

Feeding and the Radula in the Marine Pulmonate Limpet

Trimusculus reticulatus

BY

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(1 Plate; 4 Text figures)

INTRODUCTION

THE MARINE PULMONATE limpet *Trimusculus reticulatus* is found on the west coast of North America. The first detailed in-life observations of a trimusculid limpet were made on this species by YONGE (1958). Particular attention was paid to the mantle cavity and some aspects of behaviour. Observations were also made on mucus secretion, the role of the large cephalic lobes, odontophore extrusion and the use of the radula in "effectively scraping fine encrusting vegetation from the surface of the rock." More recently two other species have been looked at in detail. These are the New Zealand *Gadinalea nivea* (WALSBY, MORTON, & CROXALL, 1973) and the Australian *Trimusculus* (*Gadinia*) *conica*, (HAVEN, 1973). The latter work is principally concerned with the reproduction and development of the brooded young. Some notes on feeding demonstrate that it "takes place while the animals are stationary" and whilst it is admitted that no evidence of feeding behaviour was obtained in the laboratory she claims circumstantially that food is obtained by grazing the small area in front of the shell, of diatoms and settled debris. Walsby *et al.* describe the feeding mechanism and ecology of *Gadinalea nivea* in which habit and habitat are closely related. Feeding involves the utilization of the water turbulence and the animal orientates to the predominant current. In its normal position it hangs upside down and lowers the shell so that the water current enters from behind. Lavish mucus is produced from glands of the mantle lip and the front and sides of the foot. Mucus secreted as a curtain in front of the head overlies the mantle and is ballooned out by the current. Particles of phytoplankton are trapped by the mucus curtain acting like a "fly paper" rather than a sieve. After inspection by the extended oral lobes the curtain may then be enclosed by a hood formed by these lobes and ingested by means of the protrusible odontophore.

On a brief visit to the Hopkins Marine Station, Pacific Grove, California, in July 1972 opportunity was taken for a complementary study in life of *Trimusculus reticulatus*. Preserved and living specimens were transferred to the Marine Research Laboratory, Leigh, New Zealand for comparison with *Gadinalea nivea* and of these 4 were kept alive for over a year and two for over two years.

Yonge's in life description of *Trimusculus reticulatus* was found to be comprehensively informative but my observations and conclusions varied with his over feeding and motility. Like *Gadinalea nivea* (WALSBY *et al.*, 1973), *T. reticulatus* is a passive filter feeder trapping suspended particles from the sea water with secreted mucus, although the details of the food collection vary slightly. In this paper aspects of the habits and habitat are reappraised in the light of the filter feeding behaviour; factors which facilitate this and which would preclude grazing as a food collecting mechanism.

HABITAT

Like YONGE (1958) I also found *Trimusculus reticulatus* in large colonies on the under surfaces of large overhanging blocks, on cave roofs and on the upper surfaces of slanting crevices, in the intertidal zone on exposed shores. These were always sites of low light intensity extending to complete darkness. About 50 were found on the inside of the roof of a redundant sea-water system intake sump well. This well was normally open only by a bottom grating, to turbulent water exchange. The animals were in almost total darkness and the shells clean, uneroded and creamish white. Clearly any growth of attached photosynthetic diatoms was not possible. In the most illuminated sites where the animals were found, deep in open shore crevices, the shells were normally tainted a dull grey-green by algal growth. However algal growth can be considered to be

minimal in such sites and was never sufficiently marked to smooth over the delicate ribbing of the shells. Analysis of incident light and chlorophyll α concentrations from surface scrapings (WALSBY *et al.*, 1973) show that in such dark places, even where there may be some tainting, available alga for grazers is negligible. This is reflected by the absence of recognized grazers in these sites. Animals associated with *T. reticulatus* were all known filter feeders; tube worms and barnacles. YONGE (1958) showed that like *Gadinalea*, (WALSBY *et al.*, *op. cit.*), *T. reticulatus* has poor cleansing ciliation, principally a narrow band conducting particles along the pallial groove on each side of the foot. It is therefore important that the animals inhabit a site free from sediment and this would help to explain why they are only found on the roofs of caves and under-surfaces. YONGE, (1953) suggested that *T. reticulatus* occupies much the same habitat as the sessile limpet *Hipponix antiquatus*. He has shown this animal to feed indiscriminately on large particles such as segments of calcareous algae that come within the very limited area of the front of the shell, by catching them with the active muscular proboscis and large distensible mouth, aided by the lateral terminal lobes flanking the mouth. Further observations on the relationship between *Hipponix* and *Trimusculus*, (YONGE, 1960) showed that whilst closely associated their precise habitats are quite distinct. An extreme storm which overturned massive blocks on the shore led Yonge to observe that "*T. reticulatus* is just as confined to the roof of these crevices as *Hipponix* is to the floor." With habitat so clearly differentiated, albeit on a micro-scale, it is reasonable that habit should also be distinct.

ACTIVITY AND LOCOMOTION

YONGE (1958) described *Trimusculus reticulatus* as a mobile animal because it moved freely in aquaria before finally establishing position above the water line. However, apparently animals on the overturned blocks did not move and in this study *T. reticulatus*, whilst capable of movement in unnatural situations, has been found to be essentially sessile. One of the four animals studied in detail has not moved or changed orientation for nearly two years and the others after settling have remained immobile between experiments for up to seven months. Thus adults retain the ability to move efficiently but probably only rarely do so. This is quite reasonable as the same muscles are used in both locomotion and attachment. MILLER (1974) demonstrates that for maximum stationary tenacity shell length to foot length ratios of 1.5, together with foot length to foot width ratios of between 1.1 and 1.5, are

optimal. It is interesting that in *T. reticulatus* these are 1.5 and 1.15 respectively, indicating excellent adaptation to the sessile habit.

In *Gadinalea* the adult shells are commonly misshapen through mutual lateral compression and marked jigsawing and even piling of two or three layers of animals, within a colony, results. This is generally less well marked in *Trimusculus reticulatus* but they are found closely aggregated, frequently show marginal shell conformity to the rock surface, and limited jigsawing and one example of piling was found. This must therefore preclude regular movement by the animals.

MUCUS SECRETION

When freshly collected I also found "great quantities of very viscous mucous, stringy and tenacious in quality" was secreted (YONGE, 1958). However this only occurred so long as the beasts remained unattached. From YONGE's drawing (1958: fig. 2) it may be seen, by the in-folding of the margins of the base of the foot that this study was made with the animal unattached. When the animals are attached, for example, to a glass or clear acrylic plate in-life examination is not impeded by copious mucus secretion.

Histological sections show that like *Gadinalea nivea*, *Trimusculus reticulatus* has a profusion of mucus glands over the mantle lip and also on the front of the foot and the latero-dorsal areas of the head. Under simulated natural conditions there appears to be a steady streaming of mucus which is collected by repeated odontophore protrusion and withdrawal when the animal is feeding. The steady mucus secretion may be effected by sustained or rhythmic contraction of the fine muscular trabeculae dividing the large mantle lip blood lacunae which radiate out across the mantle and can act as an incompressible hydrostatic skeleton behind the epithelial layer rich in mucus glands. In the foot these large blood spaces do not occur and the frontal epithelial mucus glands directly overlie the foot muscle. Presumably muscle ends reticulating between the mucus cells to the surface epithelia are able to exert an opposing steady compression force to exude mucus when the pedal muscle contracts against the substrate. When the animal is detached and the foot distorted through unnatural contraction, controlled secretion is lost and copious mucus secretion results.

THE ORAL HOOD AND MOUTH PARTS

Morphologically the oral hood is very similar to that of *Gadinalea nivea*. A clear mucus curtain characteristic of

G. nivea has not been observed nor the hood behaviour of scanning associated with its filtrant loading. Normally the hood is held within the confines of the shell. However, occasionally it has been observed to extend the oral lobes up to 3 mm beyond the shell margin with the tips of the lobes turned down over the shell margin, away from the substrate (the animal being naturally in the inverted position). Odontophore protrusion never occurs whilst the hood is so extended and whilst the function of this purposeful activity is uncertain, sensing of the water outside may be involved.

With the animal attached to a false transparent roof, appropriately sloped, odontophore protrusion may be readily observed during the feeding bursts. During such a burst the odontophore is protruded rhythmically about once per second and uninterrupted bursts have been observed to last as long as 20 minutes. This sustained activity is unlike that reported for any other gastropod while stationary and is more reminiscent of barnacle cirral feeding strokes. In the feeding position the mouth is a slit normally perpendicular to the substrate rather than one in the same plane and opposed to the substrate as in known grazers such as *Siphonaria*. Odontophore protrusion is forward with a terminating dorsal inflection away from the substrate which would preclude normal grazing activities but serve well to drag food-bearing mucus overlying the mantle lip and streaming off the foot, into the mouth.

Occasionally the oral lappets, which normally overlap slightly, are drawn apart and the odontophore protrusion directed towards the substrate before the upward inflection away from it. This falls far short of the grazing stroke of say, *Siphonaria zelandica* in which the mouth is opposed to the substrate and the grazing stroke, seen through a glass plate, runs the backwardly inflected tip of the radula along the surface. In *Gadinalea nivea* odontophore protrusion, to ingest the mucus curtain, occurs with the shell retracted to the substrate. This protrusion appears similar to that observed in *Trimusculus reticulatus* when not retracted. Further observations of *G. nivea* have shown that under conditions of decreased turbulence protrusion similar to that in *T. reticulatus* may occur though only for short bursts.

The odontophore is large and when withdrawn it is infolded and fully fills the buccal cavity. To observe it whole it is necessary to remove the buccal mass by dissection. The front of the foot is cut away to expose the ventral side of the head. A ventral incision is made to separate the oral lobes which are then trimmed away back to the mouth. The incision is continued back through the "neck" into the visceral mass. The lateral walls of the neck are trimmed and the antero-lateral pedal musculature cut away affording access to the buccal mass which may then be excised

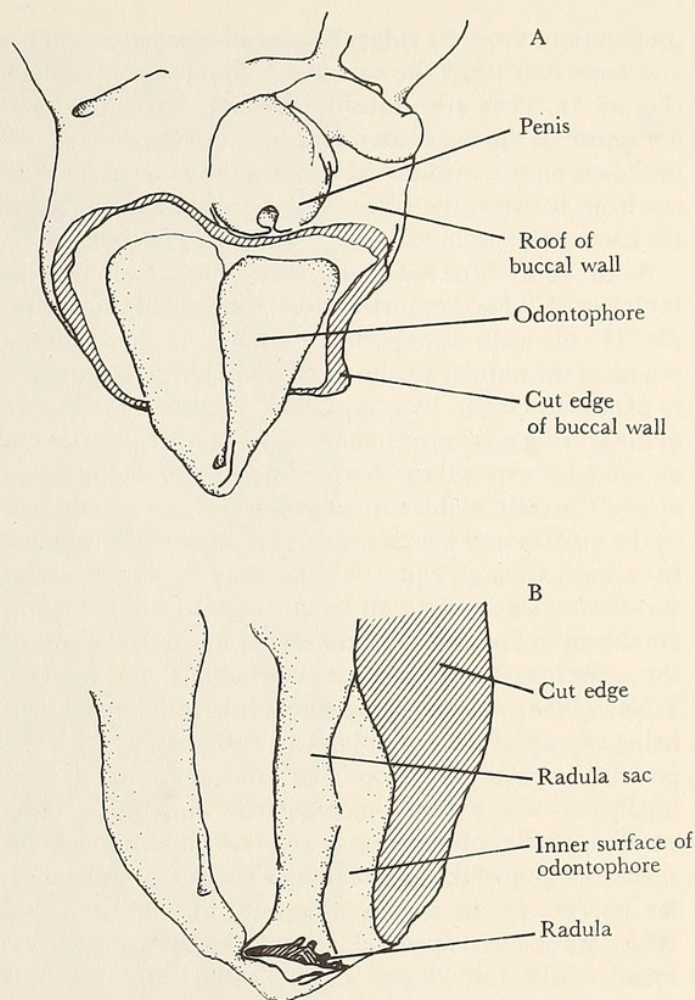


Figure 1

- A. Excised buccal mass of *Trimusculus reticulatus* with front and side walls cut away to expose the odontophore
 B. Odontophore with left infolded section cut away and the right infolded side inflected back to expose the odontophoral trough, radula sac and opening and the tip of the radula

entire. It is turned over and the lips and walls around the mouth cut away to expose the heart shaped proboscis (Figure 1A). The fleshy proboscis is infolded dorsally so that there is slight overlapping medianly. The inner surface of the proboscis is inspected by cutting away one lateral infolded side and inflecting back the other. Along the floor lies a slightly raised tube which is the radula sac. It opens by a narrow window anteriorly, to expose the very tip of the radula (Figure 1B).

Both inner and outer surfaces of the proboscis are finely ridged. During proboscis eversion the floor is pushed out and up and the lateral infoldings open to flatten out the "U" shaped form of the withdrawn proboscis. Histological

preparations show the ridges to be spade shaped in section and some four times the size of the minute radular teeth (Figure 5). They are probably the main surface for the encapture of the food laden mucus. The infolding of the proboscis on the withdrawal stroke must squeeze the mucus from between the ridges and then posteriorly out of the back of the proboscis flask, towards the oesophagus.

At the base of the radula sac the radula develops as an intucked "U". Farther forward this is unrolled into a simple "U", the teeth cusps pointing inward. At the tip, in the mouth of the radular sac the transparent radula is flattened to expose the teeth. By comparison (Figure 2) the radula of the grazing marine pulmonate *Siphonaria zelandica* has an extended exposed tip sharply turned over and directed down. The teeth of this turned-over section are worn down in the median and lateral regions especially. The radulae from approximately equal sized *S. zelandica*, *T. reticulatus* and *Gadinalea nivea* (shell length 14 mm, width 11 mm) are shown in Figure 2. The difference in size and shape of the siphonariid and trimusculid radulae are marked. YONGE (1958) reports seeing the radula of *T. reticulatus* being exposed during odontophore extrusion under a low power binocular microscope. However, as the radula is so small, and only exposed momentarily during the rapid eversion strokes, observation is very difficult, although the surface ridging of the proboscis may be seen under binocular low power. In section (Figure 5) the odontophoral ridges are spade shaped, 50-60 μm in length and 40 μm broad whilst the longest radula teeth cusps are only about 13 μm long and 3 μm wide at the base similar to the needle shaped teeth of *G. nivea* (WALSBY *et al.*,

1973). Although the teeth of pulmonate limpets are in all cases small by comparison with those of mesogastropods, these sizes are particularly small. Those of *S. zelandica* for example, have a cusp length of about 30 μm and width 15 μm ; clearly much more robust for abrading the substrate.

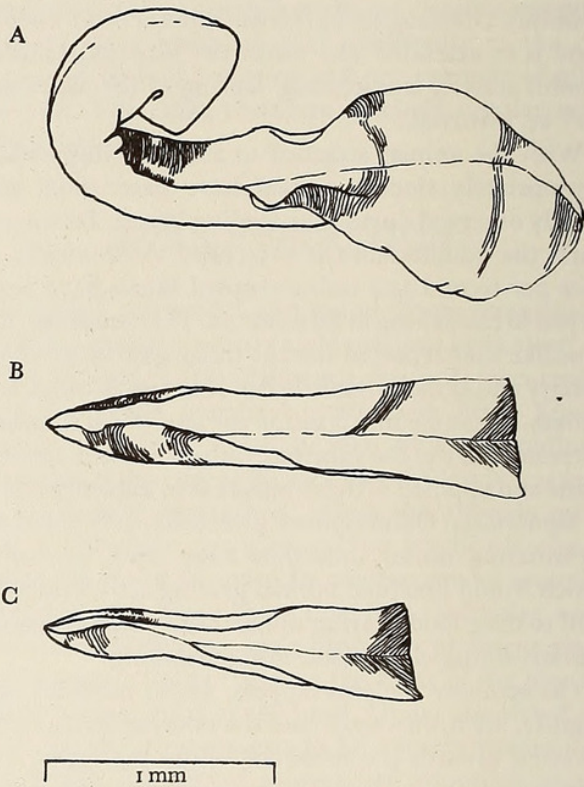


Figure 2

The radulae from equal sized specimens of:

- A. *Siphonaria zelandica* B. *Trimusculus reticulatus*
C. *Gadinalea nivea*

Table 1

Comparison of whole radula of *Siphonaria zelandica*, *Trimusculus reticulatus* and *Gadinalea nivea*. All from animals with approximate shell dimensions 14mm long \times 11mm wide.

	Radula length mm	Radula width mm	Dental formula
<i>Siphonaria zelandica</i>	3.87	0.97	30-1-30 143
<i>Trimusculus reticulatus</i>	2.10	0.71	102-1-102 176
<i>Gadinalea nivea</i>	1.61	0.48	45-1-45 116

Tables 1 and 2 show clear differences of the radula and radula teeth of trimusculids from a siphonariid. Those of the two trimusculids are much less suitable for a feeding habit that involves substrate abrasion and the absence of both the jaw and large internal salivary glands would seem to preclude grazing in the normal way.

The teeth of *Gadinalea nivea* and *Trimusculus reticulatus* are quite similar although the radula of *T. reticulatus* is substantially longer and broader and quite flattened distally. This flattening extends back about $\frac{1}{3}$ the length from the tip and here the teeth may be slightly tainted. Possibly this much is protruded during the feeding stroke. In the resting position however, the radula is contained



Transverse section through the head region of *Trimusculus reticulatus*

- | | |
|--|----------------|
| B. Buccal cavity containing food-bearing mucus | |
| C. Odontophoral cartilage | F. Foot muscle |
| L. Ciliated dorsal lining of buccal cavity | M. Mantle |
| R. Radula on floor of radula sac | |
| S. Ridged surface of odontophore, infolded | |

Table 2

Comparison of the dimensions of the first marginal tooth in *Siphonaria zelandica*, *Trimusculus reticulatus* and *Gadinalea nivea*. All sizes in μm .

	Whole length cusp tip to base edge =	Base length	Base width	Cusp length (unworn)	Cusp width
<i>Siphonaria zelandica</i>	41	32	20	29	8
<i>Trimusculus reticulatus</i>	16	5	6	13	3
<i>Gadinalea nivea</i>	15	8	5	10	3

in the radula sac though its tip may be seen through the opening. In *T. reticulatus* the radula probably plays a bigger role in the drawing in of mucus than in *G. nivea* but in both, the ridged surface of the odontophore appears the most important.

GUT AND FAECAL ANALYSIS

Food taken in has been studied from the consolidated faecal pellets and also from the gut contents. When animals preserved in Bouins are dissolved in 15% NaOH all parts are digested except for the radula and frequently the mid and hind gut contents which remain as a continuous string consisting of mucus and food particles. The majority of the identifiable particles are diatoms. Sponge spicules and odd small ecdysed limbs or limb segments from crustacean larvae are also present. There is no evidence of whole small crustacea being taken in, for example from larvae freshly settled on the substrate. The diatoms in the gut contents studied here have been identified by Dr. F. J. Taylor as mostly attached species. However it appears that these are individuals which have been washed from the rock surface. Those diatoms at the front of the intestine, where little digestion can have occurred, consist of both empty and full frustules indicating that both living and dead diatoms were trapped, and that these were therefore washed-off specimens. Only very small rock particles were ever found and were rare. Radula teeth were also found along the gut string showing that the radula is used actively during feeding. However, more important was the fact that the teeth showed very little wear. By comparison the terminal teeth of *Siphonaria zelandica* showed a reduction in the length of the main cusp from 29 to 19 μm , due to wear. It is therefore clear that the delicate teeth of *Trimusculus reticulatus* scarcely abrade the substrate although they are used to "graze" food bearing mucus from the mantle cavity.

FEEDING RATES

Particle removal experiments were performed in two types of apparatus. One was the same apparatus that was used for *Gadinalea nivea* (WALSBY *et al.*, 1973) and the other, easier to run for long periods, a simple closed circuit recirculation system (Figure 3), in which the sea water of known particle concentration was circulated by means of a small air lift pump having a siphon overflow. This allowed water to be delivered into the animal chamber in small surges simulating wave action. Cultured *Dunelliella salina* was used for the food particles. Figure 4 shows a typical decline in particle concentration. The bars indicate observed periods of odontophore protrusion and withdrawal. After these periods, the samples always showed a reduced particle count. Control experiments showed either little

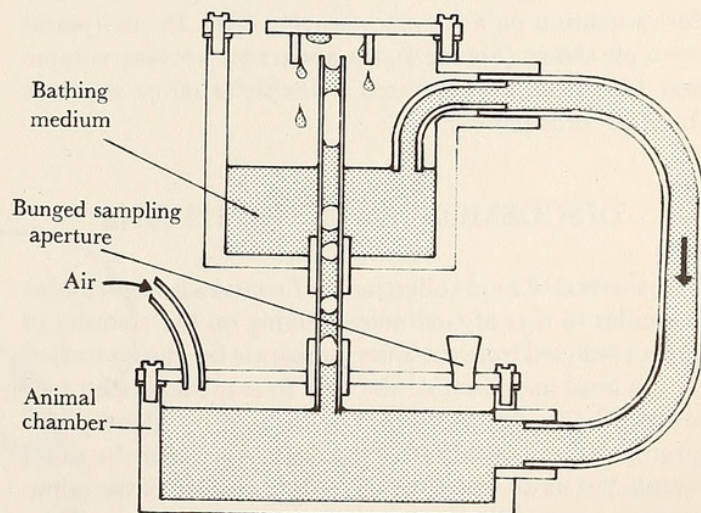


Figure 3

A closed circuit system for circulating a small volume of medium with surging water movements



Walsby, John R. 1975. "FEEDING AND THE RADULA IN THE MARINE PULMONATE LIMPET TRIMUSCULUS-RETICULATUS." *The veliger* 18, 139–145.

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