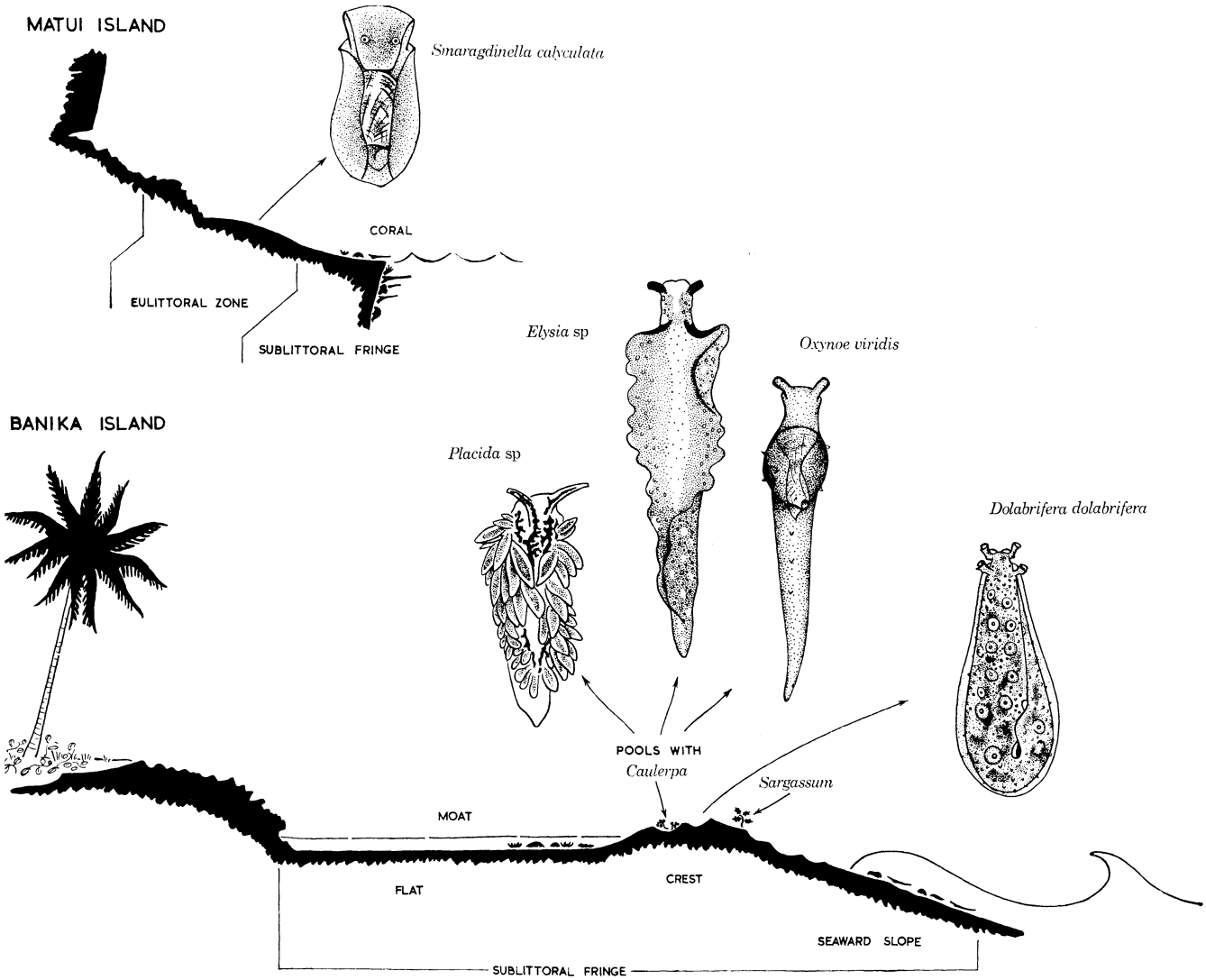


FIGURE 186. The distribution of opisthobranchs which live on the coral reef of a moderately exposed northern coast (Matui Island; the reef is about 11 m wide) and of a 'weather coast' (Banika Island; the reef is about 30 m wide).

thrust raises the animal off the bottom. The lateral waves, of great amplitude, push the body forwards. When swimming the crimson and blue colouring near the edge of the mantle is prominently displayed. At rest, or when crawling, the large lateral flaps are rolled up with the under surface outermost; the red and white mottling of the under surface of the mantle and side of the body matches perfectly the mid-dorsal region and the

* Edmunds has just presented a more detailed analysis of the swimming and posturing of *Hexabranchus marginatus*.

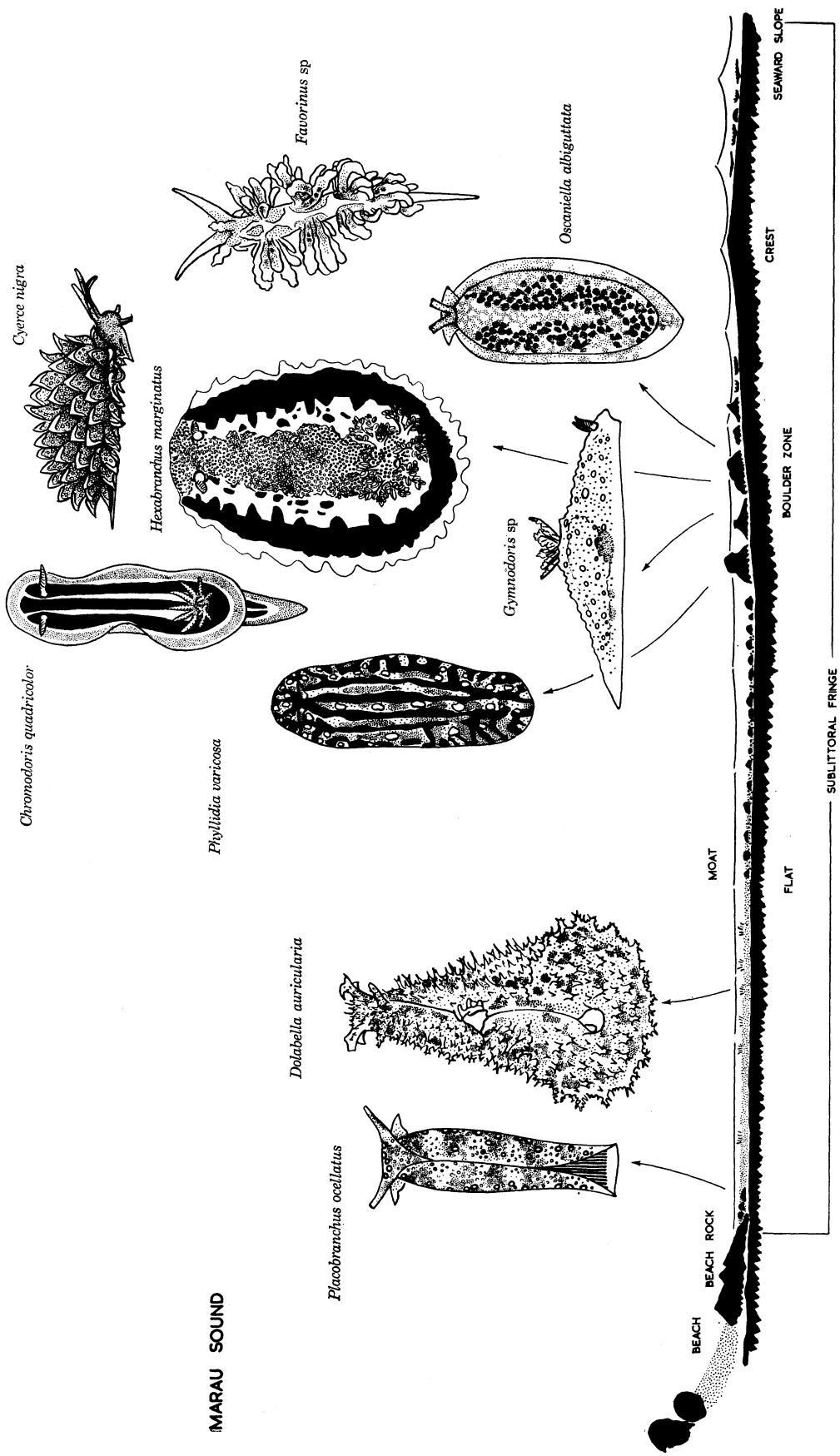


FIGURE 187. The distribution of some of the opisthobranchs which inhabit a fairly sheltered reef (Marau Sound; the width of the reef is about 500 m).


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animal is extremely difficult to see in this pose against the floor of the moat. Only three species of aeolid (normally hydroid and sea anemone feeders) were collected, all of them belonging to the one family, the Facelinidae. One species of aeolid, *Favorinus* sp. (possibly *F. gouaroi* Risbec), was found eating the spawn of *Oscaniella albiguttata* Bergh, attached to the side of a *Porites* micro-atoll. Other selective carnivores taken in the boulder zone were pleurobranchs which usually feed on sea squirts; the three species found were the large reddish brown *Oscanius weberi* Bergh, the mottled reddish brown *Oscaniella albiguttata* and the bright orange *Berthella delicata* (Pease). Two species of *Chelidonura* were found crawling across coral rock and small living coral colonies. These carnivores feed on mobile prey, e.g. annelid worms, other opisthobranchs, and probably roam throughout the boulder zone searching for their food. Some herbivorous forms also live in the boulder zone; *Lobiger viridis* Pease (order Sacoglossa) was found on small clumps of *Caulerpa racemosa* and *Elysia marginata* (Pease) on *Enteromorpha* sp. or just crawling across the side of the coral rock. Here, too, was found the spectacular black and gold *Cyerce nigra* Bergh feeding on the dark green filamentous alga *Chlorodesmis comosa*. *Cyerce nigra* swims actively, though rather inefficiently, when dislodged—it propels itself forwards, backwards or sideways in a somewhat fitful way. Swimming is jerky and violent and is caused by the alternate up and down bending of the broad, flattened cerata. There are several rows of cerata along each side of the body and the movements of these are synchronized; during the effective (down) stroke, which is very strong, the lowermost row bends down first followed in turn by each of the other rows; in the recovery (up) stroke the sequence is reversed.

### *Living coral*

The only opisthobranchs found on living coral were three species of *Phyllidia* (order Nudibranchia), *P. varicosa* Lamark, *P. pustolosa* Cuvier and *P. nobilis* (Bergh). Some individuals of all three species were crawling on branched *Acropora*, but were not observed eating it; their diet may be be the living coral polyps or sponges growing on the lower branches of the colony.* The method of feeding must be suctorial since they have a small mouth and no buccal hard-parts.

### *Inner part of the flat*

In the quiet waters nearer the beach where the finer sediments accumulate live several herbivores, *Dolabella auricularia* (Solander), a large sea hare, amongst the sea-grass *Thalassia hemprichii*, *Stylocheilus longicauda* (Quoy & Gaimard), a much smaller sea hare, and *Placobranchus ocellatus* van Hasselt, a sacoglossan, on lumps of coral rock covered with *Enteromorpha*.

## Discussion

A fairly exact comparison of the coral reef and temperate rocky shore as a habitat for opisthobranch molluscs can be made since the same basic life zones, as described by T. A. and Anne Stephenson (see Lewis 1964), can be identified on both kinds of shore. On temperate hard shores most opisthobranchs live in the sublittoral fringe, though some species can be raised to the midlittoral zone when large rock pools are present there.

* In Fiji (Rava reef, near Vitonga Bay, Viti Levu) I found a specimen of *Phyllidia nobilis* feeding on a sponge.


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Euryhaline forms like *Limapontia capitata* (Müller) often live in shallow pools near the upper limit of the mid-littoral. The opisthobranchs of the coral reef are restricted to the fringe whether it is the crest of a fairly exposed part or the flat of a somewhat sheltered sector. The moat covering the reef flat is comparable to a large rock pool in the sublittoral fringe of a temperate shore which, at low tide, may be completely separated from the sea or may remain connected by a gully. In temperate regions quite a number of opisthobranchs, e.g. dorid and dotid nudibranchs, are found living at the very top of the sublittoral fringe and thus may be out of the water for as long as 3 h. This is rarely so in the tropics as the drying action of the wind and the heat of the sun are so great. A soft-bodied animal such as an opisthobranch would soon perish if uncovered for a short period, even if it is lying beneath a coral rock. *Smaragdinella calyculata*, the only opisthobranch found stranded by the ebbing ride, lives in moist crevices very close to the extreme low-water mark.

Since opisthobranchs of the coral reef flat are always submerged, their daily activities are not interrupted by the receding tide. Many continue to wander about the floor of the lagoon at low water, within the limits of their particular habitat. Quite a number of coral reef opisthobranchs can swim, though this is hardly surprising since the lagoon offers a very wide expanse of still water of a moderate depth to be exploited. The swimming action is always vigorous but inefficient and seems more likely to be used for escape than as a normal mode of progression.

What limits opisthobranchs to fairly well-defined areas of the coral reef? Food would appear to be the answer though, through lack of exhaustive observation, it is not possible to be dogmatic about this. I and others (Miller 1961; Thompson 1964) have found that in temperate parts of the world food is the dominating influence—the lives of opisthobranchs are completely governed by the distribution and abundance of their food organisms. Opisthobranchs have very special diets, and naturally, are commonest where their food is plentiful. Other factors, however, must sometimes operate for an opisthobranch may never occur at certain places where one of its food organisms is often abundant. Silt, wave action, exposure to wind and sun appear to be most important in determining where the food organisms occur.

A striking feature of the collection is the small number of aeolids (order Nudibranchia). Other workers have found that this group is poorly represented in the tropics. Eliot, who studied the Indo-Pacific forms fairly intensively, found few aeolids on the reefs, so did Farran, and both remarked on their paucity (see Risso-Dominguez 1962). Risbec, who collected opisthobranchs for two years on the reefs of New Caledonia found more aeolids than anyone else—some 30 species (though I suspect that some of his species are merely colour varieties of others). The total for the tropical Indo-West Pacific, however, still falls short of the number recorded in temperate seas. Although my own collecting was in no way exhaustive, I do believe that aeolid nudibranchs are poorly represented both in species and individuals, certainly on top of the reef.

Why are aeolids so rare? More might have been expected since zoantharian coelenterates, which some aeolids are known to eat, are so dominant. I did not see aeolids feeding on coral polyps and no one else has reported them doing so. The reason for the small numbers is possibly the rarity of their food for both hydroids and sea anemones


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which they normally eat, are uncommon on the reef. The three species of aeolid collected in the British Solomon Islands belong to the family Facelinidae and facelinids are reported as predominant elsewhere in the Indo-West Pacific. Their pre-eminence is perhaps the consequence of a more catholic taste in food, for facelinids are known to eat opisthobranch eggs and other aeolid nudibranchs as well as hydroids. One species collected by me was feeding on the eggs of *Oscaniella*.

Little can be said about the geographic distribution of the opisthobranchs found in the British Solomon Islands. Those species which have been identified at this stage (33) are characteristic members of the shelf fauna of the Indo-West Pacific region—some of them, e.g. *Placobranchus ocellatus* and *Dendrodoris nigra*, are recorded from Zanzibar and Hawaii, i.e. at or near the eastern and western edges of the faunal region. There are indications that the opisthobranchs of the Indo-West Pacific are not evenly distributed throughout the faunal region but this cannot yet be convincingly demonstrated for the systematics of a great many of the species need revision. The *Siboga* Expedition (Bergh 1905) collected 166 species in the East Indies and Risbec 140 in New Caledonia (only 25 and 15, respectively, of these species were found in the Solomons), but though the total numbers are close, there are quite considerable differences between the faunas of these two areas. Such discrepancies, however, may well be the result of muddled systematics or inadequate collecting.

## Postscript

A recent (May 1968) collecting trip to Viti Levu in Fiji has confirmed the observations and their interpretation which I have presented above. At least 20 of the 44 species collected in Fiji have also been found in the British Solomon Islands. In Fiji, I collected two infaunal species (none was taken in the Solomons), a bubble-shell *Pupa sulcata* (Gmelin) living in coarse sand at the landward edge of the moat and an aeolid, *Cerberilla annulata* (Quoy & Gaimard), burrowing in an area of coarse sand in a channel near the edge of a sheltered reef.

The drying effect of both sun and wind certainly influence the distribution of opisthobranchs at low tide. At Momi in Viti Levu (Fiji) the fringing reef is wide and has no moat —when the tide ebbs only shallow pools are left, both on the broad mud flat (with sea grass) and on the landward slope (very gentle) of the coral part of the reef. The opisthobranch molluscs (several individuals of eight species were collected) were found only under coral rocks and boulders lying in these pools—none was found under a rock left dry by the retreating tide. Silt too was found to be limiting. At Vunda Point, near Lautoka, the reef which is fairly wide (about 350 m) is at certain places so extensively covered with mud (and the mangrove *Rhizophora*) that the living coral part of the reef is reduced to a very narrow strip; here there is only a line of boulders clear of sediment and the nudibranchs are confined to it. The limiting effect of the fine deposit is probably indirect since it restricts the occurrence of the organisms which are the food of the opisthobranchs.

The swimming forms *Cyerce* and *Hexabranchus* were both very common and were often seen swimming in the moat. At Natandola Harbour one small individual of *Hexabranchus* was observed swimming in very turbulent water, caused by the water of the moat spilling over the end of the reef where it abuts on the sandy beach at the head of the bay. *Bornella*


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*digitata* Adams & Reeve, another swimming nudibranch, was very common at Vunda Point. This animal swims by single, violent side to side flexions of the body. At the end of each stroke made by the tail the edge of the foot on the concave side of the body is turned upwards and remains so at the start of the return stroke; probably the transversely inclined foot gives some lift to the body. The animal moves head first; progression is slow and the course followed rather irregular. Risbec (1953) mentions that this species swims feebly, but I have found that the bending movements are very vigorous and are maintained for several minutes.

I wish to thank the Royal Society of London for inviting me to be a member of their expedition to the British Solomon Islands Protectorate. I am greatly indebted to Professor J. E. Morton and other members of the marine party for their prodigious help in collecting opisthobranchs. I am very grateful to the South Pacific Research Programme Committee of the University of Auckland for paying my return air-fare to Honiara and for granting me a small special clothing allowance.

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