

Form and Habit in Some Small Gastropods of New Zealand Boulder Beaches

BY

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(10 Text figures)

INTRODUCTION

THE SMALL GASTROPODS living in the deeper layers of boulder beaches form a distinctive ecological grouping. The New Zealand species have parallels in many parts of the world, as on British and North American shores (STEPHENSON & STEPHENSON 1950) and in the tropical Pacific (MORTON & CHALLIS 1969). Especially typical are the mesogastropod families Assimineidae and Caecidae, and the primitive pulmonates of the Ellobiidae. Such snails are generally small and pale, living permanently away from light; though occurring in great local abundance, they are seldom much observed by collectors.

The commonest New Zealand species at the high-tidal margin of boulder beaches are the assimineid *Suterilla neozelanica* (Murdoch, 1899), selected for fullest treatment in this paper, and the ellobiid *Marinula filholi* (Hutton, 1878). On the same shores but typically on the sunwarmed tops of boulders is found the littorinid *Melarhaphe oliveri* (Finlay, 1930), an extremely widespread gastropod of New Zealand shores.

MORTON & MILLER (1968) gave a general account of the boulder beach habitat of New Zealand shores, but the earliest ecological description of boulder beach molluscs is Powell's paper (1933) dealing with the high tidal Mollusca of Rangitoto Island.

¹ ROSEWATER (1970), Indo-Pacific Mollusca 2 (ii) has shown that the name *Littorina (Austrolittorina) unifasciata antipoda* (Philippi, 1847) must be used for what has been known as *Melarhaphe oliveri* Finlay. In view of its wide currency in ecology, the old name is for the present retained here.

ECOLOGICAL NOTES

Beaches of pebbles, flattened stones or wave-rounded boulders form the steeply ramped, semi-mobile shoreline in many localities with greater than average wave-exposure. Good examples are found at Smuggler's Bay, Whangarei Heads, on both coasts of the Coromandel Peninsula, and on offshore islands of the Hauraki Gulf, such as Little Barrier, and Otata, in The Noises Group. Typically the substrate is composed of stones up to a foot or more in diameter, subject to constant shifting by waves, especially at the unstable level of the littoral fringe. Life exposed on the surface is sparse and restricted to few species. The

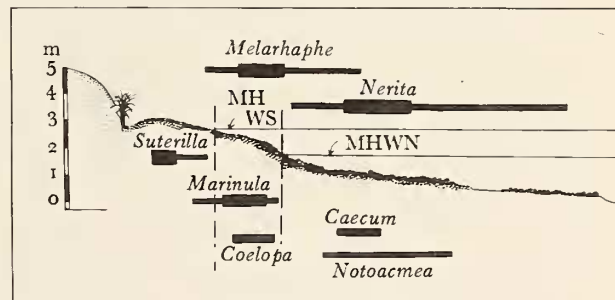


Figure 1

Boulder beach at Smuggler's Bay, Whangarei Heads
Profile of shore showing the ranges and maximum abundance of the gastropods *Suterilla neozelanica*, *Marinula filholi*, *Melarhaphe oliveri*, *Nerita melanotragus*, *Notoacmea daedala* and *Caecum digitulum*. The distribution of the larva of the kelp fly *Coelopa littoralis* is also included

unshaded rocks often bake in the sun for long periods. The effects of surge and wave-splash are largely precluded, because swash cannot sweep far up the shore, but percolates immediately between the boulders. Thus, most of the beach is left dry and bare, with the principal fauna seeking refuge in the deeper layers (Figure 1).

In the eulittoral zone, algae are almost absent; but in the sublittoral fringe crusts of basal *Corallina officinalis*, and films of *Ralfsia verrucosa* and *Hildenbrandtia crouani* form a conspicuous pink and brown zone. At and below the wave-break line of low spring tides, the furoid algae (*Carpophyllum maschalocarpum*, *C. plumosum*, *Cystophora retroflexa* and *Xiphophora chondrophylla minor*, in northern New Zealand) cover the sides and tops of the largest boulders.

In many ways the exposed surfaces of a boulder beach could be compared with a littoral fringe which is extended far down the shore, to mean sea level at least, as a result of the high insolation and the difficulty of retaining surface water. The normal mid-littoral zone, characterised in northern New Zealand by the barnacle *Chamaesiphon columna*, the rock oyster *Crassostrea glomerata* and the tubeworm *Pomatoceros caeruleus*, is thus displaced to lie as a narrow strip just above the algal zone (MORTON & MILLER, 1968). Such a downward regression of the littoral fringe in a boulder beach is the converse of its more obvious upward extension, often for several metres, under the effects of splash and spray on steep rocky shores.

The fauna under stones falls into two sections, characteristic of the littoral fringe and of the eulittoral zone. In the littoral fringe there are two very characteristic elements of mobile species, arthropods and gastropods.

The arthropods are represented by the actively running wingless beach earwig, *Anisolabis littorea*, the oniscoid isopod *Ligia novaezelandiae* and the small, swift grapsid crabs, *Cyclograpsus lavauxi* and *C. insularum* (BACON, 1971). A little lower down, but still out of the water for most of the tidal period, is the jumping shrimp *Betaeus aequimanus*.

The two characteristic gastropods of the littoral fringe are *Suterilla neozelanica*, with its maximum at the spring tide drift-line, and *Marinula filholi* commonest at the neap drift-line, especially where decaying algal wrack forms a thick, viscid layer between the boulders. The top-shell *Zediloma digna* Finlay, 1927 is occasionally found in the same habitat though commoner in southern New Zealand (see Figure 1 b).

In the eulittoral zone, the fauna under the larger boulders includes several sessile filter-feeders, all with prolonged emersion between tides: the light-avoiding bar-

nacle *Tetraclita purpurascens*; the tubeworms *Spirorbis* species, *Hydroides norvegicus* and *Pomatoceros caeruleus*, as well as small rock oysters *Crassostrea glomerata*. Very large and stable boulders harbour the stalked barnacle *Mitella spinosa* and the pulmonate limpet *Gadinalea nivea* (Hutton, 1878). A constant member of the same under-boulder community is the deep-red shade anemone *Isactinia tenebrosa*. The crabs of the eulittoral form a characteristic series. The larger purple to black *Leptograpsus variegatus* is active here, and smaller specimens may overlap with *Cyclograpsus* higher up. The fast-scuttling half-crab *Petrolisthes elongatus* is very common, and there are two slow xanthid crabs, *Heterozius rotundifrons* and *Ozius truncatus*.

The chief gastropods found under stones in the eulittoral zone are herbivores which may emerge to graze from the sides and tops of stones at night or at high tide. They include the top-shells *Zediloma atrovirens* (Philippi, 1851) (sometimes accompanied by *Z. arida* (Finlay, 1927) and *Z. digna*), and *Anisodiloma lugubris* auct. Very characteristic of under-surfaces are two small, thin-shelled limpets, *Notoacmea daedala* (Suter, 1907) and *Atalacmea fragilis* (Sowerby, 1823). Barker (unpublished results 1969) has made a careful study of this group of gastropods in the Leigh area, North Auckland. He determined the extent of their feeding migrations, and estimated by pigment determinations the resources of available algal food on the seemingly bare rock surfaces.

Two minute gastropods have a permanent habitat under stones in the eulittoral zone, feeding from diatoms and plant debris in the water film, the rissoid-like *Dardanula olivacea* (Hutton, 1878) and the tusk-shell *Caecum digitulum* Hedley, 1904.

The ecological factors controlling the distribution of these communities would appear to be high humidity, and permanently low levels of light and temperature. The same faunas can thus be found not only in boulder beaches, but on the open surface of the walls of eulittoral caves with a periodically high wave action. A striking similarity is apparent between dark cave walls and boulder beach habitats. Sessile species common to both include the barnacles *Tetraclita purpurascens* and *Mitella spinosa*, and the anemone *Isactinia tenebrosa*. The pulmonate limpet *Gadinalea nivea* and the patelloid *Notoacmea daedala*, as well as the boulder beach crab *Leptograpsus variegatus* are also found on cave walls. In total darkness at the extremity of the cave, *Marinula filholi* and the larva of the kelp-fly *Coelopa littoralis* crawl about on the open walls. *Ligia novaezelandiae* is everywhere abundant here.

THE SMALL GASTROPODS

Occurrence and Mode of Life

(a) Assimineidae

There are two New Zealand representatives of this small high-tidal family placed by THIELE (1931) in the super-family Rissoacea of the order Mesogastropoda. One, *Assiminea vulgaris* (Webster, 1905), is not studied in detail here, but POWELL (1933) has described its ecology, as an inhabitant of the *Salicornia* salt meadow zone at Rangitoto Island. It is generally confined to coasts of greater shelter than mobile boulder shores, being rather constantly found with the upper shore ellobiid *Ophicardelus costellaris* (H. & A. Adams, 1854). Such an association may be compared with the British assimineid-ellobiid species pair, which are *Assiminea grayana* (Leach in Fleming, 1828) and *Ovatella myosotis* (Draparnaud, 1801), found in a closely similar habitat, with the salt-meadow succulent *Obione portulacoides* (MORTON & MACHIN, 1959).

The second New Zealand assimineid, *Suterilla neozelanica*, was also found by Powell at Rangitoto, but is more typical of exposed boulder beaches. It occupies a very narrow belt, at the upper edge of the littoral fringe, generally in the highest tier of boulders, where it is restricted to the damp surfaces of stones deep enough for a constant low temperature and saturated atmosphere. On stones 15 to 30 cm down, with a permanent water film, *Suterilla* is abundant, having its greatest density at about the level of the high water table. Unlike the periwinkle, *Melarhappe oliveri*, this snail is not adapted to intermittent dryness and desiccation. In normal daylight it soon ceases to crawl about. Immersed in water it keeps the operculum tightly sealed, remaining completely inactive in either light or dark, though it clearly tolerates short periods of submersion by normal high tides. Though an air-breather, it shows little capacity for full terrestrial life, maintaining its high shore level by restriction to the narrow confines of darkness, low and uniform temperature and high humidity.

Little wave-borne marine detritus appears to lodge at this level; but the finer debris of sub-littoral plants may wash down, to cover the boulders with a thin nutritive film. By contrast with the ellobiid snail *Marinula filholi*, at the next level down the shore, *Suterilla neozelanica* avoids the richest areas of decaying algal wrack; it appears to be a discriminating browser. The radula is kept constantly at work, sampling from the water-filmed surface as the snout forages forward in front of the foot. *Suterilla* is a virtually continuous feeder, taking in the finest com-

minuted particles. Its diet and its radula contrast strongly with those of the deposit feeders *Melarhappe* and *Marinula* (see later).

Suterilla neozelanica is strongly negatively phototactic. The exposed parts are translucent white, and the pale, horn-coloured shell offers little protection from light. The light avoidance reaction predominates over the negative geotaxis generally present in small upper shore snails. Both components are found in the orienting behaviour of the *Melarhappe* periwinkles (see the classic study by FRAENKEL (1927) of the European *M. neritoides* (Linnaeus, 1758)).

(b) Littorinidae

The small high tidal periwinkle *Melarhappe oliveri* is frequently found on the sun-warmed upper surfaces of stones and boulders, and avoids only the most mobile of boulder beaches. In its ecology and adaptations it contrasts strongly with *Suterilla*. It is a robustly built snail, subsisting upon the thin surface films of the black lichen *Verrucaria maura*, or on wave-lodged deposits, including diatoms, accumulating in small crevices at a high shore level. *Melarhappe* is highly tolerant of exposed, apparently inhospitable rock surfaces. Its upper limit is set by the requirement of regular wave-splash or spray. Those *Melarhappe* species whose breeding biology is known depend on the liberation of free-swimming veliger larvae, effectively limiting their spread as possible land colonists (for reproduction of littorinids, see FRETTER & GRAHAM, 1963). The spawning and larvae of the New Zealand species, *M. oliveri* and *M. cincta* (Quoy & Gaimard, 1833) have been described by PILKINGTON (1971). Foster (unpublished results) has made a detailed study of the orienting and zone maintenance of *M. oliveri*.

Most closely related to the littorinids and resembling them in its feeding habits is the small high-tidal snail *Rissellopsis varia* (Hutton, 1873) which is found clustering in pits and concavities on the surfaces of large, stable boulders.

(c) Ellobiidae

In these primitive pulmonate snails, the mantle cavity always remains air-filled during tidal immersion. They fall ecologically into two classes: dull, brown pigmented forms such as *Ophicardelus* and *Ovatella* species, living in salt meadows, and the smaller, pale or colourless species, represented in New Zealand by *Marinula filholi*, *Rangitotoa insularis* Powell, 1933 and *Leuconopsis obsoleta* Hutton, 1878, that have retreated to a permanently

deep habitat in rock crevices or between intertidal boulders (MORTON, 1955 b).

Marinula filholi lives on New Zealand boulder shores at the next level below *Suterilla*, generally at or around HWN. It may slightly overlap with *Suterilla* but soon altogether replaces it. The shell is larger and stronger than that of *Suterilla*, and pinkish brown or buff. The exposed parts of the animal are translucent and unpigmented. *Marinula* feeds on the rich deposits of decaying brown algae at the drift line of high neap tides. Such material forms a thick, viscous covering beneath boulders, sometimes filling all the interspaces between them. Throughout this layer, *Marinula* abounds, raking up large amounts of the soft food with the radula. The digestive system (see later) is typically that of an unselective deposit feeder.

On sheltered shores, as at Rangitoto Island, with stable boulders buried in mud, *Marinula* is found with the two minute, pale ellobiids *Leuconopsis obsoleta* Hutton, 1878 and *Rangitotoa insularis* Powell, 1933, never recorded from mobile boulder beaches. Both species were found by POWELL (1933) to be organic deposit feeders, occurring sporadically in large numbers on the under-sides of stones that are in contact with the mud.

The different niches occupied by the small gastropods in relation to boulder surfaces and shell gravel are summed up in Figure 2. The habitats include both mobile boulders of a wave-washed ramp, and the pitted basalt blocks lying upon organic mud on sheltered shores, as at Rangitoto (POWELL, 1933).

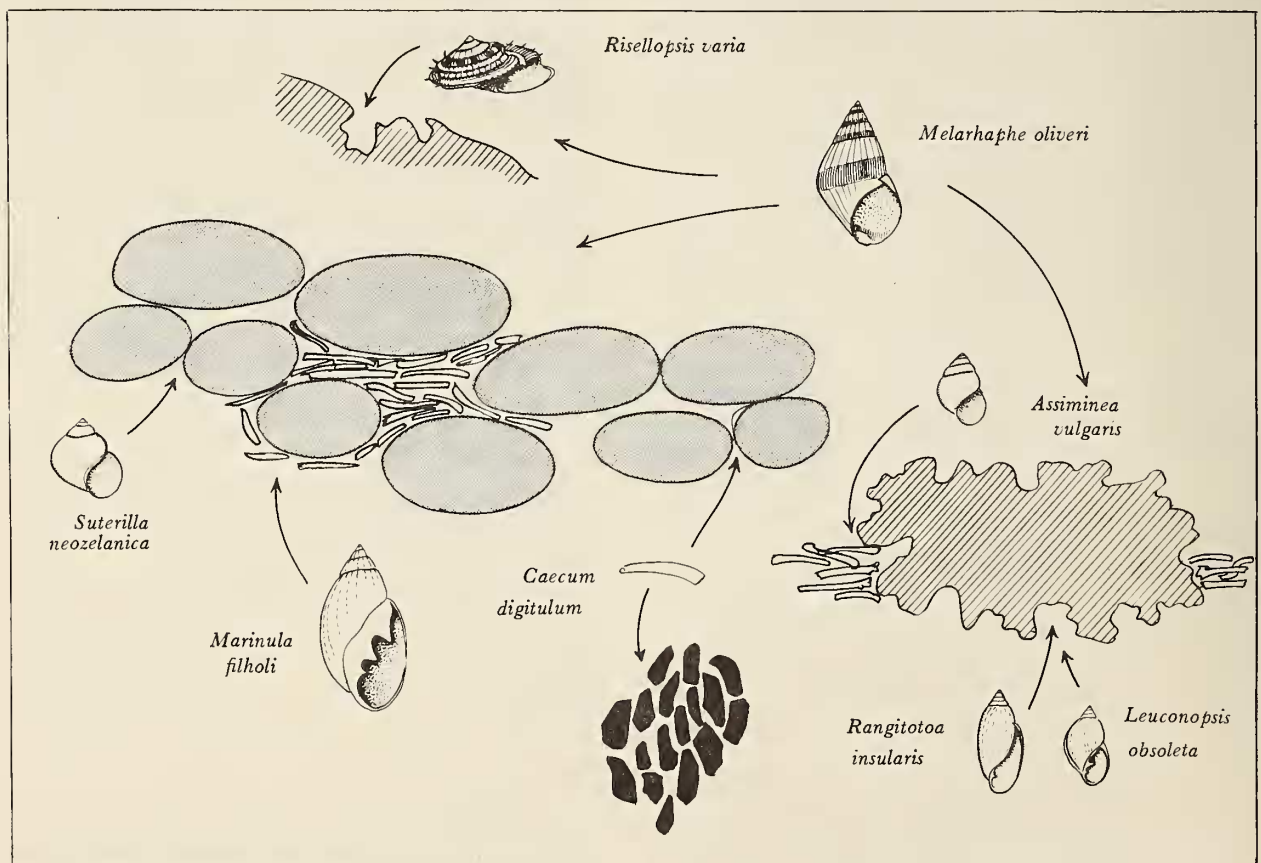


Figure 2

The ecological distribution of the small gastropods of high tidal boulder beaches. Among smooth, mobile boulders are *Suterilla neozelanica*; *Marinula filholi* (especially where decaying algal wrack is mingled with the boulders); and *Caecum digitulum* (also found interstitially in clean, coarse sand — inset).

Melarhaphé oliveri lives on sun-warmed upper surfaces and *Rissellopsis varia* in pits and concavities of stable boulders. On stable, irregular boulders situated in sediments, with algal wrack, are *Assimineæ vulgaris* (also found in *Salicornia* salt meadows), *Leuconopsis obsoleta* and *Rangitotoa insularis*

Comparable habitats in the boulder-strewn littoral fringe have closely similar faunules in many parts of the world. In the "grey zone" of the Florida Keys, STEPHENSON & STEPHENSON (1950) mention three ellobiid species (two *Melampus* and a *Detracia*) as well as two species of the hydrobiid genus *Truncatella*. A reef recently studied by the writer (unpublished) near Waikamilo on Kauai Island, Hawaii, presented a strong parallel to the New Zealand pattern. Loose boulders lying on top of moist sand had *Littorina pintado* (Wood, 1828) and *Nerita picea* Récluz, 1841 on the pitted, sun-warmed surface. Underneath, in moist depressions occurred an *Assimineae* species and the following small, deposit-feeding ellobiids: species of *Plectotrema*, *Laimodonta* sp., *Melampus castaneus* (Mühlfeldt, 1818), *M. semiplicatus* (Pease, 1860) and *Pedipes sandwicensis* Pease, 1860.

(d) Caecidae

The minute, tusk-shaped mesogastropod *Caecum digitulum* has a restricted range on boulder beaches. It is never air-breathing, being found lower on the shore than *Suterilla* and *Marinula*, on the under-surfaces of clean, smooth boulders at about MTL. It may be found under "papa" mud-stone slabs at Hobson Bay, Auckland Harbour. It also occurs on mobile boulder beaches of open shores, as well as under loose boulder cover at Goat Island Bay, near Leigh, and at Taurikura Bay, Whangarei Heads. *Caecum digitulum* may also be found (D. A. Challis—personal communication) in the water-filled interstitial spaces of coarse shell sand, near mid-tide mark. Its minute size gives it an adaptive versatility wherever a permanent water film is present.

The mantle cavity of *Caecum digitulum* is filled with water and the animal (unlike *Suterilla*) is small enough to renew this from the water film left on the rock surface between tides. *Caecum digitulum* is no more than 2.5 mm long and 0.5 mm in maximum diameter, simplified in shape and ideally adapted for life on smooth boulder surfaces. By its small size, *C. digitulum* can apparently remain active and fully mobile between tides so long as the rock surface is wet. When the animal is extended from the shell, the convex side of the tube is held uppermost. The water film is sufficient to maintain it against the surface and still permit traction by the sole of the foot. The arch of the shell retains water beneath, allowing a current to and from the mantle cavity. The slender proboscis is extended with the mouth against the substratum, gleaning diatoms and other particles. When the animal is withdrawn and the operculum closed, the shell lies on its side, held to the rock by surface tension.

FORM AND FUNCTION

A detailed account is given of *Suterilla neozelanica*, which belongs to a family anatomically little known. Comparative notes are given for other species, especially for the organs of feeding and digestion.

(a) *Suterilla neozelanica*

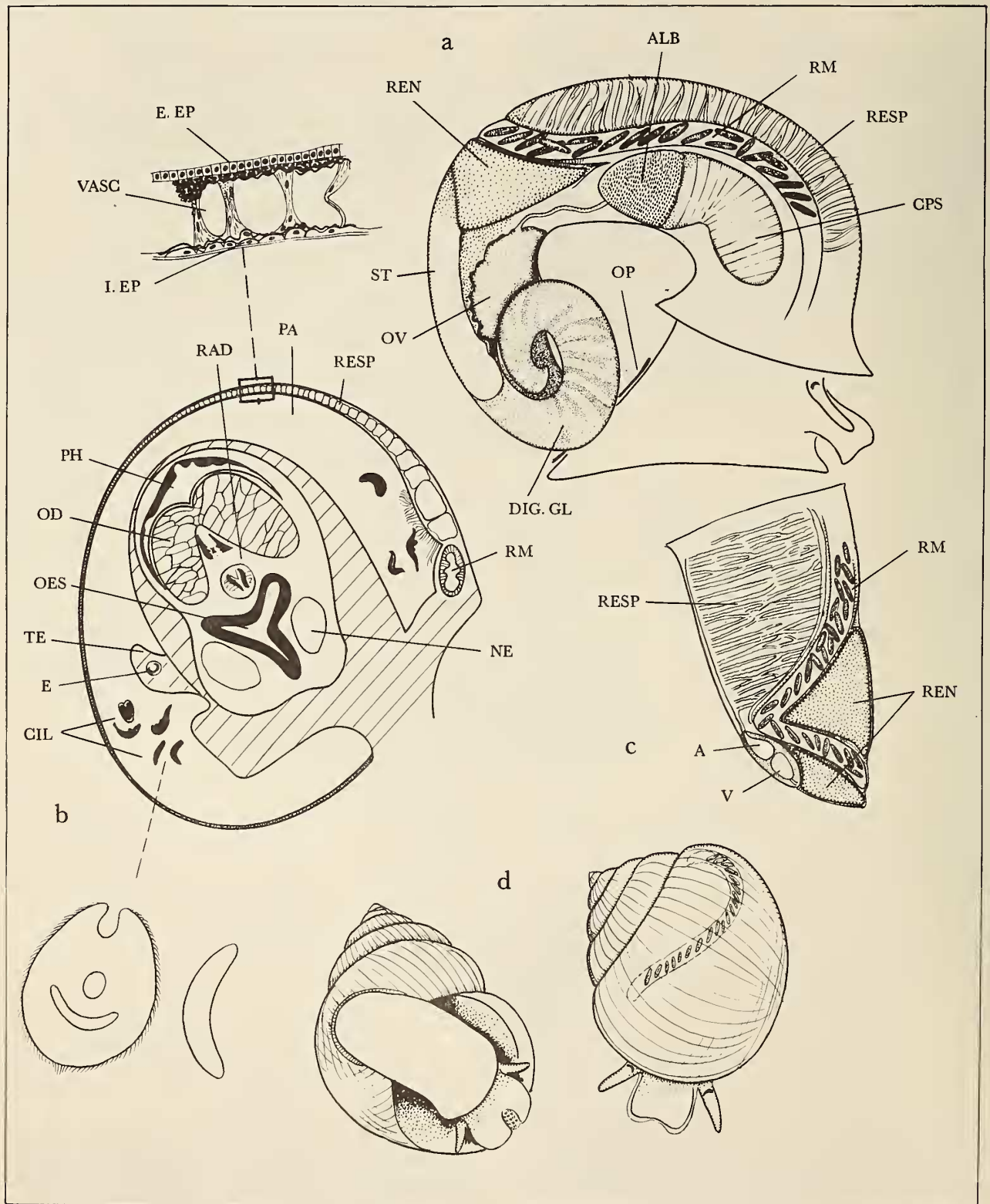
The general arrangement of the pallial organs is illustrated in Figure 3. The pallial cavity of *Suterilla* is air-filled and has lost the ctenidium; but there is no specialised 'lung' as found in pulmonate snails. The cavity opens freely to the exterior all round its margin, being temporarily closed by pressing the pallial skirt against the body wall. With no water circulation, pallial cilia are of reduced importance and the hypobranchial gland is absent. In place of the ctenidium a series of fine, parallel or anastomosing blood vessels runs across the mantle roof from right to left. The respiratory surface has a thin, non-ciliated epithelium with vascular spaces beneath it. Occasional clusters of mucous cells discharge into the pallial cavity.

The mantle roof is traversed by the intestine, embayed by the renal organ on the left. The female genital duct lies on the right. The anus is placed far forward and compact, cigar-shaped faecal pellets are discharged clear of the pallial cavity. The renal organ has the typical prosobranch form, with no distinct ureter as in pulmonates. The renal pore lies far back on the right side, and a ciliated furrow runs forward from it.

A notable feature of the mantle cavity is the presence of small saucer-shaped ciliates of an undescribed species congregating numerously in the water film covering the wall. They possibly serve as scavengers of waste particles that would normally be removed by cilia. In their account of the marine pyramidellid *Odostomia* (also gill-less) FRETTER & GRAHAM (1949) remark upon the great attraction to ciliates presented by the respiratory and excretory areas of the mantle wall. In *Odostomia*, amoeboid excretory cells pass with their contents into the mantle cavity.

"Wherever one of these cells is found in a pallial blood space or making its ways through the epithelium of the mantle, there will always be found at least one ciliate hovering directly over it, presumably for the sake of ingesting the material which the cells are about to empty into the mantle cavity."

Though *Suterilla* relies, so far as could be determined, on normal renal excretion, ciliate scavengers may have assumed an auxiliary role in the absence of water-borne removal of waste.



The alimentary canal of *Suterilla* has most of the features typical of microphagous style-bearing mesogastropods. The spherical buccal mass fills the snout and showing through by its pink colour. On its roof lies a pair of mucus-secreting salivary glands with short ducts. The radula sac is short and recurved, with a bulbous tip, where the ribbon and its attached teeth are secreted. The teeth (see Figure 6 c) are very distinctive, forming delicate instruments not for abrading but for raking up particles. Each transverse row is widened by the special development of the outer marginals. The central tooth is a transverse rectangle with a row of small, blunt cusps. The laterals are stout and falcate, strongly erectile so as to converge towards the centre. The marginal teeth are finely fashioned. The first, next to the lateral, has a crescentic border with sharp, slender cusps, about 9 in number. The second is broad and somewhat fan-shaped, with about 16 small, blunt cusps. These are formed by the hooked tips, slender rod-like components, fused to form a single compound tooth-plate. The outermost cusp is broader and somewhat splayed; it is separately illustrated in Figure 6 c. The form of the second marginal is reminiscent of the condition in the rhipidoglossan radula where numerous separate marginals are used with a brush-like action to sweep a wide surface. The appearance of the radula was probably responsible for the former placement of *Suterilla neozelanica*, as *Cirsonella neozelanica*, in the Cyclostrematidae among the Rhipidoglossa (see SUTER, 1907). Similar first

and second marginal teeth are illustrated by POWELL (1933) for *Assimineea vulgaris* (see Figure 6 d).

The oesophagus is a simple tube with a pair of strongly ciliated dorsolateral folds, twisted to the left at the site of torsion. Mucous and ciliated cells are abundant, but there is no trace of the oesophageal pouches found in primitive mesogastropods, including the Littorinidae.

The stomach is a short triangular sac pointed behind and embedded on either side in the digestive gland. It is prolonged in front into a thimble-shaped style sac, having a common lumen with the first part of the intestine which separates from it just behind the apex. The interior of the

(← on facing page)

Figure 3

Suterilla neozelanica

- (a) animal removed from shell, seen from the right side;
 (b) transverse section of the head and pallial cavity with (inset above) pallial epithelium, with blood vascular spaces, and (inset below) ciliate protozoans from the pallial cavity in surface and edge view;
 (c) surface view of roof of the pallial cavity showing extent of respiratory space in relation to rectum and renal organ;
 (d) animal in the shell from below (left) and above (right).

A - auricle ALB - albumen gland

CIL - symbiotic ciliates in mantle cavity CPS - capsule gland

DIG. GL - digestive gland E - eye

E. EP - external epithelium of mantle

I. EP - internal epithelium of mantle

NE - pleural ganglia of nerve ring OD - odontophore

OES - oesophagus OP - operculum OV - ovary

PA - pallial cavity PH - pharynx (lumen)

RAD - radula sac REN - renal organ

RESP - respiratory area RM - rectum ST - stomach

TE - cephalic tentacle V - ventricle

VASC - vascular channel of respiratory area

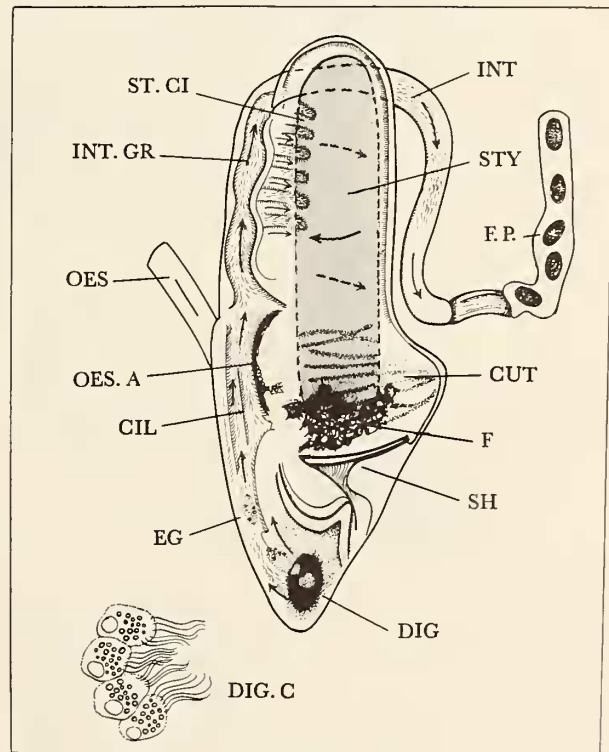


Figure 4

Suterilla neozelanica

interior of the stomach as seen by transparency, with the course of the ciliary currents arrowed, and the position of the crystalline style shown in broken outline — (inset) long-ciliated cells of the digestive diverticula

CIL - ciliary folds CUT - cuticle

DIG - digestive diverticulum DIG. C - digestive gland cells

EG - egesta from digestive gland F - food mass

F. P. - faecal pellet INT - intestine

INT. GR - intestinal groove OES - oesophagus

OES. A - oesophageal aperture SH - gastric shield

STY - style ST. CI - style sac cilia

stomach, as depicted in Figure 4, is occupied in life by a delicate, crystalline style, hyaline and semifluid, lasting only a short time after the removal of the animal from its feeding site. The style head rotates against a thick sheet of cuticle projecting on the right side of the stomach to form an anvil-shaped gastric shield. The oesophagus enters the stomach to the left of the shield.

The stomach contains an assortment of fine particles with diatom frustules often prominent. The single aperture of the digestive gland leads from the stomach apex, well behind the gastric shield. A ciliated channel runs forward from it on the left side, bringing rejected particles or excreta from the digestive gland to the intestinal groove. Transverse ciliary currents round the confluence of the stomach and style sac converge on the intestine.

The intestine bends to the right beneath the style sac, being lined by two ridges with strong ciliary currents beating towards the anus. Here the cigar-shaped faecal pellets are constructed, being moulded and nipped off by strong peristaltic contractions. They are rotated and given a final mucus coat by ciliary action. The rectum widens as it runs along the mantle and contains one or sometimes two obliquely stacked rows of pellets.

The digestive gland is unusual for the regular arrangement of its tubules, which are long and unbranched, and set parallel so as to encircle the visceral mass. Macerations of living gland cells reveal active cilia, rather longer than the cells, reaching right across the lumen. Their beat assists the flow of particles in and out of the diverticula.

REPRODUCTIVE SYSTEM

The egg masses of *Suterilla neozelanica* are still unknown, but the morphology of the female genital system would indicate that the eggs, as in related mesogastropods, are laid together, within a common mucilaginous spawn mass. The female duct lies on the right wall of the mantle cavity below the rectum, its pallial part representing a tubular infolding of a glandular tract of the mantle wall. Posteriorly the narrow ovarian duct leads from the ovary, an irregular yellowish patch on the surface of the digestive gland. (see Figure 3 a)

The pallial genital duct has two parts. The short albumen gland is translucent and hemispherical, continuing at its straight side into a longer, opaque capsule gland (Figure 5c, d). This gland opens into the mantle cavity at its rounded anterior end. There is no special jelly gland, distal to the capsule gland, as in some littorinids. A separate sperm storage sac is also lacking, spermatozoa being temporarily attached by their heads within the lumen of the albumen gland.

The male genital system (Figures 5 a, 5 b) is simpler than the female. The testis is a cluster of white lobules attached to the digestive gland. Sperm are conducted forward by a convoluted vas deferens, running beneath the pallial floor to the base of the penis. This is a muscular appendage, L-shaped and laterally compressed, attached behind the head and reflected back within the mantle cavity. The vas deferens traverses the penis to the tip, and the penial integument carries two tracts of mucous gland cells.

(b) *Melarhaphé oliveri*

Though classed in broad terms like *Suterilla* as a microphagous herbivore, *Melarhaphé oliveri* has a wholly different feeding niche, and a distinctive morphology of the gut. The periwinkles of the littoral fringe probably experience the hardest regime of any intertidal gastropods. They are very intermittent feeders, and they may remain dry and sealed by the operculum for long periods at a time. The rock surface is scraped by the radula for maritime lichens or inconspicuous blue-green algae. The wave-lodged detritus accumulating in moister crevices must also be an important food source.

The surface-abrading habit is reflected in the length and robustness of the radula, contrasting strongly with that of *Suterilla*. The teeth are massive and heavily cusped (see Figure 6 a), lacking any sharp, or finely pointed denticles. With constant abrasion of the rock surface, the teeth are evidently rapidly expended and replaced. The radula sac is extremely long, forming a double-coiled spiral, equalled in relative length only by that of a patellid limpet.

Among herbivorous mesogastropods, the broad evolutionary trends in the gut have been

- (a) The reduction of the radula to a narrow ribbon of only seven rows of teeth,
- (b) the shortening of its length as compared with that of archaeogastropods,
- (c) the reduction of the salivary glands,
- (d) the simplification of the oesophagus with its loss of glandular pouches, and
- (e) the increased emphasis on the style sac, gastric shield and sorting area.

The littorines are primitive in having achieved only the first of these features. The stomach is a spacious sac with a long extension behind the entry of the oesophagus, serving as a storage chamber for coarse, intermittently ingested food. FRETTER & GRAHAM (1962) have well described the stomach of the larger *Littorina littorea*, (Linnaeus, 1758), and a briefer account for *Melarhaphé oliveri*

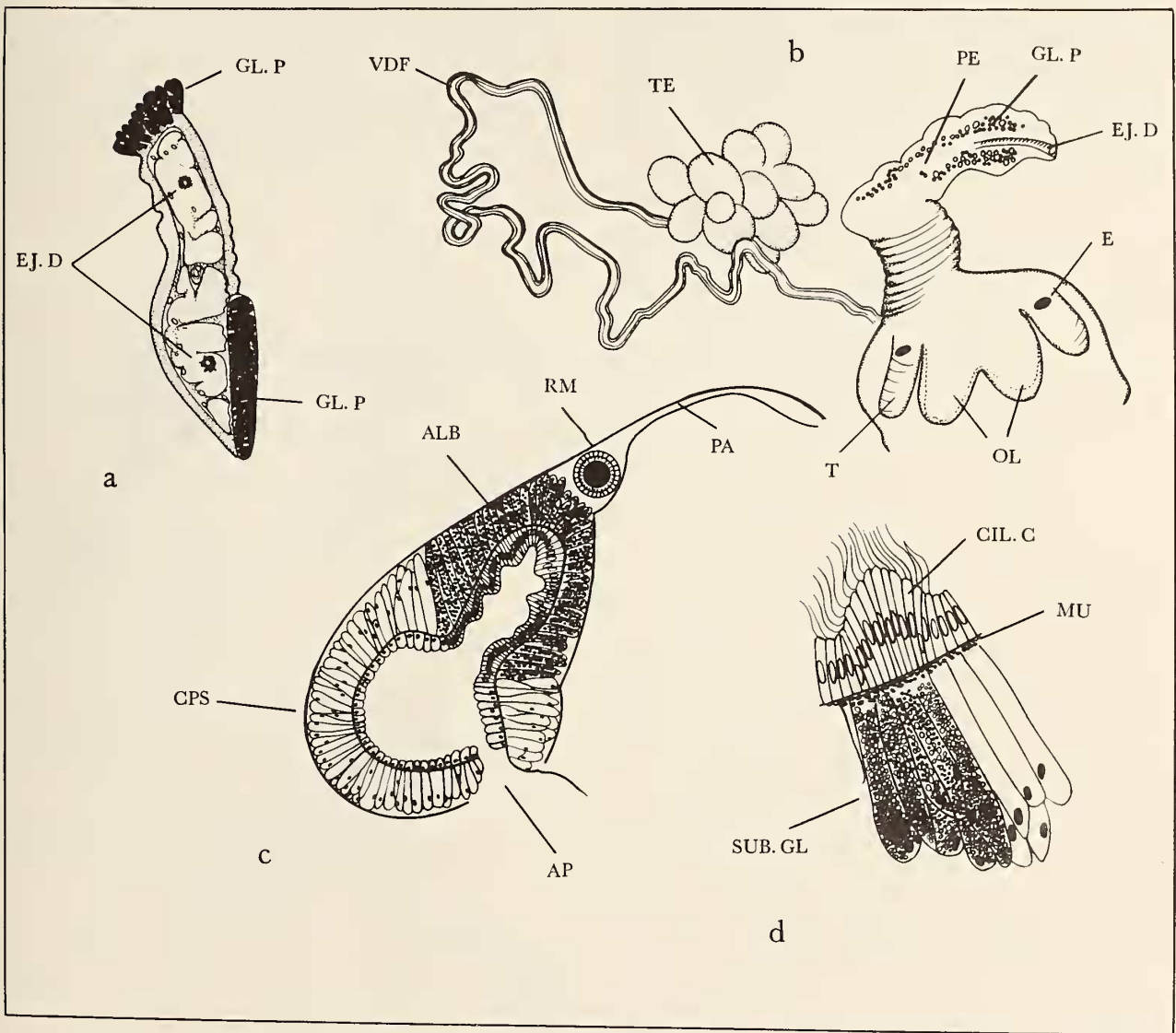


Figure 5

Suterilla neozelanica

- (a) the distal part of the penis in oblique section, ejaculatory duct sectioned twice;
- (b) the male genital system, showing the unraveled vas deferens and the penis in relation to the head;
- (c) transverse section of the female genital duct and rectum, slightly oblique to show the communication of albumen and capsule gland;
- (d) detailed histology of the capsule gland.

ALB - albumen gland	CIL. C - ciliated cells
AP - ventral aperture of capsule gland to mantle cavity	E - eye
CPS - capsule gland	EJ. D - ejaculatory duct
GL. P - epithelial glands of penis	OL - oral lappets
MU - muscle fibres investing gland cell layer	
PA - mantle wall	PE - penis
SUB. GL - subepithelial gland cells	RM - rectum
	T - tentacle
	TE - testis
	VDF - vas deferens

will here suffice. (Figure 7 b) There is no crystalline style, though the first part of the intestine is the structural equivalent of the style sac. Its cilia rotate a cord of mucus-compacted food and debris that extends back into the rest of the stomach. The stomach lining has only three weakly

ciliated tracts. A broad ridge carrying a ciliary current leads back from the oesophagus around the fundus, and returns forward on the right, served by feeble tributary ridges. On the ventral wall, a wider ciliated tract runs forward to the intestine. The gastric shield is hardly dis-

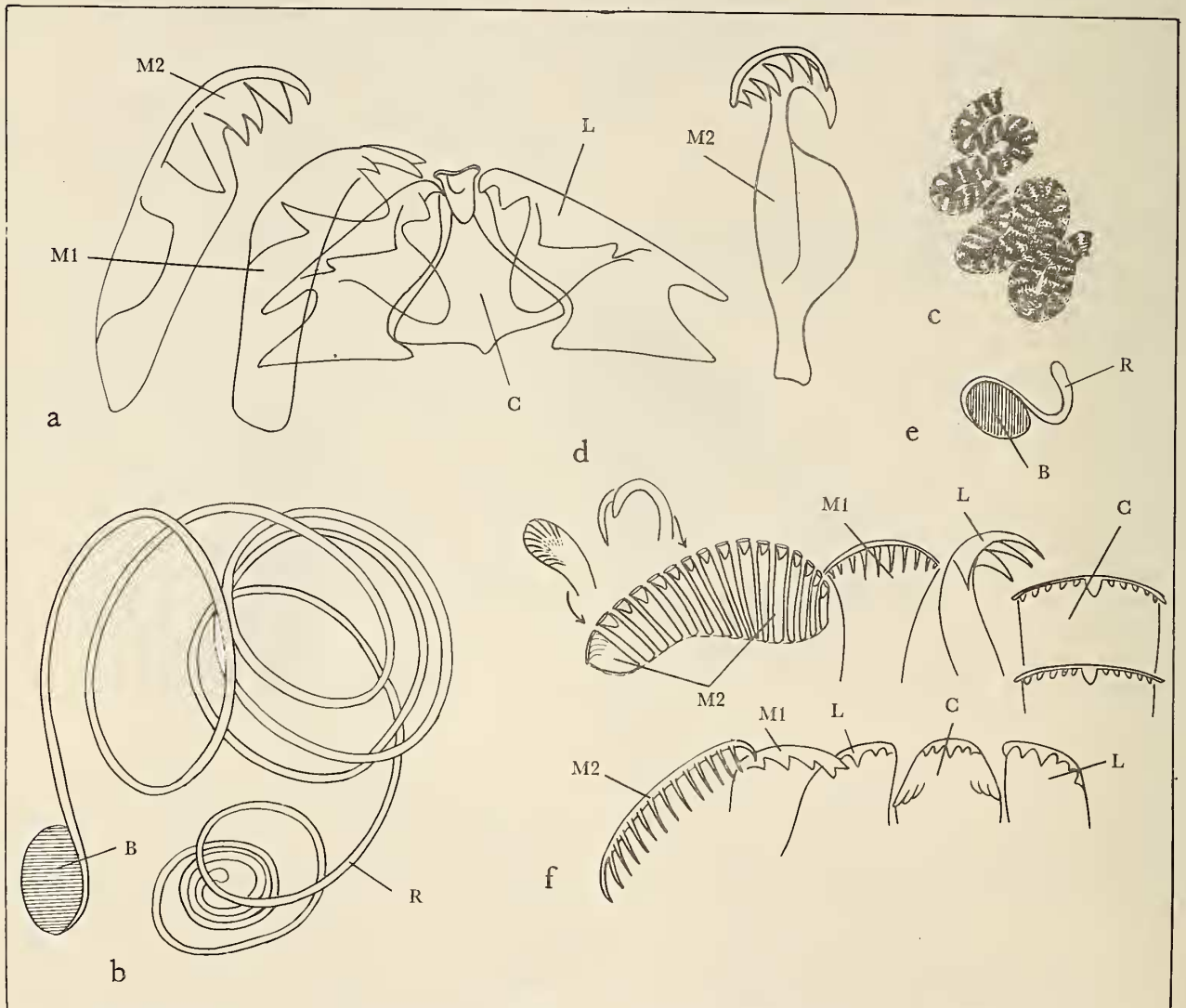


Figure 6

- (a) teeth of radula of *Melarhaphé oliveri*; an outer marginal tooth is separately shown, reflected to show mesial aspect;
 - (b) relative proportions of radula and buccal mass of *Melarhaphé oliveri*;
 - (c) portion of meandering grazing trail of *Melarhaphé oliveri*;
 - (d) teeth of radula of *Suterilla neozelanica*;
 - (e) relative proportion of radula and buccal mass of *Suterilla neozelanica*;
 - (f) teeth of radula of *Assiminea vulgaris* (from POWELL, 1933).
- B - buccal mass C - central L - lateral
 M1, M2 - first and second marginal teeth R - radular caecum

tinct from the surrounding cuticle. The openings of the digestive gland lie near the junction of the stomach with the style sac. The wall of the stomach is muscular and freely contractile; the large bulk of food evidently undergoes efficient extraction without ciliary sorting. Digestion evidently begins with the admixture of enzymes from the oesophageal pouches.

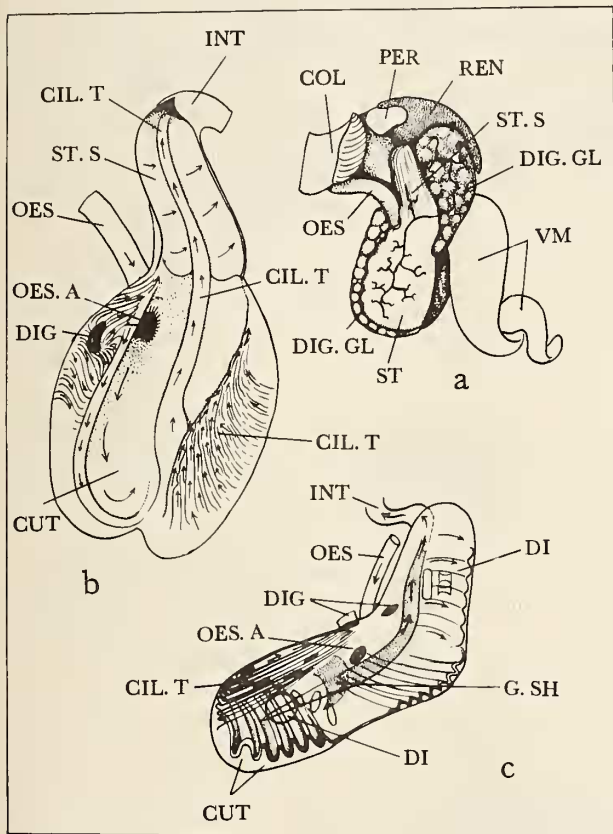


Figure 7

The stomach of Littorinacea

- (a) *Melarhappe oliveri*, interior of the stomach, showing the course of the ciliary currents;
 (b) *Melarhappe oliveri*, external view of the stomach and visceral mass;
 (c) *Rissellopsis varia*, the stomach as seen by transparency, for comparison with *Melarhappe*.
- CIL. T - ciliary tract COL - columellar muscle
 CUT - cuticle DI - diatom within stomach
 DIG - apertures of digestive gland DIG. GL - digestive gland
 G. SH - gastric shield INT - intestine OES - oesophagus
 OES. A - oesophageal opening PER - pericardium
 REN - renal organ ST - stomach VM - visceral mass
 ST. S - first part of intestine, corresponding with style sac

Rissellopsis varia, also a member of the Littorinacea, is our only New Zealand example of the family Bembiciidae, a group more numerous represented in Australia. *Rissellopsis* is a minute snail, normally lodging within the crevices or empty barnacle shells in the upper or middle eulittoral zone (MORTON & MILLER 1968). Like *Melarhappe*, this species is an intermittent feeder, but experiences a longer tidal immersion; its small size gives it access to a richer diet, largely of wave-lodged diatoms collecting in the recesses that can be scoured with the radula. The stomach of *R. varia* is illustrated in Figure 7 c, for comparison with *Melarhappe*. It can be seen that ingested diatom frustules are rather large objects in relation to the size of the stomach. The gut resembles that of *Melarhappe* not only in the stomach structure but in the retention of oesophageal pouches, and in the long, many-coiled, radular sac.

(c) *Caecum digitulum*

In its diet and digestive system, this minute mesogastropod is somewhat like *Suterilla*, having a well-defined style sac with a delicate semifluid crystalline style. Food is secured by continuously gleaning individual particles from the surface of the rock even when the tide is out. In relation to the size of the buccal mass, even a diatom 50 μm long is a large object, separately picked up with the radula and carried along the oesophagus by peristalsis.

The radula (Figure 8 b) is short and delicate, with about 13 transverse rows. The central tooth has a semicircle of minute denticles and the lateral is also lightly denticulate. The marginal teeth are long and slender, with claw-like terminal cusps, themselves with minute denticles. Their function is evidently to seize whole diatoms or particles of similar size as the proboscis explores the ground ahead of the advancing foot.

The narrow oesophagus has neither pouches nor any other distinctive features. The stomach is small and triangular, with a thimble-shaped style sac, the whole fitting into a notch in the single lobe of the digestive gland. (Figure 8a). Strong cilia rotate the crystalline style, which has a mass of food particles agglutinated to its head. The dimensions of the food are too large in relation to stomach size for ciliary sorting to be effective. Food appears to be digested extra-cellularly by the enzymes secreted from the digestive gland cells. The intestine which forms a double loop on the mantle wall, has a strong ciliary beat throughout. A single diatom strongly distends the lumen and is not built into a faecal pellet. Pellets are formed however from the outflow of waste from the digestive gland and from finely comminuted food remains; these are nipped off separately from the faecal cord by peristalsis, and

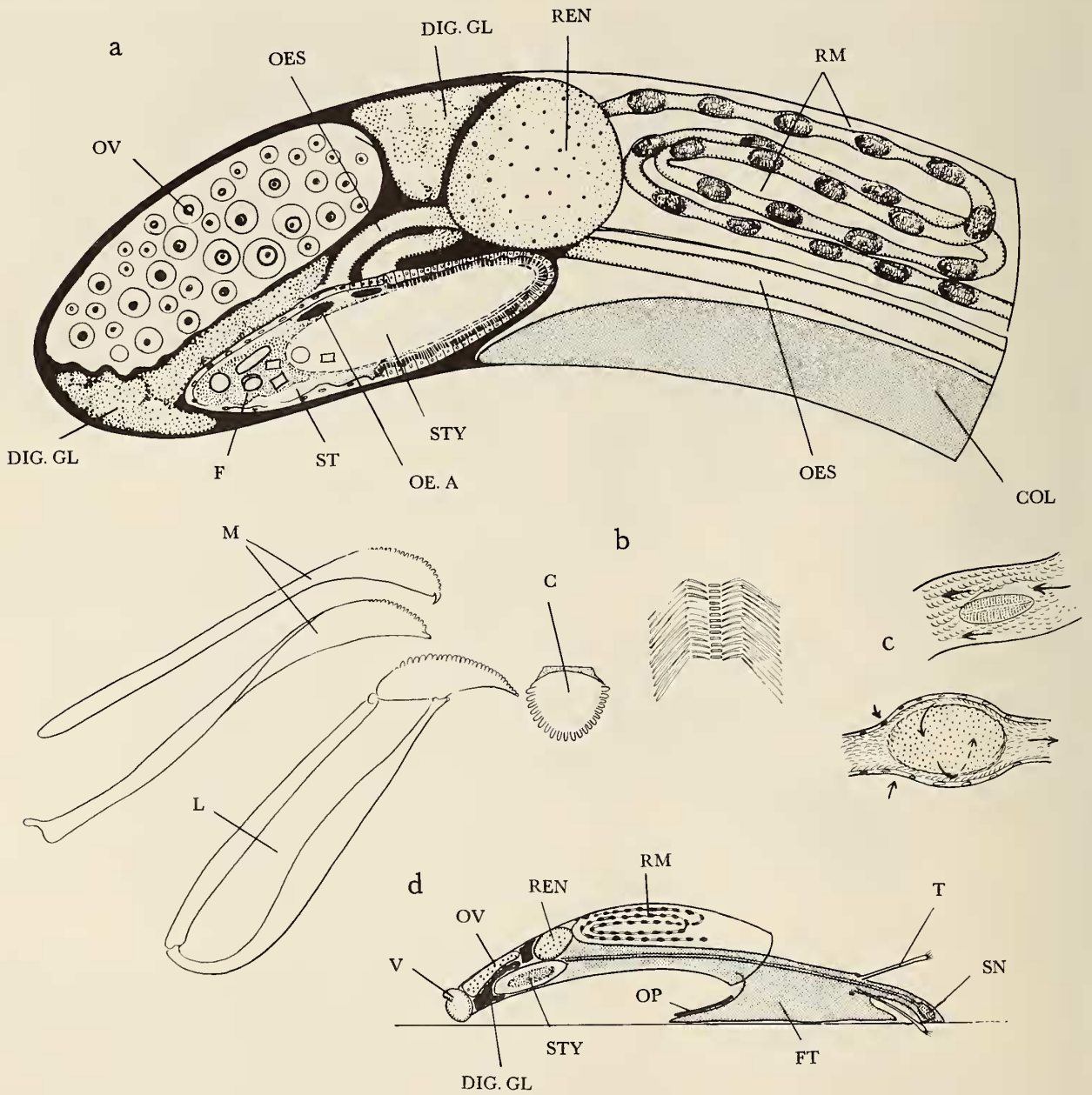


Figure 8

Caecum digitulum

- (a) visceral mass removed from the shell and viewed as by transparency from the right side;
- (b) the radula, with several rows intact (right) and with details (left) of median, lateral and marginal teeth;
- (c) details of movement of materials within the gut; ciliary propulsion of a diatom in the oesophagus (above) and peristaltic and ciliary movement of a faecal pellet in the intestine (below);
- (d) the extended animal moving forward with the shell in upright posture.

C - columellar or median tooth COL - columellar muscle
 DIG. GL - digestive gland F - food mass in stomach
 FT - foot L - lateral tooth M - marginal tooth
 OES - oesophagus OP - operculum OV - ovary
 REN - renal organ RN - rectum with faecal pellets
 SN - snout with buccal mass ST - stomach
 STY - crystalline style T - head tentacle V - visceral coil

turned and compacted with mucus by transverse ciliary beat. (Figure 8 c).

(d) *Marinula filholi*

The Ellobiidae are all deposit feeders with a muscular gizzard-like stomach. Like most of the Pulmonate sub-order Basommatophora they ingest large volumes of surface deposits or plant detritus. The general characters of the ellobiid gut (MORTON 1955 a) show a very different pattern from that of the mesogastropods so far described. Food is not abraded from a hard substratum, as in limpets or littorinids, but is raked in without selection by the broad, widely sweeping radula. As in the great majority of pulmonates, the radula of *Marinula* has many teeth to a row; POWELL (1933) recorded the formula as 121 · 1 · 121. The central tooth is narrowly compressed and the inner members of the lateral series, equipped with single, hooked cusps, resemble it. The outer laterals, that may be referred to as marginals, have several cusps, 4 at first, but increasing to 7 at the extreme edge of the radula. (Figure 9 c).

The oesophagus of *Marinula* is a narrow ciliated tube; the stomach forms an ovoid or pear-shaped gizzard, invested at its greatest diameter with a coat of circular muscle (Figure 9 a). Both the oesophagus and intestine open at the proximal end. As in other ellobiids, the wide posterior part of the apparent oesophagus is properly part of the stomach, for it receives the wide opening of the anterior (larger) of the two digestive diverticula. The second diverticulum is small and easy to overlook, as in the simplified diagram given by MORTON (1955 b); it opens through the wall of the gizzard which is otherwise lined with cuticle. At the apex of the stomach is a small annexe containing a fold of ciliated epithelium of unknown function. The muscular coat of the gizzard constantly contracts during life, serving to squeeze out from the food mass nutritive material which is digested extracellularly by enzymes within the stomach. Fine material in suspension appears to be conveyed under pressure to the digestive diverticula. Cilia beat from both diverticula back into the stomach. By periodic relaxations of the intestinal opening, a coarser residue (sand grains from the stomach as well as unassimilated egesta from the diverticula) is allowed to pass out of the stomach. There is neither a style sac, nor ciliary sorting area; and unlike some primitive ellobiids (e.g. *Ophicardelus costellaris*), *Marinula filholi* has lost the original ciliated channels leading from each digestive diverticulum to the intestine.

The stomach of the minute *Rangitotoa insularis* Powell, 1933 (Figure 9 b) is essentially like that of *Marinula*, but the gizzard is relatively stronger and more spherical, well

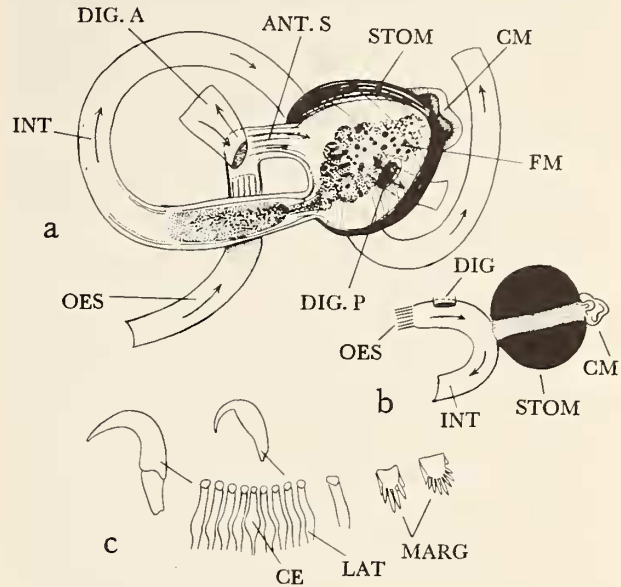


Figure 9

ELLOBIIDAE

- (a) stomach and portions of the oesophagus and intestine of *Marinula filholi*, viewed diagrammatically as a transparent object. Food passage indicated by arrows
 (b) stomach of *Rangitotoa insularis*;
 (c) teeth of radula of *Marinula filholi*.

ANT.S - anterior chamber of stomach CE - central tooth
 CM - caecum DIG - aperture of digestive gland
 DIG.A - anterior digestive diverticulum
 DIG.P - posterior digestive diverticulum
 FM - food mass in stomach INT - intestine
 LAT - lateral teeth MARG - marginal teeth
 OES - oesophagus STOM - stomach with muscular wall

marked off from the thin-walled anterior chamber which receives the single digestive diverticulum.

STYLE SAC OR GIZZARD:
 COMPARATIVE DISCUSSION

The four sorts of gastropod described here show two broadly alternative types of stomach for dealing with finely particulate food. The occurrence of the crystalline style and style sac in gastropods was first discussed by GRAHAM

(1939), who concluded that the style is a device possessed by slow, continuous feeders. It is thus absent in those intermittent feeders that take large amounts of food, with interruption by tidal exposure. This rule still largely holds good, as exemplified in patellid limpets and upper shore littorinids. The essential functions of the crystalline style have been set out by MORTON (1952, 1960 a): as well as a store of amylolytic enzyme, it serves as a rotating capstan permanently attached to a mucous food string and regulating its passage into the stomach.

Feeding may be essentially continuous even with intervals of tidal emersion. Whereas *Melarhapha* and *Risellopsis* appear to be inactive for long periods when the tide is out (Beckett, unpublished 1969), *Caecum* goes on browsing so long as the rock surface is moist with a water film, and *Suterilla* lives and feeds in a permanently saturated atmosphere, being covered only briefly and infrequently by the tides.

Regularly associated with the style in prosobranch gastropods is the ciliary sorting area of the stomach, serving to grade and regulate a constant flow of particles. Sorting is effected by the removal of heavier material thrown by the rotation of the style against the ciliated folds and ridges. The finest particles are kept in suspension, eventually to reach the digestive diverticula, while the rejected material is carried along the grooves to reach the intestine. A stomach with a style sac is characteristic, then, of prosobranchs in which ingested food is mixed with much unassimilable debris.

The simpler gizzard type of stomach, with the style undeveloped and the sorting area lacking, is found in gastropods where the food intake is of relatively large volume and is squeezed or triturated without the separation of coarse from fine particles. Such food may consist of relatively pure plant material, such as lichens in *Melarhapha* where the stomach approximates to the gizzard form, or decaying algae, as in the Ellobiidae that possess a strong gizzard.

The gizzard would appear to be a special feature of those deposit-feeding basommatophoran pulmonates in which the volume of ingested food is too great for ciliary sorting. The mud-flat dwelling Amphibolidae (FARNIE, 1919) have acquired a highly specialised stomach, with a triturating gizzard, serving to squeeze out the nutriment from heavy swallowings of organic deposits. In current studies by Mr Ian Briggs, *Amphibola crenata* (Gmelin, 1791) has been shown to feed unselectively from the organic surface layer of mudflats. In cleaner habitats it may swallow large amounts of sand grains, apparently utilising from these the surface flora of bacteria or diatoms. The Siphonariidae, pulmonate intertidal limpets, possess a spacious oesophageal crop and muscular stomach, in some

respects convergent with the gut of the patellid limpets (unpublished personal observations).

Among the style-bearing Prosobranchia, the size of the style and its power of traction, as well as the dimensions and complexity of the sorting area, appear to vary widely according to the coarseness and bulk of the particulate diet. In ciliary feeders, such as Calyptraeidae, Turritellidae, Struthiolariidae, and Siliquariidae, and in the Vermetidae which feed by cilia and mucous traps (MORTON,

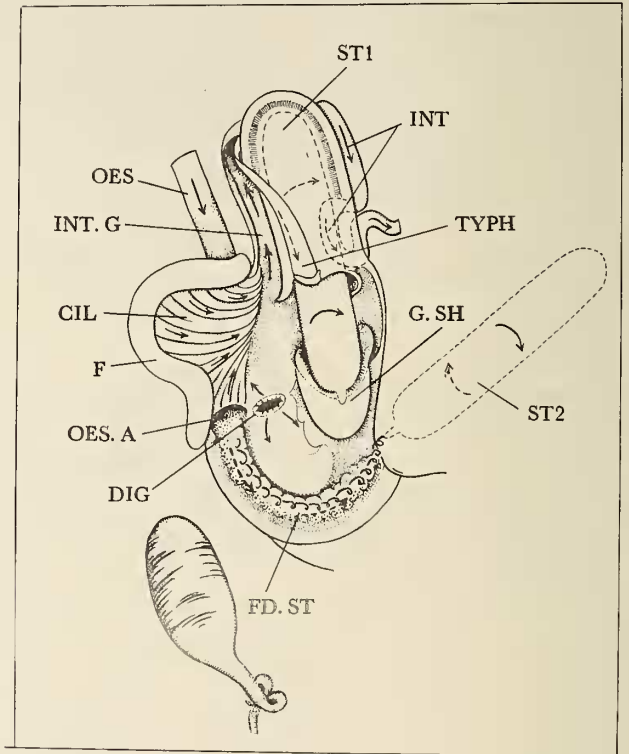


Figure 10

Zeacumantus lutulentus (family CERITHIIDAE)

- (a) Diagram of interior of stomach and style sac, showing the attachment of the tightly twisted food string to the crystalline style. The style is represented *in situ*, and in diagrammatic outline lifted away from its sac.

Zemelanopsis trifasciatus (family MELANIIDAE)

- (b) the stout, heavy crystalline style with its direct continuation into a food string.

CIL - ciliary sorting area DIG - digestive diverticulum
 F - fold bounding sorting area FD.ST - food string
 G.SH - gastric shield INT - intestine
 INT.G - intestinal groove OES - oesophagus
 OES.A - oesophageal opening ST 1 - style in style sac
 ST 2 - style (outline) removed from style sac
 TYPH - typhlosole

1960 a), the style is slender and of a more fluid consistency, like that of *Suterilla* and *Caecum*. In those mesogastropods, by contrast, that take in coarser food, mingled with shell fragments and sand grains, the style is heavier and more robust, with a strong food cord attached. The sorting area is also very extensive. Good examples are the melaniid snail *Zemelanopsis trifasciata* (Gray, 1843) (see MORTON 1952) where the style is firm and almost cartilaginous in texture and the Cerithiidae, as illustrated by *Zecumantus lutulentus* (Kiener, 1842) (Figure 10). A crystalline style of maximal length and traction power is found in the Strombidae, where the style sac is prolonged far forward into the mantle. These large tropical mesogastropods graze upon small algae as well as ingesting large amounts of soft nutritive deposits (ROBERTSON, 1961). Among the Bivalvia, a similar relation between deposit-feeding and a heavy crystalline style has been demonstrated by YONGE (1949) for the Tellinacea.

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Literature Cited

- BACON, M. R.
1971. Distribution and ecology of the crabs *Cyclograpsus lavauxi* and *C. insularum* in northern New Zealand. *New Zeal. Journ. Marine & Freshwater Res.* 5 (3, 4): 415-426
- FARNIE, W. C.
1919. The structure of *Amphibola crenata* Martyn. *Trans. New Zeald. Inst.* 51: 69-85
- FRAENKEL, GOTTFRIED S.
1927. Geotaxis und Phototaxis von *Littorina*. *Zeitschr. f. vergl. Physiol.* 5: 585-597
- FRETTER, VERA & ALASTAIR GRAHAM
1949. The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. *Journ. Mar. Biol. Assoc. U. K.* 28: 493-532
1962. British prosobranch molluscs, their functional anatomy and ecology. London, Ray Soc. xvi+755 pp.; 316 figs.
- GOETZE, E.
1938. Bau und Leben von *Caecum glabrum* (Montagu). *Zool. Jahrb. (Abt. Syst. & Ökol.)* 71: 55-122
- GRAHAM, ALISTAIR
1939. The alimentary canal in style-bearing prosobranchs. *Proc. Zool. Soc. London, Ser. B.* 109: 75-112
- MORTON, JOHN EDWARD
1952. The role of the crystalline style. *Proc. Malacol. Soc. London* 29: 85-95
- 1955a. The functional morphology of the British Ellobiidae (*Leuco-phytia bidentata*, *Ovatella myosotis* and *Carychium tridentatum*). *Philosoph. Trans. Roy. Soc. London, Ser. B:* 239: 89-160
- 1955b. The evolution of the Ellobiidae with a discussion on the origin of the pulmonates. *Proc. Zool. Soc. London* 125: 127-168
- 1960a. The functions of the gut in ciliary feeders. *Biol. Rev.* 33: 92-140
- MORTON, JOHN EDWARD & D. A. CHALLIS
1969. The biomorphology of Solomon Islands shores with a discussion of zoning patterns and ecological terminology. *Philos. Trans. Roy. Soc. London, series B:* 255: 459-516
- MORTON, JOHN EDWARD & M. C. MILLER
1968. *The New Zealand Sea-shore.* Collins, London, 638 pp.
- MORTON, JOHN EDWARD & J. MACHIN
1959. A key to the land snails of the Flatford area, Suffolk. *Field Studies* 1 (1): 1-11
- PILKINGTON, M.
1971. Eggs, larvae and spawning in *Melarhaphé cincta* (Quoy and Gaimard) and *M. oliveri* Finlay (Littorinidae, Gastropoda). *Austral. Journ. mar. Freshwat. Res.* 22: 79-90
- POWELL, ARTHUR WILLIAM BADEN
1933. The high-tidal Mollusca of Rangitoto Island, Auckland, with descriptions of a new genus and two new species. *Trans. New Zeal. Inst.* 63 (2): 144-153
- ROBERTSON, ROBERT
1961. The feeding of *Strombus* and related herbivorous marine gastropods. *Notulae Naturae* 343: 1-9
- STEPHENSON, T. A. & ANN STEPHENSON
1959. Life between tide-marks in North America. 1. The Florida Keys. *Journ. Ecol.* 38: 354-402
- SUTER, HENRY
1907. *Manual of the New Zealand Mollusca.* Government Printer, Wellington, 1120 pp.
- THEILE, JOHANNES
1931. *Handbuch der systematischen Weichtierkunde.* Fischer, Jena, 788 pp.
- YONGE, CHARLES MAURICE
1949. On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. *Philos. Trans. Roy. Soc. London (B)* 234 (609): 29-76; 29 text figs. (5 September 1949)

