Feeding and Digestion in the Bivalvia

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I. INTRODUCTION

The primitive mollusc was probably a fine-particle feeder using a protrusible radula to collect and ingest material into the cavity of a muscular buccal bulb (Morton and Yonge, 1964). The remainder of the alimentary canal consisted of an esophagus, stomach, and intestine, and three associated glandular areas (Owen, 1966b). These were salivary glands opening into the buccal cavity, esophageal pouches, and midgut glands or digestive diverticula opening into the stomach. The stomach was probably pear-shaped with the wider anterior region consisting of an extensive nonciliated, cuticle-covered area, and a ciliated area of grooves and ridges associated with the openings of the ducts of the digestive diverticula. The tapering posterior region, the forerunner of the style sac, was the passageway to the intestine and here a fecal string of mucus-embedded material was rotated and moulded by the combined action of cilia and muscle before passing to the intestine. The finely divided ingested material was probably subjected to an initial extracellular digestion within the gastric cavity and this was completed intracellularly within the cells lining the tubules of the digestive diverticula.

In the Bivalvia, following the enclosure of the body within the shell, the head, together with the radula, buccal mass, and associated glands

have been lost (Yonge, 1953a). The early bivalves probably c particulate material directly from the substratum by means of oral appendages and from this ancestry three main lineages, distin by their feeding mechanisms have survived to the present day (P 1968). These are the protobranchiate, septibranchiate, and lame chiate bivalves.

II. Feeding Methods

The Protobranchia, with the exception of the Solenomyidae 1961), feed primarily by means of ciliated palp proboscides. Thes into the substratum and collect particles which are carried to lamellae for sorting prior to ingestion. The sorting appears to be if not entirely, quantitative since the gut in these animals is in filled with mud and sand grains in addition to diatoms and organ tus. Particulate material is also collected by the ctenidia, but t of the contribution from this source is unknown (Stasek, 196 It is possible that it varies with the species but the gut of s of *Nucula sulcata* when kept in suspensions of particulate ma relatively empty compared with that of animals allowed to bur the substratum.

Knowledge of the food and feeding processes of the Septibr still based on the work of Yonge (1928). The ctenidia in these are modified to form muscular septa which can be raised and to drive water through the mantle cavity. Unlike all other biva are no longer ciliary feeders but scavengers, ingesting whole bodie ments of dead or moribund animals together with any other p material which enters the mantle cavity.

The main food collecting organs in the lamellibranchiate bi the greatly enlarged ctenidia disposed on either side of the visc and foot. They are primitively respiratory organs, but the varic tracts serve not only to create a current of water but also sort, and transport particulate material to the labial palps a or to appropriate areas for subsequent expulsion from the man as pseudofeces. As in most ciliary feeding animals, the cilia v form these functions are arranged in well-defined tracts along t surfaces of the elongate filaments which make up the ctenidia.

Powerful cilia, arranged in continuous tracts along the lat serve to drive water between the filaments and are responsi inhalant and exhalant currents which enter and leave the man It is these tracts in particular which have attracted the a workers interested in the structure and physiology of cilia. S coordinating mechanisms for cilia have been fairly well estab a series of progressive neuroid impulses and second, mechanic

ence (Sleigh, 1962, 1969). The possibility that the beating of the lateral cilia in *Mytilus edulis* is under nervous control was earlier demonstrated by stimulation and severing of the branchial nerve (Aiello, 1960; Papero and Aiello, 1970). Papero (1972) has now traced nerve fibers from the visceral ganglia to the ciliated epithelium of the gill filaments where they penetrate the basal lamina and lie adjacent to cells bearing the lateral cilia. Only certain cells appear to have this close association with nerve fibers, suggesting that they may act as pacemakers and that cells less favorably placed may be excited indirectly. Serotonin (5-HT), which has a cilio-excitatory effect on the gills of *Mytilus* (Aiello, 1962; Aiello and Guideri, 1965), was identified within the branchial nerve (Papero, 1972). Nervous control of the lateral cilia may well prove significant in an understanding of the fluctuations in pumping rates which have been recorded for many bivalves.

Cilia on the frontal surfaces of the filaments serve to transport material to the tracts leading to the mouth or to the rejection areas. Peculiar to lamellibranchiate bivalves, among animals employing ciliary feeding mechanisms, are the compound laterofrontal cilia, or cirri, which lie between the frontal and lateral tracts. They occur at intervals of 2–3 μm in most species and stand out from the laterofrontal faces of the filaments to form a sort of grating between them; they beat at right angles to the long axis of the filaments. Most workers accept that they serve as the primary filtering mechanism of the lamellibranchiate gill, although the precise manner in which this is achieved has until recently not been fully understood (see Section IV). Material collected by the ctenidia is passed to the mouth by way of the labial palps, and during the course of this transfer it may undergo further vigorous sorting and selection. Details of the labial palps are reviewed by Owen (1966a) and Purchon (1968).

The form of the gills and the fascinating and intricate sorting mechanisms associated with them vary in the different species (Atkins, 1936, 1937a,b, 1938, 1943) and have been reviewed by Jørgensen (1966), but in general the lamellibranchiate bivalves exhibit some monotony of feeding methods. The main variation appears to be between deposit and suspension feeding although the distinction is admittedly one of degree, since most deposit feeders almost certainly supplement their food intake by filtering suspended matter (Braefield and Newell, 1961; Pohlo, 1969). Reid and Reid (1969), on the basis of siphon behavior, selection in the mantle cavity, stomach morphology, and stomach contents, grouped eight species of *Macoma* into three feeding categories. *Macoma secta, M. inquinata,* and *M. calcarea* all moved the inhalant siphon around on the surface of the substrate to suck up masses of surface particles. The ciliary mechanisms of the pallial organs of *M. secta,* however, were less selective

than those of the other species studied, and it was concluded tha of its nutrients must come from microbial colonies on the larg grains which it ingests. Of the remaining five species, only *M. br* casionally took up finely divided deposit material. The other four never allowed the opening of the inhalant siphon to come into with the substrate and were classified as suspension feeders.

In another intertidal tellinid, *Scrobicularia plana*, Hughes (1969) that during high tide, deposit feeding tended to be limited to th and mouth of the burrow and was probably supplemented by sus feeding. The more obvious deposit feeding activities of the i siphon took place throughout the period of low tide, provided th table remained at the surface. The inhalant siphon could be e some 5–8 cm over the surface of the mud, and during this exte was periodically swept from side to side while the tip of the plucked at the surface of the mud. Particles of sediment, some size to the lumen of the siphon and often accompanied by air passed down the siphon. This activity continued for some 2–4 was followed by withdrawal of the siphon for periods averaging but on occasions extending to 30–40 min. The direction in whic phon was extended altered, so that eventually a full circle was d This activity resulted in considerable quantities of bottom mater taken into the mantle cavity and the production of pseudofece were expelled every 10–20 min, exceeded the defecation rate 300 times. Moreover, the pseudofeces still contained large am organic matter and it would appear that little of the organic ma tained in the sediment taken up by the siphon is actually Hughes (1969) suggests that the rarity of horizontal migration *bicularia*, compared with some other tellinids, may well be correl the abundance of organic material in its environment. The intak siderable quantities of bottom material also appears to be correl the pumping activities of the gills. While the filtering efficien gill of *Scrobicularia* is comparable with that of solely suspensi bivalves, the pumping rate is much lower. Indeed, it is these the feeding activities of bivalves, namely, the rate of passage through the mantle cavity and the efficiency and mechanism retention, which have received particular attention over rece

III. Pumping and Filtration Rates

Methods used to study the rate of passage of water through cavity of bivalves fall broadly into two main categories. Dire attempt to separate and measure the exhalant flow while indire

use the rate of removal of suspended material from a known volume of water to estimate the rate of flow through the mantle cavity. Direct methods measure the "pumping rate" while indirect methods measure the "filtration rate," and unless evidence is produced to show that all the suspended particles are being retained, this will be less than the pumping rate. The advantage of direct methods is that the pumped water is collected and measured directly and, moreover, by means of a flow meter (Drinnan, 1964) or other recording device (Davids, 1964; Sawyer, 1972) can be continuously monitored. It is, however, particularly important to ensure that the animal is neither pumping against an appreciable back pressure nor allowing water to siphon through the mantle cavity. The "constant level" chamber (Galtsoff, 1928) embodies this principle and with various modifications has been employed by many subsequent workers (Loosanoff and Engle, 1947; Tammes and Dral, 1955; Drinnan, 1964; Davids, 1964).

The main disadvantage of direct methods is that the separation and collection of the exhalant flow requires that the animals undergo special treatment which may possibly affect their normal behavior. Moreover, such methods are difficult to use with siphonate bivalves and attempts have been made to overcome these difficulties by including dyes or particles in the water, thus allowing direct observation of the flow. Hersh (1960) used dilute suspensions of aluminum dust and recorded the movements of the particles in the exhalant current photographically. This information, together with measurements of the size of the siphonal apertures, enabled him to calculate the rates of the through-current. Coughlan and Ansell (1964) used nontoxic soluble dyes in the water supplied to the animal and this enabled them to regulate the supply to a point where it just provided the whole of the inhalant flow.

Investigations of the filtering rate using indirect methods usually assume that (a) the reduction in the concentration of particles is due to filtration, (b) the animal's pumping rate is constant, (c) particle retention is 100% efficient, alternatively a known constant percentage is retained, and (d) the test suspension is at all times homogeneous (Coughlan, 1969). Various equations differing only in notation have been employed to calculate the filtering rate (Fox *et al.*, 1937; Jørgensen, 1949; Theede, 1963), and Coughlan (1969) has suggested that in practice the simplest to apply is that given by Quayle (1948).

$$m = \frac{M}{nt}\left[\left(\log_e \frac{\text{conc}_0}{\text{conc}_t}\right) - \left(\log_e \frac{\text{conc}_{0'}}{\text{conc}_{t'}}\right)\right]$$

Conc_0 and conc_t are the concentrations initially and after time t in the test suspension while $\text{conc}_{0'}$ and $\text{conc}_{t'}$ are those in a control suspension

TABLE I
PUMPING AND FILTRATION RATES

Species	Length (mm)	Temp. (°C)	Method	Rate (ml/hr/animal)	F
Mytilus edulis	25	18	Direct	800	Qurai
	29	18–20	Direct	350–1000	Davi
	24–39	17	Indirect	110	Aller
	32	13–14	Indirect	1500	Jørg
	48	12–15	Indirect	1100	Will
	68	12–15	Indirect	1700	Will
Ostrea edulis	19–39	17.5	Indirect	200–1000	Aller
	—	18.5	Direct	4000	Drir
	70–86	12–13	Indirect	100–700	Mat
Crassostrea angulata	70–90	12–13	Indirect	200–1680	Mat
Pecten irradians	38–44	22–26	Indirect	3260	Chij
					H
Anodonta cygnea	80–100	18–20	Direct	250–300	de I
					I
Cardium edule	30–40	17–19	Indirect	500	Wil
Venus striatula	21–28	17	Indirect	40	All
Mya arenaria	57–82	17.5	Indirect	600–1300	All
Scrobicularia plana	40	16.5	Both	350	Hu
Dreissena polymorpha	29	—	Indirect	5–180	Mc

and give a measure of the rate at which particles settle out
Where settling is negligible the final term of the equation ca
M is the volume of suspension, n the number of animals an
ing rate per animal. A selection of results obtained by va
using both direct and indirect methods is given in Table I. M
lists are given by Hughes (1969), Winter (1969), and A

The selection serves to illustrate the wide range of pumpi
rates in different species from the relatively low figure of
animal in *Scrobicularia* to the much higher rates in the la
of *Mytilus*, *Ostrea*, and *Pecten*. Meaningful comparisons o
filtration rates in different species, and in different sized
the same species are, however, difficult. Before valid comp
made, a standard method of presenting the results, partic
of the size of the animal must be adopted. Shell length
Table I is of limited use. Hughes (1969) expressed the p
tion) rates of a number of bivalves on a per unit gill are
that differences in the pumping rates may be due to di
properties of the gills and there appeared to be some corr
the pumping rate per unit gill area of a species and its

Mercenaria mercenaria, *Mytilus edulis*, and *Cardium edule* all have high pumping rates per unit gill area (6.05, 0.89, and 1.87, respectively) and live in situations where the water contains relatively little suspended material. *Scrobicularia plana* and *Mya arenaria*, on the other hand, both have low pumping rates (0.3–0.5, depending on temperature, and 0.56, respectively) and both live in situations where the inhalant current is likely to include large amounts of particulate material. The value of results presented in this form is uncertain, since calculations of the gill area do not appear to have taken into account whether or not the gills are plicate. Both *M. mercenaria* and *C. edule* possess plicate gills, while those of *Mytilus*, *Mya*, and *Scrobicularia* are flat.

Most workers prefer to relate the pumping (filtration) rate to the weight of the animal and to express results in terms of a specific filtration rate, i.e., milliliters per gram per unit of time. Ali (1970) used the whole weight of the animal but this has been criticized on the grounds that it gives excessive regard to the shell weight. The use of wet (Winter, 1969) or dry (Walne, 1972) meat weights have been criticized on the grounds that they may be affected by the amount of storage products and the stage of development of the gonad (Allen, 1962; Ansell, 1964). Nevertheless, Walne (1972) found that dry meat weight gave the best measure of size.

In general, the specific filtration rate decreases with increasing size. Applying the allometric equation

$$F = aW^b$$

the values for b, i.e., the relationship between the specific filtration rate F and the body weight W tend to fall between —0.7 and —0.8 (Winter, 1969; Walne, 1972); the value of b should approximate to —0.67 if the decline in filtration rate with increasing size is related to the surface area of the body. As in other similar cases, the significance of the higher values for b are not known.

The influence of temperature on the pumping (filtration) rate varies with different species. Over the range 10° to 20°C the filtration rates of *M. edulis* (Theede, 1963; Walne, 1972), *Arctica islandica* (Winter, 1969), *Crassostrea virginica* (Walne, 1972), and *Hiatella arctica* (Ali, 1970) increase by some 15–35% and of *Ostrea edulis* (Walne, 1972) and *S. plana* (Hughes, 1969) by 100% or more. The differences probably reflect differences in the optimal range for the filtration rate in the different species and comparisons between species should be made at temperatures close to the optimal temperature for the species (Ali, 1970).

Although not generally realized in the past, it is now clear that the rate of water movement over the animal has an effect on the pumping

TABLE II
THE EFFECT OF FLOW RATE ON THE FILTRATION RATE[a]

Species	Specific filtration rate[b]	
	Flow rate 200 ml/min	Flow rate 300 ml/min
Ostrea edulis	117.8	146.6
Crassostrea gigas	120.2	164.1
Mytilus edulis	50.7	63.5
Mercenaria mercenaria	55.5	75.5
Venerupis decussata	55.5	76.0

[a] Data from Walne (1972).
[b] The rates are for animals of 1 gm dry meat weight.

(filtration) rate. Table II shows the specific filtration rates of five of bivalves, each of 1 gm dry meat weight, at flow rates of 200 ml/min. In each case the filtration rate is increased at the high rate. The causal connection is unknown but there appears to be r tion of the water somehow forcing itself through the mantle ca the animal (Walne, 1972). This effect of the flow rate on the fi rate, and therefore on the feeding activities of the animal, offers a nation for the views of earlier workers that bivalves such as *Cra* (Galtsoff, 1964) and *Agropecten* (Marshall, 1960) grow best in where there is a steady nonturbulent flow of water. From expe extending over the relatively short period of 14 days, Walne (19 able to demonstrate an increased growth rate in small specime *edulis* and *C. virginica* at a flow rate of 180 ml/min compared ml/min. More extensive experiments on the influence of water the growth rate of *Agropecten irradians* have been reported by Smith (1972), although in this case, the flow rates ranged fron 35,000 ml/min. At the higher flow rates growth almost ceased, creased as the rate of flow decreased to reach a maximum in t of 500 to 1000 ml/min. It is presumably within this range that mals reach a maximum filtering rate and the limiting factor bec concentration of suspended food present in the water. Kirk (1972) has suggested that the most efficient system for culturi *radians* might be one in which the rate of water flow is such outflow contains not less than 60% of the suspended food prese inflow.

The effects of the nature and concentration of suspended mate ent in the water on the pumping and filtration rates of bival

been the subject of many investigations and much of the earlier work is reviewed by Jørgensen (1966). Results vary both with the species and the investigator, but in general, high concentrations of algae, on the order of 10^5 to 10^7 cells per milliliter, effect a reduction in the filtration rate. These concentrations exceed those normally encountered by the animal and while different species are able to tolerate different concentrations of suspended material in the environment (Mathers, 1973b), the reduction at these relatively high concentrations may, in many cases, simply be due to the overloading of the sorting and filtering mechanisms of the gill. Alternatively the medium, particularly under experimental conditions, may contain inhibitory substances which depress the activity of the gill. Suspensions of *Chlorella*, and the filtrate of such suspensions, depressed the pumping rate of *Mytilus edulis* (Davids, 1964).

Changes in the concentration of particles present in the water available to the animal can also affect the pumping and filtration rates. The introduction of suspended particles into clean sea water resulted in an increase in the pumping and filtration rates of *M. edulis* (Theede, 1963; Davids, 1964). Moreover, this increase in activity occurred with both algal suspensions and inert particles such as activated charcoal, suggesting that the receptor system concerned is both mechanosensory and chemosensory (Thompson and Bayne, 1972). The observation by Mathers (1973b) that the addition of small numbers of *Isochrysis galbana* to dilute suspensions of colloidal graphite (Dag 554) greatly increased the filtration rate of *O. edulis*, but markedly decreased the filtration rate of *Crassostrea angulata*, similarly suggests that both qualitative and quantitative factors may be significant. Davids (1964) reported that a decrease in the concentration of particles, or the complete removal of particles, usually resulted in an increase in the pumping rate of *M. edulis*, but both Theede (1963) and Thompson and Bayne (1972) found that the removal of the particulate stimulus resulted in a marked decrease in the filtration rate.

Of particular interest is the effect of nonparticulate stimuli on the pumping and filtration activity. Theede (1963) found that the addition of glucose to the medium induced an increase in the filtration rate of *M. edulis* and a similar effect has been reported by Thompson and Bayne (1972) using extracts of algae, filtered culture medium, and glucose. There is some controversy over whether dissolved organic material may contribute significantly to the nutrition of bivalves (Collier *et al.*, 1953; Galtsoff, 1964), but as Thompson and Bayne have shown, there is no doubt that dissolved material can affect the filtration rate, although this does not necessarily imply that such material has any nutritional value. It is interesting, however, that preliminary work, as yet unpublished, indicates that the gills of bivalves possess active carrier-mediated transport

systems for the absorption of neutral amino acids and hexose charides (D. R. Bamford, personal communication).

It is the relationship between the filtering activities of the a the efficiency of food utilization which is perhaps the significar in the context of bivalve nutrition, since variations in the filt are in effect a measure of variation in the food ration ingeste of time. Thus as Walne (1972) has argued, a more biologicall measurement would be estimates of the food ration in various This measurement, coupled with information on the assimi ciency of the animal, could provide a more significant assessn feeding activity. Unfortunately, there is as yet little data a these aspects of bivalve feeding and nutrition. Investigating t ity of *M. mercenaria* to different food concentrations, Walne verted the filtered algal material to a food ration, expresse micrometers of algal material filtered per hour. The result species of algae are shown in the following table.

Algal sp.	Max. ration	Cubic microme animal per h
Dunaliella tertiolecta	16.6×10^4	4.98×1
Isochrysis galbana	38×10^4	2.17×1
Phaeodactylum tricornutum	90×10^4	4.50×1

The small size of the *Isochrysis* ration is probably related nutrition value of this alga (Table III). For the other two it is interesting to note that although there is a great diffe number of cells filtered per hour, the ration in terms of cubic of algal material is more or less similar. Table III shows food value of different algae to young specimens of *O. ed mercenaria*. The data, taken from Walne (1972), are based o of juvenile bivalves kept in various concentrations (usually algae over a period of 21 days. This ensured that at leas tests was at a favorable concentration of the food. Of the fou to be as good or better than *Isochrysis* for *Ostrea*, two, *Mo Dicrateria*, are not so good for *Mercenaria*. Why different should vary in their food value is not clear. It does not related to differences in amino acid composition of the a suggestion that forms with a rigid wall (e.g., *Chlorella* an *monas*) are not readily assimilated does not explain the poor by the related *Dunaliella* which has no rigid cell wall.

TABLE III
THE FOOD VALUE OF DIFFERENT ALGAE TO JUVENILE BIVALVES[a]

Species	Index of food value[b]	
	Ostrea edulis	*Mercenaria mercenaria*
Monochrysis lutherii	1.36	0.59
Tetraselmis calcitrans	1.20	1.11
Skeletonema costatum	1.01	3.30
Isochrysis galbana	1.00	1.00
Dicrateria inornata	0.94	0.67
Cricosphaera carterae	0.62	0.70
Chlorella stigmatophora	0.60	0.31
Phaeodactylum tricornutum	0.59	0.44
Olisthodiscus sp.	0.56	0.75
Nanochloris atomus	0.54	0.92
Micromonas pusilla	0.44	0.74
Dunaliella tertiolecta	0.39	0.14
Chlamydomonas coccoides	0.30	0.19

[a] Data from Walne (1970).

[b] Based on the growth of juveniles when fed various foods compared with the growth of controls fed on *Isochrysis* (some on *Tetraselmis* for *Mercenaria*). The index is calculated by dividing the mean size measured at 21 days from the commencement of the test, by the mean size of the control on that day.

Winter (1969, 1970) investigated the food utilization or protein efficiency of *Arctica islandica* and *Modiolus modiolus* under different environmental conditions by comparing the protein content of the algae removed from suspension with that of the feces produced during the experimental period. Results for *Arctica* show that while an increase in the concentration of algal cells from 10^3 to 20^3 cells per milliliter results in a decrease in the filtration rate from 100 to 65 ml/min, the total amount of algal material filtered is increased from 120 to 162 mg dry wt/24 hr. The percentage food utilization, however, drops from some 88% to 67%, and at both concentrations approximately the same amount of algal material is utilized by the animal. At higher cell concentrations (40^3 cells per milliliter at 12°C), the filtration rate is greatly depressed and, moreover, considerable amounts of the algae filtered are accumulated as pseudofeces suggesting that the sorting mechanisms of the gill are overloaded.

The effect of body size on food utilization appears to differ in the two species. In *A. islandica*, increase in size is accompanied by a marked in-

crease in the total amount of algae filtered (30–280 mg dry wt/2 but the percentage food utilization decreases from 75 to 43%. *modiolus*, the increase in the amount of algae filtered with incr size of the animal is less (20–100 mg dry wt/24 hr) but the perc food utilization remains more or less constant at 87%, suggestin in this species food utilization is independent of food avail Thompson and Bayne (1972) expressed the assimilation efficiency *edulis* kept in different concentrations of *Tetraselmis sp.* in terms ratio of ash-free dry weight to dry weight of the feces. At concent of 1×10^3 cells per milliliter, the assimilation efficiency was 89 as the cell concentration increased, the assimilation efficiency de approximately linearly to reach zero at a concentration of 25×1 per milliliter.

The development of techniques which allow the maintenance of stant concentration of food particles (Winter, 1969), the correla filtering rates with estimates of the assimilation efficiency (Winte Thompson and Bayne, 1972), and the data on optimum flo (Walne, 1972; Kirby-Smith, 1972) offer the hope that studies on t ing of lamellibranchiate bivalves have reached a stage where t contribute not only to an understanding of the animal's reactio environment, but also to useful predictions for the culture of econ important species. It is important, however, that investigators in t express their results, whenever possible, in a form which will all comparisons to be made with those of other workers.

IV. Efficiency and Mechanism of Filtration

Data on the filtering efficiency of the lamellibranchiate gill s siderable variation. Particles in the size range 3–10 μm are re be retained in any percentage between 0 and 100, while the of smaller particles varies between 0 and a maximum dependi size of these particles. Jørgensen (1949, 1960) found that certain were able to retain particles of a few microns in diameter efficie he suggested that the differences in the results were due to d in technique. He concluded that maximum performances wer be expected from absolutely undisturbed animals. Under such it would appear that most lamellibranchiate bivalves are able completely particles of a diameter of 3 to 4 μm and above.

Hughes (1969) found that the filtration rate of *Scrobicular* mined by the indirect method and using talc particles of ab

equalled the pumping rate, indicating a filtration efficiency of 100% for particles of this size. Haven and Morales-Almo (1970) analyzed the filtration of particles by *C. virginica* by measuring differences in the numbers of particles in the size range 1.0–12 μm in the water before and after it had flowed over the animals. A significant feature of their results was that above a particle size of 2 to 3 μm there was no further change in efficiency suggesting that filtration of particles of this size and above was 100%. Also relevant was the high retention of particles in the 1–3 μm range. Although the filtration efficiency for these particles was less than 100%, nevertheless, owing to their greater numerical abundance, they constituted in terms of volume the largest single fraction within the size range 1–12 μm. Thus it seems clear that any proposed filtration mechanism for the lamellibranch gill must explain not only the complete retention of particles larger than 2–3 μm but also the significant retention of particles in the 1–3 μm range and possibly smaller.

To explain the retention of small particles, MacGinitie (1941, 1945) suggested that the lamellibranch gill, when functioning normally, is covered by a continuous sheet of mucus which serves as the filter. Most workers, however, prefer the classic theory—namely, that it is the laterofrontal cirri which are primarily responsible for the filtering activity of the gill. The main difficulty is that the distance between adjacent laterofrontal cirri is some 2.0 to 3.5 μm, depending on the species, and while this might allow for the efficient retention of particles above 3–4 μm, it does not explain the high retention of smaller particles. It has been suggested that the laterofrontal cirri are sticky and that it is this property which accounts for the high retention of small particles (Wallengren, 1905; Tammes and Dral, 1955; Dral, 1967).

A recent paper by Moore (1971) offers a fascinating and convincing explanation for the filtering efficiency of the lamellibranch gill. Each laterofrontal cirrus consists of a double row of cilia (20–25 pairs) which, in the active gill, beat as one in a plane at right angles to the long axis of the filament. Examination of the cirri under the scanning electron microscope (Fig. 1B) reveals that each pair of cilia bends, one on either side of the main axis of the cirrus, to extend across the intercirrus space. This bending occurs at regular intervals along the length of the cirrus for each pair of cilia, and the cirrus ends with a bifurcation formed by the separation of the longest pair of cilia. The effect is to form a meshwork between the cirri and between adjacent filaments (Fig. 1A). Detailed measurements are given by Moore (1971) but in *M. edulis*, for example, the arrangement forms a filter with a mesh size of 2.7×0.6 μm. A number of questions remain unanswered, but this arrangement

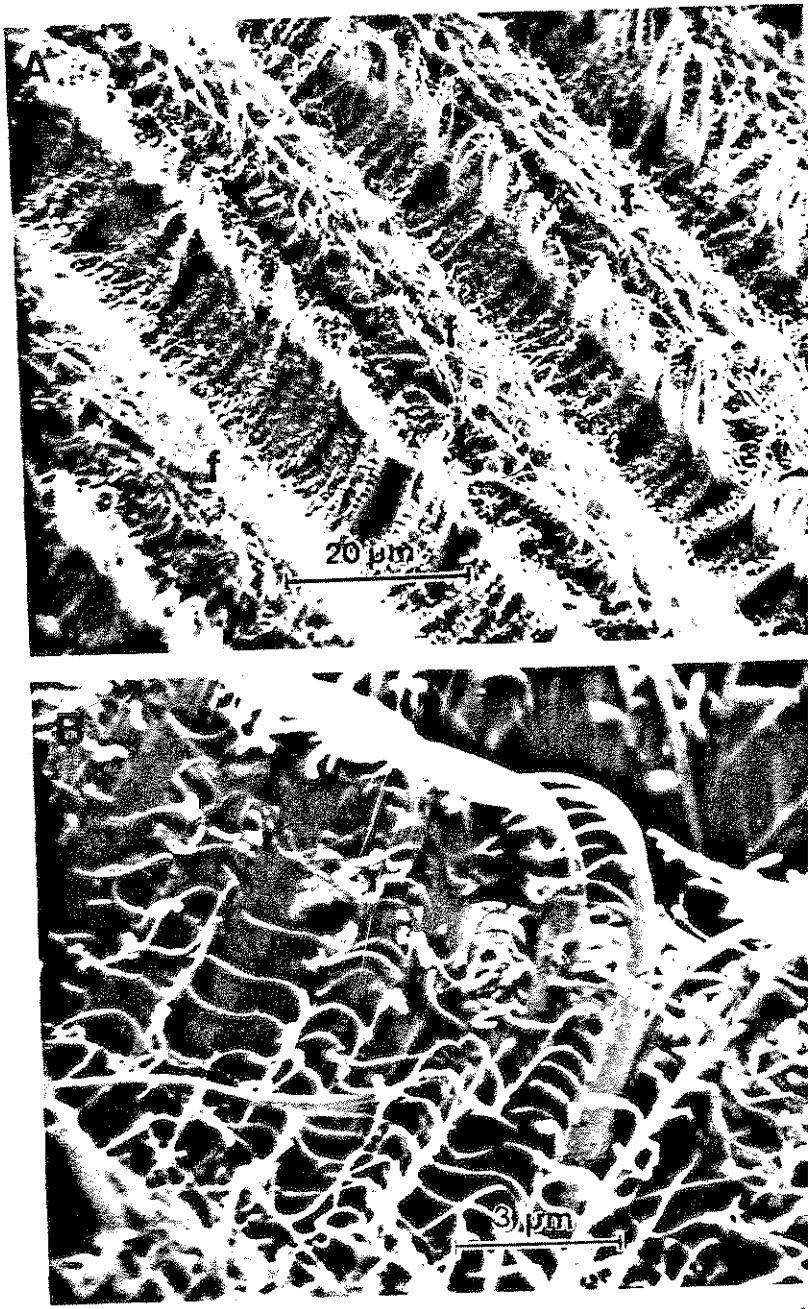

FIG. 1. *Mytilus edulis*. Scanning electron micrographs of (A) the frontal of the gill viewed at an angle of 45° and showing the frontal faces filaments (f) with the laterofrontal cirri extending across the interfilamen (×1200) and (B) the detail of the laterofrontal cirri (×7000).

clearly offers an explanation of the high retention of particles of 1–2 μm recorded for this species by a number of workers.

V. The Digestive System

The alimentary canal in the Bivalvia consists of a simple tubular œsophagus, a complex globular stomach and style sac, with associated midgut glands or digestive diverticula, and a variously coiled intestine somewhat arbitrarily divided into a midgut and hindgut. The stomach, style sac, and digestive diverticula are the most complex regions of the gut and show considerable variation throughout the class. Essentially, the stomach is a globular structure with much of the internal surface of the left wall covered by a variously developed gastric shield and the remainder ciliated. The ciliated region may be thrown into a complex pattern of folds and ridges to form sorting areas associated with the apertures of the ducts to the digestive diverticula and the opening to the intestine. In the Protobranchia, the style sac forms a passageway between the stomach and the intestine, but in the remaining bivalves the style sac is functionally, and frequently morphologically, isolated from the adjacent intestine and contains a crystalline style which projects into the stomach (Owen, 1966b). The digestive diverticula consist of numerous blind-ending tubules which communicate with the stomach by a system of ducts.

Ingested material passes from the esophagus into the stomach where it is subjected to the action of enzymes released from the crystalline style, also possibly the digestive diverticula and gastric wall, and to the ciliary sorting mechanisms of the stomach. The effect of the latter is that "accepted" material is directed toward the openings of the ducts leading to the diverticula, while "rejected" material is passed to the intestine. Of particular significance in this context is the intestinal groove and associated major and minor typhlosoles. The groove serves to convey material from the stomach, and in many cases from the digestive diverticula to the intestine. Thus, the disposition of the groove has a major influence on the passage of material through the stomach.

There is general agreement that the digestive diverticula function primarily as organs of intracellular digestion and absorption, but it is possible that in certain bivalves they also have a secretory function and produce enzymes which act extracellularly. Earlier workers considered that the intestine served solely for the conduction and formation of fecal material, but it now appears, as will be discussed later, that the digestive and absorptive roles of the intestine, at least in certain bivalves, are greater than had been previously realized.

The association of zooxanthellae with members of the Tridacı well known, and it has been suggested that the remarkable hype of the siphonal tissues in these bivalves is correlated with their uti or "farming," of the algae as a holozoic food source (Yonge, 1936, Fankboner (1971) has suggested that the relationship cannot l considered as farming but rather as a slow systematic removal and degenerate zooxanthellae which may represent a hazard to th They are intracellularly digested by amebocyte lysosomes both circulatory system and in the intertubular spaces of the digestiv ticula. Electron micrographs show that the microvillous borde hypertrophied siphons endocytoses considerable amounts of mate the seawater, and Fankboner suggests that this may make a si contribution to the nutrition of the animal. In a recent paper *et al.* (1973) conclude that the Tridacnidae appear to obtain the benefit from their zooxanthellae by way of photosynthetates rat by digestion of older algal cells with amebocytes.

A. *The Stomach and Style Sac*

Purchon (1959, 1963) has suggested that variation in the mc of the stomach is of phylogenetic significance. On the basis of th tion of the intestinal groove and associated typhlosoles, and t tionship to certain ducts from the digestive diverticula, he has r five main types as a basis for taxonomic division. These are th proteia (Protobranchia), Gastrodeutia (Septibranchia), Ga (most of the Filibranchia), Gastrotetartika (the remainder of branchia and many Eulamellibranchia), and the Gastropempt mainder of the Eulamellibranchia). On the basis of the numbe opening into the stomach, the five orders are grouped into two s The Protobranchia and Septibranchia, as bivalves with few duc into the stomach are placed in the Oligosyringia, while the three orders, in which many ducts open into the stomach, are the Polysyringia; they constitute the lamellibranchiate biva

The proposal to unite the Protobranchia and Septibranchia same subclass on the basis of the number of openings of th the digestive diverticula into the stomach has been criticized mani (1967). In both, the diverticula communicate with the s two or three openings, but in the Nuculidae the duct syste branched, while in the Septibranchia there is practically no d Dinamani concludes that the simple stomach of the Septibr pears to have no relationship with the stomach types of othe It is worth noting, however, that the Nuculanidae, in cont

Nuculidae, possess a group of "specialized" diverticula in which the duct system, like that of the Septibranchia is poorly developed (Owen, 1959).

Irrespective of whether the five characteristic stomach morphologies described by Purchon have any taxonomic significance, they do appear to be related to patterns of digestion. In the Protobranchia, digestion appears to be largely extracellular and takes place within the lumen of the stomach. Indeed, it was originally believed to be entirely extracellular in the Nuculidae (Owen, 1956), but electron microscopic examination has shown that the digestive cells lining the tubules possess a well-developed lysosomal system and do ingest material derived from the stomach (Owen, 1973). Little is known of the digestive processes in the Septibranchia, but the cells lining the tubules of the diverticula are capable of ingesting relatively large particles. In the Polysyringia (lamellibranchiate bivalves), the distribution of enzymes suggests that while digestion is largely intracellular in the Gastrotetartika, there is increased extracellular digestion in the gastric cavity of both the Gastrotriteia and Gastropempta; in the latter the role of the midgut as an organ of digestion and absorption is also much increased (Reid, 1966, 1968).

1. *The Gastric Shield*

An extensive cuticle covered region of the stomach wall appears to have been a feature of the primitive mollusc (Morton, 1953) and occurs in the Septibranchia (Yonge, 1928) and Protobranchia (Owen, 1956). In most bivalves, however, the cuticle is stouter, usually modified into one or more toothlike thickenings, and reduced in area to form the gastric shield. It covers that region of the stomach wall against which the crystalline style impinges and is generally regarded as serving to hold the head of the style, and, according to some workers, to assist in the trituration of the gastric contents by a type of pestle and mortar action. Earlier workers (Berkeley, 1935; Shaw and Battle, 1959) demonstrated the chitinous nature of the gastric shield, but until recently there had been few investigations of its structure and properties, possibly because it has been regarded as an inert structure serving primarily to protect the underlying epithelium.

Kubomura (1959) described the gastric shield of *Meretrix meretrix* as lying freely on a ciliated epithelium and consisting of an outer, probably collagenous layer and an inner, harder chitinous layer. Chitin has also been recorded in the gastric cuticle and shield of *Nucula sulcata* (Halton and Owen, 1968) and *Lasaea rubra* (McQuiston, 1970), respectively; and while electron microscopic studies did not confirm the presence of cilia, they did show that microvilli extend from the underlying epithelial cells

through the matrix of the cuticle and shield to the free surface. Mor
it now appears that like the so-called stomachal plates of the op
branch gastropods, *Dolabella scapula* (Hashimoto *et al.*, 1951
Aplysia punctata (Stone and Morton, 1958), the gastric shield is
matically active. Kubomura (1959) found the amylase activity
gastric shield of *Meretrix* to be greater than that of the stomacl
style sac, and crystalline style, while Halton and Owen (1968) d
strated a strong reaction for acid phosphatase and weaker reactic
nonspecific esterase and arylamidase in the gastric cuticle of *Nucu*
significance of the enzymes associated with the gastric shield is unc
It has been suggested that the production of a chitinous matrix b
the microvilli may serve to protect them from the head of the cry
style while still allowing the underlying epithelium to continue it
tory functions (Halton and Owen, 1968).

2. *The Crystalline Style*

A crystalline style is found in all bivalves except the Protob
and consists of an elongated hyaline rod, the outer layers of wl
relatively firm and which surround a more liquid core. Since th
review (Owen, 1966b), additional information has been publishe
secretion (Goreau *et al.*, 1966; Morton, 1969a; Wada, 1969a,b
1970), chemical nature (Doyle, 1966; Bedford and Reid, 19
physical properties (Kristensen, 1972b) of the style.

It now seems clear that the matrix of the style is secreted by
of the typhlosole, although the rate of secretion would appear
in different species. Wada (1969b) found that in the pearl oyst
tada fucata, in which the styles had disappeared after a period i
sea water, some 9–14 days were required for the reformation of
when the animals were returned to natural conditions. Kristense
left animals in sea water containing trypan blue until the st
uniformly stained (12–18 hr); they were then transferred to
water. The results indicated that the styles of *Abra nitida* wer
every 4 hr and those of *Macoma balthica* every 24 hr.

Investigation of the chemical nature of the crystalline style
and *Cardium* showed that some half of the organic matter of
was protein, at least some of which was closely bound to car
(Doyle, 1966). The carbohydrate content included the neut
mannose, galactose, fucose, xylose, deoxyribose, and glucose
amino sugars glucosamine and galactosamine; the hexosamines
titatively the most important sugars in the style. The ratio of de
phosphorus in both styles was close to 1:1 *M*, and Doy

TABLE IV
pH OF REGIONS OF THE GUT OF *Ostrea edulis*

	Yonge (1925)	Mathers (1973c)	
		Mean	Range
Stomach contents	5.5	6.0	5.5–7.2
Digestive diverticula	5.7	6.15	5.8–7.2
Crystalline style	5.2	6.6	6.3–7.2
Midgut	5.7	7.1	6.5–7.7
Rectum	6.0	6.4	6.2–6.5

that this is more likely to indicate a nucleotide than a nucleoside, as earlier suggested by Hashimoto and Sato (1955) from their study of the style of *Mactra*. Kristensen (1972b) has reported on certain physical properties of solutions of style material. The surface tension is lowered, the viscosity increased, and oil is efficiently emulsified in such solutions, and he suggests that these factors may be important in the sorting of particulate material in the stomach.

Earlier statements (Owen, 1966b) that the crystalline style is the most acid structure in the bivalve gut and that the pH of the gastric fluid varies little, if at all, must be reconsidered (Purchon, 1971). It now seems clear that the style is not the most acid part of the gut and that the pH of various regions of the gut, including that of the style, may vary considerably (Table IV). Langton (1972) found that the mean pH of styles of *O. edulis* collected from the shore was 6.5 (range 6.0 to 6.8) while the mean of specimens kept totally immersed in an aquarium tank was pH 6.0 (range 5.8 to 6.5). As will be discussed later, it would appear that variations in the pH of the style are associated with the feeding activities of the animal. When oysters are actively ingesting food, the pH of the style rises, but when food is not being ingested, the pH of the style falls. Mathers (1973c) suggests that the acidity of the gastric contents, which may be as low as pH 5.5, is due to the dissolution of the style and to acid secretions from the digestive diverticula.

B. *The Digestive Diverticula*

There have been a number of investigations of the ultrastructure and histochemistry of the digestive diverticula since the previous review (Owen, 1966b). They confirm that the numerous spheres which characteristically fill much of the cytoplasm of the acidophilic or digestive cells

lining the blindly ending tubules form a lysosomal system which to process exogenous material ingested by endocytosis from the of the tubule (Owen, 1972b). In the various species examined, ther been identified (a) small coated pinosomes in the apical cyt (Owen, 1970); (b) larger, often irregularly shaped heterophagoso the subapical region and within which the exogenous material i accumulates (McQuiston, 1969; Pal, 1972); (c) spherical hete somes (characterized by a pronounced "halo" beneath the limitin brane), the contents of which give positive reactions to tests f hydrolases (Sumner, 1966a,b, 1969; Owen, 1972b); and (d) bodies typically enclosed by two membranes (Owen, 1970, 197 all the species examined, the dispersed Golgi bodies or dictyos the digestive cell show a characteristic structure. The distended eral regions of each Golgi saccule contain membranous elements representing small disc-shaped vesicles packed closely together (I ton, 1969; Owen, 1970, 1973; Pal, 1972). It is possible that prima somes originate from the dictyosomes.

The structure and function of the digestive diverticula of th branchiate bivalve, *Nucula sulcata*, were reported to differ fro of lamellibranchiate bivalves (Owen, 1956). Apart from the uniq tion of the duct system, feeding experiments as evaluated by ligh scopy, showed no evidence of phagocytosis or of intracellular within the cells lining the tubules, and it was concluded that was exclusively extracellular. Feeding experiments with ferritin, by electron microscopic examination, have shown that the diges lining the tubules do possess a lysosomal system within which e material is digested (Owen, 1973). It would appear, however, mode of functioning of the diverticula is such that only fluid and of macromolecular dimensions resulting from the extensive ext digestion in the gastric cavity are able to enter the diverticula. I branchiate bivalves, relatively large particles up to and includ algal cells may reach the tubules of the diverticula to undergo en by the digestive cells (Mathers, 1972).

The precise nature and role of the darkly staining cells, whi the well-defined crypts of the tubules of eulamellibranchs an clusters between the digestive cells of protobranchs and filibr mains uncertain. Observations on the repair of digestive tubule *sostrea gigas* (Mix and Sparks, 1971) damaged by ionizing rad pear to support the earlier view that the darkly staining cells nests of young cells serving to replace the digestive cells (Yo Regeneration of the tubule epithelium started with the app nests of darkly staining cells formed, it was suggested, by t

division of either uninjured or repaired "crypt" cells. Electron microscopic examination of the crypt cells of normal animals indicates, however, that while in some species they appear to consist of but one cell type—the so called basophilic cell—in other species, more than one cell type is present (Owen, 1972b).

The basophilic cell, as originally described by Sumner (1966b), appears to be invariably present; it exhibits features normally associated with the synthesis and export of protein (McQuiston, 1970; Owen, 1970; Pal, 1971). It is pyramidal in shape and much of the cytoplasm is filled with a rough endoplasmic reticulum. The well-developed Golgi apparatus is quite unlike that of the digestive cell and gives rise to membrane bound vesicles which migrate to the tapering apical region of the cell bordering the lumen of the tubule. In *N. sulcata,* where it appears to be the only type of cell forming the nests of darkly staining cells, it bears a single flagellum (Owen, 1973).

In *Cardium edule,* a slender, columnar, flagellated cell is also present in the crypts in addition to the nonflagellated basophilic, pyramidal cells, and Owen (1970) has suggested that the former may serve to replace the digestive cells. In *Tridacna,* three types of cell have been described within the nests of crypt cells. In addition to basophilic and flagellated cells, there are smaller stem cells which do not extend to the lumen of the tubule. Fankboner (1970) has concluded that it is these stem cells which give rise to both the flagellated cells and basophilic cells and, while the former represent mature cells, the latter represent transitory stages in the formation of mature digestive cells. Thus while some workers (Sumner, 1966b; McQuiston, 1969; Owen, 1970) believe that the pyramidal, basophilic cell, represents a mature secretory cell, possibly producing enzymes which act extracellularly, it is also clear that the nests of darkly staining cells remain a possible source for the replacement of the digestive cells.

Experimental proof of what has been suspected for some time, namely, that the ducts may play a significant role in the digestive and absorptive functions of the diverticula, has been provided by Mathers (1972). Specimens of *O. edulis* fed algal cultures labeled with ^{14}C showed that soluble or finely particulate material was quickly absorbed by the brush border epithelial cells lining the ducts. The experiment also provided support for the counter-flow hypothesis originally proposed to explain a simultaneous two-way flow within the ducts although the cilia present all beat toward the stomach (Owen, 1955). ^{14}C activity appeared first (within 10 min) in those regions of the ducts lined by a brush border epithelium and did not occur in the lumina of the ciliated gutters until some 90 min after the start of the experiment.

Peroxisomes, previously demonstrated in vertebrates and
in the animal kingdom, have recently been identified in the
the digestive diverticula of certain bivalves (Yokota, 1970, 19
1972a; Pal, 1972). In castor bean endosperm, peroxisomes are
with the key enzymes of the glyoxylate cycle and serve for the
of the fat stores of the seed into utilizable carbohydrates (Beev
In the protozoan, *Tetrahymena*, only the glyoxylate bypass e
associated with peroxisomes and again they are thought to be
in gluconeogenesis (Müller *et al.*, 1968). Large amounts of g
known to accumulate in many bivalves and there exists the
that peroxisomes, linked with glyoxylate cycle enzymes, may
in this process and capable of utilizing certain amino acids
fatty acids for glycogen formation. A recent examination of t
adductor muscle of *M. edulis* for malate synthase and isoc
gave negative results (de Zwaan and van Marrewijk, 1973). T
summary of their paper suggest that the results can be exte
whole animal, but it is clearly desirable that similar tests
out on extracts of the digestive diverticula. One would ex
glyoxylate cycle enzymes in tissues with a high lipid content.
occurrence of these enzymes in bivalves is still unanswered.

C. *Enzymes*

Histochemical surveys of the alimentary tract of bivalves
hydrolytic enzymes are located chiefly in the digestive divert
ing the epithelia lining the ducts, certain regions of the gas
sac epithelia, and in the epithelium lining the midgut (S
Reid, 1968; Mathers, 1973a). Of particular interest is the
activity associated with the ducts of the digestive div
Mathers (1972) concluded, on the basis of the increased ac
the cells and lumina of fed animals, that they are active
zyme secretion. Indeed, while there is general agreement
in the bivalves is predominantly intracellular, there is an in
of opinion that extracellular processes may be of greater sig
previously realized.

A wide range of carbohydrases capable of degrading m
galactosides, and a number of polysaccharides have been
the digestive tract of bivalves (Kristensen, 1972a; Mather
presence of amylase in the crystalline style has been report
and in general exhibits greater activity than that of the d
ticula (Owen, 1966b). In the deep sea scallop, *Placopecte*
acetone powder extracts of the style gave a specific activi

protein compared with the low value of 0.04 U/mg protein for similar extracts of the digestive diverticula (Wojtowicz, 1972). Amylase activity has also been reported in the gastric shield of *M. meretrix* (Kubomura, 1959) and extracts of the gastric wall of *O. edulis* (Mathers, 1973d). The styles of a number of bivalves show high activity for "laminarinase," probably a multicomponent enzyme which includes exo- and endo-hydrolytic β-1,3-glucanases and β-glucosidases (Sova *et al.*, 1970; Wojtowicz, 1972). Carbohydrases associated with the digestive gland include α- and β-glucosidase, α- and β-galactosidase, and chitiobiase (Sumner, 1969; Wojtowicz, 1972; Mathers, 1973d).

It is provisionally accepted that the degradation of native cellulose to glucose requires three enzymes. First, a true cellulase (C_1) capable of acting on native cellulose, second, a poly-β-glucosidase (C_x) acting on regenerated cellulose, soluble cellulose derivatives such as carboxymethyl cellulose and the products of cellulase activity, and third, β-glucosidase, such as cellobiase, capable of converting the oligosaccharides produced by the first two enzymes to glucose. The distribution of digestive cellulolytic enzymes, as recorded by earlier workers but interpreted in the light of the above scheme and based on the specificity of the enzymes involved to particular substrates, has been tabulated by Payne *et al.* (1972). Crosby and Reid (1971) concluded that high cellulase activity was related mainly to the cellulose content of the food. This conclusion needs to be reexamined, however, since their assessment of digestive cellulolytic activity did not meet the criteria outlined above. It would appear that a true cellulose (C_1) has in fact been demonstrated in the crystalline style and digestive diverticula of only a limited number of bivalves, in contrast to poly-β-glucosidase (C_x) and β-glucosidase activity, which are widespread in the class. A comparison of the digestive cellulolytic activity of the style of *Cardium edule* and the crop juice of the gastropod *Helix pomatia* indicate that while the latter possesses a true cellulase (C_1), and two parallel working enzymes (C_x, a and b) acting on degraded celluloses, the former does not possess a true cellulase, and the breakdown of degraded celluloses is mediated by a single enzyme (Koopmans, 1970).

In *Scrobicularia plana* a true cellulase (C_1) together with a poly-β-glucosidase (C_x) occurs in the crystalline style, digestive diverticula and midgut; β-glucosidase activity is exhibited only by the digestive diverticula and midgut (Payne *et al.*, 1972). The β-glucosidase activity of the digestive diverticula showed two peaks of maximal activity at pH 5.5 and 4.45, suggesting that there are two β-glucosidases associated with cellobiose hydrolysis and the authors suggest that one may be concerned with extracellular and one with intracellular digestion. Of particular in-

terest is the complete cellulolytic system associated with the midgut, i cating again that this region may play a more important role in dige and absorption in the bivalves than previously realized. It would ap that the ability of *Scrobicularia* to digest cellulose is a property o animal itself, since none of the seventeen bacterial strains isolated the gut showed any cellulolytic activity.

A comparative study of the proteinases of a wide range of marin vertebrates, including extracts of the digestive diverticula of a nu of bivalve species, show that the class exhibits relatively weak protec activity (Kozlovskaya and Vaskovsky, 1970). Under the conditio the survey no activity was recorded for some species, and even th *Mya arenaria*, which had the highest level of activity among the biv tested, was well below that of members of the Cephalopoda, Crus and Asteroidea. As indicated in the earlier review (Owen, 1966b) greater part of protein digestion in bivalves takes place intracell within the digestive cells of the tubules of the diverticula. In a nu of bivalves, the pH activity for the enzymes involved showed three at about pH 3, pH 5.5, and pH 7.5 to 8 (Reid and Rauchert, 1970, The alkaline endopeptidase has chymotryptic activity and Rei Rauchert suggest that the acid endopeptidase with an optimum region of pH 3 may be similar to vertebrate cathepsins D and E. Gastrotetartika, all three endopeptidases showed similar activity the Gastrotriteia and Gastropempta the chymotryptic activity is and the greater part of the intracellular digestion of protein is unc influence of acid endopeptidases (Reid, 1968). Extracellular tryptic ity, pronounced in the Gastropempta, has been recorded in the juice. Reid and Rauchert (1972) believe it may be derived from the tive diverticula and suggest that there is possibly a phylogenetic of intracellular chymotrypsin and extracellular trypsin in the bi Tryptic activity has also been recorded from the midgut of the pempta (Reid, 1968).

Reid (1968) also studied the distribution of esterases in bival a pattern somewhat similar to that for proteases emerges. In a to the expected activity in the style sac and digestive diverticu Gastropempta exhibited strong esterase activity in the stomach a gut, compared with the moderate to weak activity of these re the Gastrotriteia and Gastrotetartika. In an analysis of the este the stomach and digestive diverticula of eight species of *Mactr* and Dunnill (1969) found that one aliesterase was common to species while *M. secta* differed from the other species in that gastric and diverticular zymograms were identical. They conclu

in this species, the diverticula actively secrete esterases to an extent which is unusual in lamellibranchiate bivalves. In this context, it is interesting to note that Mathers (1973a), using histochemical techniques for the demonstration of nonspecific esterases, found that the epithelium of the ducts of the diverticula, stomach, and midgut, together with the gastric shield, showed the greatest activity in *O. edulis* and *C. angulata*. Esterase was also demonstrated in the lumen of the digestive diverticula ducts of fed animals.

VI. Feeding and Digestive Rhythms

It has been generally assumed that the processes of feeding and digestion in lamellibranchiate bivalves, provided the environmental conditions are satisfactory, take place more or less continuously and simultaneously. A periodicity is imposed on the feeding of the small intertidal bivalve *Lasaea rubra* which, at its upper littoral limit, may be submerged for an average of only 1 hr in 12 hr (Morton *et al.*, 1957). The style is partly dissolved as the tide ebbs and rapidly reforms again on the return of the tide (J. E. Morton, 1956). Although there is no period when all the cells lining the tubules of the digestive diverticula are at a particular stage, it is possible to recognize a well-marked predominance of activity which can be correlated with the various times of submergence and exposure by the tide. The phases of activity are absorption, intracellular digestion, and excretion or fragmentation, until finally, after some 8 hr exposure, many of the tubules are devoid of cells.

The same four stages were recognized in *Lasaea* by McQuiston (1969), but he found that two opposing stages of the cycle, rather than one, predominated at any given time. He interpreted this to mean that a complete cycle for a given tubule took place every 24 hr and not every 12 hr as suggested by Morton. Thus, in a single tidal cycle roughly half the tubules comprising the digestive diverticula started in a mature condition and finished empty, while the remainder started empty and finished in the mature phase. McQuiston related this diphasic cycle to the requirements for both intracellular and considerable extracellular digestion which occur in this animal in each tidal cycle (Ballantine and Morton, 1956).

It has been suggested that a rhythmic mode of feeding and digestion may apply to bivalves in general, each cycle comprising well-defined phases of feeding, extracellular digestion, and intracellular digestion (B. Morton, 1969a,b, 1970a,b, 1971a). Morton (1969a) found that the

freshwater bivalve, *Dreissena polymorpha*, possessed a diurnal r
of adductor activity in which the shell valves were shut on aver
hr a day and for the remaining 12 pumped water into and out
mantle cavity by phasic contractions of the adductor muscles. Th
mals filtered and ingested material only during the periods of acti
duction and this rhythmic feeding regime was correlated with w
fined and separate periods of extra- and intracellular digestion. Th
was secreted during the periods of active adduction and underwe
solution during quiescent periods.

A similar cycle, in this case correlated with the tidal cycle, ha
outlined for *Cardium edule* and *Ostrea edulis* (Morton, 1970a,
Feeding occurs over the high tide period, and it is claimed that i
material is not passed to the digestive diverticula until the suc
rising tide; during the intervening period of low tide it undergoes
cellular digestion in the gastric cavity. Intracellular digestion is f
during the ebb and low tide periods by the fragmentation of the d
cells and the preparation of the tubules for a fresh influx of n
on the following rising tide. In *Ostrea*, the volume of the style
a decrease from 25 mm^3 to 1–4 mm^3 during each tidal cycle.

The correlation of the feeding and digestive processes of *Ostr*
the tidal cycle is particularly interesting since, unlike *Cardium*,
mals used by Morton did not occur intertidally; they were collect
Burnham-on-Crouch where they were covered by some 10 ft o
at low tide. Specimens were transported to Portsmouth where th
kept totally immersed in a large sea water tank for 2 days prio
start of the experimental period. The rhythm of feeding and d
outlined above was correlated with the tidal cycle at Burnl
Crouch.

Morton's interpretation of the digestive cycle has been pres
some detail since, if accepted, it will require a complete reapp
the mode of functioning of the stomach and digestive diverticula
libranchiate bivalves (Purchon, 1971). The main features of
hypothesis are that feeding in the bivalves is rhythmic and, c
with this, extracellular digestion in the stomach and intracellul
tion in the digestive diverticula are organized in strictly al
phases. As a consequence the processes of regeneration, absorptic
tion, and disintegration by the digestive cells show a pronoun
chrony throughout the diverticula.

Winter (1969, 1970) reported that the filtration rates of *Ar*
Modiolus, both sublittoral bivalves, showed two phases of high
which alternated with two periods of low activity during a 24-h
Hughes (1969) was unable to find any evidence of an endogenou

in the pumping rate of the intertidal bivalve *Scrobicularia plana* and could not induce a rhythm in animals subjected to alternating 6 hr periods of exposure and submersion. Rao (1953) claimed that a tidal rhythm in the pumping rates of *Mytilus edulis* and *M. californianus* persisted for some weeks under constant laboratory conditions, but this has not been confirmed by other workers (Jørgensen, 1960; Theede, 1963; Davids, 1964). Thompson and Bayne (1972) concluded that *M. edulis* filters continuously if food is present and provided the particle concentration does not exceed certain limits. Thus, the evidence for a rhythmic pattern of feeding in bivalves, other than that imposed by environmental factors, is equivocal. Moreover, while certain bivalves may exhibit a diurnal rhythm of adductor activity, there is some doubt that bivalves pump water and ingest food only during periods of active adduction. Drinnan (1964) records that in the absence of shell movement *O. edulis* maintained a steady pumping rate of 4 l/hr.

It is clear, however, that a rhythmic pattern of feeding is imposed on intertidal bivalves, and the important question is how this may affect the pattern of digestion. Langton (1972) collected oysters from the level of low-water spring tides at regular intervals of time over the tidal cycle; they were exposed to air at low water. Generally, large amounts of food were found in the stomachs of samples taken during high tide, while the stomach was apparently empty in those taken during low tide. The latter is the period when, according to Morton, material collected during the preceding high tide is undergoing extracellular digestion within the gastric cavity. Morton also recorded during each tidal cycle a decrease in the volume of the style of *O. edulis* equal to some 85% of the maximum style volume, but out of 100 specimens examined by Langton only two had no style and the largest recorded difference was from 32 mm^3 to 15 mm^3, i.e., a 53% decrease in volume.

Langton found a significant correlation between the total style protein and the tidal cycle when this was shifted —3 hr out of phase with the sample time; i.e., the protein content of the style was at a maximum 3 hr after high tide. There was a highly significant correlation between the total style protein and amylase protein, implying that there is also a tidal rhythm for style amylase. The pH of the style also varied with the tidal cycle, ranging from pH 6.0 at low tide to about pH 6.8 at high tide. No correlation was found between either the amylase activity or the pH of the digestive diverticula (approximately 6.5) and the tidal cycle. Langton did find, however, a significant difference in the α-amylase activity of the digestive diverticula of oysters collected at night (low) compared with those collected during daytime (high), suggesting the existence of a diurnal rhythm. The correlations between the tidal cycle and

the pH and protein content of the crystalline style were not maint
in animals kept continuously immersed in aquariums under labor
conditions (Langton and Gabbott, 1974).

Langton noted that while the pH and size of the style of *Ostrea* v
systematically with the tidal cycle, the maximum style size correspo
to the time when there was the greatest amount of food in the sto
Thus the changes in the style may simply reflect variations in ava
food levels rather than a pattern of rhythmic digestive activity.

Owen (1972b) has suggested that the activity of the digestive
ticula may be similarly controlled by available food levels rather
by any rhythmic pattern of digestion. Certainly the claim that ma
ingested during one high tide is held in the stomach to undergo extra
lar digestion during the low tide period, before being passed to the
tive diverticula on the following rising tide is difficult to maintain.
is ample evidence that particulate material, once ingested, passes r
into the digestive diverticula. Mathers (1972) found ^{14}C activity p
in the lumina and epithelia of the ducts and tubules of the digestiv
10 min after feeding *O. edulis* with ^{14}carbon-labeled algae; within 9
active material was moving out of the tubules toward the stoma

Owen (1972b) examined sections of the digestive diverticula of *C.*
taken at short intervals of time over the whole tidal cycle. He sug
that during the period when food is not available, i.e., at low tic
digestive cells lining the tubules assume a similar appearance wh
termed the "holding phase." When the animals are covered by the
tide, food is ingested and rapidly reaches the tubules of the dive
to be endocytosed by the digestive cells and to undergo intracellu
gestion within the lysosomal system. During this process the cells i
in height and residual bodies are formed. In *Cardium*, these are
nated within the abstricted apices of the cells, which subsequently
to a low cuboidal form. At all stages during this cycle the digesti
continues to endocytose material from the lumen of the tubule a
cycle is continued as long as food is available. Moreover, individ
bules or groups of tubules pass through the cycle at different rates
bly due to variation in the "delivery" of food to different regions
diverticula. As a consequence, the homogeneous or synchronous
ance of the diverticula is gradually lost during feeding. When the
are again uncovered by the tide, or the food supply is exhaust
cycle is continued only to the holding phase and this is maintain
food is again available.

Variations of this cycle as outlined for *Cardium* clearly exist i
ent species of bivalves. Owen (1972b) suggested that such variati
be dependent on (a) whether feeding is correlated with externa

ternal rhythms, (b) the nature of the food ingested, and (c) the mode of release of the residual bodies, i.e., whether or not the individual digestive cells break down completely in each cycle. In any case it would appear that the alimentary canal of lamellibranchiate bivalves is designed to process particulate food more or less continuously and that extracellular digestion in the stomach and intracellular digestion in the digestive diverticula are not organized in strictly alternating phases as suggested by Morton. The extent to which any particular item of food is subjected to extracellular processes in the gastric cavity will depend rather on the nature and size of the food particle and the amount of food present in the stomach.

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