

A NEW THEORY OF FEEDING AND DIGESTION IN THE FILTER-FEEDING  
LAMELLIBRANCHIA

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## ABSTRACT

Recent observations regarding the feeding and digestive processes of the filter-feeding Lamellibranchia do not find accord with the currently accepted concept of continuous and simultaneous feeding and digestion in these animals.

A new theory embracing both the old and the new facts is put forward in which these processes are considered to be rhythmic in nature.

## INTRODUCTION

Amongst the Bivalvia, the Lamellibranchia form a relatively homogenous grouping but most taxonomists agree are distinct from the Protobranchia, e.g., Ridewood (1903), Pelseneer (1911), J. E. Morton (1967), Owen (1959), Purchon (1959), Yonge (1959). The Septibranchia are linked by some with the Lamellibranchia, e.g., Newell (1965), J. E. Morton (1967), but not by others, e.g., Pelseneer (1911), Purchon (1960, 1962).

In the primitive Protobranchia the digestion of food is considered to be mainly extra-cellular (Owen, 1956), whilst there is a paucity of information on the feeding and digestive processes of the scavenging Septibranchia (Yonge, 1928).

The Lamellibranchia (constituting the majority of the Bivalvia) exhibit a wide variety of form and exploit a wide range of aquatic environments. They do, however, possess many common features not the least of which is that they are mostly filter-feeders and that the process of digestion is both extra-cellular and intra-cellular.

The processes of feeding and digestion in the Lamellibranchia are considered to be continuous and simultaneous. Owen (1966) states that "the more or less continuous mode of feeding which characterises the majority of bivalves would seem to preclude a synchronous activity of the digestive system." Purchon (1968) can also be quoted as reporting that "It is generally considered that feeding and digestion are continuous processes in bivalves, new food material being added all the time, and unwanted material being as constantly eliminated by passage into the mid gut." Purchon (1971) has, however, subsequently suggested, in the light of new evidence, that these processes may not be continuous and that a reappraisal of current thought on this subject is called for.

Owen (1955) showed how such a continuous system could operate, and there can be little doubt that the components of the feeding and digestive processes he elucidated do operate in the Lamellibranchia. This is not questioned. The purpose of this paper is to demonstrate that these component processes do not necessarily occur simultaneously and continuously and to show that feeding and digestion in the Lamellibranchia is a dynamic process.

## THE PRESENT THEORY

It is generally assumed that members of the Lamellibranchia are filtering suspended or deposited material from the water continually, this process being the function of the ctenidia.

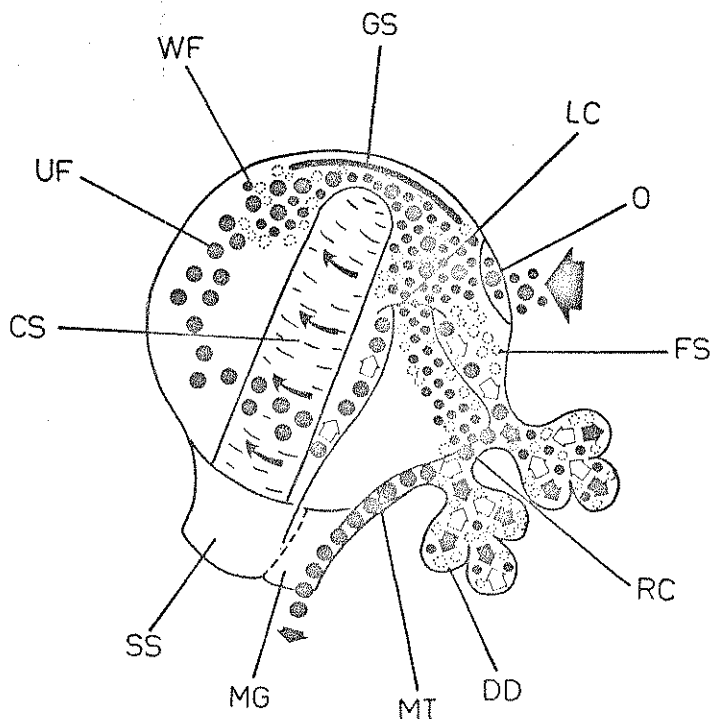


FIG. 1. A diagrammatic representation of the suggested functioning of the stomach and digestive diverticula of the Eulamellibranchia, CS, Crystalline style; DD, Digestive diverticula; FS, Fragmentation spherules; GS, Gastric shield; LC, Left caecum; MG, Mid gut; MT, Major typhlosole; O, Oesophagus; RC, Right caecum; SS, Style sac; UF, Large unwanted particles; WF, small food particles. (After Owen, 1955.)

As the water is passed through the ctenidia exchange of oxygen and carbon dioxide takes place and particulate material is abstracted and passed either up or down the gill lamellae to be concentrated in mucoid strings and passed anteriorly. Large particles are removed by ciliary sorting mechanisms on the ctenidia and also by powerful ciliary tracts on the mantle and visceral mass and passed posteriorly to be ejected as pseudofaeces via the inhalant opening. From the ctenidia particles are passed to the labial palps where further rigorous sorting takes place. Finally, particles of a suitable size are passed to the mouth where they are ingested (Atkins, 1936, 1937a, b, 1938).

In the stomach the mucoid food string becomes wound around the crystalline style (Fig. 1, CS) which acts as a capstan, winding in the string. The tip of the style revolves against the gastric shield (GS) and it is assumed that this action mechanically breaks up the food material; the style dissolves as it rotates, releasing extra-cellular enzymes bound up in its matrix. Since the style is continually dissolving distally it must be continually secreted at its basal end. As the food is broken up it is subjected to further sorting in the stomach and large indigestible particles are passed to the mid gut (MG) in the intestinal groove of the major typhlosole (MT). Small particles are continually being passed to the digestive diverticula (DD) where they are phagocytosed, subjected to intra-cellular digestive processes and finally assimilated. Waste from the diverticula is passed back to the stomach in fragmentation spherules (FS) which probably break up and aid in the primary extra-cellular digestion of newly arriving food material by release of small quantities of enzymes derived from the digestive diverticula.

TABLE 1. A summary of the species of lamellibranchs in which rhythmicity has been detected. The environmental variables to which the rhythms have been correlated have also been indicated with the authority.

Species	Rhythms detected	Authority
A. Freshwater		
<i>Anodonta cygnea</i>	Endogenous	Barnes, 1952, 1955
<i>Anodonta cygnea</i>	Daily	Sälanki, 1964; Sälanki & Vero, 1969
<i>Unio pictorum</i>	Daily	B. S. Morton, 1970b
<i>Hyridella australis</i>	Daily	Hiscock, 1950
<i>Dreissena polymorpha</i>	Daily	B. S. Morton, 1969b
B. Marine		
<i>Venus mercenaria</i>	Daily	Thompson, 1970
<i>Venus mercenaria</i>	Daily	Bennett, 1964
<i>Venus mercenaria</i>	Daily, monthly, 27-day	Brown <i>et al.</i> , 1956
<i>Crassostrea virginica</i>	Tidal, daily, monthly, 27-day	Brown, 1954; Brown <i>et al.</i> , 1956
<i>Crassostrea virginica</i>	Tidal	Haskin, 1964
<i>Crassostrea virginica</i>	Tidal	Carriker, 1951
<i>Crassostrea virginica</i>	Tidal	Kunkle, 1957
<i>Crassostrea virginica</i>	Tidal	Nelson, 1918, 1920, 1925, 1933
<i>Crassostrea virginica</i>	Tidal, daily	Loosanoff & Nomejko, 1946
<i>Ostrea edulis</i>	Tidal, daily	B. S. Morton, 1971
<i>Cardium edule</i>	Tidal	B. S. Morton, 1970a
<i>Cerastoderma (=Cardium) edule</i>	Tidal	Farrow, 1972
<i>Arctica islandica</i>	2 x Daily (Tidal ?)	Winter, 1969, 1970
<i>Mytilus edulis</i>	Tidal	Gompel, 1937
<i>Mytilus edulis</i>	Tidal	Rao, 1954
<i>Mytilus californianus</i>	Tidal	Rao, 1953
<i>Modiolus modiolus</i>	2 x Daily (Tidal ?)	Winter, 1969, 1970
<i>Modiolus demissus</i>	Tidal	Nagabhushanam, 1963
<i>Macoma balthica</i>	Tidal	B. S. Morton, 1970c
<i>Macoma balthica</i>	Tidal	Thorpe, 1972
<i>Donax semignosus</i>	Tidal	Mori, 1938, 1950
<i>Donax denticulatus</i>	Tidal	Trueman, 1971
<i>Scrobicularia plana</i>	Tidal	Thorpe, 1972
<i>Mya arenaria</i>	Tidal, daily, monthly	Dicks (pers. comm.)
<i>Lasaea rubra</i>	Tidal	J. E. Morton, 1956
<i>Lasaea rubra</i>	Tidal	McQuiston, 1969
<i>Teredo navalis</i>	Daily	B. S. Morton & McQuiston, 1973
<i>Pecten jacobaeus</i>	Daily	Sälanki, 1966
<i>Lithophaga lithophaga</i>	Daily	Sälanki, 1966

## RHYTHMICITY IN THE LAMELLIBRANCHIA

### Occurrence

Examination of the literature reveals that many lamellibranchs possess rhythms of activity (Table 1).

Pavlov (1885) first noted that the spontaneous activity of the adductor muscles of *Anodonta* assumed a regular periodicity. Marceau (1906, 1909) later showed that very many lamellibranchs of widely differing structure and mode of life exhibited a rhythmic-

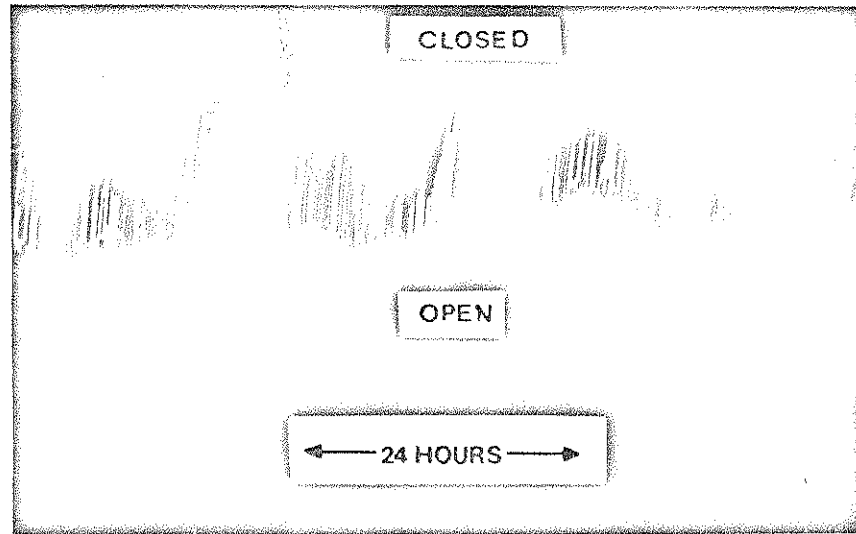


FIG. 2. A kymograph record of the activity of *Dreissena polymorpha*.

cal activity of the adductors. Subsequent research has shown that in most cases the rhythms so described can be correlated in some adaptive fashion with the rhythms of the environment. *Anodonta* apparently possesses an endogenous rhythm (Barnes 1952, 1955) although recently Sálanki (1964) and Sálanki & Vero (1969) have suggested that this species may also possess a rhythm related to the phases of night and day.

Littoral lamellibranchs are affected by the rhythm of the tide and can be expected to respond to such environmental extremes. What is of interest, however, is that freshwater and sub-littoral forms also possess rhythms of activity and inactivity related to another environmental variant - night and day.

Monthly or semi-lunar cycles of activity are produced by the summation of tidal and diurnal rhythms in littoral bivalves, and may play an important role in the timing of breeding in these genera, as will be discussed later.

#### Nature

The rhythmical nature of lamellibranch behaviour has been recorded in various ways, e.g., by measuring the variation in water propulsion (siphoning) (Hopkins 1936; Rao, 1953, 1954) or oxygen consumption (Gompel, 1937) but by far the most revealing method is to record the shell valve movements directly by means of a kymograph (Barnes, 1955; Koshtoyants & Sálanki, 1957). In every case which has been studied it has been shown that the period of activity is characterised by rapid phase contractions, whilst the period of rest is characterised by either closure or gaping of the shell valves (Fig. 2) according to the species (Marceau, 1906, 1909). The phase contractions rapidly close the shell valves, but relaxation of the adductor muscles allows the elastic ligament to force the shell valves open. This process is repeated many times during the period of activity. The "quick" portion of the adductor muscle might be responsible for phasic adductions whilst the "catch" portion of the adductor muscles might be responsible for the maintained closure of the shell valves during the quiescent period. In those lamellibranchs which gape during their quiescent period it would seem the "catch" mechanism is only used when the animal is disturbed.

## Effect

The phasic contractions characteristic of the period of activity serve as a pump. Rapid closure of the shell valves forces filtered water (lacking in oxygen but rich in carbon dioxide) out of both inhalant and exhalant apertures and pseudofaeces and faeces out of the inhalant and exhalant apertures respectively. Opening of the valves again, reduces the pressure in the mantle cavity relative to the outside and fresh water enters via the inhalant aperture. Sálanki & Lukacsovics (1967) have shown that *Anodonta* is rapidly filtering at this time and that oxygen consumption is also high.

During the period of quiescence the shell valves either close or gape according to the genus (Marceau, 1906, 1909). Whichever action is utilised the effect is the same, the water in the mantle cavity is not replenished by muscular action and filtration all but ceases. Sálanki & Lukacsovics (1967) have shown for *Anodonta* that filtration is minimal and oxygen consumption negligible at this time. It has also been shown for *Dreissena* that filtration ceases at this time (B. S. Morton, 1970e) and in *Cardium edule* and *Teredo navalis* (B. S. Morton, 1970a; B. S. Morton & McQuiston, 1973) that the pH of the fluid in the mantle cavity falls, indicating that it is being depleted of oxygen and greatly enriched with carbon dioxide. Koch & Hers (1943) reported a similar rhythmicity in siphonal activity and oxygen uptake in *Anodonta* and Galtsoff (1964) and Sálanki & Lukacsovics (1967) have recommended that shell valve activity be taken into account when studying filtration in lamellibranchs.

The regularity of these alternating processes of adduction and of quiescence in so many lamellibranchs precludes artefacts and to the contrary suggests that it is extremely important and is an intrinsic lamellibranch character.

## FILTER FEEDING

It has been shown in many bivalve genera that the rhythmical nature of the adduction of the shell valves has a profound effect upon feeding. The phasic adductions characteristic of the period of activity greatly enhance the food trapping mechanisms by constantly replenishing the water in the mantle cavity. It has been considered that the ctenidia themselves were solely responsible for the inhalant stream; it now seems likely that this action is supplemented by the pumping motion of the shell valves. The long periods of quiescence observed in lamellibranchs limit feeding while the shell valves are shut or gaping. It would seem therefore that a high level of filter feeding in the Lamellibranchia is not necessarily continuous.

## FUNCTIONING OF THE STOMACH AND DIGESTIVE DIVERTICULA

Unless such genera possess mechanisms for converting an irregular supply of food material into a constant stream then their digestive processes can not be continuous and simultaneous. It can be assumed that shortly after the last phasic adduction of a period of activity the mantle cavity is comparatively free of particulate material and all acceptable material has been passed to the stomach. In rare exceptions food may be stored in special organs associated with the stomach, e.g., the appendix of the Teredinidae. However, as will be discussed later the appendix generally has quite a different function. For most lamellibranchs it must be assumed that the cessation of feeding has a profound effect upon the digestive process.

## The stomach contents

It has been shown for *Ostrea edulis* (B. S. Morton, 1971) that the constituents of the stomach fluids change considerably over the tidal cycle. The same is true for the appendix of *Teredo navalis* (B. S. Morton & McQuiston, 1973).

When *Ostrea* is feeding the stomach is full of ingested material. At the start of feeding this is in the form of distinct mucoid food strings. These strings are not present for long and it is not considered that the style is continually winding in food chains as previously thought. Later the food disappears from the stomach and for a short time the stomach fluid is relatively clear. Still later the stomach begins to fill with fragmentation spherules derived from the digestive diverticula; eventually these disappear and food begins to enter the stomach with the recommencement of feeding.

Diurnal changes were also observed in the appendix of *Teredo navalis* and these reflected the changes occurring in the much smaller stomach, and showed a close similarity to the changes observed in the stomach of *Ostrea*, with the additional complication of the presence of wood fragments in the former (B. S. Morton & McQuiston, 1973).

#### The crystalline style

One of the most important single factors that has led to the acceptance of a concept of continuous feeding and digestion in the Lamellibranchia was the belief that the slow dissolution of the crystalline style released a constant supply of the enzymes that effect extra-cellular digestion of food material in the stomach. Constant dissolution assumed constant secretion at the basal end (J. E. Morton, 1952). Mitra (1901), however, believed the dissolution of the style to be periodic. Nelson (1918, 1920, 1923, 1933) showed that the style of *Ostrea virginica* was not always present and that on a rising tide it was a large firm rod, but on a falling tide it was reduced to an amorphous gelatinous mass. He further showed that the style of *Ostrea* could be reformed in 15 minutes. J. E. Morton (1956) similarly showed that the style of *Lasaea rubra* was formed and dissolved during every tidal cycle. Owen (1966) has stated that the style of lamellibranchs dissolves when the animals are kept out of water, under anaerobic conditions (also noted by Berkeley (1923)) or when the 2 valves are clamped together. Under natural conditions littoral animals are out of water at low tide; anaerobic conditions exist in the mantle cavity at certain times (i.e., during the quiescent phase) and very often lamellibranchs clamp their shell valves together for long periods of time.

My own studies on *Dreissena polymorpha*, *Cardium edule* and *Ostrea edulis* (B. S. Morton, 1969b, 1970a, 1971) have shown that the style dissolves either just before or during the early stages of feeding. This agrees with the findings of J. E. Morton (1956) on *Lasaea*. In *O. virginica* (Nelson, 1920), *O. edulis* (B. S. Morton, 1971) and *Lasaea rubra* (J. E. Morton, 1956) the style dissolves completely. This is not so in *D. polymorpha* and *C. edule* (B. S. Morton, 1969b, 1970a) in which it only partially dissolves. The enzymes of the crystalline styles of numerous lamellibranchs are well documented (Owen, 1966; Purchon, 1968) but since the style only dissolves occasionally these enzymes are released only intermittently and consequently extra-cellular digestion in the stomach is rhythmic too. The site of secretion of the matrix of the style is now generally assumed to be the typhlosole, e.g., List (1902), Nelson (1918), Lazier (1924), Graham (1931), Goreau *et al.* (1966), B. S. Morton (1969a, 1970a,d), Giusti (1970). The ciliated cells of the style sac itself probably only serve to rotate the style though they may also be responsible for the secretion of some enzymes.

The laminar nature of the style (Nelson, 1918; Kato & Kubomura, 1954; B. S. Morton, 1969a, 1970a) suggests that it is secreted intermittently. It is now postulated that at the time of secretion (Fig. 3,A), style material is poured into the style sac and coats the surface of the style; this has the effect of pushing the style forward, and this process is aided by the cilia which rotate the style. Eventually the newly produced style material solidifies and secretion stops. Dissolution begins (Fig. 3,B) and ceases when the thin basal end of the style is no longer in contact with the cilia of the style sac and cannot be pushed forward any further. This process in all probability occurs in those



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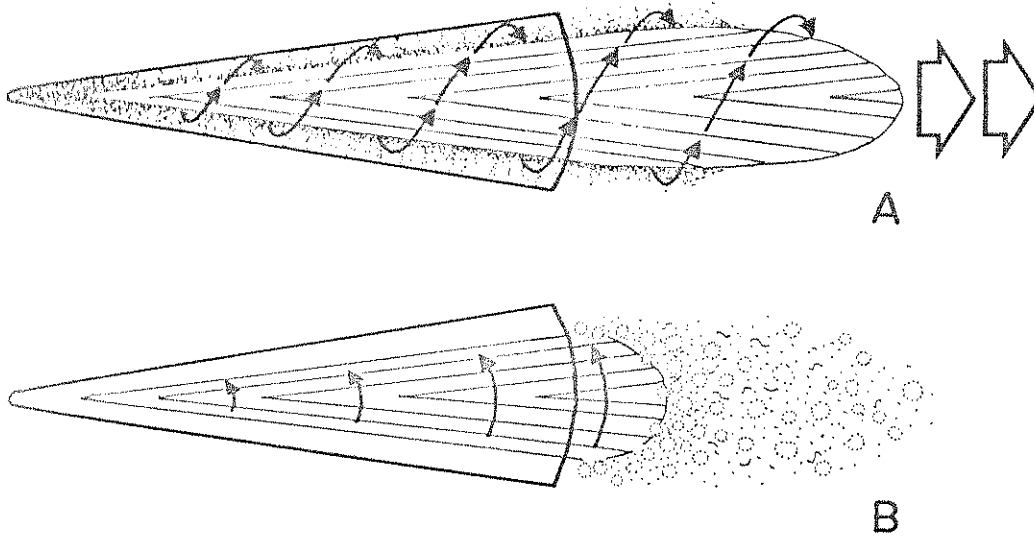


FIG. 3. A diagrammatic representation of the 2 processes of (A) secretion and (B) dissolution of the crystalline style of the Lamellibranchia.

bivalves in which the style does not dissolve completely, and accounts for the known facts regarding the lengthening and thickening of the style. In those bivalves in which the style dissolves completely, e.g., *Ostrea* and *Lasaea*, the process is much simpler although probably the same principles are involved; the style is secreted at one time and dissolved at another.

One of the commonest misconceptions regarding the crystalline style of lamellibranchs is that it is the most acid organ in the gut (Yonge, 1925, 1926a). In bivalves examined subsequently (B. S. Morton, 1969b, 1970a, 1971) the style has been approximately neutral, or at the most only slightly acid. The digestive diverticula appear to be the most acid region of the gut and in most species (but not in *Ostrea edulis*), the style does not buffer the stomach contents. This is true for *Dreissena* and *Cardium* where the pH of the stomach fluids varies widely over the course of the diurnal and tidal cycle respectively (B. S. Morton, 1969b, 1970a). In *O. edulis* the pH of the stomach contents remain fairly stable over the tidal cycle.

#### The gastric shield

The gastric shield of the Lamellibranchia is largely restricted to the left dorsal wall of the stomach. It has generally been regarded as protecting the stomach wall from the abrasive effect of the rotating crystalline style, though it may (Yonge, 1949) assist in

the trituration of stomach contents. Halton & Owen (1968) have shown that the gastric shield of the protobranch *Nucula sulcata* is enzymatically active. They further suggest that the gastric shield of lamellibranchs may also be enzymatically active, an observation supported by the recent work of McQuiston (1970), and not simply an inert protective structure. Should it subsequently be proven that the gastric shield generally plays an active role in digestion it is possible that this function would be closely associated with the functioning of the crystalline style and as such similarly regulated.

#### The sorting areas of the stomach

Purchon (1956, 1957, 1958, 1960) has made an especial survey of the stomach in the Bivalvia. In the Lamellibranchia the stomach possesses sorting areas that principally function by removal to the mid gut of large or indigestible particles leaving a suspension of fine particles for primary extra-cellular digestion by enzymes liberated by the style and subsequent transmission to the digestive diverticula for intra-cellular digestion.

Since it has been shown that lamellibranchs are not continually feeding, food is not always in the stomach and it therefore follows that the sorting areas are not always sorting potential food material. This is particularly true for the eulamellibranch sorting area type C (Reid, 1965b) in the digestive caeca. It is probable that in this organ the sorting mechanism manipulates food at one time and waste material at another.

#### The appendix

As noted earlier the contents of the appendix of *Teredo navalis* vary systematically over the course of 24 hours. Wood is always present, but at certain times either fragmentation spherules or filtered material too large to be digested are also found. As in *Ostrea* particulate material other than fragments of wood never occurs simultaneously with the fragmentation spherules. It appears that the appendix of *Teredo* serves partly as a temporary store of unusable or unwanted material and perhaps also as a reserve of potential food material. Purchon (1960) and Reid (1965b) have suggested the former function for the appendix of the Tellinacea which is homologous with the appendix of the Teredinidae (Yonge, 1949). Reid (1965b) further suggested that contraction of the adductor muscle periodically emptied the appendix of *Lima hians*.

#### The digestive diverticula

The digestive diverticula of the Lamellibranchia all possess a striking similarity. Their function has been elucidated by Yonge (1926b) and Owen (1955) who subsequently (Yonge, 1939; Owen, 1956) also showed that they differ fundamentally from those of the Protobranchia.

The digestive diverticula are organs of absorption and intra-cellular digestion (List, 1902; Vonk, 1924; Yonge, 1926b; Owen, 1955; Dinamani, 1957; Saleuddin, 1965; Sumner, 1966a,b; B. S. Morton, 1969a, 1970a,d). Mansour (1946), Mansour & Zaki (1946) and Mansour-Bek (1946) also considered them to be organs of secretion. It was considered by Owen (1955) that this secretory function could be derived from the disruption of fragmentation spherules, carrying the waste products of intra-cellular digestion, in the stomach. Subsequently Sumner (1966a,b) and McQuiston (1969) attributed a secretory function to the basophil cells or "nests of young cells" of Yonge (1926b) which were considered to be responsible for the replacement of old spent digestive cells and the formation of new tubules (Yonge, 1926b; J. E. Morton, 1956; B. S. Morton, 1969b, 1970a,b,c, 1971).

Owen (1970) has now apparently clarified the issue and shown that the "nests of young cells" are composed of two cell types, one of which is secretory, the other perhaps being responsible for the replacement of both secretory and absorptive cells.



The location of the digestive diverticula in relation to the stomach varies from species to species, but in the Lamellibranchia they are mainly restricted to caeca. In many, but not all cases, the openings to the digestive diverticula are associated with an in-pushing of the major typhlosole which projects into the duct leading to the diverticula (sorting area type C (Reid, 1965b)). Particles of food enter the caeca where they are transported to the openings of the ducts. It was assumed that small particles were continually entering the ducts and that the digestive diverticula were continually absorbing fluid and phagocytosing small particles. It was necessary to postulate a two way flow in the ducts supplying the diverticula in order to explain how the waste products of digestion could pass out while food material was entering. The counter-current theory (Owen, 1955) explained how this system could operate. Undoubtedly the principle underlying this theory is correct. The food entering the ducts does travel in the "upper" part of the duct and waste does travel out of the diverticula in the "lower" part of the tube (Mathers, 1972). The system, however, is not necessarily a counter-current since food is not necessarily entering the diverticula at the same time that waste is leaving the diverticula. It has now been established for *Dreissena*, *Cardium*, *Anodonta*, *Macoma*, and *Ostrea* (B. S. Morton, 1969b, 1970a,b,c, 1971) that the digestive diverticula undergo a pattern of cytological changes that is related to the feeding and digestive rhythm. This pattern closely approximates to that demonstrated by J. E. Morton (1956) and subsequently confirmed by McQuiston (1969) for *Lasaea* and the stages can be defined as 1) Formation, 2) Absorption and phagocytosis, 3) Digestion, 4) Breakdown, 5) Development and Formation (1). To this sequence must now be added the secretory function described by Sumner (1966a,b), McQuiston (1969) and Owen (1970). The enzymes are probably secreted prior to or during the absorptive phase.

During breakdown of the diverticula, the absorptive cells disintegrate releasing fragmentation spherules which pass into the stomach. Owen (1955) has suggested that their disruption in the stomach may aid primary extra-cellular digestion. This is probably true for some genera, e.g., *Lasaea rubra* (J. E. Morton, 1956), but since they are probably more acid than the organ that produces them, they may more importantly, also initiate style dissolution. pH may not be solely responsible for dissolution of the style at this time since the proteinaceous style (Bailey & Worboys, 1960) would be liable to dissolve if a protease were present (Reid, 1965a). Such a protease could be found in fragmentation spherules containing excess intra-cellular proteases derived from the digestive diverticula (Yonge, 1923; Rosen, 1949; Ganapati & Nagabhushanam, 1956).

#### Movement of food and waste in the stomach

Ciliary mechanisms have been considered as the main propulsive source for the movement of particles in the stomach of lamellibranchs. It has, however, been shown that the cilia at the opening of the caeca into the stomach usually beat out of the caeca thereby apparently hindering the entry of food material, but also probably more importantly, thereby preventing blockage of the openings (Purchon, 1955). Since the counter-current theory explaining the two way passage of material in the ducts of the diverticula may not necessarily function as originally envisaged since the inhalant and exhalant streams are separated temporally as well as spatially, it is necessary to find an alternative mechanism to account for the transport of material between the stomach and the digestive diverticula.

The tubules of the digestive diverticula are surrounded by a meshwork of muscle fibres. Owen (1955), Millar (1955) and J. E. Morton (1956) have all suggested that contraction of these muscles would expel waste from the diverticula. The last two authors report observing this action in *Ostrea* larvae and in *Lasaea* respectively. Reid (1965b) has suggested that the appendix of *Lima* is emptied by the contraction of the adductor

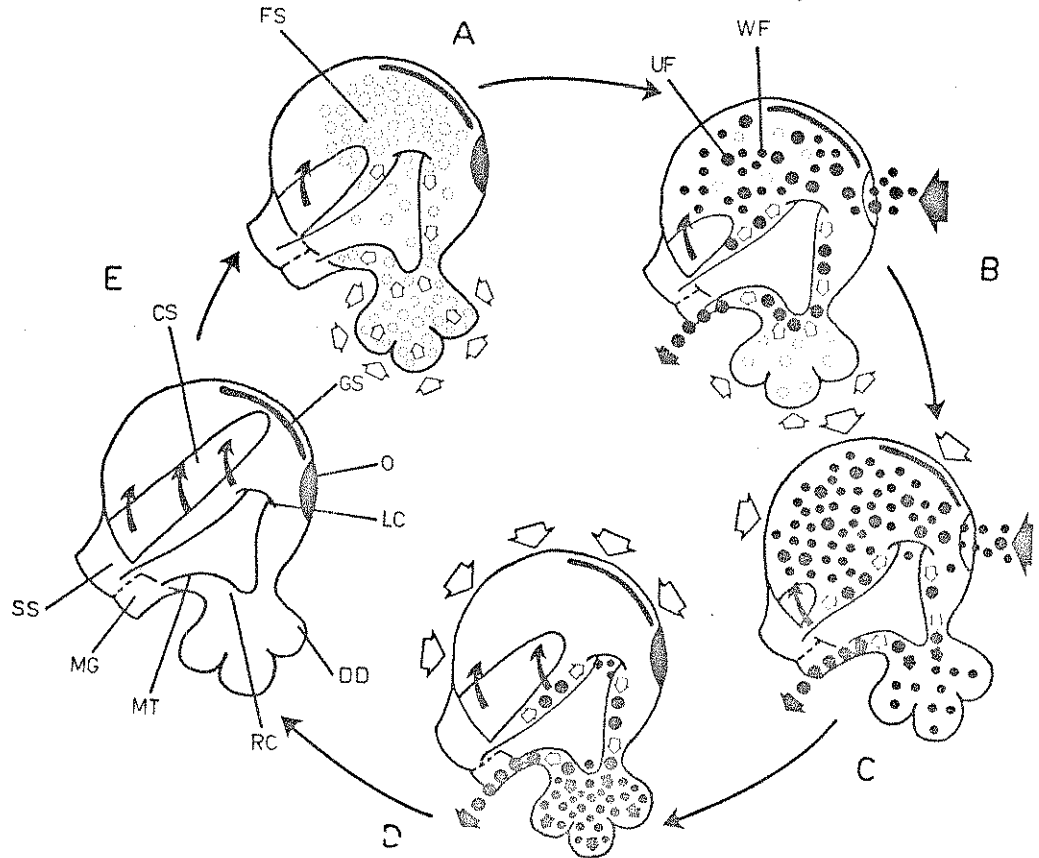


FIG. 4. Diagrammatic representations of the stomach in the Lamellibranchia showing how the digestive processes can be divided into a number of phases. (For lettering see Fig. 1.)

muscles, whilst the appendix of *Teredo* could be emptied by nothing other than by muscular activity (Purchon, 1960).

Possibly rapid phasic adductions of the adductor muscles at the time of feeding in lamellibranchs may also serve the subsidiary function of squeezing the products of extra-cellular digestion in the stomach into the diverticula, and at other times contractions of the muscle fibres investing the diverticula may help to pass waste materials into the stomach. As originally postulated by Graham (1949), Owen (1953) and Purchon (1955) opposing muscular forces acting on a fluid medium may be the principal agency for the transference of particulate material from one part of the alimentary tract to another in the Lamellibranchia.

#### DISCUSSION

Critical analysis of the available information suggests that the currently accepted theory of a steady state in feeding and digestion in the Lamellibranchia cannot account for many of the changes observed in the feeding and digestive processes and which are of a cyclical nature.

For those species examined the following sequence of events has been determined.

The animal feeds for a period of time. This action is characterised by rapid phasic contractions of the adductor muscles which serve to pump water into and out of the mantle cavity, thereby supplementing the inhalant ciliary currents produced by the

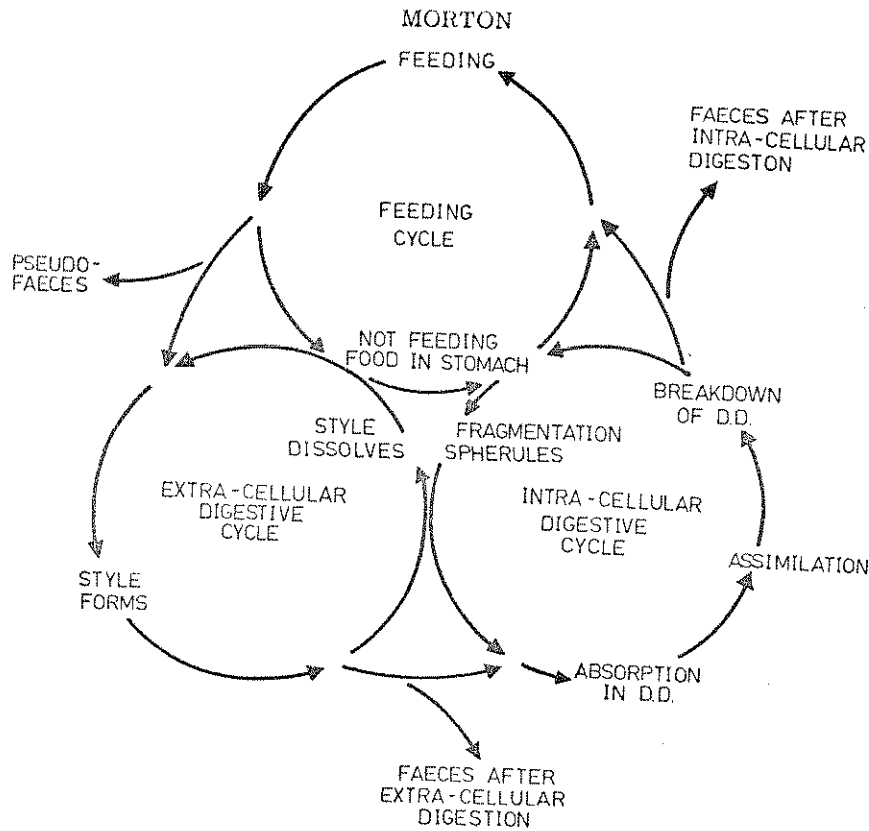


FIG. 5. A schematic representation of the rhythmic nature of the feeding process and extra-cellular and intracellular digestive mechanisms in the Lamellibranchia.

ctenidia. The ctenidia also serve to effect the filtration of the water once it is in the mantle cavity and to initially sort the food. Material of an acceptable size is passed to the labial palps for further rigorous sorting and ultimately selected material is transported to the mouth for ingestion.

The food arrives in the stomach at a time when the style (Fig. 4, CS) has either wholly or partly dissolved (Fig. 4, A), e.g., *Ostrea edulis* (B.S. Morton, 1971) or the arrival of food in the stomach initiates style dissolution (Fig. 4, B), e.g., *Dreissena polymorpha* (B.S. Morton, 1969b). In the former case the dissolution of the style is considered to have been caused by the arrival in the stomach of the fragmentation spherules (FS) derived from the digestive diverticula (DD). In the stomach the enzymes released from the dissolving style act upon the food to break it up. The partly digested food is then sorted in the stomach, large unwanted particles (UF) are passed to the mid gut (MG) in the intestinal groove of the major typhlosole (MT) (Fig. 4, B, C, D) and food material of an acceptable size is passed to the digestive diverticula for further extra-cellular digestion (Owen, 1970), absorption and phagocytosis, intra-cellular digestion and final assimilation. Passage of food material into the diverticula may be assisted by the phasic contractions of the adductor muscles that are occurring at this time.

When the animal ceases to feed (Fig. 4, D) (during the period of adductor quiescence) the mouth (O) may shut, remaining waste is passed to the mid gut and remaining food passed to the diverticula. The final closing action of the shell valves probably also removes the last pseudofaeces from the mantle cavity. The crystalline style now reforms and the epithelium of the digestive diverticula commence the process of breakdown (Fig. 4, E) eventually passing assimilated products to the rest of the body and producing fragmen-

tation spherules which are ultimately passed to the stomach (Fig. 4, A) probably by contraction of the meshwork of muscle fibres surrounding each digestive tubule. The digestive diverticula reform in preparation for another cycle whilst the fragmentation of spherules begin to act upon the now fully formed style causing it to dissolve once again.

The process varies, as would be reasonably expected in such a diverse assemblage of animals, but the essential principle (Fig. 5) is evident in all those examined, and is usually regulated by an environmental rhythm.

It would seem to be generally accepted that the evolution of the Lamellibranchia occurred in the shallow coastal waters. Such animals would have been subjected to the twin environmental rhythms of the tide and night and day. These rhythms are apparently retained in modern littoral lamellibranchs (Table 1). Adaptive radiation of the Lamellibranchia into the sublittoral zone of the sea and into fresh waters removed the effect of the tide. Sublittoral forms now possess diurnal rhythms only. Similarly modern fresh water forms also possess diurnal rhythms although *Anodonta* may have taken the process one step further and evolved an endogenous rhythm; feeding as the necessity arises. Apparently the Lamellibranchia have retained either the primitive feeding mechanisms related to the tidal cycle or have transferred their feeding rhythm to the subsidiary rhythm of night and day. In littoral lamellibranchs, e.g., *Crassostrea virginica* (Brown *et al.*, 1956), *Ostrea edulis* (B. S. Morton, 1971) and *Mya arenaria* (Dr. B. Dicks, pers. comm.), it has also been suggested that summation of the tidal and daily rhythms produce a third rhythm related to the phases of the moon. Brown *et al.* (1956) have shown this rhythm to be of 14.8 days duration, being thus semi-lunar.

Spawning and the liberation of larvae in *Ostrea edulis* occurs at fortnightly intervals in relation to the phases of the moon (Korringa, 1947; Knight-Jones, 1952). This confirmed the earlier work of Orton (1926) who showed that in this species young larvae are more abundant in the gills of the adult immediately after the full moon whilst mature larvae showed peaks of abundance later. A lunar periodicity in spawning has also been shown for *Chlamys opercularis* (Amirthalingham, 1928) and *Pecten maximus* (Mason, 1958). The triggering mechanism for the release of larvae or gametes may be synchronised by the semi-lunar rhythm built up by the summation of the tidal and diurnal rhythms. Temperature may also play a role in ensuring that the gametes or larvae are not liberated in the wrong lunar cycle. Such a mechanism has obvious survival values.

It would appear that rhythmicity in the Lamellibranchia is widespread, regardless of the habitat and is important in correlating the various components of the complex feeding and digestive cycle.

#### SUMMARY

It has hitherto been believed that in the filter-feeding Lamellibranchia the processes of feeding and digestion were both held in a steady state. Careful study of both of these processes in a number of genera, both freshwater and marine in relation to the time factor, has shown this view to be untenable. These processes comprise a rhythmic sequence of phases related to environmental rhythms. Two alternate phases can be detected. In the first food is collected, filtered, selected and passed to the stomach. Food collection then ceases and the accumulated food material is digested. The complex organs of feeding and digestion in the Lamellibranchia are co-ordinated to a fine degree and the processes they initiate achieve a refinement hitherto unsuspected. Feeding and digestion in the Lamellibranchia is a dynamic process both temporally and spatially.

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