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THE STOMACH IN THE BIVALVIA

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CONTENTS

The Protobranchia, with a stomach of type I (Gastroproteia), comprise one of only two subclasses of Bivalvia. The stomachs of members of the deposit-feeding Nuculacea and Nuculanacea are basically comparable and differ from those of all filter-feeding bivalves in some important respects. There are only three slender ducts from the digestive diverticula (Oligosyringia). There is no clear crystalline style, but the wide proximal expansion of the mid gut houses an amorphous, viscous secretion in lieu. The intestinal groove does not obviously extend forwards from the mid gut into the stomach. A gastric shield and a dorsal hood are present, but there are no other stomach caeca. Any sorting areas present differ in disposition from those in filter-feeding bivalves. In the Solemyacea the alimentary canal including the stomach is much reduced and simplified, and in one species is wholly lacking.

In the subclass of filter-feeding bivalves there are many ducts from the digestive diverticula into the stomach (Polysyringia) and the intestinal groove extends forwards from the mid gut into the stomach, protected throughout its course by the overhanging major typhlosole. Six of the superfamilies in the Pteriomorpha have stomachs of type III, in which the diagnostic feature is a long slender tongue of the major typhlosole which penetrates the food-sorting caecum to its apex, accompanied throughout by the intestinal groove. This feature is so remarkable that it cannot have evolved more than once and it must indicate that these six superfamilies have a common source. Other possible criteria for the clustering of superfamilies in the Pteriomorpha have been considered individually and all have been rejected for reasons given. The superfamilies Arcacea, Limopsacea, Mytilacea, Pinnacea, Pteriacea and Ostreacea, all of which possess a stomach of type III, are judged to compose a natural assemblage, the Gastrotriteia.

The review of the Gastrotriteia reports upon 27 genera assembled in ten families and six superfamilies. Two species, *Trisidos semitorta* and *Pteria penguin* are described in detail. A type B sorting mechanism, which links the apex of the typhlosolar tongue with the apex of the dorsal hood, has been found in two families, the Pteriidae and Mytilidae, and this implies phyletic affinity between these families. Tabulation of variation in the internal structure of the stomach in this group fails to reveal any other subordinate clustering. Extensive sorting areas may be present or absent, and the duct orifices may be arranged in an extended series or may form clusters, and such variation is best interpreted as random.

Stomach type IV is characterized by a major typhlosole and intestinal groove which emerge from the mid gut and curve evenly to the left across the stomach floor, without production of a typhlosolar tongue and without entering into an embayment on the right anterior side of the stomach. Thirteen superfamilies exhibit this type of stomach, and analysis of structural variation shows that these may be arranged in three groups.

(i) In the Pectinacea, Limacea and Anomiacea there are many duct orifices, either scattered or clustered, the major typhlosole passes towards the left pouch, and there is a conspicuous sorting area on the anterior floor of the stomach.

(ii) In the Pandoracea and Clavagellacea the duct orifices are concentrated into a few embayments of the stomach wall, the major typhlosole and intestinal groove are short and either very posterior in position or pass towards the left caecum (Laternulidae). There is a conspicuous anterior sorting area on the stomach floor between the oesophageal orifice and the intestinal groove.

(iii) In the remaining eight superfamilies there is not an extensive anterior sorting area on the stomach floor. The major typhlosole and intestinal groove pass towards the left caecum (Trigonacea, Crassatellacea, Carditacea, Hiatellacea and Pholadomyacea), or penetrate the left caecum (Unionacea, Leptonacea and Gastrochaenacea). The last three of these superfamilies are intermediate in this respect between stomach types IV and V, and it is possible that one or more of these superfamilies may have reverted from stomach type V to type IV.

Finally there are some taxa which have most certainly reverted from stomach type

V to type IV. This has been clearly demonstrated in the Lucinacea (in the families Lucinidae and Thyasiridae), the Corbiculacea (for example in *Sphaerium corneum*), the Chamacea (in *Chama multisquamosa*) and the Tellinacea (in *Donax faba* and *D. semigranosus*). These changes can be variously explained as simplification of the stomach permitting opportunism in feeding in nutritionally poor habitats (Lucinidae); as the outcome of adoption of small size as a strategy for survival (*S. corneum*); as paedomorphosis (*D. semigranosus*). Consideration should be given to the possibility of other cases of reversion from stomach type V to type IV, especially among taxa with greatly simplified stomachs, and with a small body size.

Of the 13 superfamilies that exhibit a stomach of type IV, the eight that are listed in group (iii), above, should be set on one side for the present time in view of the possibility that further examples of reversion from a stomach of type V may yet be identified. The remaining five superfamilies, the Pectinacea, Limacea, Anomiacea, Pandoracea and Clavagellacea compose a distinct phylogeny of bivalves, the Gastrotetartika. Within this restricted group the review reports on 14 genera assembled in nine families and five superfamilies. One species, *Chlamys crassicostata* is described in detail. Among the remaining eight superfamilies the review treats 20 genera assigned to 15 families, while two species, *Velesunio ambiguus* and *Aspatharia brumpti*, are described in detail. Within the Pholadomyacea, the genus *Parilimya* has a stomach which is in a state of transition between stomach type IV and type II. This provides valuable support to the proposition that the septibranchs have evolved from anomalodesmatan ancestors taxonomically close to the Verticordiidae.

The septibranchs are carnivorous and have stomachs of type II (Gastrodeutera); they include the families Verticordiidae, Poromyidae and Cuspidariidae. In each of the verticordian genera *Halicardia*, *Policordia* and *Lyonsiella* individual species show different degrees of specialization towards the carnivorous habit, those least specialized having stomachs that still possess a dorsal hood, a small sorting area of ciliated folds, a small major typhlosole and an intestinal groove. In the more highly specialized carnivorous taxa all these structures are lacking, and the stomach forms a powerful crushing gizzard with a thicker outer muscular coat and a thicker inner lining of scleroprotein. There are only two slender ducts from the digestive diverticula into the stomach (Oligosyringia). These data support the concept of transition from a delicate ciliary microphagous habit to a convulsive muscular carnivorous habit without loss of efficiency during an intermediate opportunistic omnivorous phase. Although the septibranchs are polyphyletic as indicated by the very different feeding methods of the Verticordiidae and Cuspidariidae, they may nevertheless have originated from an even earlier common ancestry in the Anomalodesmata. Although this would place the septibranch families as components of the Anomalodesmata, their extreme structural and functional specialisms may justify the award of independent taxonomic status at a level equivalent to each of the three phylogenies within the filter-feeding bivalves. Review of the Gastrodeutera reports upon seven genera of septibranchs, assigned to three families placed in either one, or two, superfamilies.

Recognition of stomach type V is simple, being dependent upon the presence of a semicircular or elongated flange of the major typhlosole, accompanied by an extension of the intestinal groove, which projects into the right caecum. As regards the large assemblage of bivalves which possess this type of stomach (Gastropempta), tabulation of details of internal structure has failed to indicate any natural subdivisions. This paper reports upon the stomachs of 76 genera, assigned to 24 families and to 14 superfamilies. To this phylogeny should be added three further families, the Lucinidae and Thyasiridae (Lucinacea) and the Pisidiidae (Corbiculacea), and a few species in the genera *Donax*, *Tellina* and *Chama* in which the stomach has reverted from type V to type IV. The internal structure of all stomachs of types IV and V was therefore examined in detail to define more thoroughly the differences between these two types of stomach, with a view to identifying any further taxa which may have

reverted from type V to type IV. It was found that the ultimate destination of the major typhlosole and intestinal groove in the stomach was within the left caecum in all examples of stomach type V, and also in the Unionacea, Kelliidae (Leptonacea) and Gastrochaenacea, but in no other taxa with a stomach of type IV. This suggests that the Unionacea, Leptonacea and Gastrochaenacea are either transitional between types IV and V, or may have partly reverted from type V to type IV.

Stomach types IV and V differ as regards the distribution of the sorting areas. In stomachs of type IV sorting areas 1, 3 and 8 are common, numbers 6 and 7 are occasional, numbers 4 and 5 are rare. In stomachs of type V sorting areas numbers 3 and 6 are almost universal, numbers 5, 7 and 8 are common, number 1 is rare and number 4 is absent. Other variations in internal structure of the stomach are without taxonomic significance. These concern the size of the oesophageal orifice, the size and location of the gastric shield, the ciliated pathway from the oesophageal orifice to the dorsal hood, and the relationship between the style sac and the mid gut. Advantage is taken of this further information to supply more extensive definitions of stomach types III, IV and V.

Attention is drawn to a curved flange that lies on the posterior floor of the stomach in certain members of the Leptonacea and of the Tellinacea, and that might indicate a phyletic affinity between these superfamilies. There are a number of similarities between the stomachs of *Glauconome* (Veneracea) and *Geloina* (Corbiculacea), and also between *Petricola* (Veneracea) and *Trapezium* (Arcticacea). A conical mound on the floor of the stomach appears to be diagnostic of families in the Unionacea. Attention is drawn to the need for further studies on the stomach in species of *Chama*.

INTRODUCTION

Early interest in the internal structure and ciliary sorting mechanisms of the stomachs of bivalve molluscs was much encouraged by the publication of the more wide-ranging study of the molluscan stomach by Graham (1949). A general review revealed the occurrence of five distinct types of stomach in the Bivalvia (Purchon 1956*b*, 1957*b*, 1958, 1960*a*). It was later concluded that these stomach types were largely indicators of five distinct phylogenies, though these phylogenies were partly obscured by some unexpected results, for example, in *Donax faba* and in *Chama multisquamosa* (Purchon 1958, 1960*a*). The condition in *D. faba* was explicable in terms of paedomorphosis, which may or may not apply to the other case. Unexpected results were also obtained for the Lucinidae and Thyasiridae, which differ significantly from the related Ungulinidae. This may be attributable to the fact that the Lucinidae and Thyasiridae are specializing as colonists of nutritionally impoverished marine sediments, and simplification of the stomach permits opportunism in acceptance of food material (Allen 1958*a*).

Major contributions to the subject have been made by Reid (1965) and by Dinamani (1967), while many authors have contributed descriptions of the interior of the stomach in individual species. The relevant literature is now extensive, sufficient data are available for simple analysis, and a thorough review is now practicable and desirable.

The present review covers 261 species of bivalves, assigned to 157 genera, to 68 families, and to 37 superfamilies. It is dependent on the accurate location of these taxa, and upon the correctness of the drawings and interpretations made by a large number of authors; in only a few cases it has been considered necessary to offer a different interpretation.

For the majority of species investigated the interior of the stomach conforms closely to one of a few basic patterns and it is easy to identify the various structures therein. In a few examples, for instance among the Lucinacea and Pandoracea, significant differences in layout make it difficult to ensure a correct interpretation. Where there are deviations from the normal dispositions of parts it is important that terms such as 'right caecum', 'left caecum' and 'left pouch' should only be applied where homology with the typical structures can reasonably be inferred. It is clear that in *Donax semigranosus*, with a stomach of type IV–V, the embayment on the right anterior stomach wall is homologous with the 'right caecum' seen in stomachs of type V, so this expression has been applied here, and elsewhere as seems appropriate in examples of stomach type IV. Similarly the term 'left caecum' has been used in descriptions for several superfamilies in which the stomach is of type IV although only in the Unionacea and Gastrochaenacea is it penetrated by the terminal sector of the major typhlosole and the intestinal groove as always occurs in stomachs of type V. Again, it has seemed reasonable to use the term 'left pouch' in a few taxa in which its posterodorsal margin is not invested by an extension of the gastric shield, where the duct orifices lie in a separate hollow nearby, or even when no duct orifices lie in this region of the stomach wall. These decisions have been necessary for comparisons among taxa, and for simple analysis of structural variation.

The sorting areas within the stomach have been designated numerically according to their positions, but it has not been practicable also to quantify the extent to which each may develop. Sorting area number 3 is highly variable in extent, in some taxa being confined to the dorsal hood, but in other taxa it may spread over the roof of the stomach and expand on its right side as the 'posterior sorting area' of Graham (1949). Ansell (1961) has criticized the practice of describing as a 'sorting area' any set of ciliated folds which only exhibits one ciliary pathway and which therefore cannot itself sort particles into different grades. I have not followed this very reasonable recommendation because (i) particularly where only one specimen is available for dissection, an investigator may fail to observe all the ciliary pathways which are present; (ii) the folded area in question may have lost one or more ciliated pathways, but it remains homologous with sorting areas in that position in other taxa.

For each of stomach types III, IV and V exhaustive descriptions and detailed original drawings are provided for a number of species not previously investigated. These indicate the degree of detail which is desirable for this survey. For all five stomach types the literature is reviewed and for each superfamily a condensed description and a simplified diagram is provided, drawing together the reports on all taxa within that superfamily. These simplified diagrams conform to a common pattern, thereby facilitating comparison.

The present review has confirmed the original recognition of five types of stomach in the Bivalvia, each representing a distinct phylogeny save for a few cases of reversion from stomach type V to type IV due to paedomorphosis, or secondary structural and functional simplification. Stomach type I (Gastroproteia) is confined to the predominantly deposit-feeding nuculoid Protobranchia. Stomach type II (Gastrodeutera) is highly adapted to form a muscular crushing gizzard in the carnivorous Septibranchia. Both of these stomach types lack any conspicuous extensions from the intestinal typhlosoles and intestinal groove, and only receive a few (three or two, respectively) ducts from the digestive diverticula (Oligosyringia). In contrast, stomach types III, IV and V are specialized primarily for microphagous suspension-feeding and are characterized by a large number of orifices of ducts from the digestive diverticula (Polysyringia), and by the conspicuous extension of the major intestinal typhlosole and intestinal groove across the floor of the stomach. Stomach type IV is deemed to be a basic feature of the filter-feeding Lamellibranchia, occurring even in relatively primitive superfamilies in this subclass. From such an origin stomach type III (Gastrotriteia) evolved in a majority of the pteriomorpha in which the major typhlosole bears a conspicuous tongue bordered on both sides by the intestinal groove. Stomach type V (Gastropempta) typifies a phylogeny including many superfamilies of higher Eulamellibranchia in which the major typhlosole and intestinal groove extend into the left and right stomach caeca, cleansing the vicinity of the orifices of ducts leading to the digestive diverticula. Stomach type V has developed from an ancestry possessing stomachs of type IV, and this is also true for stomachs of type II in the Septibranchia which evolved from an anomalodesmatan ancestry (see figure 16 I–V).

A few diagrams have been redrawn with little change from the original, and the sources of these are acknowledged as follows: figure 10*d*, *e,f*, *Donax semigranosus* (Nakazima 1965*a*, plate 14); figure 10*h*, *Chama multisquamosa* (Purchon 1958, figure 9); figure 11*a*, *Pholadomya candida* (Morton 1980, figure 39); figure 11*b*, *Parilimya fragilis* (Morton 1982, figure 30); figure 11*c*, *d*; *Cuspidaria cuspidata* (Purchon 1956*b*, figures 4 and 5); figure 11*e,f*, *Lyonsiella abyssicola* (Allen & Turner 1974, figures 17*b* and 101*d*; figure 16 I–V (Purchon 1959, figures 1 and 2).

Stomach type I: Gastroproteia

Nuculacea

Review of literature

Nuculidae (figure 1, p. 189)

Nucula hanleyi Winckworth, 1931	(Yonge 1939; Graham 1949)
Nucula layardi A. Adams, 1856	(Dinamani 1967)
Nucula nucleus (L., 1758)	(Yonge 1939; Purchon 1956)
Nucula sulcata Bronn, 1831	(Owen 1956)
Nucula turgida Leckenby & Marshall, 1875	(Owen 1956)

Nuculanacea

Review of literature

Nuculanidae

Malletia obtusata (Sars, 1872)	(Yonge 1939)
Nuculana minuta (Müller, 1776)	(Purchon 1956)

Relatively few examples of the nuculoid Protobranchia have been investigated with respect to the structure and organization of the stomach. It appears from these studies that the stomachs of the Nuculacea and of the Nuculanacea are basically comparable, and one account can suffice for both of these superfamilies. Yonge (1939) described the stomach of *Malletia obtusata* in some detail, but for the Nuculidae he only mentioned the differences noted, and the only macroscopic difference that he claimed was that there are only two ducts from the digestive diverticula in the Nuculidae, but three in the Nuculanidae. In this he followed the conclusion of Heath (1937), but this was incorrect as subsequently established by Graham (1949), Owen (1956) Purchon (1956) and Dinamani (1967) for *N. hanleyi*, *N. sulcata*, *N. nucleus* and *N. layardi*. The stomach is globular and communicates ventrally with a very wide, conical style sac from the base of which the mid gut arises. An intestinal groove passes up the right side of the style sac, protected on its left and right sides by the major and minor typhlosoles, respectively. Both typhlosoles apparently pass forwards into the stomach, but Dinamani (1967) thinks otherwise with respect to *Nucula layardi*. The minor typhlosole is developed into a large, **U**-shaped structure on the

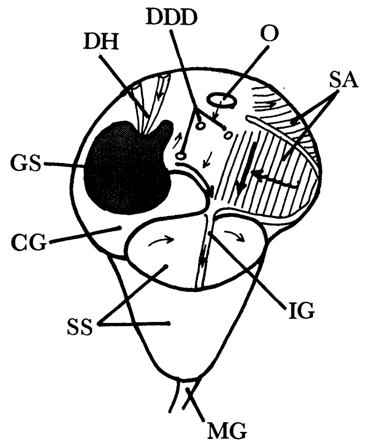


FIGURE 1. Nuculacea. Diagrammatic representation of the interior of the stomach after opening on the right side from near the oesophagus (O) towards the mid gut (MG). There is an extensive sorting area (SA), a gastric shield and chitinous girdle (GS, CG) and a dorsal hood (DH). There are only three orifices of ducts from the digestive diverticula (DDD). The proximal part of the mid gut is enlarged and serves as a style sac (SS) with an intestinal groove (IG). The stomach in the Nuculanacea differs only in details.

right side of the stomach, the arms of which enclose the parallel folds of an extensive sorting area. The major typhlosole passes across the stomach floor to the left, on the anterior side of a chitinous girdle which protects the left and posterior walls of the stomach. The intestinal groove apparently ends at the junction of the style sac and the stomach, but a rejection tract serving the same purpose accompanies the course of the major typhlosole and discharges waste from the stomach into the intestinal groove in the style sac. In some species of *Nucula* this rejection tract comprises a series of four or five parallel folds, but in *N. turgida* it consists of only one fold. In *Nuculana minuta* there is no such rejection tract, but the intestinal groove itself passes forwards on the floor of the stomach. There is a well developed dorsal hood on the roof of the stomach and curving over to the left side. A gastric shield lies on the left side of the stomach, extending into the mouth of the dorsal hood; it is in direct contact with the chitinous girdle mentioned previously.

The stomach of the nuculoid Protobranchia differs from those of all filter-feeding 'lamellibranch' bivalves in a number of important respects.

(i) The wide-mouthed style sac does not contain a clear, firm crystalline style, but an amorphous mucoid mass within which the food material ingested becomes incorporated.

(ii) There are only three slender ducts from the digestive diverticula into the stomach, not many such ducts. Owen (1956) has established that these ducts in the nuculoid Protobranchia have a fundamentally different organization from those in the filter-feeding 'lamellibranch' bivalves. Purchon (1963) recognized the importance of the numerical difference, proposed two subclasses for the Bivalvia, the Oligosyringia and the Polysyringia, and included the Septibranchia in the former.

(iii) There are no structures corresponding with the left pouch, the food sorting caecum (Filibranchia), the left caecum and the right caecum (Eulamellibranchia).

(iv) If the intestinal groove, or its homologue, passes forwards from the style sac into the stomach, it is not arched over and protected from the manipulative and digestive processes in the lumen of the stomach by a flap-like major typhosole as it is in most filter-feeding bivalves.

For these and other reasons it was concluded that there should be two subclasses in the

Bivalvia, for the Protobranchia and for the remainder respectively (Cox 1959; Owen 1959; Purchon 1959; Yonge 1959). Although Cox (1960) advised otherwise, the term Lamellibranchia is now generally accepted as the title of this second subclass.

Solemyacea

Review of literature

Solemyidae

Nucinella serrei Lamy, 1912	(Allen & Sanders 1969)
Solemya parkinsoni Smith, 1874	(Owen 1961)
Solemya sp.	(Reid 1980)
Solenomya togata (Poli, 1795)	(Yonge 1939)

The stomach of *Solenomya togata* is a simple swelling which possesses an anterior ciliated part into which open two ducts from the digestive diverticula, a middle part, which is ciliated ventrally but is otherwise lined by a chitinous girdle, and a posterior style sac with a ciliated waste tract on its right side. There is no ciliary sorting mechanism within the stomach, which is thought to exhibit secondary simplification (Yonge 1939). The stomach of *Solemya parkinsoni* is basically comparable, though relatively smaller in size, and serial sections show that there is a small caecum which corresponds with the dorsal hood of other bivalves (Owen 1961). The species of *Solemya* investigated by Reid (1980) was found to be unique among bivalves in lacking a gut. Feeding is presumably by uptake of dissolved organic materials.

The stomach of *Nucinella serrei* is larger than that of *S. parkinsoni*, but is considerably simpler. A narrow anteroventral ciliated channel directs material from the oesophagus to the relatively enormous single aperture leading from the stomach floor to the digestive diverticula. The remainder of the stomach wall, even anterior to that orifice, is completely lined by a chitinous sheath. Posteriorly a ciliated channel, flanked by the typhlosoles, leads from the diverticular aperture into the combined style sac and mid gut. The diverticula themselves are arranged in two groups; an anterior group with a wide lumen and which may be concerned with intracellular digestion, and a posterior group which may be concerned with secretion and extracellular digestion.

Accepting that the stomach in the Solemyacea shows secondary simplification, it must be emphasized that the phyletic origins of the group are not known and there are no grounds for thinking that it was so derived from a stomach of the nuculoid type.

STOMACH TYPE III: GASTROTRITEIA

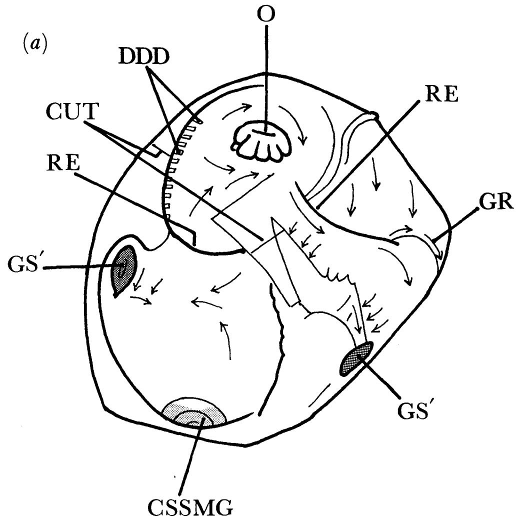
Arcacea

Description of fresh material

Trisidos semitorta (Lamarck, 1819)

The oesophagus (O) enters the stomach anterodorsally, its lips bulging into the lumen of the stomach and their disposition differing somewhat in the various dissections, presumably due to variations in muscular tonus and blood pressure locally.

The combined style sac and mid gut (CSSMG) leaves the posterior wall of the stomach and passes downwards into the visceral mass. The crystalline style was not seen. The minor



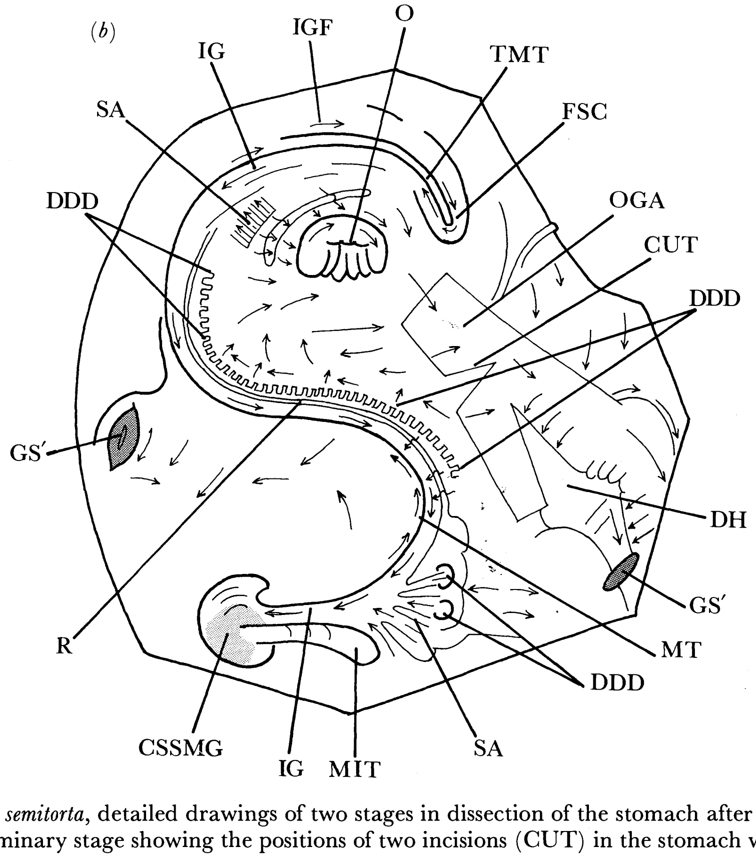


FIGURE 2. *Trisidos semitorta*, detailed drawings of two stages in dissection of the stomach after opening on the right side. (*a*) Preliminary stage showing the positions of two incisions (CUT) in the stomach wall to permit a more extensive display of the interior (magn. × 8). (*b*) The dorsal hood (DH) has been carried over to the right side and the gastric shield (GS′) has been cut in two (magn. × 8). There is a long curvilinear series of duct orifices (DDD) but the sorting area associated with these in other arcoids is much reduced.

typhlosole (MIT) extends a short distance out of the mid gut and on to the right posterior wall of the stomach. The major typhlosole (MT) and intestinal groove (IG) extend far into the stomach in a broad curve first to the right, and then across to the left side of the stomach, and up its left wall. A tongue of the major typhlosole (TMT) extends over the anterior roof of the stomach, above the oesophageal orifice, this tongue being accompanied on both sides by the intestinal groove (IG, IGF). Unfortunately it was not possible to follow the whole course of the major typhlosole and its tongue, and to determine the exact point of origin of the forwardly directed component of the intestinal groove (IGF). Nor was it possible to ascertain whether there was a type B sorting mechanism (Reid 1965) at the apex of the food-sorting caecum (FSC).

Below the oesophageal orifice there is a broad flat area of stomach wall which is bordered by a very regular series of orifices of ducts from the digestive diverticula. In the large specimens that were dissected here (maximum shell length 10.6 cm) there were as many as 38 duct orifices in this series. Each duct orifice lay at the head of a narrow slit lying between closely placed, parallel, tumid lips. Morton (1983) interprets this system of tumid folds as a sorting area, with duct orifices lying individually between the adjacent folds. His figure 20 depicts these folds as being considerably larger, compared with other features in the stomach, than they are seen to be in the present investigation. Ciliary currents in the vicinity of these duct orifices are as indicated (figure 2*b*), and it is probable that they serve to sort particulate material, probably restricting admission of all but the smallest particles into the ducts leading to the digestive diverticula. However, I am inclined to reject the definition of this system as a 'sorting area' with respect to the customary usage of that expression. I know of no examples in which duct orifices lie between adjacent folds of a 'sorting area', except *Pseudopythina*. In *Anadara granosa* the duct orifices lie in a regular series along the margin of a conventional sorting area and the folds of the sorting area pass into the duct orifices (Purchon 1957). It is true that in *Lima fragilis* and in *Pecten maximus* groups of duct orifices lie within the boundaries of sorting areas, but individual folds of the sorting areas pass into these orifices (Purchon 1957; Graham 1949). In *Trisidos semitorta* the situation is otherwise and the short, parallel, tumid folds form the lips of the duct orifices.

A small portion of a conventional sorting area, with closely spaced parallel folds, was found on the left side of the oesophageal orifice, near the mouth of the food sorting caecum. The whole sorting area was probably much more extensive than the portion figured (SA). A small sorting area of irregular form was found on the right posterior wall of the stomach, near the mouth of the mid gut. This sorting area comprised a few large, irregular folds which focused upon the intestinal groove, into which its ciliary pathways discharged. At the outer margin of this sorting area there were two orifices of ducts to the digestive diverticula (SA, DDD).

A further point needs to be made with respect to this series of 38 plus two orifices of ducts to the digestive diverticula. In the course of the dissection the stomach wall has been cut at two selected points (CUT), and the stomach has been stretched backwards to be able to represent the whole uninterrupted series of duct orifices in the figure. However, in the undissected state the 38th duct orifice would lie close to the right side of the oesophageal orifice, which is where it was found in the first of the dissections reported here.

In all studies on the structure of the bivalve stomach it has been customary to depict the dorsal hood on the left side, where its functional relations with the gastric shield, the left pouch, and the tip of the crystalline style can best be illustrated. Had it been possible to make one further dissection of this species, it would have been my intention to transfer the dorsal hood to the left side of the diagram in conformity with this practice. It is here shown on the right side (DH), together with a fragment of the gastric shield (GS).

Review of literature

Arcidae (figure 3*a*, p. 194)

Anadarinae	
Anadara granosa (L., 1758)	(Purchon 1957*a*)
Anadara senilis (L., 1758)	(Yoloye 1975)
Anadara trapezia (Deshayes, 1840)	(Sullivan 1960)
Bathyarca glacialis (Gray, 1824)	(Oliver & Allen 1980*a*)
Trisidos semitorta (Lamarck, 1819)	(Morton 1983)
Arcinae	
Arca avellana Lamarck, 1819	(Purchon 1957*a*)
Arca concamera Bruguière, 1789	(Dinamani 1967)
Arca inaequivalvia Bruguière, 1789	(Dinamani 1967)
Arca rhombea Born, 1780	(Dinamani 1967)
Bentharca nodulosa (Müller, 1776)	(Oliver & Allen 1980*a*)

Anadara granosa is typical (figure 3) with a well developed sorting area of parallel folds lying at right angles to the major typhlosole and its tongue, extending from the apex of the food-sorting caecum across the floor of the stomach almost to the orifice of the mid gut. Orifices of ducts from the digestive diverticula are equally spaced along the anterior border of part of the sorting area ventral to the oesophageal orifice. The style sac and mid gut are conjoined, and the minor typhlosole ends close to the orifice of the mid gut into the stomach. The left pouch receives two ducts from the digestive diverticula on the left side of the body. The intestinal groove arises outside the mouth of the left pouch, and circumnavigates the tongue of the major typhlosole. The gastric shield invests the ventral border of the dorsal hood, and the posterior border of the left pouch. Figures of the stomachs of *Anadara granosa* (Purchon 1957*a*) and of *T. semitorta* (Morton 1983) suggest presence of a hood groove linking the apex of the food-sorting caecum with the dorsal hood, and possibly signify the presence of a sorting mechanism of type B (Reid 1965).

There are considerable variations from this pattern within the family Arcidae, particularly with respect to the long series of ducts from the digestive diverticula, and the extent of the sorting area. These differences do not relate to the division of the family into two subfamilies. There may be as many as 38 duct orifices (*Trisidos semitorta*), or as few as eight (*Anadara senilis*); alternatively the series is broken into four clusters of four orifices each (*Arca concamera*), or two clusters of two orifices each, in a deep embayment (*Bathyarca glacialis*). The sorting area is extensive in *Anadara granosa*, *A. senilis*, and *Arca concamera*, but is wholly lacking in *Trisidos semitorta*. In *T. semitorta* two ducts from the digestive diverticula open separately on the right side of the stomach, close to the orifice of the mid gut, but separated from it by a small sorting area of irregular radiating folds. Careful study of the description of *Bathyarca glacialis* suggests that the food-sorting caecum and the left pouch have been interpreted collectively as the left pouch, since the tongue of the major typhlosole would be expected to enter the caecum, and very rarely enters the left pouch (as in *Atrina vexillum*).

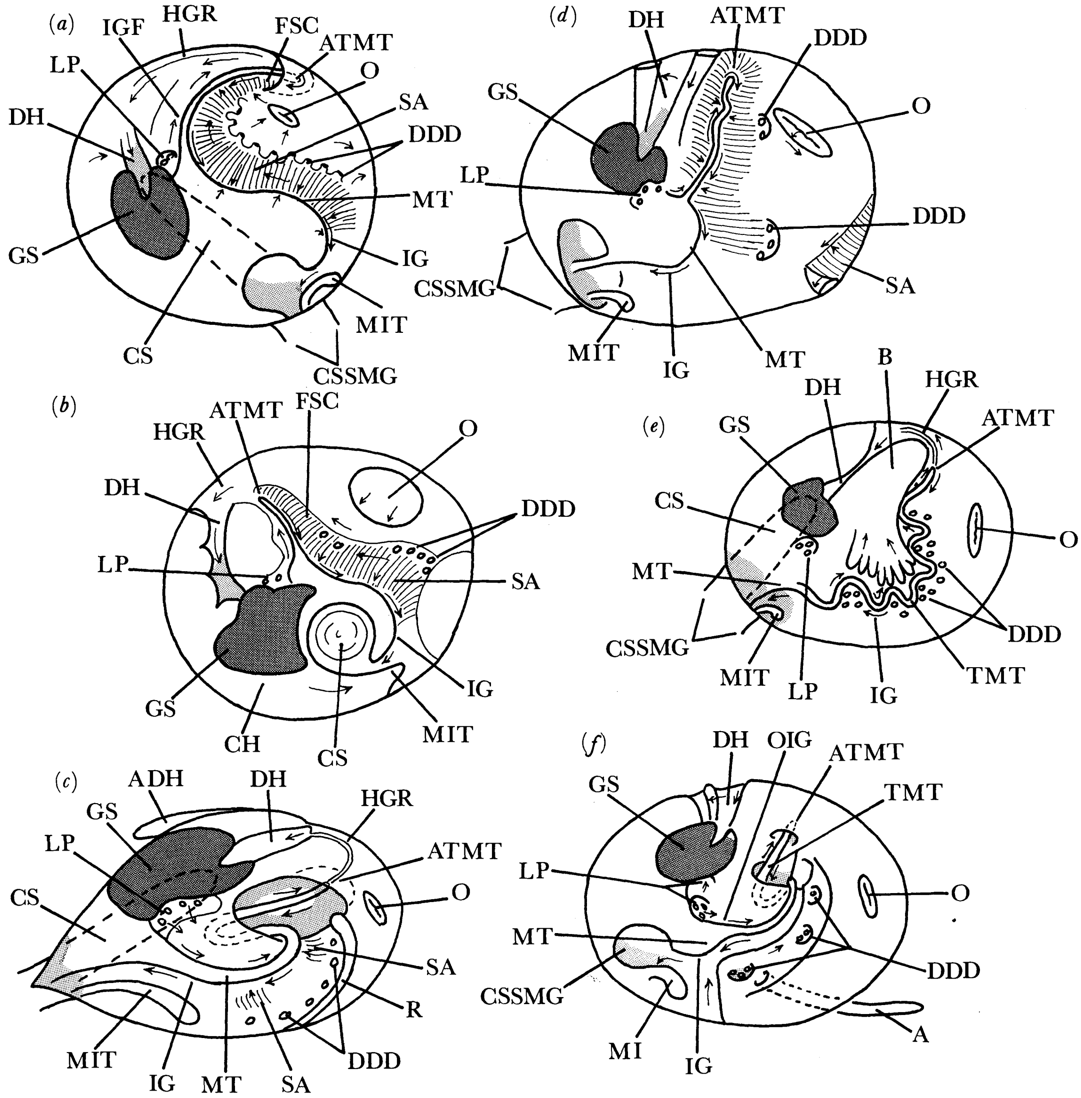


FIGURE 3. Diagrammatic representations of the interior of the stomach in the Gastrotriteia, after opening on the right side. (*a*) Arcidae; (*b*) Limopsidae; (*c*) Mytilidae; (*d*) Pinnidae; (*e*) Pteriidae and Vulsellidae; (*f*) Ostreidae. In all examples the major typhlosole is developed into a long, slender tongue that penetrates deeply (ATMT) into a food-sorting caecum (FSC). In the Mytilidae, Pteriidae and Vulsellidae (*c*, *e*) note the hood groove (HGR) which links the apex of the typhlosolar tongue with the dorsal hood. A left pouch (LP) is present and contains duct orifices. In the Glycymeridae there is a minor difference from the Arcidae in the much smaller number of duct orifices.

Limopsacea

Review of literature

Glycymeridae

Glycymeris glycymeris (L., 1758) (Graham 1949; Reid 1965)
Glycmeris violacescens Lam., 1819 (Purchon 1957*b*)

Graham's figures 1 and 1A indicate the disposition of the tongue of the major typhlosole and intestinal groove. He discriminates between a sorting area of the food-sorting caecum and a posterior sorting area, these being separated by a slender ridge which then borders the intestinal groove in the caecum. The anterior border of the sorting area of the caecum bears a slender pleat which enters in turn each of the five ducts from the digestive diverticula entering the stomach here in an evenly spaced linear series. Reid reports that this pleat forms a continuous typhlosole separating the ciliated and non-ciliated components of each duct. Reid found 'about seven' ducts in this series, each lying within a vertical fold of the stomach wall, a condition suggestive of that described for *Trisidos semitorta* (Arcidae). Graham asserted that the caecum could be closed from the main gastric cavity by apposition of the smooth areas lying anteroventrally and posterodorsally, opposite the oesphageal orifice. All the ducts from the digestive diverticula on the left side of the body open into the left pouch.

In *G. violacescens* a few differences are noted. The sorting area was not divided into anterior and posterior components, and no longitudinal ridge separated the sorting area from the intestinal groove. The digestive diverticula of the right side opened into the stomach by only four orifices and these orifices were judged to represent embayments of the stomach wall, each receiving a group of ducts from the digestive diverticula. Reid did not comment on this and it is uncertain whether the Glycymeridae are characterized by clustering of the ducts into a few *embayments*, a significant difference from the condition observed in the Arcidae, or whether there are only a few *ducts* which subdivide almost immediately. The sorting area of the food sorting caecum extended round the tip of the typhlosolar tongue in *G. violacescens*, and extended on to the posterior wall of the caecum. This observation precludes the occurrence of a type B sorting mechanism (Reid 1965), which supports Reid's conclusion that in *G. glycymeris* the tongue of the major typhlosole represents 'part of a type B sorting mechanism'. Taking into account these minor interspecific differences, figure 3*a* may be taken to represent both the Arcidae and the Glycymeridae.

Limopsidae (figure 3*b*, p. 194)

Limopsis aurita (Brocchi, 1814)	(Oliver & Allen 1980*b*)
Limopsis belcheri (Adams & Reeve, 1850)	(Dinamani 1967)
Limopsis vaginatus Dall, 1891	(Purchon 1957*b*)

Only preserved specimens of *L. belcheri* and *L. vaginatus* were available, but Oliver & Allen (1980*b*) studied living material and their figure 4 gives basic information on ciliary currents in the stomach. The studies on these three species are in general agreement. The oesophagus is decidedly large, as also is the crystalline style. The style sac and mid gut are conjoined, the minor typhlosole ends on the stomach wall close to the orifice of the mid gut, and the major typhlosole sends a long slender tongue up the left side of the stomach into a food-sorting caecum. Oliver & Allen's statement that the left pouch 'is penetrated by a tongue of the major typhlosole' is based on misinterpretation. The ducts from the digestive diverticula open into the stomach in three clusters; two ducts enter via the left pouch, two ducts enter the anterior face of the stomach, below and to the left of the oesophageal orifice, and four or five ducts enter on the right side, either near the oesophageal orifice or further posteriorly, close to the mid gut. There is a well developed dorsal hood, bounded by longitudinal ridges anteriorly and posteriorly. In *L. aurita* there is a deep and strongly ciliated tract which carries particles to the dorsal hood, apparently from the head of the food-sorting caecum. In Oliver & Allen's figure 4 this could be interpreted as merely a component of the dorsal hood, but it might possibly represent the hood tract of a type B sorting mechanism (Reid 1965). The general structure of this part of the stomach is reminiscent of that of *Pteria penguin*, though in the latter the buttress (= axial fold) is more powerfully developed and stretches across the floor of the stomach from left to right as a series of finger-like processes (figure 3*e*).

Oliver & Allen mention the presence of a sorting mechanism of type A (Reid 1965), but do not depict this clearly in their figure 4. However, Dinamani (1967) shows this sorting area as a narrow strip of regularly arranged transverse folds lying along the right side of the major typhlosole and its tongue. The gastric shield is large and sends one flange into the mouth of the dorsal hood, and another into that of the left pouch. The crystalline style may not be long, but it is evidently a thick structure. In *L. aurita* the posterior floor of the stomach was unciliated, but covered by a thin coat of material comparable to the gastric shield in transverse section. This fact, together with the remarkably wide oesophagus, suggests that it may be able to ingest and digest occasional large items of food. The Limopsidae are categorized as epibenthic suspension feeders by Oliver & Allen, but it seems distinctly possible that they are opportunists which feed upon anything available, including all forms of plankton and carcases of small crustaceans. For what other reason should the oesphagus be so wide, and the interior of the stomach protected by a chitinous sheath? The rather weak development of the sorting area in *L. aurita* may indicate a less rigorous sorting of particulate food than is typical of shallow water suspension feeders. Figure 3*b* indicates some similarities with the Arcacea (figure 3*a*), but also some specialized features.

Philobryidae
Philobrya munita Finlay, 1930 (Morton 1978)

The specimens studied were of very small size and the only information available was that obtained by reconstruction from serial transverse sections. The style sac and mid gut are conjoined, the minor typhlosole enters the stomach and ends on its right side close to the orifice of the only duct from the digestive diverticula on the right side of the body. The digestive diverticula of the left side have only one duct, which enters the stomach via the left pouch. The major typhlosole crosses the stomach and ends near the mouth of the left pouch, having given rise to a tongue which arises on the *right* side of the stomach and passes forward into a food-sorting caecum on the *right* side of the oesophagus. This disposition does not support Morton's (1978) assertion that 'the structure of the stomach of *P. munita* closely conforms to that of *Limopsis vaginatus* and *Glycymeris violacescens*'. The gastric shield invests the posterodorsal border of the left pouch, but does not support the mouth of the dorsal hood. No information is available regarding sorting areas in the stomach. The small number of ducts from the digestive diverticula, and the apparent simplicity of the interior of the stomach is presumably attributable to the small size of the animals studied. It is frequently noted among bivalves that there is a greater number of ducts from the digestive diverticula on the right side of the stomach than on the left. If hypertrophy of the digestive diverticula of the right side is a characteristic of bivalve molluscs, but has not occurred in these small specimens, this might account for the position of the typhlosolar tongue, and the food-sorting caecum in these specimens. Had growth been continued, these structures might have been pushed further to the left.

Mytilacea

Review of literature

Mytilidae (figure 3*c*, p. 194)

Arcuatula elegans (Gray, 1828)	(Morton 1977*b*)
Arcuatula sp.	(Dinamani 1967)
Adula (*Botula*) *falcata* Gould, 1851	(Fankboner 1971)
Botula cinnamomea (Lamarck, 1819)	(Dinamani 1967)
Limnoperna fortunei (Dunker, 1856)	(Morton 1973)
Lithophaga gracilis Philippi, 1847	(Dinamani 1967)
Lithophaga nasuta (Philippi, 1846)	(Purchon 1957*b*)
Modiolus metcalfei (Hanley, 1843)	(Morton 1977*c*)
Modiolus modiolus (L., 1758)	(Reid 1965)
Modiolus striatulus (Hanley, 1843)	(Dinamani 1967)
Modiolus undulatus (Dunker, 1857)	(Dinamani 1967)
Musculista senhausia Benson, 1842	(Morton 1974*a*)
Mytella charruana (d'Orbigny, 1846)	(Narchi 1983)
Mytilus edulis L., 1758	(Graham 1949; Reid 1965)
Perna viridis (L., 1758)	(Dinamani 1967)

The internal structure of the stomach of several genera in the family Mytilidae is thoroughly documented by recent studies which are broadly in agreement. A general statement can be made, to which only minor amendments are required to suit individual examples. Save for *Mytella charruana*, *Muscalista senhausia* and *Arcuatula elegans*, the style sac and mid gut are conjoined, and leave the posterior end of the stomach. The minor typhlosole emerges from the mid gut and terminates on the right side of the stomach nearby. At the posterior end of the stomach the major typhlosole has a relatively broad base in *Mytilus edulis* and in *Lithophaga nasuta*, but it is typically slender at its base, and almost the whole of the major typhlosole can be designated as its tongue. The tongue of the major typhlosole reaches its maximum development in *Perna viridis*, in *Modiolus undulatus*, and in *Arcuatula* species, in which it coils twice within the food-sorting caecum before ending on its left anterior wall, on the left of the oesophageal orifice. Typically the tongue is shorter and simpler in form; it crosses the floor of the stomach from right to left, it turns downwards into the food-sorting caecum on the left anterior floor of the stomach, and then turns forwards to its apex at the anterior end of the caecum (figure 3*c*). Similarly the food-sorting caecum varies in size and in complexity. In some species there is a type B sorting mechanism (Reid 1965) at the apex of the food-sorting caecum, a ciliated hood groove carrying selected particles from the caecum to the dorsal hood, for example, in *Mytilus edulis*, in *Adula falcata*, and probably in *Musculista senhausia* in which a ciliated hood tract is figured, suggesting the presence of a type B sorting mechanism.

Generally in the Mytilidae the floor of the stomach is dominated by the tongue of the major typhlosole and by the left and right duct tracts, while folded sorting areas are notably absent. However, in *Limnoperna fortunei* there is a sorting area of parallel ridges and grooves above the mouth of the food-sorting caecum, separating this from the left pouch.

The intestinal groove arises at the base of the typhlosolar tongue, on its left side, and accompanies the tongue throughout the food-sorting caecum, around its apex and then backwards into the mid gut. At the site of the type B sorting mechanism a ciliated hood groove departs and conveys selected material into the dorsal hood. The gastric shield lies on the left side of the stomach, and is held firmly in position by a saddle-shaped flange which enters the lower or posterior border of the mouth of the dorsal hood, and by another flange which invests the mouth of the left pouch a little lower down. The dorsal hood extends backwards from the left roof of the stomach, tapering towards its apex. The left pouch serves to secure the gastric shield, it receives ducts from the digestive diverticula on the left side of the body, and the left duct tract originates here. The intestinal groove arises outside the left pouch, on the left side of the typhlosolar tongue.

The ducts from the digestive diverticula on the left side of the body open into the stomach via the left pouch and the left duct tract (Reid 1965), while the ducts of those on the right side of the body open into the stomach via the right duct tract. These two duct tracts accompany the typhlosolar tongue and the intestinal groove into the food-sorting caecum, carrying particles inwards to the apex of the caecum. In a few cases these duct tracts have developed a series of transverse ridges and grooves, on which cilia beat over the crests of the ridges into the caecum, and along the grooves into the intestinal groove. Such a system of ciliated folds has been termed a type A sorting mechanism by Reid (1965), and this was found to be very weakly developed in *Lithophaga nasuta* and in *Perna viridis*, but more strongly so in *Modiolus modiolus* and in *M. metcalfei* (figure 3*c*). A similar weak sorting area of type A was found at the posterior end of the right duct tract, where it discharges waste material into the intestinal groove, in *Lithophaga nasuta* and in *Perna viridis*.

On the left side of the body the digestive diverticula open into the left pouch or into the left duct tract nearby, usually in small clusters, but sometimes in a regularly spaced series as in *Perna viridis*. The digestive diverticula on the right side of the body usually open in small groups, but in a regularly spaced series in *Botula cinnamomea*, in *Modiolus* species and in *Perna viridis*. *Modiolus metcalfei* and *Limnoperna fortunei* are unusual in having a small group of duct orifices lying within the food-sorting caecum, on its anterior side. This group has presumably moved from a more characteristic position a little below and to the left of the oesophageal orifice.

An appendix was found on the right posterior wall of the stomach in *Mytilus edulis*, in *Modiolus metcalfei*, and in *Adula falcata*. It was thought to be non-functional by Reid (1965) in *M. edulis*, but to be concerned in removal of excess material from the mucus-bound bolus in the lumen of the stomach of *A. falcata* by Fankboner (1971).

Reid (1965) observed regular contractions in the stomach wall of *M. edulis*. The stomach had been fully exposed by dissection, but had not been cut open. Muscular contractions occurred about twice per minute, and took about 20 seconds to pass round the whole stomach wall. Observations were continued for as long as two hours, and were repeated on a number of specimens. The effect of these contractions was thought to be a temporary widening of the rejectory grooves within the stomach, which would augment the rate of rejection of excess material.

Mytella charruana is atypical in that the mid gut and the style sac are wholly separate (Narchi 1983).

Pinnacea

Review of literature

Pinnidae (figure 3*d*, p. 194)

Atrina vexillum (Born, 1778)	(Purchon 1957*b*)
Pinna bicolor Gmelin, 1791	(Dinamani 1967)
=*P. atropurpurea* Sowerby, 1825	(Purchon 1957*b*)

The oesophagus is wide and dorsoventrally flattened, and the combined style sac and mid gut leaves the stomach posteriorly. The minor typhlosole ends at the orifice of the mid gut. The major typhlosole curves across the floor of the stomach to the left, gives rise to a long and slender tongue, and then ends outside the left pouch. The typhlosolar tongue passes far up the left side of the stomach in the food-sorting caecum. The floor of the stomach, and that of the caecum, are dominated by a large type A sorting mechanism (Reid 1965) whose folds lie at right angles to the typhlosolar tongue and extend round its apex on to the posterior side of the caecum. The food-sorting caecum extends over the roof of the stomach and far downwards on the right side. The presence of this sorting area precludes the occurrence of a type B sorting mechanism (Reid 1965) at the apex of the caecum. A large and fleshy axial fold separates the caecum from the dorsal hood, which is well developed, with substantial ridges on its posterior wall. The small and compact gastric shield is held in position by saddle-shaped flanges which invest the lower border of the mouth of the dorsal hood above, and the upper border of the mouth of the left pouch below. About 15 ducts from the digestive diverticula on the left side of the body open into the left pouch. Three ducts open via an embayment of the anterior wall of the stomach lying below the oesophageal orifice, while the remainder open by about 12 ducts discharging via a wide embayment on the right side of the stomach.

A. vexillum differs from the above account in one major respect. Is is unusual, perhaps unique, in that the major typhlosole sends a secondary tongue into the left pouch. The intestinal groove arises posterior to this secondary tongue, it enters the left pouch, passes round the tongue and then emerges from the left pouch anteriorly to penetrate the food sorting caecum in the customary fashion. In *A. vexillum* there is an additional duct embayment below the oesophageal orifice.

The stomach in the Pinnidae differs from those in the Arcidae and Glycymeridae in that the sorting area does not extend back to the orifice of the mid gut; however, there is a general resemblance with the stomach of the Glycymeridae, especially if the duct orifices in the Glycymeridae prove to be clusters of ducts opening via an embayment of the stomach wall.

Pteriacea

Description of fresh material

Pteriidae (figure 3*e*, p. 194)

Pteria penguin (Röding, 1798)

The upper and lower lips of the mouth were very deep, and the mouth was broad. The oesophagus (O) was wide and flat throughout its length, and lay close beneath the mantle crest, and slow ciliary currents were found over its whole internal surface. The entrance of the oesophagus into the stomach was marked by a transverse ridge (R) on which cilia beat

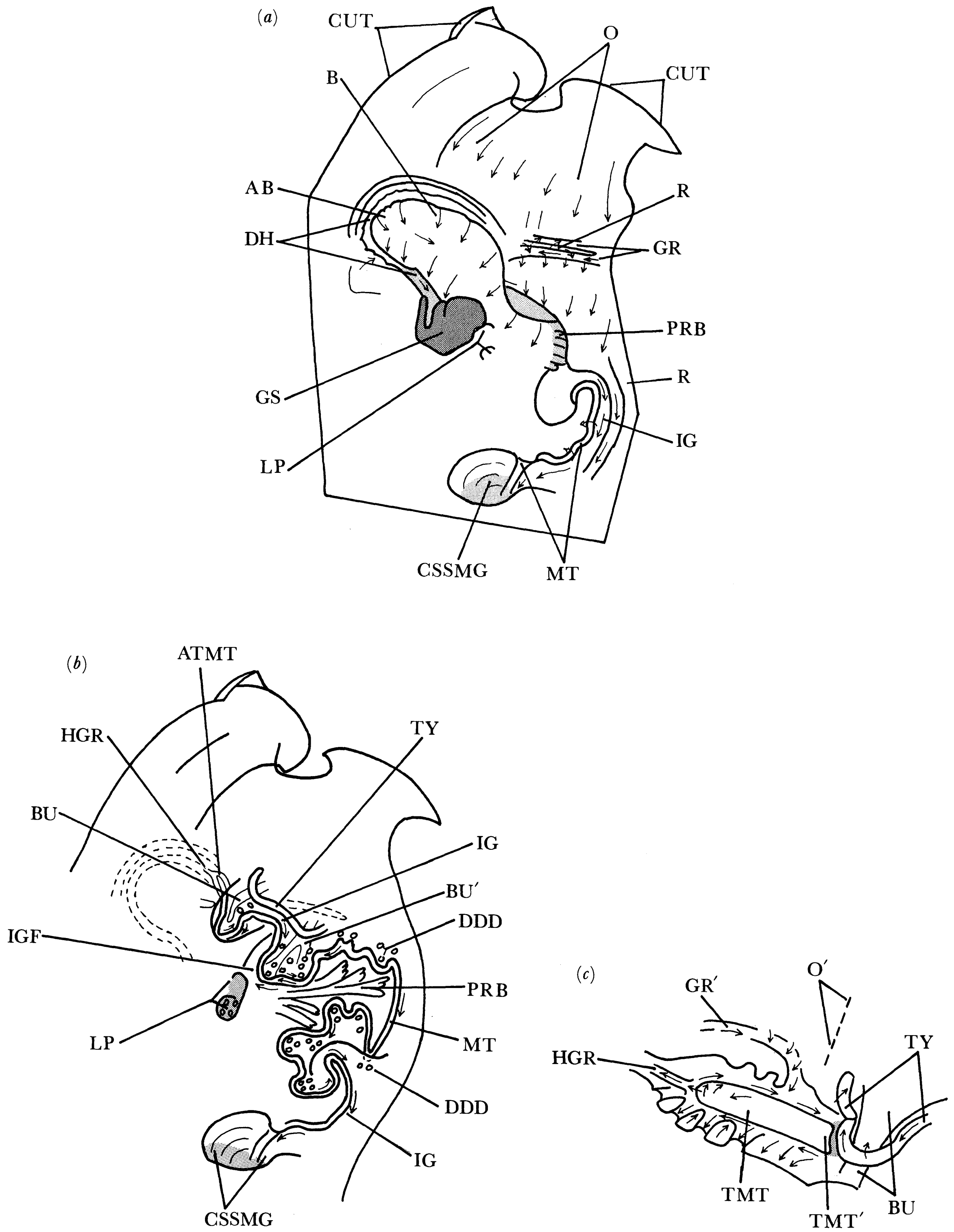


FIGURE 4. *Pteria penguin*, three stages in dissection of the stomach from the dorsal surface. (*a*) A preliminary stage (magn. × 5); (*b*) the full course of the tongue of the major typhlosole (MT) and the hood groove (HGR), and the positions of all the duct orifices (DDD) (magn. × 5); (*c*) details of the type B sorting mechanism at the apex of the typhlosolar tongue and origin of the hood groove (magn. × 20).

transversely from left to right and also into two grooves (GR) lying anterior and posterior to the ridge. Immediately posterior to the transverse ridge and grooves, cilia on the anterior floor of the stomach conveyed material posteriorly and on to the right side of the stomach, along another ridge (R) which isolated this material from the intestinal groove (IG) nearby, and carried particles past the orifice of the combined style sac and mid gut (CSSMG) towards the dorsal hood (DH).

On the left side of the stomach a fleshy buttress (B) extended downwards on to the floor of the stomach, over which it spread to the right as a series of finger-like processes (PRB). A deep U-shaped groove encompassed the upper part of the buttress, and the portion of this groove from the apex of the buttress (AB) to the gastric shield was the dorsal hood (DH), a deep but featureless hollow. Cilia on the surface of the buttress beat strongly backwards into the dorsal hood, and also into the left pouch (LP).

At the posterior end of the stomach the combined style sac and mid gut (CSSMG) passed downwards into the visceral mass; the major intestinal typhlosole (MT) and the intestinal groove (IG) passed forwards into the stomach along its right side in an arc which dipped out of sight in the first phase of the dissection. By further dissection the two structures were followed forwards in a series of five roughly semicircular flares, the first of which has just been described. The second and third flares lay on the right side of the stomach, the fourth lay on its right anterior wall, while the smaller fifth flare lay on the left side of the median line. The tongue of the major typhlosole reached its apex (ATMT) anteriorly on the left side, ventral to the left border of the oesophageal orifice into the stomach. A considerable length of the major typhlosole was accompanied by the intestinal groove on both sides, the cilia in the groove on the posterior side beating towards the apex of the tongue, while those in the groove on the anterior side were beating towards the mid gut. This sector of the major typhlosole was therefore the 'tongue', but I did not succeed in ascertaining the position of the origin of the outwardly running sector of the intestinal groove, and it was therefore not possible to determine the point of origin of the tongue.

Beneath the left and right margins of the oesophageal orifice into the stomach two small buttresses (BU, BU′) pressed downwards and backwards, apparently pushing the tongue of the major typhlosole backwards at these points, just as the finger-like processes of the large buttress (PRB) apparently push the major typhlosole and intestinal groove across to the right. A secondary typhlosole (TY) passed transversely across the left and right buttresses (BU, BU′) and cilia on this secondary typhlosole beat strongly to the left, and also anteriorly away from the intestinal groove, thus preventing newly arrived particles from being trapped prematurely in the intestinal groove. The apex of the tongue of the major typhlosole (ATMT) lay in a pocket on the left side of the median line. Here there was a type B sorting mechanism (Reid 1965) from which a groove (HGR) conveyed selected particles round the apex of the buttress (AB) and thence into the dorsal hood.

Thirty two orifices of ducts from the digestive diverticula were found in association with the major typhlosole, all of these lying on the same side of the typhlosole and in close association with the intestinal groove. No ducts were found in the region of the posteriormost semicircular flare of the major typhlosole. In addition to the above, four ducts to the digestive diverticula were found entering a shallow depression on the floor of the stomach (LP) which was judged to be the left pouch although it was unusual in not receiving an extension of the gastric shield into its mouth.

Review of literature

Pteriidae (figure 3*e*, p. 194)	
Pinctada vulgaris (Schumacher, 1817)	(Herdman 1904; Purchon 1957*b*)
Pteria chinensis (Leach, 1814)	(Purchon 1985)
Pteria penguin (Röding, 1798)	

The wide oesophagus is flattened dorsoventrally and enters the stomach anteriorly, while the conjoined style sac and mid gut leaves posteroventrally. The minor typhlosole ends on the right side of the stomach near the orifice of the mid gut. The left anterior side and the floor of the stomach are dominated by a fleshy buttress which passes downwards and spreads outwards to the right in an array of finger-like processes closely approaching the tongue of the major typhlosole. These processes of the buttress perform a ciliary directive function on the stomach contents, but there is no conventional sorting area in the stomach. The typhlosolar tongue passes forwards from near the mid gut, travelling round the right and anterior sides of the stomach in a series of semicircular flares which increase its length and bring it in close association with the large number of orifices of ducts from the digestive diverticula. Finally the tongue passes up the left anterior side of the stomach, ending near the left corner of the oesophageal orifice. The typhlosolar tongue is particularly long in large specimens of *P. penguin*, but less so in *P. chinensis* and in *Pinctada vulgaris*.

There is a type B sorting mechanism (Reid 1965) at the apex of the food-sorting caecum, and this communicates with the upper border of the dorsal hood by a ciliated hood tract. Four ducts from the digestive diverticula open into the left pouch and the remainder open by a large number of orifices arranged in irregular groups of three or four along the anterior and right side of the typhlosolar tongue and intestinal groove. In a large specimen of *Pteria penguin* there were 32 duct orifices, all unclustered, while in *Pteria vulgaris* there were 23 ducts, arranged mainly in three clusters. The dorsal hood forms a deep but narrow cleft on the left side of the stomach, above the left pouch. The gastric shield is secured in position by a flange which enters the ventral border of the dorsal hood and another which enters the left pouch. In *Pinctada vulgaris* a ciliated pathway leads from the floor of the left pouch to the origin of the intestinal groove. The dorsal hood and the gastric shield were relatively smaller in *Pteria penguin* than in *Pinctada vulgaris*.

In the Pteriidae it seems that the ciliary mechanisms in the stomach are primarily designed for preliminary acceptance of particulate food material; this may relate to the position adopted by these bivalves among gorgonians, where the water should be relatively clean.

Isognomonidae	
Crenatula modiolaris (Lamarck, 1819)	(Reid & Porteous 1980)
Isognomon nucleus (Lamarck, 1819)	(Dinamani 1967)
Malleidae	
Malleus albus Lamarck, 1819	(Purchon 1957*b*)
Vulsella vulsella (L., 1758)	(Reid & Porteous 1980)

The stomach in these families is basically comparable with that in the Pteriidae (figure 3*e*), but is very much simpler, partly due perhaps to the smaller size of the specimens studied. The axial fold is not developed into a robust buttress, but the finger-like processes radiating from its base are much the same, though smaller in *V. vulsella* than in *M. albus*. No finger-like processes were found in *I. nucleus*. In these families the tongue of the major typhlosole is less tortuous, but in *M. albus* it still twists in and out of embayments of the stomach wall receiving duct orifices. In *V. vulsella* the tongue is very short and simple, and forms the greater part of the major typhlosole. In *V. vulsella* a type B sorting mechanism (Reid 1965) is present, a ciliated hood groove passing from the apex of the simple food-sorting caecum to the dorsal hood. As in the Pteriidae, there is no conventional sorting area in the food-sorting caecum or on the anterior floor of the stomach in these families. Dinamani (1967) reported that the stomach of *I. nucleus* is fashioned on the mytilid pattern, but here it is judged to be more similar to the pteriid pattern, which had not been studied by Dinamani.

Ducts from the digestive diverticula on the left side of the body open into or near the left pouch, four in the case of *V. vulsella*, and two in *M. albus*. The remainder of the ducts from the digestive diverticula open on the right side of the stomach, usually in a few groups, though in *I. nucleus* one group of six ducts is arranged in an evenly spaced series below the oesophageal orifice, on the anterior side of the food-sorting caecum. In *M. albus* the ducts open in clusters into three deep embayments of the stomach wall, into which the typhlosolar tongue penetrates, and this is also true for the posteriormost cluster of ducts in *I. nucleus*.

In *M. albus* it was reported by Purchon (1957*b*) that there was an interruption in the course of the major typhlosole and the intestinal groove, within the posteriormost stomach embayment. No such condition has been reported for other members of the Vulsellidae, and the condition observed may have been an individual abnormality, or it may have been based on a misinterpretation. *C. modiolaris* is unusual in that the major typhlosole has a muscular lobe which appears able to close off the intestinal groove. The intestinal groove arises in the left duct tract, outside the left pouch, and near the base of the major typhlosole. This is especially clearly demonstrated in *V. vulsella*.

The dorsal hood lies high up on the left side of the stomach, above the left pouch, and the gastric shield is secured in position by marginal flares which pass into the mouths of these two features. The style sac and mid gut are conjoined in all cases, and leave the stomach posteriorly. The minor typhlosole ends on the right side of the stomach, close to the orifice of the mid gut. In *V. vulsella* a secondary intestinal groove, associated with the minor typhlosole, passes round the right side of a group of 12 ducts which open a little distance from the true intestinal groove. In *C. modiolaris* there is a comparable group of duct orifices, but ciliated ridges emerge from these orifices, and merge into a single ridge which carries particles away from the duct orifices and into the dorsal hood.

Ostreacea

Review of literature

Ostreidae (figure 3*f*, p. 194)

Ostrea edulis L., 1758	(Yonge 1926; Graham 1949; Reid 1965)
Ostrea forskali Gmelin, 1791	(Dinamani 1967)
Ostrea madrasensis Preston, 1916	(Dinamani 1967)
Ostrea parasitica Gmelin, 1791	(Purchon 1957*b*)

The wide oesophagus is dorsoventrally flattened and enters the stomach anteriorly, and the combined style sac and mid gut leaves posteriorly. The minor typhlosole ends on the right side of the stomach, close to the orifice of the mid gut. A minor intestinal groove is deeper, and more strongly ciliated in *O. edulis* than in *Mytilus edulis.* The major typhlosole passes forwards on the floor of the stomach and almost immediately develops as a slender tongue with a wide left duct tract and the intestinal groove on its left side. The typhlosolar tongue passes far to the left in the food-sorting caecum. There are no sorting areas on the floor of the stomach, though Reid (1965) reports that in *O. edulis* the left and right duct tracts develop marked transverse ridges within the caecum. He compared the stomach of *O. edulis* with that of *Mytilus* edulis, while Purchon (1957*b*) compared the stomach of *O. parasitica* with that of *Lithophaga nasuta.* A very weak sorting area along the ventral margin of the axial fold of *O. parasitica* indicates some similarity with stomachs in the Pteriacea. However, there is a major difference from the stomachs of the Mytilacea and the Pteriacea in that the ducts from the digestive diverticula are not scattered, but are concentrated into only a few embayments of the stomach wall. Yonge (1926) showed by means of gelatin casts that in *O. edulis* the digestive diverticula communicate with the stomach at only two points, the left pouch, and the floor of the food sorting caecum below the oesophageal orifice. Graham (1949) recorded that in *O. edulis* a group of four ducts enters the floor of the caecum, and a fifth duct opens nearby. In the remaining species the floor of the caecum receives three groups of ducts.

The dorsal hood is well developed, and passes waste matter into a hollow passing over the roof and down the right posterior side of the stomach, to discharge into the intestinal groove near the orifice of the mid gut. The left pouch comprises two hollows, with four ducts from the digestive diverticula opening into the lower hollow. The gastric shield invests the upper border of the upper hollow, which is blind, and also invests the lower margin of the dorsal hood. A blind appendix was found on the right side of the stomach of *O. edulis* and *O. forskali* by Reid (1965) and Dinamani (1967), respectively. This appendix may be homologous with the posterodorsal caecum of the Tellinacea (Yonge 1949) and with the appendix of the Pholadidae and Teredinidae (Purchon 1955*b*, 1960*a*). Failure to find an appendix in *O. parasitica* may have been due to misidentification of a small aperture on the right side of the stomach (Purchon 1957*b*, figure 8, DDD^1).

Owing to the lack of sorting areas, and the concentration of the orifices of the ducts from the digestive gland, it is concluded that the stomach of the Ostreacea provides a sixth category of stomach in the Gastrotriteia (figure 3*f*).

Analysis

Review of the structure and function of the stomach in the six superfamilies that compose the Gastrotriteia reveals that although all examples investigated possess the tongue of the major typhlosole which is diagnostic of the Gastrotriteia, these examples do not conform to a single common plan, but must be assigned to six different subordinate types. With the information at present available, each of these stomach types is representative of one of the six superfamilies, suggesting the occurrence of an adaptive radiation within the Gastrotriteia which has affected the general organization of the stomach as much as any other organ system (figure 3). As summarized in table 1, diversification of stomach organization within the Gastrotriteia has concerned three principal features: the presence or absence of ciliary sorting areas with parallel folds lying at right angles to the major typhlosole and intestinal groove; whether the digestive diverticular communicate with the stomach via a large number of scattered duct orifices or whether the ducts have been concentrated into groups, and perhaps open via embayments of

TABLE 1. DIVERSITY OF STOMACH STRUCTURE IN THE GASTROTRITEIA

regularly folded sorting area	duct orifices scattered	duct orifices clustered
present	Arcidae Limopsidae	Pinnidae
absent	†Pteriidae †Mytilidae	Ostreidae

† A type B sorting mechanism is present.

the stomach wall; whether a type B sorting mechanism (Reid 1965) has developed at the apex of the food-sorting caecum, and links this organ with the dorsal hood by means of a ciliated hood groove.

STOMACH TYPE IV: GASTROTETARTICA

Pectinacea

Description of fresh material
Chlamys crassicostata (Sowerby, 1842)

Only one living specimen was available for investigation. The oesophagus was slit open along the mid-dorsal line, and the incision was extended down the right side of the stomach and then along the combined mid gut and style sac. This exposed a very extensive sorting area of ridges and folds (SA) on which particulate material was trapped and conveyed by ciliary action into the intestinal groove (IG) and thence into the mid gut. This sorting area invaded two large and deep pockets in each of which were found clusters of ducts from the digestive diverticula. At least seven ducts entered the pocket on the left side (PL), while at least fourteen ducts entered the pocket on the right side (PR).

On the left side of the stomach there was a large dorsal hood (DH), the posterior border of its mouth being invested by the gastric shield (GS). A sorting area (SA) extended from the stomach into the dorsal hood on its median side, and here ciliary currents passed material into the dorsal hood. The dorsal hood was unusual in structure, extending into blind, conical pockets both anteriorly (DHA) and posteriorly (DHP). A ridge (R) and a groove on the lateral wall of the dorsal hood pass backwards into the posterior pocket, and cilia beat backwards over most of this wall.

The left pouch (LP) lay median to the dorsal hood, and its posterior wall was invested by a rim of the gastric shield. There was a small sorting area in the left pouch, and here cilia beat towards the origin of the intestinal groove (OIG). Two ducts from the digestive diverticula opened into the left pouch. The gastric shield (GS) was oval in shape, and was substantially constructed.

The minor typhlosole (MIT) terminated at the orifice of the combined style sac and mid gut (CSSMG). The major typhlosole (MT), accompanied by the intestinal groove (IG) curved gently to the left across the floor of the stomach, to end just outside the mouth of the left pouch.

It is notable that the large number of ducts from the digestive diverticula, at least 23, are associated into two major and one minor cluster. In the two major clusters, located within the main sorting area of the stomach, the orifices of the ducts were generally located adjacent to areas of smooth epithelium which were bordered by a narrow opaque rim (OR).

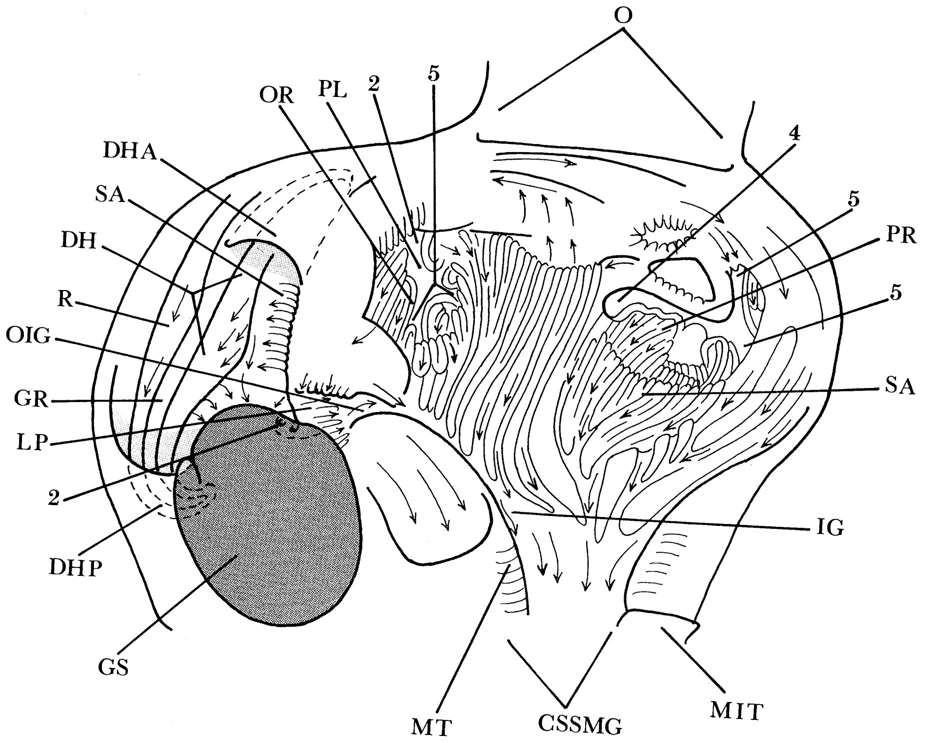


FIGURE 5. *Chlamys crassicostata*, the interior of the stomach after exposure by a mid-dorsal incision from the mouth to the mid gut (magn. × 15). The stomach is of type IV, in which the major typhlosole (MT) and intestinal groove (IG) curve across the stomach floor towards the left pouch (LP). There is an extensive sorting area (SA) on the anterior floor of the stomach. A large number of duct orifices is arranged in clusters (2, 2, 5, 4, 5, 5) in association with the sorting areas. The dorsal hood is unusually complex, with deep anterior and posterior pockets (DHA, DHP).

Review of literature

Pectinidae (figure 6*a*, p. 208)	
Chlamys crassicostata (Sowerby, 1842)	
(as *Pecten crassicostatus*, Sowerby)	(Dinamani 1967)
Chlamys opercularis (L., 1758)	(Graham 1949; Reid 1965)
Pecten maximus (L., 1758)	(Graham 1949; Reid 1965)
Spondylus hystrix Röding, 1798	(Purchon 1957*b*)

The description and illustration given by Dinamani (1967) for *Pecten crassicostatus* is basically comparable with that given for the same species in this paper, although slight differences in the strategy of dissection have resulted in differences in orientation of the two figures. Dinamani makes the point that, since the major typhlosole in this species is more or less flush with the floor of the stomach, the intestinal groove is shallow. His dissection of the left pouch revealed the presence of five or six ducts from the digestive diverticula, whereas the present study only found two. Dinamani figured the two broad pockets on the left and right sides of the extensive sorting area on the floor of the stomach, into which he showed only three and two ducts entering, respectively. The two accounts can be combined to show that in this species the ducts from the digestive diverticula open into the stomach in three comparable clusters, on the left and right sides of the stomach floor and via the left pouch.

Chlamys opercularis was described but not figured by Graham (1949), and was only briefly mentioned by Reid (1965). Graham's description for this species is in general conformity with that for *C. crassicostata*, except that he did not find two clusters of ducts entering the left and right sides of the floor of the stomach, but only two single ducts, one near the oesophageal orifice and the other a little further posterior on the right side of the stomach floor. Descriptions of the stomach of *Pecten maximus* by these authors (Graham 1949; Reid 1965) are also in accordance with the present description. Reid (1965) reported that the duct embayments are deeper in *P. maximus* than in *C. opercularis*, while Graham (1949) found there to be two ducts on each side, instead of only one as in *C. opercularis*.

The stomach of *Spondylus hystrix* was described and figured by Purchon (1957*b*), and in many respects is comparable with the above mentioned species. Six ducts were found to enter the left pouch; ducts entering the stomach elsewhere were arranged in three clusters, three ducts opened to the left of the oesophageal orifice, four ducts on the right side of the oesophageal orifice, and four more further posteriorly on the right side of the stomach. However, these duct orifices lay on the margin of the sorting area, not in hemispheric pockets within the sorting area. Another significant difference noted was the presence of a long slender process which passed backwards on the right side of the major typhlosole, which either separated the sorting area from the intestinal groove (as suggested by Purchon 1957*b*), or which caused the intestinal groove to divide, one branch passing into the left pouch and the other following the left border of the sorting area and passing into the food sorting caecum. A further difference of importance was that the sorting area of the dorsal hood passed downwards, past the mouth of the left pouch and towards the lumen of the stomach, which is true also for *Pecten maximus*, but not for *Chlamys crassicostata*.

Limacea

Review of literature

Limidae (figure 6*a*, p. 208)

Lima fragilis (Gmelin, 1791)	(Purchon 1957*b*)
Lima hians (Gmelin, 1791)	(Graham 1949; Reid 1965)

Graham (1949) noted that the general structure of the stomach of *L. hians* is reminiscent of that of *Pecten* or *Chlamys*. In *P. maximus* and in *L. hians* he figured and described a small conical pouch (Graham's figures 6 and 7, C), which I judge to be the apex of the food-sorting caecum. Reid (1965) made a very detailed study of *L. hians* and recorded in addition the presence of an appendix (Reid's figures 8 and 9, X) which usually contained sand grains. Purchon (1957*b*) had not seen such a structure in *L. fragilis*.

The structural and functional details of the stomachs of *L. fragilis* and *L. hians* are generally in close conformity. The style sac and mid gut are conjoined, the minor typhlosole curves on to the right posterior wall of the stomach where it ends, while the major typhlosole and intestinal groove curve gently to the left and end within the left pouch. The dorsal hood is large, with well developed ridges and grooves on its anterior wall, and with a sorting area of transverse ridges and grooves curving inwards to the apex of the hood. The gastric shield is apparently larger in *L. fragilis* than in *L. hians*, and only in the former species does it provide support (minimal) for the upper margin of the left pouch. On the right side of the major typhlosole and intestinal groove the chief sorting area of the stomach extends anteriorly into the

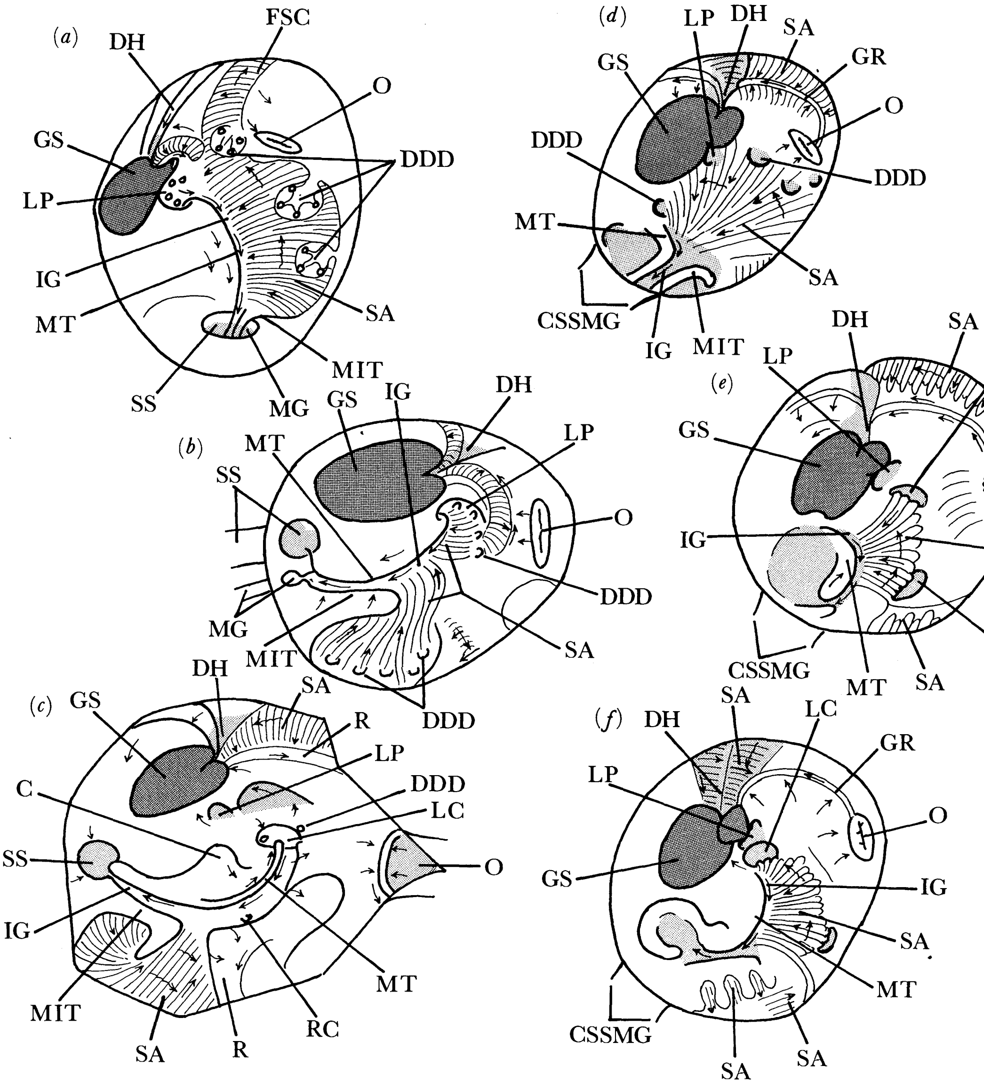


Figure 6. Diagrammatic representations of the interior of the stomach in the Gastrotetartika. This stomach, of type IV, is characterized by a major typhlosole (MT) which curves to the left across the floor of the stomach without sending a tongue into a right caecum receiving duct orifices, or into a food-sorting caecum. (*a*) Pectinidae and Limidae; (*b*) Anomiidae; (*c*) Unionidae; (*d*) Pandoridae, Chamostreidae, Myochamidae and *Cochlodesma*; (*e*) Lyonsiidae and Clavagellidae; (*f*) Laternulidae. The Unionacea are unusual in lacking an extensive sorting area on the anterior floor of the stomach, and in the penetration of the left caecum (LC) by the major typhlosole and intestinal groove. These features may suggest that in the Unionacea the stomach has reverted from stomach type V to type IV. The conical mound (C) on the floor of the stomach is apparently characteristic of this superfamily.

food-sorting caecum on the left side of the oesophageal orifice, and on to the right posterior stomach wall close to the orifice of the mid gut. Within the confines of this sorting area ducts from the digestive diverticula open into the stomach in three clusters of ten or more ducts, each cluster lying in a shallow hemispheric embayment. One of these embayments lies below the left side of the oesophageal orifice, a second lies in a comparable position on the right side, while the third lies further posteriorly. In *L. fragilis* a fourth group of nine ducts entered the stomach via the left pouch; this is probably also true for *L. hians*, but this was not reported by Reid (1965).

In *L. hians* Reid (1965) observed that the anterior border of the principal sorting area is marked by a marginal typhlosole which pushes backwards into each of the three embayments where it enters and emerges from each duct orifice in turn, thereby defining a branched non-ciliated tract on the floor of each embayment. On account of its disposition Reid called this the duct typhlosole. On the non-ciliated tract he observed a vortex created by the current from the ciliated gutter in each duct, and also saw very fine particles being drawn into the non-ciliated gutter of the duct. This was direct visual support of the counter-current theory advanced by Owen (1956). These observations that the clustered duct orifices do not enter the stomach *within* the sorting area, but along the sides of a deep and branched indentation of the margin of the sorting area provide an element of comparability with the condition in the Arcacea where, however, the line of equidistant duct orifices is clearly along the margin of the sorting area.

On the chief sorting area of the stomach an unusual feature was observed in both *L. fragilis* and in *L. hians*. In all other bivalves examined the type A sorting mechanism comprises only two contrasted ciliary pathways: at right angles over the crests of the folds towards the apex of the food-sorting caecum, and longitudinally down the grooves into the intestinal groove. In these two species of *Lima* an additional 're-sorting' current was detected on the broad posterior parts of the ridges, carrying fine particles anteriorly along the sides of the folds.

The present review re-affirms the broad similarity between the stomach in the Limidae and in the Pectinidae.

Anomiacea

Review of literature

Anomiidae (figure 6*b*, p. 208)

Anomia ephippium (L., 1758)	(Purchon 1957*b*)
Enigmonia aenigmatica (Holten, 1802)	(Morton 1976)
Placuna placenta (L., 1758)	(Purchon 1957*b*)

In several respects the internal structure of each of these examples is in conformity with a common plan. Thus the oesophagus is wide, particularly in *Enigmonia aenigmatica*, while the style sac and mid gut are wholly separate. The principal sorting area, on the floor of the stomach, is divided into anterior and posterior moeities which join basally and discharge waste material together into the intestinal groove. Morton (1976) reports this for *E. aenigmatica*, but it is less easy to discern this fact from his figure, partly because the incision in the stomach wall lay on the left side below the dorsal hood, thus apparently transferring the dorsal hood to the right side.

The minor typhlosole ends in the mouth of the mid gut in *P. placenta*, but was not seen in the other examples. In all three genera the major typhlosole and the intestinal groove curved gently to the left from the mouth of the mid gut towards the left pouch. They entered the left pouch in *A. ephippium* and in *P. placenta*, but ended close outside the left pouch in *E. aenigmatica*. The gastric shield is well developed, and invests the posteroventral border of the mouth of the dorsal hood, and also the upper margin of the left pouch, in all examples. The gastric shield is larger in *P. placenta* than in *A. ephippium*, but in *E. aenigmatica* it is especially large, covering the dorsal and posterior wall of the stomach and extending back to the mouth of the style sac.

In *A. ephippium* the dorsal hood is small and lacks a noticeable sorting area; in *P. placenta* the dorsal hood is larger, and bears two well developed sorting areas composed of transverse folds; one of these lies on the anterior face of the dorsal hood and ends on the left side of the stomach below the oesophageal orifice; the other passes over the posterior face of the dorsal hood, on to the roof and right posterior side of the stomach. In *E. aenigmatica* there are sorting areas on anterior and posterior faces of the dorsal hood, which similarly end on the anterior ventral and right posterior walls of the stomach.

The left pouch receives from two to four ducts from the digestive diverticula of the left side. The remainder of the ducts from the digestive diverticula open into the stomach in two groups, but these differ somewhat according to the genus; thus on the right posterior wall of the stomach there is a scattered cluster of duct orifices in both *A. ephippium* and in *P. placenta*, as also on the left anterior floor of the stomach of *P. placenta*. In contrast, the ducts entering on the right anterior floor of the stomach of *A. ephippium* are concentrated into a single orifice, as is also true for the ducts entering the left and right anterior sides of the stomach of *E. aenigmatica*.

In conclusion, the stomach of *E. aenigmatica* represents an extreme condition in this superfamily; the oesophagus is unusually wide, the gastric shield is unusually extensive, and the duct orifices have been reduced to a minimum. The overall similarity to the conditions described for various examples in the Cuspidariidae, Verticordiidae and Parilimyidae is obvious. The internal structure of the stomach may record an ancestral requirement in greater surf? The location of this species in the calm waters of the upper midlittoral zone of the seaward fringe of mangrove forest will minimize the need for sorting of suspended particles on the ctenidia, on the labial palps, or within the stomach. The stomach wall can scarcely require protection by an extensive gastric shield against abrasive action by sand grains. There is a very remote possibility that small planktonic larvae might be admitted through the lip apparatus, since Morton (1976) reports that the lips can open and *Enigmonia* may swallow material that has not undergone rigorous selection on the ctenidia. The adoption of a facultative carnivorous habit could be important if the sea water in the mangrove is deficient in phytoplankton through competition by other filter feeders such as *Saccostrea* and *Isognomon*.

Pandoracea

Review of literature

Pandoridae (figure 6*d*, p. 208)	
Pandora inaequivalvis (L., 1758)	(Allen 1954; Purchon 1958)
P. pinna (Montagu, 1803)	(Allen 1954)
Laternulidae (figure 6*f*)	
Cochlodesma praetenue (Pulteney, 1799)	(Allen 1958*b*)
Laternula limicola (Reeve, 1863)	(Nakazima 1957)
L. rostrata (Sowerby, 1839)	(Purchon 1958)
Cleidothaeridae	
Cleidothaerus albidus (Lam., 1819)	(Purchon 1958)
C. maorianus Finlay, 1927	(Morton 1974*b*)
Myochamidae (figure 6*d*)	
Myadora ovata Reeve, 1844	(Purchon 1958)
M. striata (Quoy & Gaimard, 1835)	(Morton 1977*a*)
Lyonsiidae (figure 6*e*)	
Lyonsia californica Conrad, 1837	(Narchi 1968)

Although each has certain characteristic features, to be mentioned below, the genera *Cleidothaerus*, *Cochlodesma*, *Myadora* and *Pandora* conform to a common pattern as regards the internal structure of the stomach. This pattern differs markedly from all other examples which have been investigated, and this may explain some of the difficulties experienced in identifying certain features in the stomachs of *Pandora* and *Cochlodesma* (Allen 1954, 1958*b*; Purchon 1958). Having compared accounts of the stomachs of these four genera it is now possible to approach these problems with greater confidence. The stomachs of *Laternula* and *Lyonsia* are markedly different, and also differ from each other in important respects. These two genera will be discussed subsequently, but it is first necessary to consider the group comprising *Cleidothaerus*, *Cochlodesma*, *Myadora* and *Pandora* which are now referred to as 'the group'.

The most striking features of the stomach in the group concern the disposition of the major typhlosole and intestinal groove, and the great extent of the folded sorting area on the floor of the stomach. The major typhlosole and the intestinal groove bend sharply to the left just outside the orifice of the combined style sac and mid gut, and form a relatively inconspicuous feature in the stomach. They do not approach the orifice of the left pouch or that of the left caecum, but terminate either just outside or just within an orifice on the left posterior floor of the stomach which receives some ducts from the digestive diverticula on that side of the stomach. This hollow cannot be the left pouch, the mouth of which is characteristically supported by a flange of the gastric shield; nor can it be equated with the left caecum, which characteristically lies on the anterior floor of the stomach, on the left side of the oesophageal orifice, and anterior to the mouth of the dorsal hood. Allen (1954, 1958*b*) considered this feature to be the right caecum in *Pandora* and *Cochlodesma*, but this cannot be so. Purchon (1958) had failed to find this orifice in *P. inaequivalvis*.

Allen (1954, 1958*b*) considered that in place of an intestinal groove there was a system of 'lateral rejection grooves' on the anterior floor of the stomach of *Pandora* and of *Cochlodesma*. He may have been influenced by the lack of a regularly folded sorting area on the anterior floor of the stomach in the superfamily Lucinacea. Certainly in the case of *Pandora*, as also in *Cleidothaerus* and *Myadora*, these folds constitute a normal sorting area, with ciliary currents passing transversely across the crests of the folds, and passing longitudinally down the grooves between the folds to discharge into the intestinal groove in the mid gut. This sorting area is unusually large in *Cleidothaerus* and in *Myadora*, while in *Cleidothaerus* there are additional sorting areas surrounding the orifice of the oesophagus, which transport freshly ingested material directly from the oesophagus to the dorsal hood. In its extreme manifestations, this type of stomach is dominated by sorting areas.

The oesophagus enters the stomach anteriorly, and the combined style sac and mid gut leaves the stomach posteroventrally. The gastric shield is well developed, especially in *Myadora* and *Cochlodesma*, and sends flares into the mouths of the dorsal hood and left pouch. The dorsal hood is well developed, its roof and anterior face bearing two sorting areas of which the anteriormost passes over the roof of the stomach accompanied by a dorsal groove to the oesophageal orifice; the other sorting area of the dorsal hood passes over the roof of the stomach, and expands on the right side of the stomach. In *Cochlodesma* an unusually large acceptance tract, of parallel longitudinal folds, passes from the dorsal hood on to the right side of the stomach. The ducts from the digestive diverticula open into the stomach at four or five sites: two orifices on the anterior face of the stomach, below the oesophageal orifice, which may be equated with the left and right caeca of other forms (there is a third orifice in *Cochlodesma*). This is reminiscent of the conditions in the Lucinacea (Allen 1958*b*). There is a left pouch, identified by its contact with the gastric shield. Finally, there is a left posterior orifice on the floor of the stomach and lying close to the end of the major typhlosole and intestinal groove. This last orifice has no counterpart in other families or superfamilies of bivalves; this and the shortness of the major typhlosole and the intestinal groove are diagnostic of this category of stomach.

The two remaining examples in the Pandoracea differ from the group described above, and from each other, in important matters in the topography of their stomachs. In *Laternula rostrata* there is no orifice on the left posterior floor of the stomach, while the major typhlosole and intestinal groove curve gently across the stomach floor and end just outside the orifice of the left caecum. There is a left pouch, but the ducts from the digestive diverticula enter the stomach only via the left caecum and the right caecum. In *Lyonsia californica* there is similarly no left posterior duct orifice, but in this example the major typhlosole and intestinal groove are very short, and curve abruptly to the left around the margin of the style sac. No ducts enter the left pouch, and all the ducts from the digestive diverticula enter the stomach only via the left and right caeca. The condition in *L. californica* is basically comparable to that in *Brechites penis* (Purchon 1960*a*). In view of the marked differences in the structure of the stomachs of *Laternula* and *Lyonsia* from the other four examples in the Pandoracea, is it legitimate to consider whether these two genera are correctly placed in the superfamily Pandoracea? It is also interesting to consider whether the similarity in stomach structure of *Lyonsia californica* and of *Brechites penis* may provide a clue as to the affinities of the superfamily Clavagellacea.

Morton (1974*b*, 1977*a*) commented briefly on the stomachs of *Cleidothaerus maorianus* and *Myadora striata*, in each case stating erroneously that stomach type IV is 'typical of the Eulamellibranchia'. This slip is repudiated since stomach type V is found in many superfamilies in the Eulamellibranchia, while stomach type III is found in the families Pinnidae and Ostreidae which may be classified either in the Eulamellibranchia or, less frequently, in the Pseudolamellibranchia.

Clavagellacea

Review of literature

Clavagellidae

Brechites penis (L., 1758) (Purchon 1960*a*)

The only information available is that which was taken from a single living specimen. The oesophagus enters the stomach by a wide circular orifice with raised lips. A ridge passes backwards from the right margin of the oesophageal orifice, over the roof of the stomach, and into the dorsal hood. Ciliary currents on either side of this ridge carry particles from the oesophagus into the dorsal hood. The dorsal hood is relatively large, and two sorting areas on its anterior face pass over the roof and on to the right side of the stomach. The style sac and mid gut are conjoined, and leave the posterior floor of the stomach. The minor typhlosole ends near the mouth of the mid gut. The major typhlosole and the intestinal groove pass forwards and to the left across the stomach floor. The left pouch is shallow, and lies anteroventral to the dorsal hood; no ducts enter the left pouch from the digestive diverticula. The gastric shield is large, extending backwards as far as the orifice of the style sac, and is held in position by two saddle-shaped flares which enter the mouths of the dorsal hood and the left pouch. The digestive diverticula communicate with the stomach by one large duct on the left side, anteroventral to the left pouch, and by one large and one small duct on the right side of the stomach. The large ducts on the left and the right sides received ten, and about 15 tributary ducts, respectively. There is a large and well developed sorting area on the anterior floor of the stomach, folds from which pass into the orifices of the ducts from the digestive diverticula. The origin of the intestinal groove lies on the anterior floor of the stomach, external to the left pouch, and external to the orifice of the duct from the digestive diverticula.

Attention is drawn to the close similarity between the stomachs of *Brechites penis* and *Lyonsia californica*.

STOMACH TYPE IVA: (UNALLOCATED)

Unionacea

Description of fresh material
Hyridellidae
Velesunio ambiguus (Philippi, 1847)

Specimens of *V. ambiguus* were studied in Singapore, having been supplied in a vacuum flask by air from Melbourne by Miss J. Hope Macpherson. Detailed records and observations were made at that time and it was briefly reported that the stomach of this species was basically comparable with that of *Anodonta cygnea* (Purchon 1958). Full details are here supplied, for comparison also with the stomach of *Aspatharia adansoni*.

The oesophagus is short, wide, and flattened dorsoventrally; it enters a broad, dorsoventrally compressed vestibule on the anterior side of the stomach, and its orifice bears tumid lips (O). On the floor of the vestibule a row of simple, flattened tubercles (TU) arises in the median line, passes to the right and joins a substantial ridge (R) which turns back over the roof of the vestibule, above the oesophageal orifice, and enters the dorsal hood (DH) on its anterior face.

The style sac (SS) and mid gut are conjoined, and pass downwards from the posteroventral wall of the stomach. The minor typhlosole (MIT) passes forwards into the stomach, and turns upwards on the right wall of the stomach. The minor typhlosole is in direct contact with a very extensive sorting area (SA) which arches over the right side and roof of the stomach, to pass into the dorsal hood on its anterior face, and from this sorting area a rejection tract (RT) conveys waste matter from the dorsal hood into the intestinal groove (IG) and thence into the mid gut groove. The major typhlosole (MT) also passes forwards on to the floor of the stomach, where it is closely associated with a large, fleshy conical prominence (C). The major typhlosole, accompanied by the intestinal groove, curves sharply to the left and passes transversely across the stomach floor (MT) towards the mouth of the left caecum (LC). It is notable that the major typhlosole and the intestinal groove do not approach, and are not associated with the orifice of the right caecum (RC). The major typhlosole and intestinal groove enter the left caecum and penetrate it to its base.

The digestive diverticula communicate with the lumen of the stomach in three groups. One large duct enters the stomach at the right caecum. This duct passes downwards, serving the digestive diverticula on the right side and beneath the stomach, from which it receives no fewer than eight tributary ducts. The walls of the stomach immediately adjacent to the mouth of this main duct are covered by a very fine sorting area of parallel ridges and grooves, on which cilia beat outwards, discharging waste material into the intestinal groove nearby. The left caecum receives about five ducts from the digestive diverticula on the left side of the stomach,

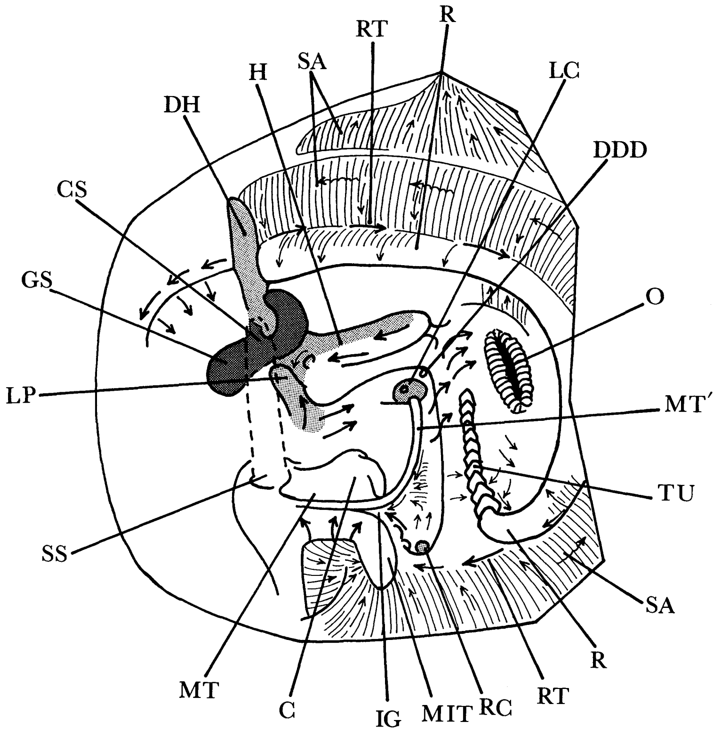


FIGURE 7. *Velesunio ambiguus*, detailed drawing of the interior of the stomach after opening by an incision in the right side. (Magn. × 10.) There are very extensive sorting areas on the anterior face of the dorsal hood, and on the roof and right side of the stomach. A conspicuous pleated fold (TU) lies on the anterior floor of the stomach, below the oesophageal orifice, and extends upwards towards the dorsal hood. The gastric shield (GS) is relatively small.

in addition to which a sixth, isolated duct (DDD) enters the stomach immediately above the mouth of the left caecum. There is a small sorting area of closely placed ridges and grooves on the floor of the left caecum, and this discharges waste into the intestinal groove. The third group of ducts from the digestive diverticula open into the left pouch (LP) the mouth of which lies anteroventral to that of the dorsal hood. The left pouch extends beneath the dorsal hood, where it receives a single large duct, and it receives five smaller ducts on its left and anterior walls.

The dorsal hood (DH) is large and well developed. On its roof and anterior wall there are sorting areas (SA) that extend over to the right side of the stomach. The chief sorting area of the dorsal hood carries three systems of cilia, one beating transversely over the crests of the folds towards the apex of the hood, one beating ventralwards parallel with the folds and discharging into a third ciliary current, which passes outwards from the apex of the hood into the stomach, discharging on its right wall into the intestinal groove. The substantial ridge (R), which enters the dorsal hood on its anterior wall, also bears a sorting area of closely spaced ridges and grooves. On the posterior wall of the dorsal hood cilia beat outwards, on to the posterior wall of the stomach.

The gastric shield (GS) is very small and flimsy, and invests the lower border of the mouth of the dorsal hood. It also invests the posterior border of a substantial hollow (H) in front of the dorsal hood and immediately above the mouth of the left pouch. The gastric shield does not reach to the mouth of what is here termed the left pouch. The above-mentioned hollow is blind, and does not receive any ducts from the digestive diverticula. It is most unusual for the gastric shield not to invest a part of the mouth of the left pouch, and it is notable that a closely comparable condition was reported for *Anodonta cygnea* (Purchon 1958).

A transverse ridge crosses the anterior floor of the stomach, in front of the transverse sector of the intestinal groove, and arching over the mouths of the left and right caeca. This ridge, and the row of tubercles, and the ciliary patterns in this region, will ensure that particles do not pass directly from the oesophageal orifice into the intestinal groove.

In one dissection a slender, weakly constructed crystalline style (CS) was seen to be revolving slowly at about four revolutions per minute.

Mutelidae

Aspatharia adansoni (Jousseaume, 1886)

Four specimens were dissected in the Department of Zoology, University of Ghana, in 1961. They had been taken from the freshwater circulating aquaria in the department, in which they had been living for months together with various other species including large specimens of the lungfish *Protopterus*. Although all four specimens were generally healthy and exhibited active ciliary systems on the organs in the mantle cavity and within the stomach, they all lacked both a crystalline style and a gastric shield.

Specimens of *Aspatharia* were dissected both from the right side and from the left side to obtain the best possible views of the interior of the stomach, and the information gained is incorporated in figure 8. The oesophagus (O) opens into the stomach anterodorsally by a broad, flattened orifice. The conjoined style sac and mid gut (CSSMG) passes downwards from the posterior end of the stomach. The major typhlosole (MT) was large and fleshy and was developed into a prominent mound (C) in the centre of the floor of the stomach. The major typhlosole passed forwards on the right side of the stomach, and then passed transversely across the stomach floor (MT′) and into the mouth of the left caecum (LC) within which it ended. The major typhlosole was accompanied throughout its course by the intestinal groove (IG) and the two structures did not enter the mouth of the right caecum (RC) on the right anterior floor of the stomach. The transverse sector of the intestinal groove was guarded by a ridge (R) which passed from above the orifice of the left caecum and ended above that of the right caecum. Anterior to this ridge cilia beat strongly forwards over a wide smooth area, ensuring that particles arriving from the oesophagus could not pass directly into the intestinal groove without having been subjected to the sorting mechanisms in the stomach. On the right anterior floor of the stomach a substantial swelling with a lobed margin (SW) served to deflect particles to the right, though the role of the sorting area (SA) on its flat surface was not ascertained.

On the right side of the stomach there was a single small orifice which lay close to the intestinal groove. Its walls bore a number of folds which were more clearly defined on its posterior than on its anterior border. This was the right caecum (RC) and when it was dissected it was found to receive ten ducts from the digestive diverticula. Ciliary currents on the floor of the right caecum all beat outwards, towards the intestinal groove. The major typhlosole and intestinal groove entered the orifice of the left caecum (LC) and terminated on its posterior wall, close to the entrance. The floor of the left caecum bore three or four ridges and grooves which were directed towards the intestinal groove. Cilia on the floor of the left caecum beat from left to right, out of the caecum towards the lumen of the stomach. The left caecum was not extensive, but the number of ducts entering it from the digestive diverticula was not recorded.

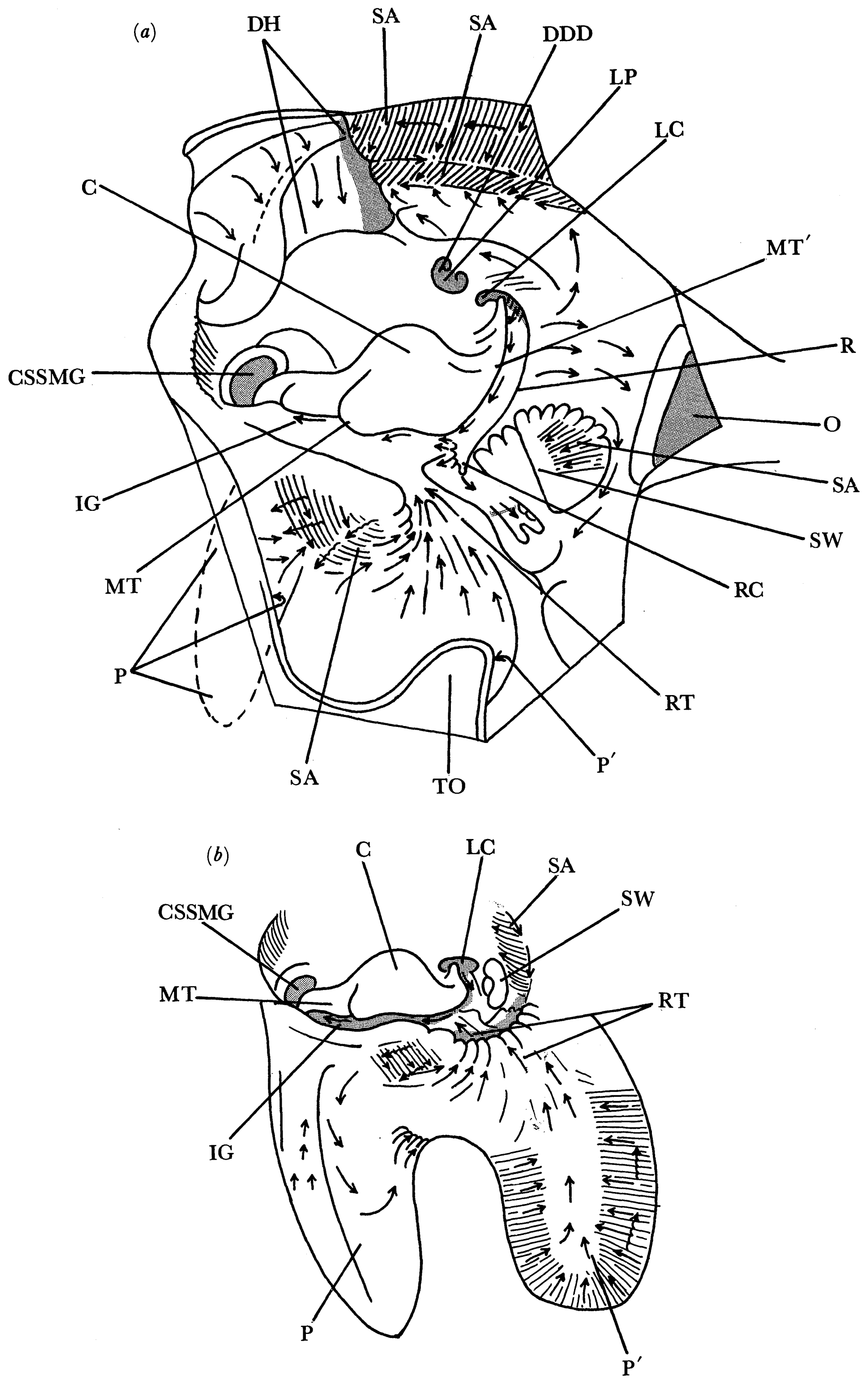


FIGURE 8. *Aspatharia adansoni*, detailed drawings of the interior of the stomach after a mid-dorsal incision from the oesophagus towards the combined style sac and mid gut (CSSMG). (*a*) General view of the dissection (magn. × 8); (*b*) details of the interiors of two deep pockets on the right side of the stomach (magn. × 8). Instead of an elongated, pleated fold on the anterior floor of the stomach, as in *V. ambiguus*, there is a lobed raised pad (SW) which bears a delicate sorting area (SA).

The left pouch (LP) comprised both a flattened semicircular pocket lying dorsal to the left caecum and also a large orifice lying a little further posterior, into which opened three ducts from the digestive diverticula on its left anterior wall and one duct on its posterior wall. The semicircular pocket was investigated and found to be blind, receiving no ducts from the digestive gland. The floor of the left pouch bore a few faint anteroposterior corrugations over which the cilia beat backwards, towards the posterior rim of the pouch. There was no indication as to whether the gastric shield would have reached the mouth of the left pouch, as is usual.

The dorsal hood (DH) was large and well developed. It opened into the stomach on its left side, and it curved downwards around the side of the stomach. On its posterior wall cilia beat strongly downwards as far as the broken line in the figure, along which particles accumulated. The broken line probably represents the position of the dorsal margin of the gastric shield. On the anterior wall of the dorsal hood there are two well developed sorting areas (SA) of closely placed parallel ridges and grooves. Over both of these sorting areas cilia beat downwards in the grooves, while on the uppermost sorting area cilia beat transversely over the crests of the folds, towards the blunt apex of the hood. Below and above the lowermost sorting area ciliary currents beat in towards the apex of the hood, and out towards the roof of the stomach, respectively. These two sorting areas extended on to the roof of the stomach, where they probably entered into association with a complex ciliary sorting system which will next be described.

On the right side of the stomach there was a complex sorting area (SA) associated with two deep, blind, upwardly projecting, conical pockets (P, P′). The whole structure presumably corresponds with the 'posterior sorting area' (SAP) of Graham (1949) and the sorting area (SA^3) of Purchon (1958). As shown in figure 8 over the whole surface of the organ cilia beat along the grooves and discharge particulate matter by a rejection tract (RT) into the intestinal groove. The nature of any relationship between this organ and the mouth of the dorsal hood was not ascertained.

Review of literature

Unionidae	
Anodonta calipygos Kobelt, 1879	(Nakazima 1957)
Anodonta cygnea (L., 1758)	(Graham 1949; Purchon 1958; Reid 1965)
Cristaria plicata (Leach, 1815)	(Nakazima 1957)
Lamellidens corrianus (Lea, 1834)	(Dinamani 1967)
Hyridellidae	
Velesunio ambiguus (Philippi, 1847)	
Mutelidae	
Aspatharia adansoni (Jousseaume, 1886)	
Etheriidae	
Etheria elliptica Lam., 1807	(Yonge 1962)
Pseudomulleria dalyi (Smith, 1898)	(Yonge 1962)

The descriptions and figures given for *Anodonta cygnea* by Graham (1949), Purchon (1958) and Reid (1965) are in general agreement, though a few points require brief comment. Graham reported the minor typhlosole as ending near the orifice of the mid gut, whereas Purchon judged that it passed forwards, separating the posterior part of the principal sorting area from the intestinal groove. Reid made a thorough study of sorting areas of the dorsal hood and showed how one of these extended on to the right posterior stomach wall as the posterior sorting area. In achieving this object his figure 11 gives inadequate attention to the anterior floor of the stomach and especially to the relative size and disposition of the major typhlosole and its attendant intestinal groove. Reid asserts that 'All the ducts of the digestive diverticula open on the left of the stomach, and it is misleading to use the terms "right" and "left" ducts'. The ducts from the digestive diverticula open into the stomach at three sites, the left pouch, an opening anteriorly on the left, and another centrally below the oseophageal orifice. Graham and Purchon, however, locate the last below the right margin of the oesophageal orifice. This difference may depend partly upon muscular tension in the wall of the dissected stomach, and may not itself be worthy of detailed discussion. However, Reid's judgement on the asymmetry of these ducts is encapsulated in his figure 14d and e, and imposes a degree of asymmetry which here seems excessive.

Graham considered the probable homologies of the three embayments through which the ducts from the digestive diverticula open into the stomach. To adopt recently accepted terminology, he deemed the left posterior duct lying close below the gastric shield to be on the site of the left pouch, and he considered the left anterior duct to be the equivalent of the 'left half of the caecum', that is, the left caecum. He was doubtful whether the right anterior duct should be regarded as representing the 'right half of the caecum', that is, the right caecum, or whether it represented a group of ducts found in many bivalves on the right posterior wall of the stomach. He was inclined to favour the latter hypothesis. My own view is that, regardless of whether the orifice is located centrally or on the right side of the stomach wall, it should be regarded as comparable (not necessarily homologous?) with the right caecum of bivalves such as *Tellina crassa*. Consideration will be given later to certain species of *Donax* and *Tellina* in which the major typhlosole has become disassociated from the lumen of the right caecum.

Yonge (1962) was only able to study preserved specimens of *Etheria elliptica* and of *Pseudomulleria dalyi*, but was able to conclude that the interior of the stomach was 'essentially similar to that of *Anodonta*, i.e. a type 4 stomach'. From inspection of his figures 7 and 17 it seems reasonable to conclude that the style sac and mid gut are conjoined, but this was not stated.

Detailed studies have been made on the stomachs of living specimens in the families Unionidae, Hyridellidae and Mutelidae, and these were found to be closely comparable in many important respects as is indicated by the following general account. The oesophageal orifice is broad and flat, and lies on the anterior face of the stomach. The combined style sac and mid gut leave the posteroventral wall of the stomach. The minor typhlosole extends forwards on to the floor of the stomach, thereby separating the intestinal groove from the greater part of the posterior sorting area. In *Aspatharia adansoni* a minor typhlosole was not identified as such, but here also the posterior sector of the intestinal groove is isolated from the greater part of the posterior sorting area by a conspicuous ridge along its right side. The major typhlosole and intestinal groove curve gently forwards and to the left, and enter the left caecum. In contrast to the Limidae, Anomiidae and Pectinidae the major typhlosole and intestinal groove do not approach the left pouch. The dorsal hood is large and its anterior wall bears well developed sorting areas which extend over the roof of the stomach and on to its right side; waste matter from the posterior sorting area on the right side of the stomach is discharged into the intestinal groove. In *Aspatharia adansoni*, however, the posterior sorting area is complicated by the development of two deep conical pouches (figure 8*a*, *b*). The digestive diverticula open into the stomach by a small number of ducts, which enter at only three sites. The left pouch receives from one to four ducts, but in *V. ambiguus* the single duct was found to receive five tributary ducts. The left caecum receives about five or six ducts, except for *Lamellidens corrianus*, in which only two ducts were recorded. On the right side of the stomach only one duct opens into the stomach, and this can be termed the right caecum. However, in *A. cygnea* two ducts enter the stomach in this area. In *V. ambiguus* and in *A. adansoni* the single duct was dissected open, and found to receive eight and ten ducts respectively.

The major typhlosole is swollen just within the stomach, and on its left side the floor of the stomach is raised into a conspicuous conical mound which appears to be diagnostic of the superfamily Unionacea, though it is less clearly indicated by Dinamani (1967) in his figure 13. A conspicuous ridge accompanies the lower border of the sorting area on the anterior face of the dorsal hood, and passes over the roof and right side of the stomach, ending on the anterior floor of the stomach below the oesophageal orifice. This recirculation ridge (Reid 1965, figure 11, RR) may be finely marked in places (*V. ambiguus*) or throughout its length (*A. cygnea*) by transverse striations. The ridge appears to be lacking in *A. adansoni*, except perhaps for its ventral end which may be represented by a broad swelling with a lobed margin. In *A. cygnea* and *L. corrianus* the ventral end of the recirculation ridge is expanded to form a broad flat plate, whereas in *V. ambiguus* the ridge ends ventrally in a regular series of transverse triangular plates. The gastric shield was not seen in *A. adansoni*, but elsewhere it is relatively small, and does not come into contact with the border of the left pouch.

Trigoniacea

Review of literature

Trigoniidae

Neotrigonia margaritacea (Lam., 1804) (Purchon 1957*b*)

The only information available is that obtained from preserved specimens. The oesophageal orifice is wide, the combined style sac and mid gut leaves the stomach posteroventrally, and the minor typhlosole ends at the mouth of the mid gut. The major typhlosole and intestinal groove pass forwards on the floor of the stomach, curve to the left and end just outside the mouth of the left caecum. The digestive diverticula enter the stomach at three sites, the left caecum which receives five ducts, the right caecum which receives four ducts, and the left pouch which receives a single large duct. The dorsal hood is very well developed, with a conspicuous sorting area which passes from the anterior face of the dorsal hood, over the roof of the stomach and expands as the posterior sorting area on the right side of the stomach. The gastric shield is extensive and strong, and invests the lower border of the mouth of the dorsal hood; it also enters the anterodorsal rim of the left pouch. Purchon (1957) considered that the stomach of *N. margaritacea* resembled those of the Limidae, Pectinidae and Anomiidae, but he overlooked some important considerations. The presence of only three duct orifices in *Neotrigonia*, instead of clusters of ducts, and the failure of the major typhlosole to reach the left pouch, indicate a greater measure of similarity between the Trigoniacea and the Unionacea.

Crassatellacea

Review of literature

Astartidae

Astarte elliptica (Brown, 1827)	(Saleuddin 1965)
A. sulcata (da Costa, 1778)	(Purchon 1958)

Crassatellidae

Crassinella mactracea (Linsley, 1845)	(Allen 1968)

Saleuddin (1965) studied all four British species of *Astarte*, but only offered a figure for the stomach of *A. elliptica*; he may have only found minor variations, unworthy of mention, in the other three species. His account differs slightly from that of *A. sulcata* by Purchon (1958), and it is possible that some features that were missed by one author may have been found by the other. Allen (1968) concluded that the stomach of *C. mactracea* corresponds closely with those of *A. elliptica* and *A. sulcata*. He judged that in *Crassinella* 'the intake of large and variable sized food is related to the virtual absence of ciliated sorting areas in the stomach and to the small size of the dorsal hood'. The small number of apertures leading from the stomach to the digestive diverticula in both *Astarte* and *Crassinella* is reminiscent of the Lucinidae (Allen 1958), and this may be attributable to the small size of the animal, or perhaps to a nutritionally impoverished environment.

The oesophagus opens on the anterodorsal face of the stomach, while the combined style sac and mid gut leaves the stomach mid-ventrally. The minor typhlosole ends close to the opening of the mid gut. The major typhlosole and intestinal groove curve forwards and to the left, and end on the left anterior floor of the stomach, external to a hollow which can be equated with the left caecum. In *A. elliptica* the major typhlosole ends in a loose spiral of two turns, but Purchon (1958) did not observe such a spiral in *A. sulcata*. In *Astarte* two ducts from the digestive diverticula enter the left caecum, and a single duct enters the stomach on the right side; in *Crassinella* only one duct was found on each side of the body. No ducts enter the left pouch in either genus. The gastric shield is comparatively well developed and is held in position by flanges which enter the mouths of the left pouch and the dorsal hood. The dorsal hood is small, and is directed forwards; it communicates with the lumen of the stomach by a deep groove which extends backwards over the roof and right side of the stomach. Purchon (1958) described a rim that encircled the orifice of the oesophagus, and a ridge that passed back from this rim on to the anterior face of the dorsal hood. Saleuddin (1965) interpreted these structures as grooves, and it was agreed that these structures serve to convey particles from the oesophagus into the dorsal hood. Saleuddin observed a folded sorting area on the anterior face of the stomach, leading up to the oesophageal orifice, but this was not seen by Purchon. In contrast, Purchon (1958) recorded a small sorting area on the roof of the stomach, between the oesophagus and the dorsal hood, and this was not seen by Saleuddin. These differences are probably due to differences in tension of the stomach walls in these regions, or to differences in illumination of the dissections. Both authors are agreed that there is no sorting area on the roof of the dorsal hood, or on the right posterior wall of the stomach. Allen (1968) also noted the lack of sorting areas in the stomach of *Crassinella.*

In view of the small size of the specimens, it seems probable that the general simplicity of

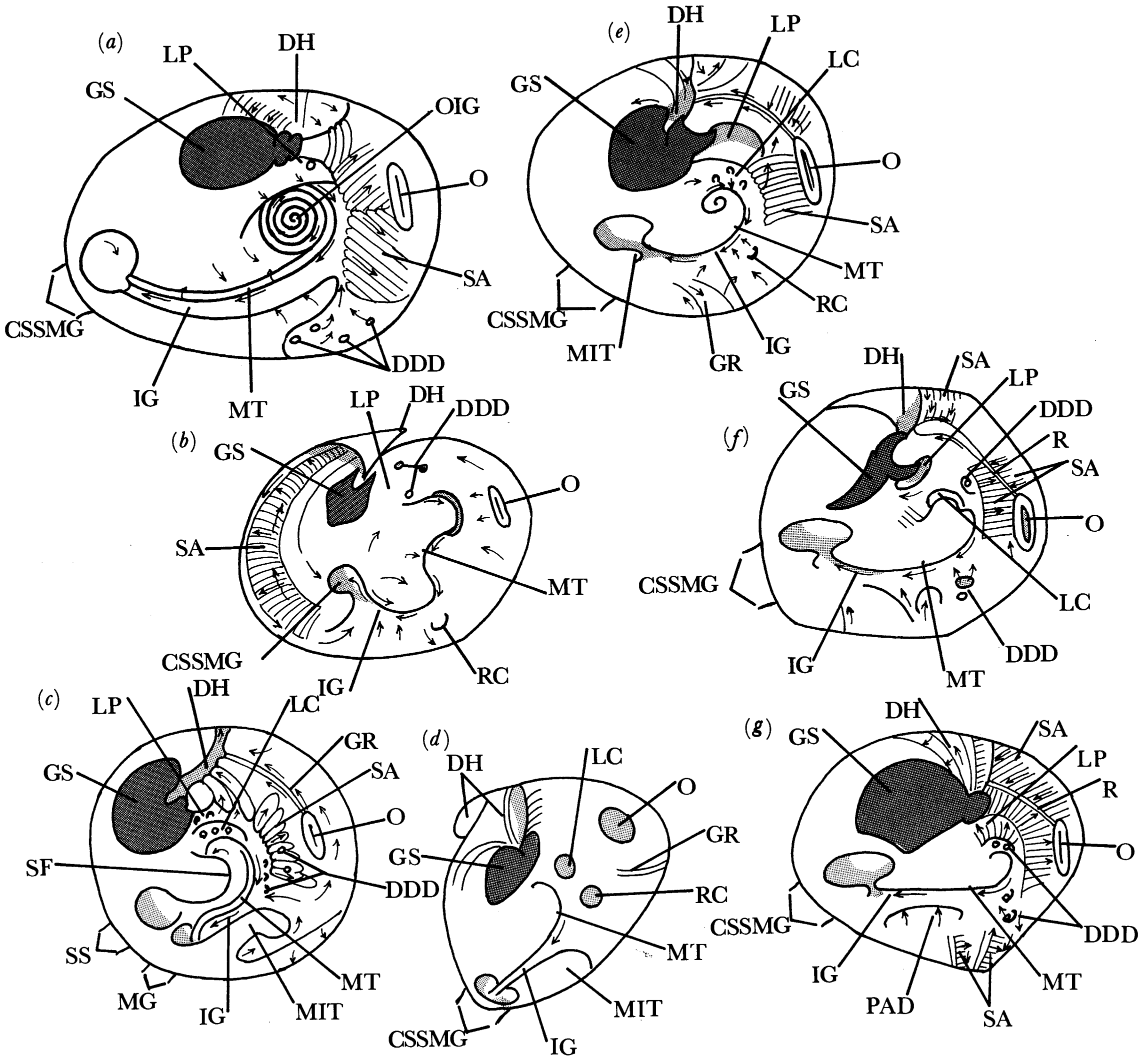


Figure 9. Diagrammatic representations of the interior of the stomach in the Gastrotetartica after opening by an incision in the right side. (*a*) Carditidae; (*b*) Pisidiidae; (*c*) Erycinidae; (*d*) Lucinidae, Thyasiridae and Montacutidae; (*e*) Astartidae and Crassatellidae; (*f*) Gastrochaenidae; (*g*) Hiatellidae. Note the simplification of the stomach in the Lucinidae and Thyasiridae which are colonists of nutritionally impoverished sediments. Note the separation of the style sac from the mid gut in the Erycinidae. The orifice of the oesophagus may communicate with the dorsal hood by means of a ridge (R) as in the Gastrochaenidae or by a groove (GR) as in the Erycinidae.

the interior of the stomach in all species investigated is a secondary feature. It is possible that, as in some species of *Donax*, the major typhlosole and intestinal groove may have withdrawn from the right caecum, and it may be prudent not to assign the Crassatellacea to any phylogeny on the grounds of stomach structure alone.

Carditacea

Review of literature

Carditidae

Beguina semiorbiculata (L., 1758)	(Purchon 1958)
Beguina variegata (Bruguière, 1792)	(Dinamani 1967)

The stomach of *B. variegata* is relatively simple, associated with the small size of the animal. It resembles that of *B. semiorbiculata* in most respects, but differs in the large numbers of ducts that enter the stomach from the digestive diverticula. The following account is mainly drawn from the more detailed information available for *B. semiorbiculata*. The oesophagus is short, and is very wide. The style sac and mid gut are conjoined. The minor typhlosole was not observed in *B. semiorbiculata* but entered the stomach for a short distance in *B. variegata*. The major typhlosole and the intestinal groove pass directly forwards on the floor of the stomach and then form a tight, flat spiral on the left anterior floor of the stomach. In *B. variegata* the spiral has fewer coils. The spiral coil of the major typhlosole and intestinal groove may be regarded as lying partly within the left caecum, though this structure is ill-defined, for a number of ducts from the digestive diverticula open nearby on the left anterior wall of the stomach.

The dorsal hood is large, with sorting areas on its anterior and its posterior surfaces; it curves downwards and forwards towards its apex, but in *B. semiorbiculata* it also possesses a blind horn which projects backwards on the roof of the stomach. The gastric shield is well developed, it invests the posteroventral border of the dorsal hood and also the dorsal rim of what is judged to be the left pouch. The gastric shield is relatively larger in *B. variegata*. The ducts from the digestive diverticula enter the stomach in three groups, five into the left pouch, four above the spiral fold, and four on the right side of the oesophagus, in *B. semiorbiculata*. In *B. variegata* the numbers of ducts are considerably larger, and those entering the stomach on its right side are arranged in two clusters. In addition to the spiral fold of the major typhlosole, another striking feature is the very extensive sorting area on the anterior face of the stomach, immediately below the oesophageal orifice. The very fine folds of this sorting area diverge to left and to right, and direct particulate material around the oesophageal orifice and towards the dorsal hood. Dinamani (1967) indicates the presence of a sorting area in the same position in *B. variegata*.

The main question concerning the stomach of *Beguina* is whether the sites of entry of ducts from the digestive diverticula on the left above the spiral fold, and on the right side of the stomach, may be designated as the left caecum and the right caecum, respectively? Arising from this, if there is a left caecum, does the spiral fold of the major typhlosole enter or lie just outside the left caecum?

Leptonacea

Review of literature

Erycinidae	
Lasaea rubra (Montagu, 1803)	(Oldfield 1955)
Kelliidae	
Pseudopythina subsinuata (Lischke, 1871)	(Morton 1972)
Galeommatidae	
Galeomma paucistriata Deshayes, 1855	(Dinamani 1967)
Scintilla hanleyi Deshayes, 1855	(Purchon 1958)
Montacutidae	
Montacuta ferruginosa (Montagu, 1808)	(Purchon 1958)
Rhamphidonta retifera (Dall, 1899)	(Bernard 1975)

It is possible to offer a generalized account of the structure of the stomach in the Leptonacea on the basis of the detailed figures and descriptions of *Scintilla hanleyi*, *Galeomma paucistriata*, and *Pseudopythina subsinuata*; some limited information is available from *Montacuta ferruginosa* (Purchon 1958; Dinamani 1967; Morton 1972). The overall simplicity of form of the minute *Lasaea rubra* is doubtless the outcome of paedomorphosis, and the meticulous studies of Oldfield (1955) are generally supportive.

The oesophagus enters the stomach on its anterior face, by a large, flattened oval orifice. The style sac and mid gut leave the stomach separately, with the exception of *Pseudopythina subsinuata* in which the mid gut becomes separate about half way along the style sac. The major typhlosole passes forwards on the floor of the stomach and curves steadily to the left, ending near or just within the left caecum. In *G. paucistriata* the tip of the major typhlosole is bent sharply backwards, while in *P. subsinuata* it emerges from the left caecum and ends on the stomach floor nearby. In *P. subsinuata* a minor typhlosole is shown as passing forwards on the right floor of the stomach. The gastric shield is well developed, covering a large area of the dorsal and posterior walls of the stomach, and sending flares into the mouths of the dorsal hood and left pouch. Several ducts from the digestive diverticula open into the stomach via the left caecum, and also via the left pouch. A further group of ducts is to be found on the right side of the stomach, a little below the oesophageal orifice, where ten or more ducts open separately in *Galeomma*, and where about ten small ducts and one large duct open in *Scintilla*; however, in *P. subsinuata* only three or four duct orifices are scattered on the anterior floor of the stomach below the oesophageal orifice and to the right of this. There is a sorting area of vertical folds on the anterior face of the stomach, immediately below the oesophageal orifice, some of the duct orifices lying within this sorting area in the case of *P. subsinuata*. A ciliated groove leads from the left corner of the oesophageal orifice into the dorsal hood, on its anterior face. No ciliated sorting areas were found within the dorsal hood, or on the right posterior wall of the stomach. A curved flange on the floor of the stomach, running approximately parallel with the major typhlosole, was found in *G. paucistriata*, in *P. subsinuata*, and in *S. hanleyi*; this may prove to be diagnostic for the Leptonacea.

As regards the family Montacutidae, the brief description of the stomach of *R. retifera* (Bernard 1975) is in conformity with the above account. In *M. ferruginosa* the gastric shield is disproportionately large, the dorsal hood is extremely small, and no sorting areas were observed; the ducts from the digestive diverticula open into the stomach by two large orifices disposed symmetrically below that of the oesophagus. This extreme simplicity of structure is attributable partly to the small size of the animal, and partly to the extremely sheltered niche occupied by this species a few inches deep in sand in association with the heart urchin, *Echinocardium cordatum.*

Hiatellacea

Review of literature
Hiatellidae

Hiatella arctica L. 1767	(Purchon 1958)
Hiatella solida (Sowerby, 1834)	(Narchi 1973)

The stomachs of these two species of *Hiatella* are closely comparable. The oesophagus enters the stomach anterodorsally by a moderately wide orifice, and the combined style sac and mid gut leaves the stomach posteroventrally. The minor typhlosole ends in the mouth of the mid gut. The major typhlosole, accompanied on its right side by the intestinal groove, passes directly forwards on the floor of the stomach to its anterior end, and then turns sharply to the left, curving in an incomplete spiral and ending outside the orifice of the left caecum. The ducts from the digestive diverticula open into the stomach at three sites, the left caecum, the right caecum and the left pouch. In *H. arctica* about six ducts were seen to enter the left caecum, and three entered via the left pouch. Two or three ducts enter the stomach on its right anterior floor, these being regarded as equivalent to a right caecum. The dorsal hood is well developed; its posterior wall bears two longitudinal folds which pass over the roof of the stomach and on to its right side; the anterior wall of the dorsal hood carries a sorting area which extends towards the oesophageal orifice, and is bordered ventrally by a longitudinal ridge with a similar disposition.

The gastric shield is well developed and sends a saddle-shaped flare into the mouth of the dorsal hood. The gastric shield also invests the posterior rim of the left pouch in *H. arctica,* but may not reach so far in *H. solida.* On the anteroventral face of the stomach a conspicuous sorting area lies between the oesophageal orifice and the transverse sector of the intestinal groove, passes over the left caecum, and enters the mouth of the left pouch. A sorting area in the dorsal hood extends over the roof of the stomach on to its right side, and discharges waste into the intestinal groove. A substantial pad on the right wall of the stomach lies below this sorting area, and isolates the posterior sector of the intestinal groove.

Gastrochaenacea

Review of literature
Gastrochaenidae

Gastrochaena impressa Deshayes, 1854	(Dinamani 1967)
Rocellaria cuneiformis (Spengler, 1783)	(Purchon 1954, 1958)

The figure and description of *G. impressa* given by Dinamani (1967) provide some support, but little new information with respect to the earlier studies by Purchon (1954, 1958). In all cases studied the specimens were small, and the simplicity of the interior of the stomach may be partly attributable to this fact. One cannot exclude the possibility that the stomach has reverted from type V to type IV by a process of paedomorphosis.

The oesophagus opens anteriorly into a globular stomach, from which the conjoined style sac and mid gut leaves posteroventrally. The minor typhlosole (wrongly labelled TY in figure 11 of Purchon (1954)) projects a short distance into the stomach. The major typhlosole is a wide, flat band which sweeps across the anterior floor of the stomach, curving to the left and ending within a broad depression on the left side of the stomach into which open six or seven ducts from the digestive diverticula. Although doubts had been expressed on the subject (Purchon 1958), it now seems appropriate to identify this depression as the left caecum. The dorsal hood is large, with a well developed sorting area on its anterior face; below the sorting area a ciliated ridge communicates with a sorting area on the left and ventral surface of the stomach near the oesophageal orifice. In *G. impressa* Dinamani (1967) observed a groove, lying between two thin folds, which passed up the right side of the stomach and into the dorsal hood. The gastric shield is very narrow posteriorly, and is held in position by two spurs which enter the mouths of the dorsal hood and of the left pouch. It was thought probable that one duct entered the left pouch, but this was not confirmed. In *G. impressa* the right caecum is represented by a saucer-shaped depression on the right side of the stomach, into which open three ducts from the digestive diverticula. In *R. cuneiformis* the right caecum is represented by one very large and one small orifice communicating with the digestive diverticula on the right side of the stomach.

Since the major typhlosole and intestinal groove do not enter into association with the right caecum it seemed reasonable to assign the stomach of *Rocellaria* to type IV in the original analysis (Purchon 1958). Having had clear evidence of reversion from stomach type V to stomach type IV by paedomorphosis in various genera (species of *Donax*, *Tellina*, and *Chama*, to be described and discussed later in this paper), it no longer seems safe to assign the Gastrochaenidae to the phylogeny of the Gastrotetartika on the basis of the present evidence. It seems possible that a similar process of simplification of the interior of the stomach *could* have taken place here also.

Pholadomyacea

Review of literature

Pholadomyidae

Pholadomya candida Sowerby, 1823	(Morton 1980)

Parilimyidae

Parilimya fragilis (Grieg, 1920)	(Morton 1982)

The only information available for both of these species was obtained by dissection and by serial sections of preserved specimens. No information is available as to the presence or absence of ciliated sorting areas in the dorsal hood, on the anterior floor of the stomach, or on the right posterior wall of the stomach. The stomachs of the two examples are similar in a number of respects. The oesophagus opens into the stomach anteriorly by a wide oval orifice which is ridged or lobed. The combined style sac and mid gut leave the stomach posteriorly in *Pholadomya*, but posteroventrally in *Parilimya*. The major typhlosole and intestinal groove pass forwards from the orifice of the mid gut, and curve steadily to the left and end just outside the mouth of the left caecum. A minor typhlosole was identified on the right posterior stomach wall in *Parilimya*, but the presence or absence of a minor typhlosole was not determined in the case of *Pholadomya*. The digestive diverticula open into the stomach at only two sites in both genera, that is, the left and right caeca. In *Pholadomya* only one duct entered the smaller left caecum; the right caecum received two ducts from the digestive diverticula. Equivalent data are not available for *Parilimya*. The gastric shield is large, and invades the mouth of the dorsal hood and that of the left pouch in each genus. In *Parilimya* it is thick, and it skirts the rim of the style sac; in *Pholadomya* it extends further backwards, to the posterior end of the stomach. The left pouch is well developed, but does not receive any ducts from the digestive diverticula in either species. In *Pholadomya* it extends forwards as a long tube on the left side of the visceral mass; it is hard to envisage the functions which may have been responsible for its unusual great size. The dorsal hood is well developed in both genera, but more so in *Pholadomya*. All the above mentioned features suggest that the two genera have a common origin.

In contrast to the above, the stomach of *Parilimya* is extended posteriorly, and here the stomach wall is surrounded by a muscular coat and its wall is thrown into about 19 longitudinal folds in a manner which is reminiscent of the septibranch *Cuspidaria* (Purchon 1956*b*). However, the inner surface of this muscular, folded extension of the stomach is not protected by a cuticular sheath as in the case of the Verticordiidae, or the septibranchs.

In view of the lack of information about the presence or absence of sorting areas in either of these genera it is not possible to judge whether any secondary simplification may have occurred. It is not possible to assign either example to a phylogeny on the basis of stomach structure. The small number and large size of the two orifices by which the digestive diverticula communicate with the stomach are reminiscent of the conditions described for the most specialized members of the Lucinacea, and the Verticordiidae (Allen 1958*a*, 1974). The great extent of the gastric shield in *Pholadomya* indicates the need for protection of the stomach from abrasion by coarse particles in the substratum, and the stomach of *P. candida* is clearly of type IV.

As regards *Parilimya fragilis*, Morton is understandably uncertain; he records it as having a stomach of type IV (p. 198), and alternatively as having a stomach of type II (p. 205), but neither of these is satisfactory. It is precluded from stomach type IV by the presence of a muscular and ridged posterior extension of the stomach. Likewise, it is precluded from stomach type II by the presence of a major typhlosole and intestinal groove on the anterior floor of the stomach. What is much more interesting is the fact that it is in a state of transition from type IV to type II, thereby endorsing the proposition that the stomach in the family Verticordiidae was derived from some ancestor in the Anomalodesmacea in much the same way. The very large orifices of the two ducts entering the stomach from the digestive diverticula suggest that this is not the lineage from which the Cuspidariidae were derived.

Stomach type IVb: Gastropempta

Paedomorphosis in stomach structure

Superfamily Tellinacea	
Family Donacidae	
Donax denticulatus L., 1758	(Wade 1969)
D. faba Gmelin, 1791	(Purchon 1960*a*)
D. gouldi Dall, 1921	(Pohlo 1967)
D. semigranosus (small) (Dunker, 1877)	(Nakazima 1965*a*)
Family Tellinidae	
Tellina ala Hanley, 1845	(Dinamani 1967)
Superfamily Chamacea	
Family Chamidae	
Chama multisquamosa Reeve, 1846	(Purchon 1958)

In the course of the original survey of stomach structure (Purchon 1956, 1957, 1958, 1960) five different types of stomach were recognized and the stomachs of a large number of species investigated were assigned as appropriate to one of these stomach types. In only two cases was there an apparent conflict in the evidence so obtained. In the Tellinacea *Donax faba* alone was assigned to stomach type IV while all other examples were of stomach type V. In the Chamacea, *Chama multisquamosa* had a stomach of type IV, while *C. lazarus* had a stomach of type V, though of a slightly unusual form. It was later concluded that these five categories of stomach structure have phyletic significance, with the exception of possible reversion from stomach type V to stomach type IV in certain cases (Purchon 1959, 1963*b*). Such a simplification of the internal structure of the stomach could arise from paedomorphosis and the adoption of a small body size, as in some species of *Donax*, or from the exploitation of nutrient-poor environments where simplification of the sorting mechanisms of the stomach could be advantageous, as in the families Lucinidae and Thyasiridae (to be discussed subsequently). However, the stomach in the family Donacidae is advanced in that the style sac and mid gut are wholly separate, which is not true for the remainder of the Tellinacea.

An apparent reversion to stomach type IV might be gained by the dissection of small specimens, the stomachs of which were still exhibiting an early stage in ontogeny. It is possible that the condition observed in *Chama multisquamosa* may be so explained, as the specimens studied were not large, though the explanation may lie in the adoption of a small size as a strategy for survival.

Detailed studies on members of the family Donacidae uphold the theory of paedomorphosis in many species of *Donax*. Stomachs of type V were found in *Egeria radiata* in specimens of shell length exceeding 5 cm (Purchon 1963*a*), as also in *Iphigenia brasiliensis* in specimens of shell length exceeding 6 cm (Narchi 1972*a*). In *Donax* stomach type V was found in *D. trunculus* and in *D. hanleyanus*, in specimens of shell length exceeding 2.5 cm, this probably being the largest species of *Donax* which has been studied in this respect (Narchi 1978). Nakazima (1965*a*) studied specimens of *D. semigranosus* of various sizes from 1.3 cm to about 1.7 cm shell length. He found that in the largest specimens the major typhlosole and intestinal groove intruded for a short distance into the right caecum, whereas in specimens of about 1.6 cm shell length the major typhlosole curved towards the orifice of the right caecum but did not enter it, and in

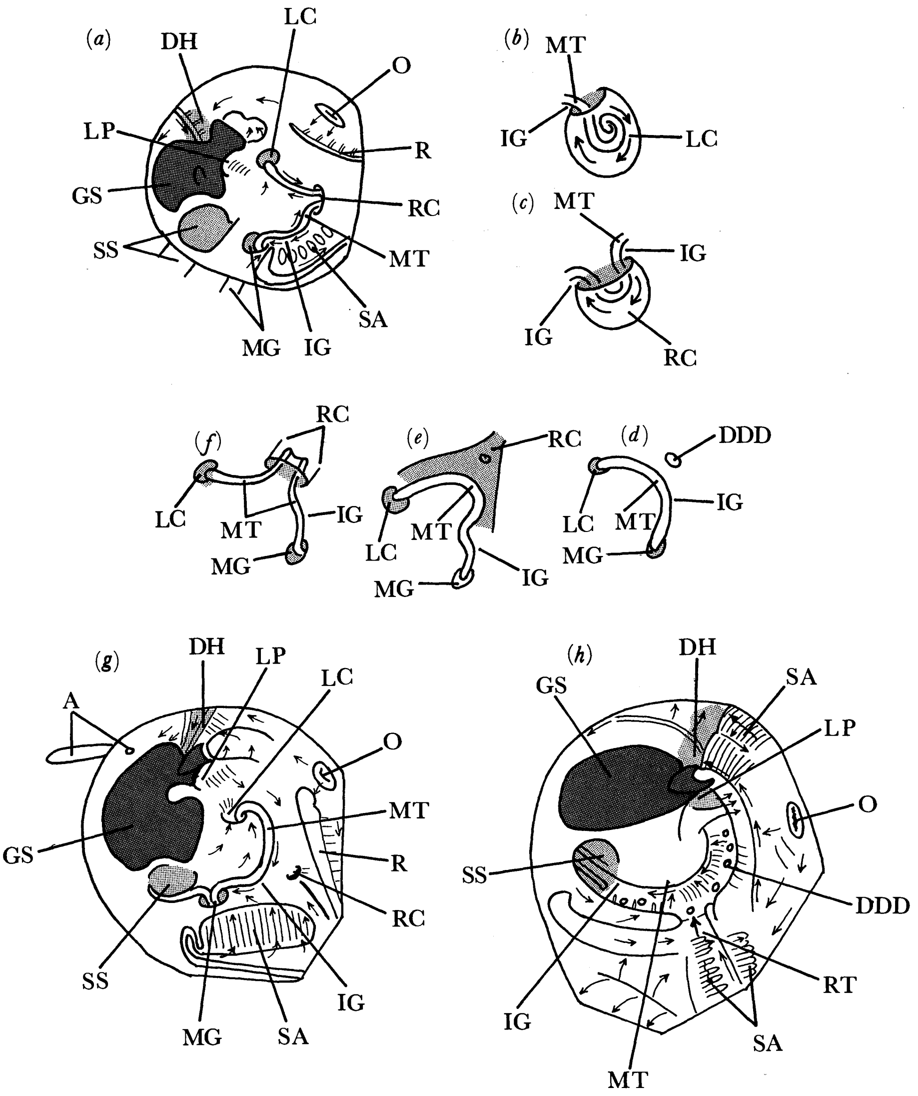


FIGURE 10. Diagrammatic representation of the interior of the stomach in three species of *Donax*. (*a*) *Donax hanleyanus* with a stomach of type V, in which the major typhlosole (MT) penetrates the right caecum (RC) and also the left caecum (LC), as also shown in the transparent enlargements of these caeca in (*b*) and (*c*), respectively; (*d*), (*e*) and (*f*), enlargements of the right caecum of *Donax semigranosus* from specimens of 1.3 cm, 1.6 cm and 1.7 cm shell length, respectively (redrawn from Nakazima (1965)). The smaller specimens have a stomach of type IV, but in the largest specimens the stomach is of type V; (*g*), *Donax faba* with a stomach of type IV. Note that the style sac (SS) is separate from the mid gut in the Donacidae, and also the presence of a posterodorsal caecum (A) in *D. faba*; (*h*) *Chama multisquamosa*. (Redrawn from Purchon (1950)).

specimens of 1.3 cm shell length the major typhlosole was completely separated from the orifice of the right caecum. Thus in *D. semigranosus* the stomach develops from type IV and may ultimately achieve type V in the largest specimens. The remaining species of *Donax* which have been investigated in this respect, namely *D. faba*, *D. gouldi*, and *D. denticulatus* have type IV stomachs.

Paedomorphosis may similarly be offered as the explanation for the occurrence of a stomach of type IV in *Tellina ala* (Dinamani 1967), whereas all other tellinids which have been investigated were shown to have a stomach of type V.

For the above reasons all these species are confidently assigned to the phylogeny of the

Gastropempta, notwithstanding the possession of a stomach of type IV in all except *Donax hanleyanus* and *D. trunculus*.

No record was kept of the size of the specimens of *Chama multisquamosa* which were dissected (Purchon 1958), but they were certainly not very large. Their possession of a stomach of type IV, and not type V as in *C. lazarus* and *C. ?brassica* (to be described later in this paper) can possibly be explained on one of the following hypotheses.

(i) The specimens were young and small and still at an early stage in ontogeny. Investigation of larger, mature specimens would have found a stomach of type V.

(ii) This species of *Chama* has undergone a process of simplification of stomach structure, possibly in association with adoption of a relatively small body size, as a result of which the stomach has reverted to an ancestral condition.

The condition of the stomach in *Donax faba* and in *Chama multisquamosa* indicates the supreme importance with respect to stomach type IVa in the assignment to higher taxonomic categories of the eight as yet unallocated superfamilies.

The conclusions of Allen (1976) regarding the stomach of *Chama multisquamosa*, based only on consideration of the Chamidae, are here repudiated. Stomach types IV and V are valid generalizations concerning internal structure of the stomach, based on a large number of observations. The distribution of these stomach types in many superfamilies of bivalves justifies the conclusion that the distinction is of phyletic significance above the level of superfamily. The only alternative hypothesis, that stomach type V had originated independently on innumerable occasions, is untenable. The occurrence of stomach type IV in a few exceptional species in the Tellinacea and Chamacea, superfamilies which are characterized by stomachs of type V, demands explanation. The simplest explanation is in terms of secondary simplification of structure in these species. There has never been any suggestion of phyletic division within the Chamidae with respect to stomach structure.

Secondary simplification in stomach structure

Superfamily Lucinacea	
Family Lucinidae	
Codakia costata d'Orbigny, 1842	(Allen 1958*a*)
C. orbicularis L., 1758	
C. orbiculata Montagu, 1808	
Divaricella quadrisulcata d'Orbigny, 1842	
Fimbria fimbriata (L., 1758)	(Allen & Turner 1970; Morton 1979)
Loripes lucinalis (Lamarck, 1818)	(Allen 1958*a*)
Lucina chrysostoma (Meuschen, 1787)	
L. pectinata (Gmelin, 1791)	(Narchi & Assis 1980)
L. pennsylvanica L., 1758	(Allen 1958*a*)
Myrtea spinifera (Montagu, 1803)	
Phacoides borealis (L., 1766)	
Family Thyasiridae	
Thyasira flexuosa Montagu, 1803	

Allen (1958*a*) studied the structure of the stomachs of thirteen species in the Lucinacea and found this to be least modified in the family Ungulinidae, and his figures clearly establish that the three species of *Diplodonta* have stomachs of type V. In contrast the stomachs of the remaining ten species in the families Lucinidae and Thyasiridae, listed above, have stomachs of type IV. *F. fimbria* also has a stomach of type IV (Allen & Turner 1970; Morton 1979). Accepting that these three families are correctly located in the same superfamily, and accepting that stomach type V cannot have evolved independently in two or more lineages, we must conclude that the stomach has become secondarily simplified in the families Lucinidae and Thyasiridae.

Therefore the family Ungulinidae serves as a 'marker' for the superfamily, which must be assigned as a whole to the phylogeny of the Gastropempta. In the Thyasiridae this secondary simplification may possibly be attributable to paedomorphosis, for *T. flexuosa* is of small size, but paedomorphosis can scarcely be relevant to larger animals, such as *Phacoides borealis*.

Allen (1958*a*) concluded that 'the Lucinacea live in environments where the food supply is so low that all available particulate food must be accepted and thus sorting mechanisms are necessarily poorly developed'. The gills and palps are modified, enabling the animals to take in large food particles. The stomach is also modified for the acceptance of larger food particles, by the loss of sorting areas, by reduction in the number of apertures leading from the stomach to the digestive diverticula, and by increase in the size of those apertures remaining.

Thus the occurrence of stomachs of type IV in the Lucinidae and Thyasiridae is the result of simplifications by means of which members of these families could successfully exploit marine sediments in habitats where nutritional resources were very poor. *F. fimbriata* occupies nutrient-deficient tropical coral sands; it also exhibits a number of comparable simplifications of gills, palps, and stomach.

Superfamily Corbiculacea
Review of literature
Pisidiidae
Sphaerium corneum (L., 1758) (Purchon 1958)

There is an apparent conflict of evidence regarding stomach structure in the superfamily Corbiculacea. Three members of the family Corbiculidae were shown to have a stomach of type V, whereas *Sphaerium corneum* has a stomach of type IV (Dinamani 1957; Purchon 1958, 1960*a*). Assuming that the families Corbiculidae and Sphaeriidae are correctly placed together in the superfamily Corbiculacea, secondary simplification must have occurred in *S. corneum*, causing reversion from stomach type V to type IV. This secondary simplification may be associated with paedomorphosis or the adoption of a small body size, or both. Stomach structure in the Corbiculidae provides a reliable 'marker', justifying location of the superfamily Corbiculacea in the phylogeny of the Gastropempta.

In *S. corneum* the oesophagus opens by a wide orifice on the anterior face of the stomach, and the combined style sac and mid gut leave the stomach posteroventrally. The major typhlosole passes forwards on to the floor of the stomach and forms two broad lobes, one of which passes to the left while the other approaches but does not enter the right caecum. The intestinal groove accompanies the right side of the major typhlosole and ends on the median side of the left pouch. The gastric shield is small and compact, and is held in position by flares which penetrate the mouth of the dorsal hood and the posterior margin of the left pouch. The dorsal hood is well developed, with a small anteriorly directed apex, and a conspicuous sorting area which passes posteriorly over the roof and onto the right side of the stomach. A rejection tract accompanies the border of this sorting area and discharges waste matter into the intestinal groove. On the left side of the body three ducts from the digestive diverticula open into the stomach via the left pouch. No information is available regarding a left caecum which may lie adjacent to the left lobe of the major typhlosole. The ducts from the digestive diverticula on the right side of the stomach open via a single aperture which may be equated with the right caecum. There are no sorting areas on the anterior floor of the stomach, or on its right side.

Analysis

An analysis of structural variation encountered in stomachs of type IV, based on the presence or absence of extensive sorting areas on the anterior floor of the stomach, and on the disposition of the orifices of ducts from the digestive diverticula, showed that the constituent superfamilies were arranged in three clusters (table 2). The Pectinacea, Limacea and Anomiacea, in which the posterior end of the ctenidium lies free in the mantle cavity, can be seen as a primitive group which may be linked with the Gastrotriteia to form the Pteriomorpha. The Pandoracea and Clavagellacea, in contrast, are highly specialized. A group of eight superfamilies which lack an extensive sorting area on the anterior floor of the stomach may *perhaps* include some which have lost a stomach of type V by secondary simplification (the Gastrochaenacea?).

Further analyses have been carried out on all examples with stomachs of types IV and V to distinguish more exactly between these two stomach types. These investigations included the ultimate destination in the stomach of the major typhlosole and the intestinal groove, and also the distribution of the various sorting areas. The results are tabulated at the end of the section on stomach type V.

TABLE 2. ANALYSIS OF VARIATION IN STRUCTURE OF THE INTERIOR OF THE STOMACH IN EXAMPLES WITH STOMACHS OF TYPE IV AND TYPE IVA

	many duct orifices, scattered or clustered	duct orifices concentrated into a few embayments	
	major typhlosole passes to the left pouch	major typhlosole passes towards left caecum	major typhlosole very short, posterior in position, not passing to either
with a conspicuous sorting area on the anterior floor of the stomach, emptying into the intestinal groove	Pectinacea Limacea Anomiacea	Laternulidae	Pandoracea (except for Laternulidae) Clavagellacea
without such a sorting area on the anterior floor of the stomach		†Unionacea Trigonacea Crassatellacea Carditacea †Leptonacea Hiatellacea †Gastrochaenacea Pholadomyacea	

† There is some evidence that these may have reverted from stomach type V to type IV.

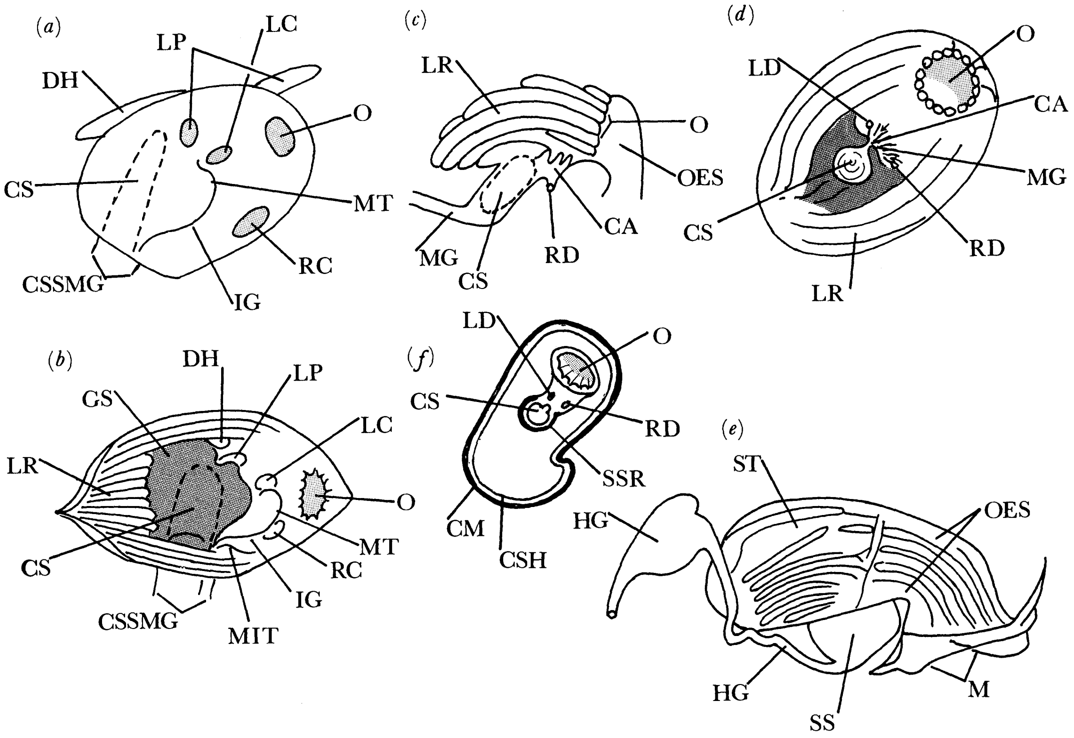


FIGURE 11. Lateral views of the stomachs in the Cuspidariidae (*c*) and Verticordiidae (*e*), and diagrammatic representations of dissections (*a*, *b*, *d*, *f*). (*a*) and (*b*) redrawn from Morton (1980, 1982); (*c*) and (*d*) redrawn from Purchon (1956); (*e*) and (*f*) redrawn from Allen & Turner (1974). In the Pholadomyidae (*a*) the stomach is of type IV, and in the Parilimyidae (*b*) the stomach is in a transitional state between type IV and type II. This suggests how the stomachs of the carnivorous Cuspidariidae and Verticordiidae probably evolved within the Anomalodesmata with the development of a highly muscular outer layer and an extensive inner lining of scleroprotein (CSH). There are only two small ducts from the digestive diverticula (RD, LD). (Magns: (*a*) ×3.5; (*b*) ×20; (*c*) ×15; (*d*) ×18; (*e*) ×38.)

Stomach type II: Gastrodeutera

Poromyacea

Review of literature

Cuspidariidae	
Cuspidaria cuspidata (Olivi, 1792)	(Yonge 1928; Purchon 1956*b*)
Cuspidaria obesa (Lovén, 1846)	(Allen & Morgan 1981)
Cuspidaria rostrata (Spengler, 1793)	(Yonge 1928)
Poromyidae	
Poromya granulata (Nyst & Westendorp, 1839)	(Yonge 1928)
Poromya tornata (Jeffreys, 1876)	(Allen & Morgan 1981)
Verticordiidae	
Halicardia nipponensis Okutani, 1957	(Nakazima 1967)
Halicardia perplicata Dall, 1890	(Bernard 1974)
Laevicardia horrida Allen & Turner, 1974	(Allen & Turner 1974)
Lyonsiella abyssicola (G. O. Sars, 1872)	
Lyonsiella alaskana Dall, 1895	(Bernard 1974)
Policordia densicostata Locard, 1898	(Allen & Turner 1974)
Policordia insolita Allen & Turner, 1974	
Verticordia triangularis Locard, 1898	

Yonge (1928) reported that the stomachs of *C. rostrata* and *P. granulata* are cylindrical and muscular, with prominent longitudinal folds in the wall, and with an extensive lining of thick cuticle. This does not cover the whole of the inner surface of the stomach in *C. cuspidata*, as was claimed for *C. rostrata* by Yonge, but leaves uncovered a small semicircular area of ciliated folds which radiate outwards from the orifice of the mid gut on the anteroventral stomach floor. The cuticular sheath encircles the protruding base of the style, preventing it from slipping further forwards into the lumen of the stomach. The orifice of the oesophagus into the stomach of *C. cuspidata* is large and circular, this being consistent with the swallowing of small crustaceans as food material. In contrast, the oesophageal orifice of *C. obesa* was found to be narrow, and guarded by a sphincter muscle, by Allen & Turner (1981). These authors found the stomach to be less muscular than the oesophagus in the Cuspidariidae, but in *Poromya tornata* the thick coat of muscle surrounding the oesophagus also extended over the whole stomach. The lumina of the style sac and mid gut are connected by a narrow longitudinal slit, and they open into the stomach anteroventrally. The style sac is a short oval cavity from which the crystalline style projects only a short distance into the lumen of the stomach. The typhlosole separating the style from the waste track in the mid gut does not pass forward into the stomach. The digestive diverticula open into the stomach by two ducts which were thought to be exceptionally wide by Yonge (1928). Allen & Morgan (1981) noted that the ducts from the digestive diverticula in *Cuspidaria obesa* were as short as they were *wide*, but the dimensions they quoted (0.04 mm) suggest otherwise. Purchon (1956*b*) decided that the ducts were *narrow* in *C. cuspidata*, for in that species the duct orifices could not be detected from within the stomach, but only by passing a bristle through the duct from the outside. There was no trace of a dorsal hood, or of a left pouch in the Cuspidariidae.

Studies on the Verticordiidae by Allen & Turner (1974), and by Bernard (1974) indicated a measure of uniformity in stomach structure in the family, although in each of the genera *Halicardia*, *Policordia*, and *Lyonsiella* individual species showed a lesser degree of specialization towards the carnivorous habit. There is a dorsal hood with a small sorting area of ciliated folds in *Lyonsiella alaskana* and in *Halicardia perplicata* (Bernard 1974), and perhaps the vestige of a dorsal hood in *P. insolita*. There is a small major typhlosole and intestinal groove in *H. perplicata*. In *P. insolita* the muscle layer is thin around the stomach and is lacking from the oesophagus, while the scleroprotein lining the stomach is thin and lacks ridges, and does not cover the right wall of the stomach. In *H. perplicata* the stomach wall is less muscularized than in other examples, and is more adherent to the adjacent viscera. A radially arranged series of ciliated folds on the stomach floor, in front of the orifice of the mid gut in *H. perplicata* is reminiscent of a similar structure in *Cuspidaria cuspidata* (Bernard 1974).

In contrast, many species are more fully adapted towards a carnivorous mode of life. In these the oesophagus is wide, with several longitudinal folds, and its orifice into the stomach may be as wide as the stomach itself. The oesophagus and stomach are invested by a thick muscular coat which assists in the swallowing of food organisms such as small crustaceans, and in the crushing of these in the stomach. The stomach wall may be separated from adjacent viscera by a haemocoele, giving added freedom for its crushing action. In such cases there are no ciliary sorting mechanisms within the stomach, while the scleroprotein cuticular lining of the stomach is very extensive, is thickened, and bears longitudinal ridges. The style sac and mid gut are conjoined and leave the stomach ventrally. The style sac is short and oval, and the style only projects a short distance into the stomach. Two ducts from the digestive diverticula open on the floor of the stomach, in front of the orifice of the mid gut, and ciliated tracts lead from their orifices to the mid gut. With the exception of *H. perplicata*, mentioned above, there is no major typhlosole and no intestinal groove. The scleroprotein lining the greater part of the stomach may be thickened around the orifices of the oesophagus and the style sac, thereby holding it firmly in position. There is no left pouch, and in most examples there is no dorsal hood.

Allen & Turner (1974) have shown that the stomach of type II in the Verticordiidae could have evolved from a stomach of type IV in an ancestral group in the Anomalodesmacea, in the course of progressive colonization of nutritionally impoverished submarine deposits, and in the gradual transition from microphagous to scavenging or carnivorous habits. Their means of trapping small crustaceans for food lie in the possession of sticky tentacles which can be periodically wiped clean at the branchial aperture. In contrast, the Cuspidariidae catch small crustaceans by means of their raptorial siphons (Reid & Reid 1974; Reid & Crosby 1980). Since the feeding strategy is different in these two families it seems probable that as regards stomach structure this is a case of convergent evolution from different origins, possibly both in the Anomalodesmacea, but not necessarily so.

STOMACH TYPE V: GASTROPEMPTA

In the very large number of examples of stomach type V there is a considerable measure of uniformity in the general organization of the stomach, including the gastric shield, the dorsal hood, the left pouch, the left and right caeca, and the route taken by the major typhlosole and the intestinal groove. It must be concluded that stomach type V has been an extremely effective mechanism for the final internal grading of particulate material for presentation to the digestive diverticula. It would seem to be unnecessary to replicate information for the above-named structures in every superfamily, insofar as they conform to a more or less standard pattern. Instead, attention will be focused upon any deviations from the norm, and variations in the disposition of the sorting areas of the stomach, which may collectively impose considerable diversity of appearance of the interior of the stomach in this group of bivalves. This diversity in form may be attributable to a number of independent factors, including:

(i) changes in shape and orientation of the stomach, imposed by the growth form and the posture adopted in each taxon;

(ii) changes imposed by the nature of the work to be done within the stomach, according to the niche occupied by the taxon, and the grades of particulate matter which are admitted into the stomach;

(iii) species specific variables, apparently of little functional significance, which can best be detected where many examples have been investigated within the same genus or family;

(iv) features that are diagnostic of certain genera, families, superfamilies, or even higher taxonomic categories.

Chamacea

Description of fresh material

Chama ?brassica Reeve, 1847

The oesophageal orifice (O) was anterodorsal in position, small in size, and surrounded by almost circular, tumid lips. It lay in a hemispheric, featureless antechamber (AC) to the stomach. Weak longitudinal ridges were seen on the posterior floor of the oesophagus. A small blind triangular pocket lay adjacent to its left border. An inconspicuous ridge (R) extended from the right side of the stomach, passed above the oesophageal orifice and thence to the left, towards the mouth of the dorsal hood. The whole area around the oesophageal orifice was generally deficient in ciliation, though a ciliary current was observed passing downwards, lateral to this ridge, on the right side of the stomach.

Below the oesophageal orifice a broad transverse belt (BE) stretched from left to right, turning downwards towards its right extremity, lateral to the opening of the right caecum (RC). There was a weak system of folds along the lower border of this belt, but it is not known whether this was attributable to contraction of tissues in this area. Over the surface of the belt cilia beat downwards, away from the oesophageal orifice. Lateral to the right end of the transverse belt there was a small sorting area (SA) of closely spaced folds, which was probably the terminal part of the large sorting area (SA) on the anterior face of the dorsal hood, for this last mentioned sorting area was seen to extend over the roof of the stomach in the second dissection. On both of these sorting areas cilia beat transversely over the crests of the folds, towards the apex of the dorsal hood. Cilia in the grooves between the folds beat ventralwards, along the grooves, and into a rejection tract which discharged into the intestinal groove nearby. It should be emphasized that, owing to differences in the strategy of opening the stomachs of the two specimens and the consequent differences in tension of various parts of the stomach wall, especially in this region, slightly different indications were gained as to the precise orientation of the ridges and grooves of the sorting area, or areas. The figure, and the above account, are deemed to be the most probable disposition of the sorting area.

The combined style sac and mid gut (CSSMG) left the floor of the stomach and passed ventralwards into the visceral mass. The minor typhlosole (MIT) extended a short distance along the right posterior wall of the stomach in the first dissection, but in the second dissection it extended further forwards above the isolated duct from the digestive diverticula (DDD) and above the right caecum. The swollen patch (PA) depicted in the figure, which was derived from the first dissection, may represent the anterior extremity of the minor typhlosole. The major typhlosole (MT) passed forwards on the right side of the floor of the stomach and entered the right caecum (RC), emerging from this to pass transversely across the anterior floor of the stomach (MT′) to enter and terminate within the left caecum (LC). Throughout its course the major typhlosole was accompanied on its anterior, or right side by the intestinal groove (IG), over which it arched closely. Ciliary currents in the intestinal groove circumnavigated each of the caeca and then passed backwards into the mid gut.

Dissection of the right caecum (RC) revealed that the major typhlosole penetrated very deeply as an oval flare circumnavigated by the intestinal groove and lying very close to at least 11 ducts from the digestive diverticula. The left caecum (LC) passed directly downwards below the stomach and parallel with the style sac. The sector of the major typhlosole within the left caecum was very long, it was accompanied by the intestinal groove, and the two structures were associated with at least six ducts from the digestive diverticula. However, it was difficult to dissect, and it is probable that several more ducts opened here. The gastric shield (GS) was relatively small, and it invested the lateroventral margin of the mouth of the dorsal hood, as also the posterior wall of the left pouch (LP). The mouth of the left pouch was approximately square in outline, and lay on the left side of the stomach anterior to the dorsal hood and the gastric shield. Three ducts from the digestive diverticula entered the left pouch. Cilia on the posterodorsal wall of the left pouch beat strongly upwards towards and into the dorsal hood on its anterior face. On the right side of the stomach, between the orifices of the right caecum and mid gut, there was an isolated aperture, through which two ducts from the digestive diverticula communicated with the lumen of the stomach (DDD). In the second dissection this aperture lay immediately dorsal to the orifice of the right caecum. This may be a matter of variation from one specimen to another, but the difference may also be partly attributable to differences in tension in the wall of the dissected stomach in this region.

The dorsal hood was not dissected further than is shown in the figure. It was a relatively large structure which curved backwards close to the left side of the stomach. On its anterior face a large sorting area of well spaced ridges and grooves (SA) extended deep into the hood; cilia on the crests of the folds carried particles towards the apex of the hood, while below the sorting area a ciliated rejection tract carried particles towards the intestinal groove on the right side of the stomach. The posterior side of the dorsal hood was not investigated.

Review of literature

Chamidae

Chama gryphoides L. 1758	(Allen 1976)
Chama lazarus L., 1758	(Purchon 1960*a*)
Chama multisquamosa Reeve, 1846	(Purchon 1958)
Chama pellucida Broderip, 1834	(Yonge 1967)
Pseudochama exogyra (Conrad, 1837)	(Yonge 1967)

Yonge (1967) did not investigate the internal structure of the stomach in *C. pellucida* or in *P. exogyra*. *C. multisquamosa* has a stomach of type IV, but *C. ?brassica*, described in detail above, *C. gryphoides* and *C. lazarus* have a stomach of type V. Allen (1976) considers that if the distinction between stomachs of types IV and V is only a matter of the degree to which the major typhlosole approaches or enters the left and right caeca, then this distinction is not one of great significance. This would be a reasonable view if it only concerned interspecific structural variation within the family Chamidae. However, the distinction between stomachs of types IV and V concerns consistent differences between two groups of superfamilies with only rare deviations in the genera *Donax*, *Tellina* and *Chama*. These deviations require explanation, and it is suggested that in *C. multisquamosa*, an animal of small size, the stomach has reverted to a simpler ancestral condition. Taking into account the universal occurrence of a stomach of type V in all species studied in 12 superfamilies and in the great majority of species in the Tellinacea and Chamacea, it is inescapable that the occurrence of a stomach of type IV in *C. multisquamosa* must be attributable to reversion.

Allen (1976) draws attention to two features that are peculiar to the family Chamidae, namely the capacious vestibule into which the oesophagus opens, and the accessory right caecum into which an accessory tongue from the major typhlosole may penetrate. However, neither of these features occurs in all species of *Chama* that have been studied. Considerable variations have been noted in the stomachs of species of *Chama*. In view of this, I have dissected many preserved specimens of species of *Chama* and have found several species to have a stomach of type V. The species concerned have not yet been identified, and the work is unpublished.

The special features in the stomach in the family Chamidae include: a well developed posterior sorting area which extends from the anterior face of the dorsal hood over the roof and on to the right side of the stomach; one or more isolated duct orifices on the right side of the stomach; a vestibule is usually, but not invariably present anterodorsally between the oesophagus and the 'stomach proper'; an accessory right caecum may be present on the right side of the stomach, and may or may not be penetrated by an accessory tongue of the major typhlosole.

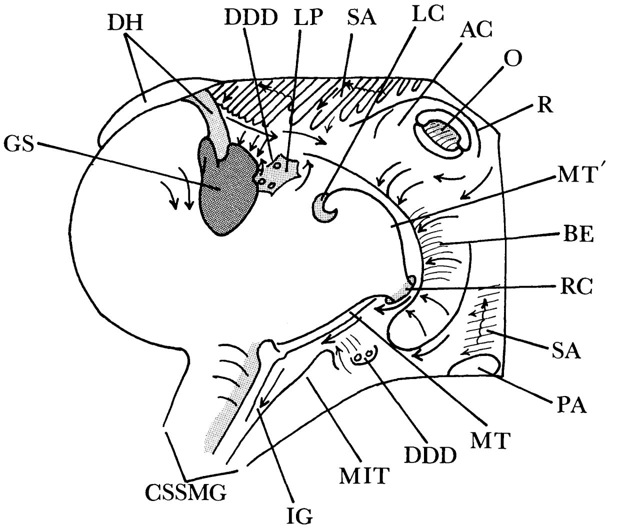


FIGURE 12. *Chama ?brassica*, detailed drawing of the interior of the stomach after opening by a mid-dorsal incision passing down through the combined style sac and mid gut (CSSMG). (Magn. × 15.) The stomach is of type V since the major typhlosole (MT) and intestinal groove (IG) pass into the right caecum (RC) before emerging and crossing the stomach floor to enter and end in the left caecum (LC). Note the presence of duct orifices (DDD) within the left pouch (LP), and also an isolated group of duct orifices on the right side of the stomach.

Tellinacea

Review of literature

Donacidae (figure 13*a*, p. 242)	
Donax hanleyanus Philippi, 1847	(Narchi 1978)
Donax semigranosus (large only) Dunker, 1877	(Nakazima 1965*a*)
Donax serra Röding, 1798	(Ansell 1981)
Donax sordidus Hanley, 1845	(Ansell 1981)
Donax trunculus L., 1758	(Mouëza & Frenkiel 1976)
Egeria radiata(Lamarck, 1805)	(Purchon 1963*a*)
Iphigenia brasiliensis Lam., 1818	(Narchi 1972*a*)
Tellinidae	
Florimetis obesa (Deshayes, 1855)	(Pohlo 1973)
Gastrana yantaiensis Crosse & Debeaux, 1863	(Nakazima 1958)
Macoma anser Oyama, 1950	(Nakazima 1957)
Macoma (8 species)	(Reid & Reid 1969)
Tellina capsoides Lamarck, 1818	(Purchon 1960*a*)
Tellina crassa Pennant, 1777	(Graham 1949)
Tellina juvenilis Hanley, 1844	(Nakazima 1958)
Tellina tenuis da Costa, 1778	(Yonge 1949)
Tellina venulosa Schrenck, 1862	(Nakazima 1958)
Semelidae	
Abra alba (Wood, 1801)	(Yonge 1949)
Abra tenuis (Montagu, 1803)	(Hughes 1977)
Scrobicularia plana (da Costa, 1778)	(Yonge 1949; Purchon 1955*b*)
Semele proficua Pulteney, 1794	(Domaneschi 1975)

Psammobiidae (figure 13*a*, p. 242)	
Asaphis deflorata (L., 1758)	(Purchon 1960*a*)
Asaphis dichotoma (Anton, 1839)	(Narchi 1980)
Gari togata Deshayes, 1854	(Purchon 1960*a*)
Orbicularia orbiculata (Wood, 1828)	(Purchon 1984)
Sanguinolaria diphos (L., 1771)	(Dinamani 1967)
Sanguinolaria nuttallii Conrad, 1837	(Pohlo 1972)
Soletellina olivacea (Jay, 1856)	(Nakazima 1957)
Solecurtidae (figure 13*b*)	
Solecurtus chamosolen (da Costa, 1778)	(Graham 1949)
Solecurtus divaricatus (Lischke, 1869)	(Nakazima 1964*a*)
Tagelus californianus (Conrad, 1837)	(Pohlo 1973)

Five species of *Donax* and one species of *Tellina* have been reported to possess a stomach of type IV and this condition has been attributed to a process of paedomorphosis in these taxa. This conclusion is supported by the fact that the largest specimens of *D. semigranosus* attain a stomach of type V owing to penetration of the orifice of the right caecum by a forward projection of the major typhlosole (Nakazima 1965); a number of other species of *Donax* and of *Tellina* have a stomach of type V as reported above. All other examples that have been investigated in this respect in the Tellinacea, in five families and 17 genera, have a stomach of type V. It can be safely concluded that this superfamily belongs to the phylogeny of the Gastropempta, notwithstanding the few exceptions noted in *Donax* and *Tellina*. Stomach type IV represents an ancestral condition and may be exhibited during an early stage in ontogeny in some taxa.

The Tellinacea comprise a very clearly defined superfamily, members of which can be recognized at a glance by the presence of a cruciform muscle in all except *Orbicularia* and *Pharus* (Solecurtidae) (Yonge 1959). In all examples investigated the stomach bears a posterodorsal caecum, which may be lobed, and which is homologous with the appendix in many members of the Pholadidae and with the wood-storing caecum of *Xylophaga* (Pholadidae) and of the Teredinidae. This may signify a phyletic bond between the Tellinacea and Pholadacea, but it will be prudent not to place much weight on this evidence in view of the occurrence of an apparently homologous stomach appendix in *Mytilus edulis*, *Ostrea edulis*, and in *Lima hians*. It is probably an archaic structure (Reid 1965).

As regards the internal structure of the stomach the tellinacean families investigated fall into two groups. In the Tellinidae, Semelidae, and Solecurtidae there are no special features to report, save for the presence of an extensive sorting area immediately below the oesophageal orifice in *Solecurtus chamasolen*, which is figured but not described by Graham (1949). Also, a single isolated duct from the digestive diverticula opens on the right side of the stomach only in *Tellina crassa* and in *Solecurtus chamasolen*. In contrast to these three families, the Donacidae and Psammobiidae exhibit a number of special features which collectively suggest an affinity between these families. Thus a substantial transverse fold crosses the stomach floor from left to right between the oesophageal orifice and the transverse sector of the intestinal groove; it passes anterior to the orifice of the right caecum, over the anterior stomach roof, and into the dorsal hood on its anterior side. This structure was found in all three genera in the Donacidae, and in three genera of the Psammobiidae, but not in *Orbicularia* or *Soletellina*. It also occurs in *Macoma*, in the Tellinidae. Second, there is a semicircular flange on the floor of the stomach, stretching from the orifice of the style sac towards that of the left pouch, and resembling a supernumerary major typhlosole, in two genera each of the Donacidae (*Egeria* and *Iphigenia*) and of the Psammobiidae (*Asaphis* and *Gari*). Finally, the style sac and the mid gut are wholly separate in all members of the Donacidae and also in *Orbicularia* only, in the Psammobiidae. Yonge (1949) has emphasized that this last character is without phyletic significance. Information on the numbers of ducts from the digestive diverticula which open into the left pouch, the left caecum, and the right caecum, is patchy, but such ducts are known to enter the left pouch in *Florimetis*, *Macoma*, *Tellina*, *Asaphis*, *Orbicularia*, and *Tagelus*.

In certain deposit-feeding tellinaceans, including *Abra tenuis*, *A. alba*, *A. nitida*, *A. prismatica*, and *Tellina tenuis*, the left pouch, left caecum and right caecum are fused to form a single, branched 'combined caecum' (Hughes 1977). This organ has been admirably described and illustrated for *A. tenuis* by Hughes (1977) who showed that the left main duct leaving the 'combined caecum' can be equated with the left pouch, for its mouth is invaded by the margin of the gastric shield, its walls bear a sorting area of parallel ciliated ridges, and it receives ducts from a digestive diverticula. As regards the identities of the left and right caeca, I am inclined to disagree with Hughes' suggestions. I suggest that the location of the terminal spiral coil of the major typhlosole must indicate the position of the *left* caecum, which is duct 1; this would leave ducts 2–5 to be representative of the *right* caecum. The same correction must be made to Hughes' brief description of stomach type V, for the major typhlosole passes into and out of the *right* caecum and terminates in the *left* caecum.

Cardiacea

Review of literature

Cardiidae (figure 13*c*, p. 242)

Cardium bechei (Reeve, 1848)	(Nakazima 1964*c*)
Cardium burchardi (Dunker, 1877)	(Nakazima 1964*c*)
Cardium edule L., 1758	(Graham 1949)
Fulvia hungerfordi (Sowerby, 1902)	Reid (personal communication)

Graham (1949) examined fresh material of *C. edule*, and his excellent figure establishes that the interior of the stomach is dominated by two large sorting areas. The posterior sorting area expands widely over the right posterior stomach wall and extends upwards over the roof towards a small and inconspicuous dorsal hood. This sorting area discharges waste material into the terminal sector of the intestinal groove. The other sorting area lies anteriorly on the stomach floor, between the oesophageal orifice and the transverse sector of the intestinal groove. Here the ciliation directs material away from the intestinal groove and towards the oesophagus. Graham illustrated this anterior sorting area but did not discuss it. Ducts from the digestive diverticula open into the stomach via the left pouch, left caecum and right caecum, and also independently on the right side of the stomach where there is a single duct in *C. edule*, but two ducts in *C. bechei* and in *C. burchardi*. The major typhlosole and intestinal groove penetrate the left and right caeca deeply in *C. edule* and *C. burchardi*, but less deeply in *C. bechei*. In *C. edule* the major typhlosole does not form a narrow tongue in the left caecum, but an open loop which encircles the caecum; in *C. bechei* the major typhlosole ends in an open spiral close to the orifice of the left caecum. In all cases there are numerous duct orifices in the left and right caeca, about eight in each caecum in *C. edule* and in *C. burchardi*, and the margin of the major typhlosole is developed into little lobes which penetrate a short distance into each of the individual ducts from the digestive gland.

Nakazima (1964*c*) examined preserved material, and concentrated on ascertaining the internal structures of the left and right caeca.

Tridacnacea

Review of literature

Tridacnidae (figure 13*d*, p. 242)

Hippopus hippopus (L., 1758)	(Nakazima, 1964*b*)
Tridacna crocea Lam., 1819	(Yonge 1936, 1953; Purchon 1958)
Tridacna derasa Röding, 1798	(Yonge 1936)
Tridacna elongata Röding, 1798	(Nakazima 1964*b*)

Yonge (1936) stated that the structure of the stomach of *T. derasa* agreed in all respects with that of *T. crocea*, which he figured and briefly described. The style sac is attached for some distance to the mid gut, later passing downwards into the substance of the foot, where it terminates. His illustration shows the crystalline style, the gastric shield, and the structures that are now known as the left pouch, the left caecum, the right caecum, and the major typhlosole. He recognized the function of the stomach as a sorting organ which normally continues the sorting process begun on the gills and the palps. However, in *T. crocea* he judged that the ducts to the digestive diverticula are exceptionally wide, and gained the general impression that so far from there being any further sorting in the stomach, every opportunity is taken of passing particulate material into the ducts. 'Only in the last resort is it passed into the mid gut.' In this he seems to have misunderstood the basic mode of action of the intestinal groove, under the protection of the major typhlosole. This is to clear the entrances to the ducts leading to the digestive diverticula and to convey waste matter unfailingly to the mid gut. Waste material is only passed to the mid gut 'in the last resort' because this is, as always, the end of a chronological sequence. It is true that the major typhlosole and intestinal groove pass deeply into the left and right caeca, and that waste material is therefore carried very close to the orifice of the ducts to the digestive diverticula, but this does *not* mean that every opportunity is taken to pass food material into these ducts. Yonge (1953) subsequently affirmed that the Tridacnidae retain the same type of ciliary sorting mechanisms in the stomach as in other eulamellibranchs.

Nakazima (1964*b*) found that the major typhlosole penetrates deeply into both left and right caeca in *H. hippopus* and *T. elongata*. In both cases the spiral coil in the mouth of the left caecum has fewer turns than in *T. crocea*. Purchon (1955) noted that nine ducts from the digestive diverticula enter the stomach via the left pouch in *T. crocea*, that the dorsal hood is well developed, and that the sorting area of the dorsal hood spreads over the roof of the stomach on to its right side. There is no anterior sorting area on the stomach floor, but there is a finely striated sorting area on the floor of the left pouch.

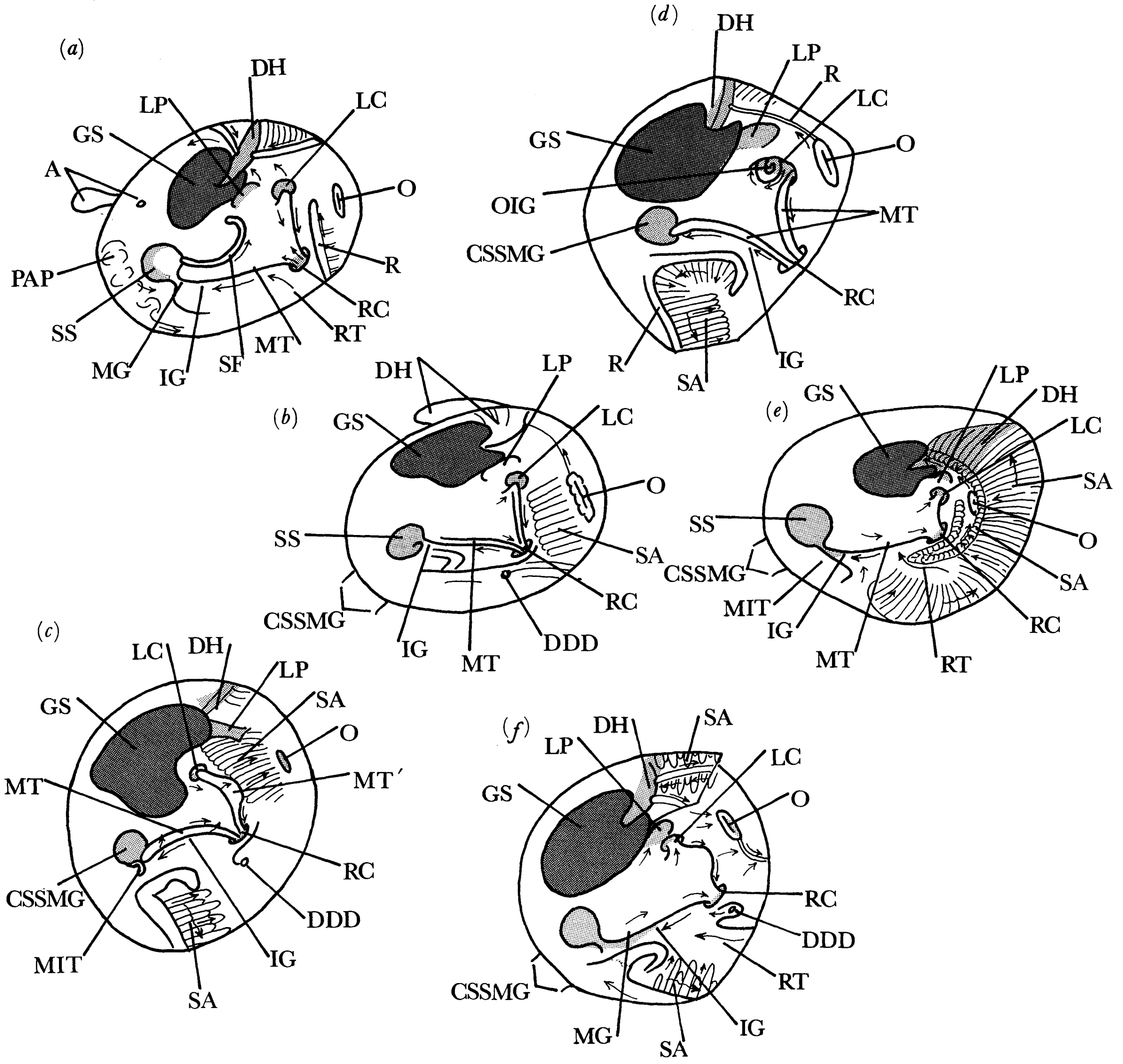


FIGURE 13. Diagrammatic representation of the interior of the stomach in various members of the Gastropempta in which the style sac and mid gut are combined (CSSMG). (*a*) Some Donacidae and Psammobiidae; (*b*) *Solecurtus*; (*c*) Cardiidae; (*d*) Tridacnidae; (*e*) Petricolidae and Libitinidae; (*f*) Isocardiidae. Note the semicircular flange (SF) on the floor of the stomach in some Donacidae and Psammobiidae. A similar structure was also found in some of the Erycinidae (figure 10*f*). Note the spirally coiled end of the major typhlosole (OIG) in the mouth of the left caecum (LC) of the Tridacnidae. A similar, but much larger spiral coil was found in the Carditidae (figure 10*d*).

Glossacea

Review of literature

Isocardiidae (figure 13*f*)

Glossus humanus (L., 1758) (Owen 1953*a*)

The stomach is globular, the oesophagus entering anterodorsally, and the combined style sac and mid gut leaving posteroventrally. The minor typhlosole ends on the stomach wall at the mouth of the style sac. The course of the major typhlosole and intestinal groove is characteristic, passing through the right and left caeca and ending on the stomach floor just outside the orifice of the left caecum. Ducts from the digestive diverticula enter the stomach via the left pouch, left caecum, and the right caecum, and a single duct enters the stomach independently on the right side close to the orifice of the right caecum. The gastric shield is large and is held in position by flanges which enter the mouths of the left pouch and the dorsal hood. The dorsal hood is unusually large; it arises from the roof of the stomach, and curves downwards on its left side. There are two conspicuous sorting areas on the roof of the dorsal hood, of which the anteriormost extends over the roof of the stomach and down its right side, being separated from the terminal sector of the intestinal groove by the conspicuous fleshy ridge. A circular ciliated groove around the oesophageal orifice passes particles into a dorsal groove which directs this incoming material into the dorsal hood, on its anterior face.

The interior of the stomach of *G. humanus* is not unlike that of the Cardiidae except that there is no sorting area below the oesophageal orifice, and it is not unlike that of the Tridacnidae except that in the Tridacnidae the major typhlosole ends in a conspicuous spiral coil, and there is no isolated duct from the digestive diverticula on the right side of the stomach.

Veneracea

Review of literature

Veneridae (figure 14*a*)	
Anomalocardia brasiliana (Gmelin, 1791)	(Narchi 1972*b*)
Anomalocardia producta Kuroda & Habe, 1951	(Purchon 1984)
Bassina calophylla (Philippi, 1836)	(Purchon 1984)
Catelysia opima (Gmelin, 1791)	(Dinamani 1967)
Chione subrostrata Lam., 1818	(Narchi & Gabrielli 1980)
Chione tiara (Dillwyn, 1817)	(Dinamani 1967)
Cyclina sinensis (Gmelin, 1791)	(Purchon 1984)
Dosinia exoleta (L., 1758)	(Ansell 1961)
Dosinia japonica (Reeve, 1850)	(Nakazima 1958)
Dosinia lupinus (L., 1758)	(Purchon 1960*a*)
Gafrarium minimum (Montagu, 1803)	(Purchon 1960*a*)
Gemma gemma (Totten, 1834)	(Narchi 1971)
Meretrix casta (Gmelin, 1791)	(Dinamani 1967)
Meretrix lusoria (Röding, 1798)	(Nakazima 1959)
Sunetta effosa (Hanley, 1842)	(Dinamani 1967)
Tivela mactroides (Born, 1778)	(Narchi 1972*b*)
Transenella tantilla (Gould, 1853)	(Narchi 1971)
Venerupis aurea (Gmelin, 1791)	(Ansell 1961)
Venerupis decussata (L., 1758)	(Ansell 1961)
Venerupis macrophylla Deshayes, 1853	(Dinamani 1967)
Venerupis pullastra (Montagu, 1803)	(Ansell 1961)
Venerupis (as *Paphia*) *pullastra*	(Graham 1949; Purchon 1960*a*)
Venerupis rhomboides (Pennant, 1777)	(Ansell 1961)
Venus casina L., 1758	(Ansell 1961)
Venus fasciata (da Costa, 1778)	(Graham 1949; Purchon 1960*a*)
Venus ovata Pennant, 1777	(Ansell 1961)
Venus striatula (da Costa, 1778)	(Ansell 1961)
Veremolpa scabra (Hanley, 1845)	(Narchi 1980*b*)
Glaucomyidae	
Glauconome chinensis (Gray, 1828)	(Nakazima 1965)
Glauconome rugosa Reeve, 1844	(Purchon 1960*a*)
Petricolidae (figure 13*e*, p. 242)	
Mysia undata (Pennant, 1777)	(Ansell 1961)
Mysia (as *Lucinopsis*) *undata* (Pennant, 1777)	(Purchon 1960*a*)
Petricola japonica Dunker, 1882	(Nakazima 1958)
Petricola pholadiformis Lam., 1818	(Purchon 1955*c*)
Petricola stellae Narchi, 1975	(Narchi 1975)
Petricola typica (Jonas, 1844)	(Narchi 1974)

The Veneridae are one of the largest and most successful of eulamellibranch families, occupying most types of soft marine substrate. Ansell (1961) concluded that the anatomy of

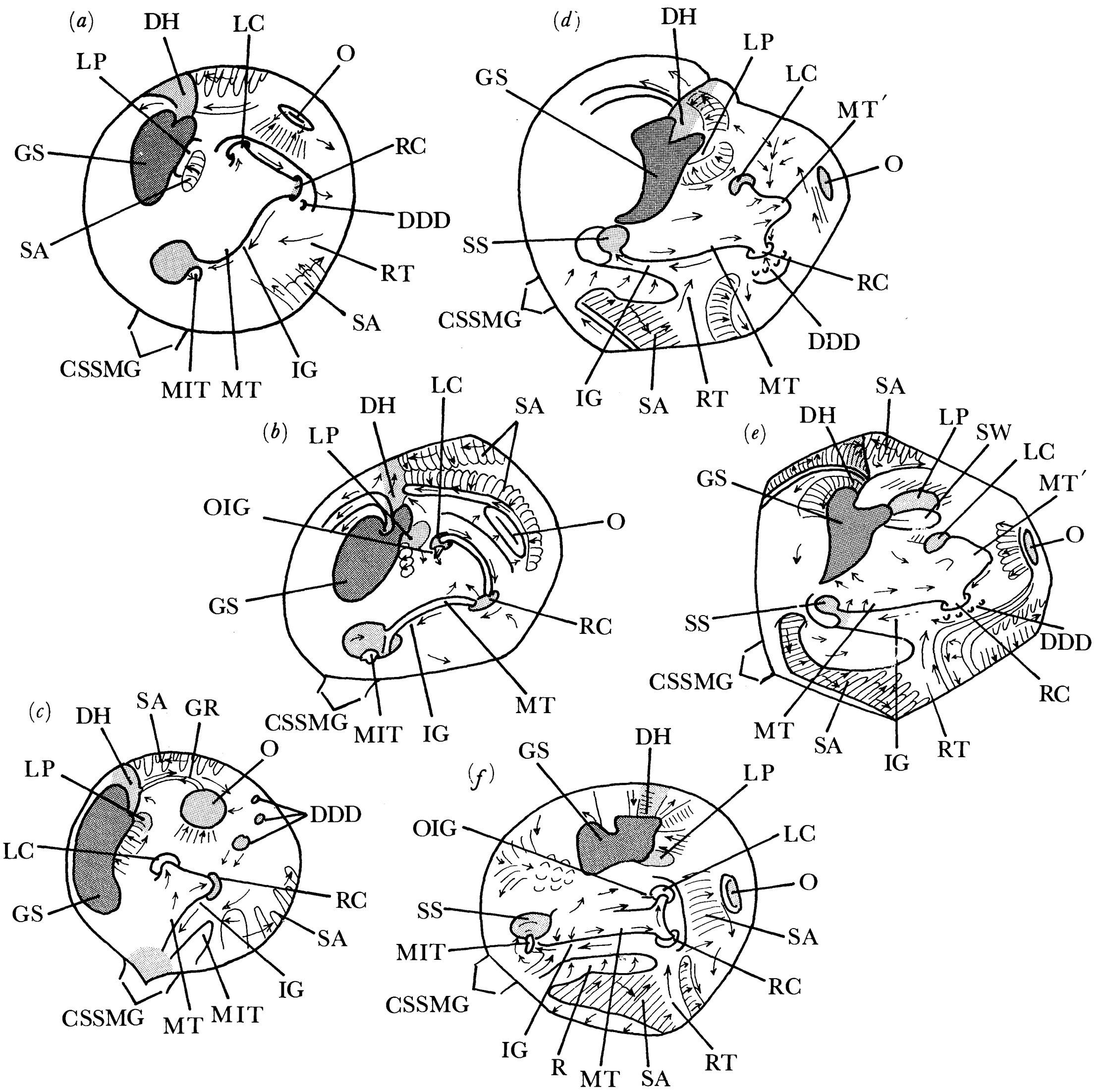


Figure 14. Diagrammatic representation of the interior of the stomach in a further group of Gastropempta in which the style sac and mid gut are combined (CSSMG). (*a*) Veneridae; (*b*) Aloididae; (*c*) Ungulinidae; (*d*) Glaucomyidae; (*e*) Corbiculidae; (*f*) Cyprinidae. Note the many points of similarity between the stomachs of the Glaucomyidae and the Corbiculidae.

the stomach was more or less the same throughout the family, and this view is supported by the present review of literature.

The stomach is globular, the oesophagus entering anteroventrally and the combined style sac and mid gut leaving posteroventrally. Exceptionally, in *Chione tiara* their orifices are placed together, but they lead into separate tubes. The minor typhlosole projects into the stomach, but ends close to the orifice of the mid gut. The major typhlosole and intestinal groove penetrate the right and the left caeca and frequently end on the anterior stomach floor, just outside the mouth of the left caecum. In *Venerupis pullastra* the major typhlosole ends just inside the left caecum, while in *Venus fasciata* the major typhlosole ends in a loose spiral within the left caecum. In *T. tantilla* and in *G. gemma* the major typhlosole makes only a very shallow loop into each of the left and right caeca, whereas in *Meretrix lusoria* it penetrates very deeply into each caecum (Nakazima 1959). In *Dosinia lupinus*, as in *Gafrarium minimum*, the right caecum is divided into upper and lower components. The major typhlosole and intestinal groove do not enter the upper component of the right caecum, into which three ducts from the digestive diverticula enter. The lower component of the right caecum and the left caecum lie close together near the median line and both are penetrated by the major typhlosole and intestinal groove. The ducts from the digestive diverticula usually enter the stomach at only three sites, the left pouch, the left caecum and the right caecum, but ducts may enter near the right caecum, for example, one in *V. fasciata* (Graham 1949) and three in *C. sinensis* (Purchon 1984). In most examples a few ducts enter the left pouch, but five are recorded as entering here in *Tivela mactroides*, eight in *Dosinia lupinus*, and 'a series' in *Dosinia exoleta*. The numbers of ducts entering the left and right caeca vary from a minimum of one and two, respectively, in *Transenella tantilla* to a maximum of 13 and seven, respectively, in *Venerupis pullastra*. This variation is undoubtedly positively correlated with the size of the specimens.

The dorsal hood is typically large, with a sorting area which may entend over the roof of the stomach and expand on its right wall as the 'posterior sorting area' (Graham 1949). In only a few examples there is a sorting area in the form of a raised lozenge in the mouth of the left pouch and extending on to the adjacent stomach floor, for example, in *Tivela mactroides* and *Gafrarium minimum*. There may also be a small and inconspicuous sorting area of vertical folds on the anterior stomach floor, between the oesophageal orifice and the transverse sector of the intestinal groove. Cilia on this sorting area beat upwards, away from the intestinal groove. This sorting area is most strongly developed in *Tivela mactroides* (Narchi 1972*b*). The gastric shield is moderately well developed, with flanges which pass into the mouths of the dorsal hood and the left pouch. In some cases on the anterior floor of the stomach there may be a transverse ridge or horizontal flap which arches over the transverse sector of the intestinal groove and passes above the orifices of the left and right caeca, as in *Cyclina sinensis*, *Anomalocardia producta* and *Bassina calophylla* (Purchon 1987).

To summarize, throughout the Veneridae there are no outstanding features in the internal organization of the stomach, but this is simpler in the smaller species. The examples studied are classified in several subfamilies, but these distinctions are not supported by corresponding differences in stomach structure.

Owen (1959*b*) recommended removing the family Glaucomyidae from the superfamily Solenacea and transferring it to the Veneracea, but attention must be drawn to the extraordinary likeness between the stomachs of *Glauconome rugosa* and *Geloina ceylanica* in the family Corbiculidae (Purchon 1960*a*) (figure 14*d*, *e*). These similarities include:

(i) the disposition of the major typhlosole and intestinal groove, with a long straight posterior sector, with a conspicuous flap pointing forwards towards the oesophageal orifice, and with the left and right caeca directed downwards, close together near the median line;

(ii) a group of four or five isolated ducts open in an arc on the stomach wall above the orifice of the right caecum;

(iii) the posterior sorting area, on the right side of the stomach, passes far back into a blind pocket close to the orifice of the combined style sac and mid gut;

(vi) the shape of the gastric shield, emarginated on its posterior border and with a posteroventral spur directed towards the rim of the style sac;

(v) the large size of the left pouch, with a substantial sorting area protruding from its mouth on to the left anterior floor of the stomach. Any one of these similarities might reasonably be dismissed as a coincidence, but taken together they offer a persuasive argument in favour of phyletic affinity. In contrast, the differences between the stomachs of *Glauconome rugosa* and *Geloina ceylanica* are few. The dorsal hood of the former is not so large, and the posterior sorting area does not extend so far into it. The conspicuous oval swelling which characterizes the mouth of the left pouch of *Geloina ceylanica* is lacking in *Glauconome rugosa*.

In the family Petricolidae Purchon (1960*a*) reported that the stomach of *Lucinopsis* (*Mysia*) *undata* was basically comparable with that of *Gafrarium minimum* in the family Veneridae. Ansell (1961) studied both *M. undata* and *Petricola pholadiformis*, but he only reported upon stomach structure in the family Veneridae. Owing to differences in presentation, it is not easy to make direct comparisons between his figure for *Venus casina* and mine for *P. pholadiformis* (Purchon 1955*c*), but they appear to be very different. Descriptions of the interiors of the stomachs of the three species of *Petricola* are in close agreement. The oesophagus enters the anteroventral face of the stomach, and its base is overhung by the dorsal hood. The combined style sac and mid gut leaves the stomach posteroventrally, and the minor typhlosole ends on the right side of the stomach close to the orifice of the mid gut. The major typhlosole and intestinal groove penetrate the right caecum and left caecum in characteristic fashion. In *P. pholadiformis* and *P. typica* the major typhlosole ends within the left caecum, but in *P. stellae* the intestinal groove is reported to arise on the stomach floor, just outside the left caecum. The left pouch has an extensive sorting area on its floor and extending out of the pouch as a beaded swelling similar to that seen in *Gafrarium minimum* (Purchon 1960*a*) and *Tivela mactroides* (Narchi 1972*b*). In *P. pholadiformis* three ducts from the digestive diverticula open into the stomach via the left pouch. No information is available regarding the numbers of ducts entering the left and right caecum, but small numbers of ducts are indicated for both caeca in *P. japonica* by Nakazima (1958). The gastric shield is of moderate size, and does not extend far towards the orifice of the style sac.

The dorsal hood is unusual in being drawn forwards so that its typically anterior face lies ventrally, and its typically posterior face lies dorsally. The dorsal hood covers the anterior part of the stomach and hides the oesophageal orifice from view in a conventional dissection. The ventral wall of the dorsal hood is covered by a very extensive sorting area, which spreads over on to the right stomach wall, a condition closely resembling that in *Trapezium* in the Libitinidae. In addition there is a further sorting area in the form of a very narrow band of transverse folds, which passes out of the dorsal hood on its ventral wall, arches over the oesophageal orifice, curves down the right stomach wall, and passes forward again to end as a horizontal band lying below the oesophageal orifice. This continuous structure in *P. stellae* incorporates those sorting areas which have been termed 'SA^8' in the dorsal hood, and 'SA^7' under the oesophageal orifice by Purchon (1960*a*); it is probably comparable with the beaded strip on the right stomach wall in the Corbiculidae.

The degree of uniformity experienced among members of the family Veneridae does not extend to the remaining families in the Veneracea, although some points of similarity have been noted between representatives of the different families in the Veneracea.

Lucinacea

Review of literature

Ungulinidae (figure 14*c*, p. 245)

Diplodonta punctata Say, 1822
Diplodonta rotundata (Montagu, 1803)
Diplodonta semiaspera Philippi, 1836
(Allen 1958*a*)

The stomach is globular in shape. A deep dorsal groove arises on the right side of the oesophageal aperture and leads particles to the anterior face of the dorsal hood. The anteroposterior sector of the major typhlosole and intestinal groove is short, penetration of the left and right caeca by the major typhlosole is not very deep, and the major typhlosole ends in a tiny spiral which comes out to the entrance of the left caecum. According to the species, there are from one to seven isolated orifices of ducts from the digestive diverticula on the right side of the stomach, the number being larger in the larger species. A well developed sorting area in the dorsal hood extends over the roof of the stomach, and down to its right side as the posterior sorting area. An acceptance tract passes from the dorsal hood over the roof and down the right side, ending in front of the orifice of the mid gut. No information is available as to whether any ducts from the digestive diverticula enter the stomach via the left pouch in *Diplodonta* species, but the large size of this embayment in *D. semiaspera* suggests that such ducts are probably present in this species.

The families Lucinidae and Thyasiridae have simplified stomachs of type IVb.

Corbiculacea

Review of literature

Corbiculidae (figure 14*e*)

Corbicula japonica Prime, 1864	(Purchon 1960*a*)
Geloina ceylanica (Lamarck, 1818, as *zeylanica*)	(Purchon 1960*a*)
Villorita cyprinoides (Gray, 1825)	(Dinamani 1957)

Living specimens of *G. ceylanica* and *V. cyprinoides*, and preserved specimens of *C. japonica*, were found to be closely comparable in the internal structure of their stomachs and it is easy to draft a general description. The oesophagus opens into an anterior prolongation from a globular stomach, and a ciliated groove around the oesophageal orifice leads via a dorsal groove into the dorsal hood. A small sorting area beneath the oesophageal orifice, with its cilia beating downwards towards the transverse sector of the intestinal groove, was observed in *G. ceylanica* but not in *V. cyprinoides*. The conjoined style sac and mid gut leaves the stomach posteroventrally, and the minor typhlosole ends on the stomach floor at the rim of the mid gut. The major typhlosole penetrates the right caecum deeply, as also the left caecum, and ends on the stomach floor just outside the left caecum. The very large, forwardly projecting lobe of the major typhlosole, which spans the space between the left and right caeca, is a characteristic feature. Within each of the caeca the margin of the major typhlosole sends a little lobe into the mouth of each duct from the digestive diverticula. The ducts from the digestive diverticula open into the stomach via the left pouch, left caecum and right caecum, and a few ducts open independently on the right side of the stomach, close to the right caecum in *G. ceylanica* (five), and in *V. cyprinoides* (one or two), but apparently not in *C. japonica.* The left pouch is a large oval cavity the walls of which bear an extensive, but very finely folded, sorting area. A few ducts from the digestive gland open into the left pouch except for *V. cyprinoides,* where this is not known for certain. An oval swelling which lies anteroposteriorly on the floor of the left pouch, and above the left caecum, is characteristic of this family. The dorsal hood is very large, and projects forwards on the left side of the stomach. There is a very extensive sorting area on its roof, and passing over the roof of the stomach and on to its right side. In each case this posterior sorting area stretches back as far as the aperture of the mid gut, but in *G. ceylanica* it leads into a blind pocket in the posterior wall of the stomach, behind the style sac. The gastric shield is of moderate size, being emarginated posteriorly in *G. ceylanica,* and sending a slender pointed prong backwards to the rim of the style sac in *V. cyprinoides.* A rejection tract passes from the dorsal hood along the anterior border of the principal sorting area, discharging into the intestinal groove. An acceptance tract passes down the posterior side of this sorting area towards the posteroventral border of the stomach in *V. cyprinoides.*

The stomach of *Sphaerium corneum* in the family Pisidiidae is secondarily simplified and has been described with other examples of stomach type IVb.

Arcticacea

Review of literature

Cyprinidae (figure 14*f*, p. 245)	
Cyprina islandica (L., 1767)	(Purchon 1960*a*; Saleuddin 1964; Reid 1965)
Arctica (= *Cyprina*) *islandica* (L., 1767)	
Libitinidae (figure 13*e*, p. 242)	
Fluviolanatus subtortus (Dunker, 1857)	(Morton 1982)
Trapezium sublaevigatum (Lamarck, 1819)	(Purchon 1960*a*)

Three illustrated accounts are available for the interior of the stomach of *Cyprina islandica.* The figure provided by Reid (1965) differs from the others in that the dorsal hood has been carried over to the right side of the stomach, and the left pouch has been widely opened. Nevertheless there is general agreement in interpretation in these accounts. The oesophagus enters the globular stomach anteriorly, its orifice being indicated by a circular ciliated groove which diverts incoming particles to the dorsal hood. A folded and ciliated area on the anterior face of the stomach, immediately below the oesophageal orifice, prevents particles from entering the transverse sector of the intestinal groove. The mid gut and style sac are conjoined, the minor typhlosole ends on the stomach wall just outside the mid gut, and the major typhlosole passes directly forwards on the stomach floor. The major typhlosole penetrates both the right and the left caeca very deeply, and ends on the stomach floor just outside the left caecum. The posterior sorting area is separated from the terminal sector of the intestinal groove by a thick longitudinal ridge; this sorting area is large, and it extends into the dorsal hood more deeply than had been indicated by Purchon (1960*a*). The gastric shield is small and flimsy and extends into the dorsal hood and into the left pouch. The left pouch has a small orifice into the stomach, but Reid (1965) has shown that it is capacious, with an extensive sorting area within.

The ducts from the digestive diverticula all open into the stomach via the left pouch, the left caecum and the right caecum. An area of folds and papillae on the posterior wall of the stomach, observed only by Purchon (1960*a*), may have been an abnormality, attributable partly to muscular tension in the stomach wall in the dissected preparation.

The stomachs of *T. sublaevigatum* and *F. subtortus* do not conform to the same general plan as that of *C. islandica*. The differences observed may be attributable partly to the growth form and partly to the habitat and mode of life favoured by each species. *C. islandica* is nearly circular in outline and is a member of the shallow infauna of intertidal muddy sands; *T. sublaevigatum* and *F. subtortus* are elongated in outline and are byssally attached, the former on the under sides of boulders, the latter on vegetation in sheltered lagoons and estuaries. Differences in the parameters of growth of the mantle or shell are likely to influence the proportions of the stomach; elongation of the mantle or shell of *T. sublaevigatum* might be partly responsible for the anterior position of the dorsal hood, overlying the orifice of the oesophagus into the stomach as in *Petricola*. Again, the observed differences in habitat of the three species are likely to influence the grades of particulate material admitted into the stomach, and so to affect the nature of the work to be done in grading the stomach contents. Such considerations are likely to influence the size and disposition of the various features of the interior of the stomach. In these various ways the *appearance* of the stomach may be changed, and this may explain why in *T. sublaevigatum* the two sorting areas on the anterior (ventral) face of the dorsal hood are so highly developed, and arch over the stomach hiding the oesophageal orifice from view. The sorting area on the posterior (dorsal) face of the dorsal hood is also enlarged. The gastric shield is larger, and stretches back to the margin of the style sac. Two further differences are the lack of a folded area between the oesophageal orifice and the transverse sector of the intestinal groove, and the presence of three ducts which open into the stomach independently on the right wall, above the right caecum.

In *F. subtortus* the following special features were recorded by Morton (1982): the style sac and mid gut are conjoined at the base, but become separate almost immediately. The gastric shield is very large, reaching the margin of the style sac as in *T. sublaevigatum*. A minor typhlosole is described as passing forwards along the right wall of the stomach, parallel with the posterior sector of the intestinal groove, and ending above the orifice of the right caecum. The configuration described seems very similar to that of the ridge described above for *C. islandica*, and I am inclined to doubt whether this is a minor typhlosole. Morton does not show what happens to the ciliated tract (his figure 15, EL); if this were to discharge into the intestinal groove posteriorly, then the longitudinal ridge (his figure 15, MT) would not be a minor typhlosole. The sorting area immediately below the oesophageal orifice appears to be wrongly homologized with the sorting area SA^7 (Purchon 1960*a*), since its principal ciliary activity is downwards, towards the transverse sector of the intestinal groove. Morton figures an acceptance tract passing up the right wall of the stomach towards and into the dorsal hood. Curiously he labels this RT, as a rejection tract. It does not seem practicable to compare the stomach of *F. subtortus* in detail with *C. islandica* and *T. sublaevigatum* until further information is available on a number of points regarding *F. subtortus*.

Dreissenacea

Review of literature

Dreissenidae (figure 15*a*, p. 254)	
Dreissena polymorpha (Pallas, 1771)	(Purchon 1960*a*; Morton 1969)
Mytilopsis sallei (Récluz, 1852)	(Morton 1981)

Morton (1981) reported that the internal structure of the stomach of *M. sallei* is very similar to that of *D. polymorpha*, but did not include an illustration. In contrast, there are two illustrated accounts of the structure of the stomach of *D. polymorpha* . In this example the style sac and mid gut are separate, but their orifices into the stomach are connected by a short groove between two fleshy ridges. The major typhlosole and intestinal groove penetrate the left and right caeca very deeply. Purchon (1960*a*) reported that the major typhlosole ended within the left caecum, but Morton (1969) observed that it emerges from the left caecum and ends on the stomach floor outside, as is also true for *M. sallei*. The ducts from the digestive diverticula open into the stomach at three sites, the left pouch (four), the left and right caeca (ten or more in each). No ducts open into the stomach independently. There is an extensive sorting area on the right side of the stomach, which extends upwards into the wide mouth of the dorsal hood, but which does not press far into it. A thick angled ridge separates the sorting area from the oesophageal orifice anteriorly, and another fleshy ridge separates the sorting area from the intestinal groove. There is a small oval sorting area on the floor of the left pouch.

Mactracea

Review of literature

Mactridae (figure 15*c*)	
Lutraria maxima (Jonas, 1844)	(Nakazima 1965)
Mactra mera Reeve, 1853	(Purchon 1960*a*, 1985)
Mactra sulcataria Deshayes, 1853	(Nakazima 1957)
Schizothaerus keenae (Kuroda & Habe, 1952)	(Nakazima 1965*b*)
Standella pellucida (Gmelin, 1791)	(Dinamani 1967)
Mesodesmatidae (figure 15*c*)	
Atactodea glabrata (Gmelin, 1791)	(Purchon 1960*a*)
Caecella chinensis Deshayes, 1854	(Narchi 1980*a*)
Caecella cumingiana Deshayes, 1854	(Purchon 1960*a*)
Mesodesma arctatum (Conrad, 1830)	(Allen 1975)
Mesodesma mactroides Deshayes, 1854	(Narchi 1981)

Yonge (personal communication) judged that the family Mesodesmatidae should be withdrawn from the Mactracea and installed in a new superfamily Mesodesmatacea. A thorough comparison of stomach structure in these two families yields a number of characters which are shared by representatives of both families, and other characters which are unique to the Mesodesmatidae. From the limited standpoint of stomach structure it is thought prudent not to enter the debate on the status of the Mesodesmatidae. However, the present writer has reservations as to the wisdom of elevating the taxonomic status of a family without exercising the greatest caution, as this puts great pressure on the upper limits of the hierarchy. No useful purpose is served by dividing the filter-feeding bivalves into four subclasses, where only one subclass should suffice (Purchon 1978).

Nakazima confined his attention to the course of the major typhlosole through the left and right caeca, so it is necessary to exclude *Lutraria*, *Mactra sulcataria*, and *Schizothaerus* from the following generalizations. With these exceptions, members of both families are characterized by the complete separation of the style sac from the mid gut and by the presence of either a lobe at the orifice of the style sac or of a ridge which passes forwards from this point, across the floor of the stomach towards the left pouch. In all cases there is also a series of lobed papillae on the anterior face of the stomach, around the oesophageal orifice. This series of papillae forms a complete circle in *Mactra mera* and in species of *Mesodesma*, but in *Caecella cumingiana* and in *Atactodea glabrata* very large and elaborate papillae diminish in size dorsal to the oesophageal orifice and intergrade with the swollen ends of folds on a sorting area passing into the dorsal hood. A comparable manifestation was reported in *Pholadidea loscombiana* in the family Pholadidae (Purchon 1955*b*). In *Mactra mera* and in *Mesodesma arctatum* a single large duct from the digestive diverticula opens on the right side of the stomach, dorsal to the orifice of the right caecum. Many ducts from the digestive diverticula open into the right caecum and into the left caecum in all species investigated, while from three to eight ducts enter the stomach via the left pouch.

In contrast to those features that are common to the families Mactridae and Mesodesmatidae, two unusual features have been found in the Mesodesmatidae alone. Thus in *A. glabrata*, *C. cumingiana*, and *Mesodesma mactroides* a scattered series of duct orifices open into the stomach dorsal to the oesophageal orifice. No such series of ducts was found in *C. chinensis*, but in this case the illustration shows that the region in which the duct orifices might have been found was at the margin of the dissection, and thus liable to damage. Again, no such ducts were reported in *Mesodesma arctatum*, though their absence may be indicated due to the presence of a single isolated duct orifice on the right side of the stomach in this species. So far as I am aware, no such system of duct orifices has been recorded in any other bivalve, and I have felt obliged to consider whether it could have been an artifact, for example, by rupture of the thin epithelium surrounding the digestive gland. This *might* have been the case in close proximity to the right caecum of *A. glabrata*, and of *C. cumingiana* (Purchon 1960*a*, figures 11 and 12), where this caecum has been partly opened, but this explanation cannot be applied to the duct orifice above the margin of the sorting area in *A. glabrata* (Purchon, figure 11, DDD^1, SA^8). In the case of *Mesodesma mactroides* the reality of this series of ducts is established beyond all doubt by the very clear illustration (Narchi 1981, figure 13). The other unusual feature of the stomach in members of the Mesodesmatidae is the presence of a very finely folded ciliated area leading into the posterior border of the orifice of the mid gut in *A. glabrata*, *C. cumingiana* and *Mesodesma arctatum.* However, this system of fine folds was not present in *C. chinensis* and *Mesodesma mactroides*.

Since these two characters have not been found consistently in all five species of Mesodesmatidae investigated, I judge that the evidence obtained from studying the structure of the stomach does not add weight to the proposal to transfer the Mesodesmatidae into a new superfamily Mesodesmatacea.

Solenacea

Review of literature

Solenidae (figure 15*b*, p. 254)	
Ensis siliqua (L., 1758)	(Graham 1949)
Pharella acuminata (Hanley, 1842)	(Owen 1959*b*)
Pharella acutidens (Broderip & Sowerby, 1829)	(Purchon 1960*a*)
Solen annandalei Preston, 1915	(Dinamani 1967)
Solen gouldi Conrad, 1867	(Nakazima 1958)

Graham (1949) provides a beautifully clear illustration of the internal structure of the stomach of *E. siliqua*, in which the principal features are the great size of the backwardly directed dorsal hood, and the enormous posterior sorting area which extends over the whole length of the right wall of the stomach and penetrates deeply into the dorsal hood. Owen (1959*b*) has emphasized that in *E. siliqua* the dorsal hood is not the small pit (P) but the large pouch (SAPC) (Graham's figure 15). The style sac is completely separate from the mid gut, and there is no minor intestinal typhlosole. All of the ducts from the digestive diverticula open into the stomach via three embayments, the left pouch, the left caecum and the right caecum. The stomachs of *P. acuminata* and *P. acutidens* were found to be closely comparable, except that in the latter the left and right caeca are much closer together than in *Ensis*, and two ducts from the digestive diverticula open by a common orifice situated a little anterodorsal to the right caecum (Purchon 1960*a*). The stomach of *Solen annandalei* resembles that of *P. acutidens* in that the major typhlosole emerges from the left caecum and ends just outside, on the stomach floor; there is a striated sorting area in the mouth of the left pouch, and there is an isolated duct orifice just outside the right caecum. *S. annandalei* differs from all other examples described in that there is a single orifice for the mid gut and style sac, though these separate almost immediately into independent tubes. The isolated duct orifice in *S. annandalei* leads into a sinuous tube which receives about eight subsidiary ducts; its wall is more like that of the stomach than that of a typical duct from the digestive gland. In *P. acutidens*, as also in *Solen gouldi* (Nakazima 1958), the major typhlosole forms a wide semicircular platform with a very frilly margin in both the right and the left caecum.

Myacea

Review of literature

Myidae (figure 15*d*)	
Mya arenaria L., 1758	(Purchon 1960*a*; Yonge 1923)
Mya japonica Jay, 1856	(Nakazima 1957)
Aloididae (figure 14*b*, p. 245)	
Aloidis (*Corbula*) *gibba* (Olivi, 1792)	(Purchon 1960*a*; Yonge 1946)

The stomach of *M. arenaria* was first investigated by Yonge (1923). The oesophageal orifice is relatively wide, and has a lobed rim. The style sac and mid gut are separate, except for a hemispherical pocket which links their orifices into the stomach, and on the border of which there is a delicate sorting area. The major typhlosole is swollen in the mouth of the mid gut; there is a distinct break in its structure, and a separate major typhlosole passes forwards into the

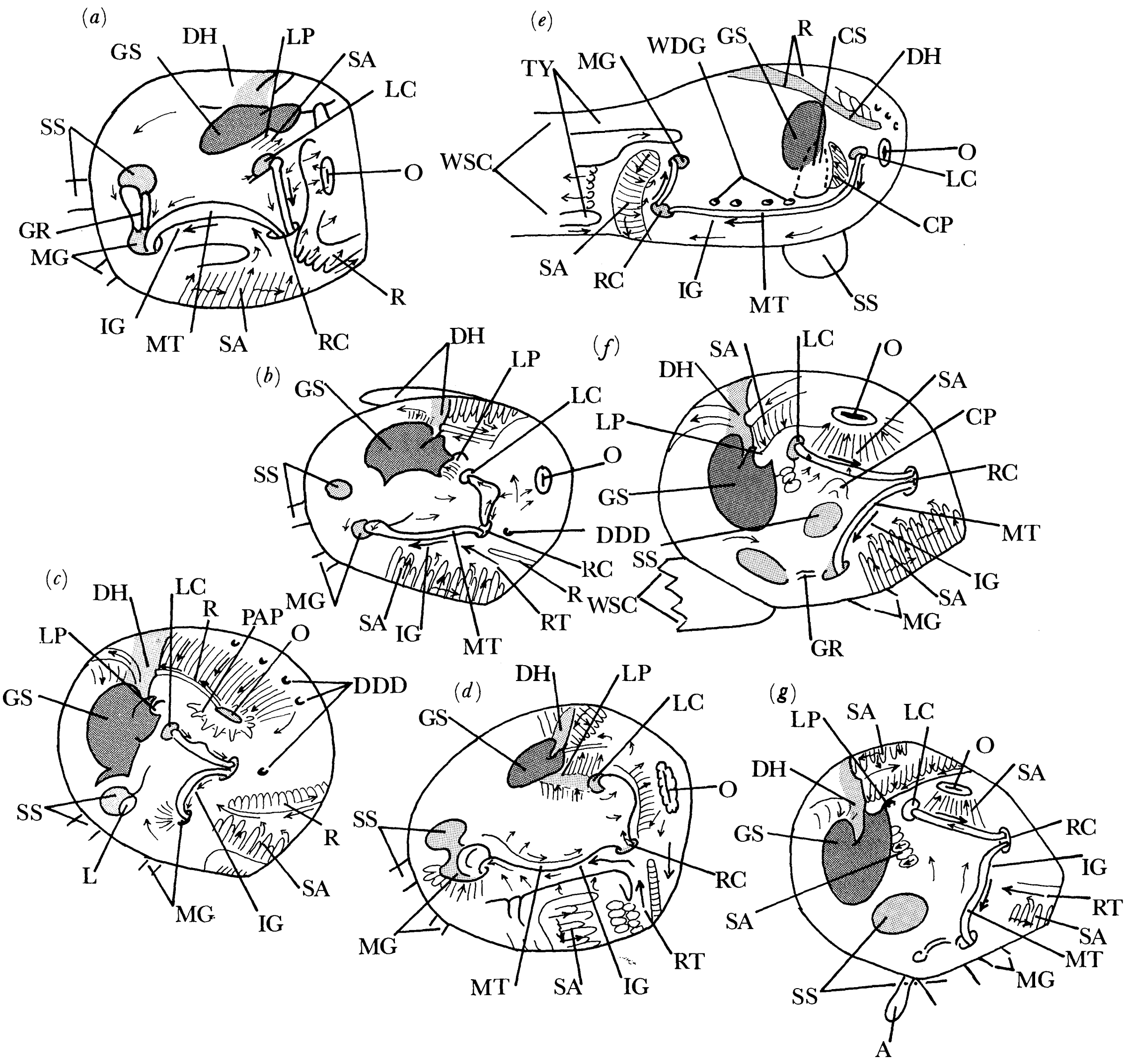


Figure 15. Diagrammatic representation of the interior of the stomach in a group of Gastropempta in which the style sac (SS) and mid gut (MG) are wholly separate. (*a*) Dreissenidae; (*b*) Solenidae; (*c*) Mactridae and Mesodesmatidae; (*d*) Myidae; (*e*) an elongated stomach in the Teredinidae; (*f*) a globular stomach in the Teredinidae; (*g*) Pholadidae. Note the circlet of complex papillae (PAP) around the oesophageal orifice in the Mactridae and Mesodesmatidae. The appendix (A) in the Pholadidae is homologous with the wood-storing caecum (WSC) in the Teredinidae and with the postero-dorsal caecum in the Tellinacea (figures 11*g* and 13*a*). In those Teredinidae with an elongated stomach the elongation has occurred in the transverse plane, widely separating the left and right caeca, this transverse axis then being turned at right angles into an anteroposterior direction. Note the series of four orifices (WDG) leading to the special wood-digesting diverticula; these orifices are situated on the left side of the major typhlosole where they are unprotected by the intestinal groove (IG) and are thereby enabled to receive fragments of wood for digestion.

stomach. The gastric shield is small and does not approach the margin of the style sac. The dorsal hood has a wide mouth, and bears two sorting areas on its roof and anterior face, which extend over the roof of the stomach and on to its right side. The anterior of these sorting areas discharges waste material by a rejection tract which lies close to the orifice of the right caecum, an unusually anterior site. A beaded ridge that lies on the anterior side of the rejection tract is directed towards the dorsal hood but does not enter it. Yonge (1923) observed what are now termed the left pouch, left caecum, and right caecum; 12 or more ducts enter each of the caeca, lobes on the margin of the major typhlosole passing into the mouths of these ducts. Nakazima (1957) reported a similar condition in *M. japonica*. The major typhlosole and intestinal groove emerge from the left caecum and end on the stomach floor just outside. The left pouch receives about 15 ducts from the digestive gland; its walls bear an extensive sorting area which emerges both above and below the pouch.

In the family Aloididae only one example has been studied, *Aloidis gibba*. The stomach of this differs from that of *M. arenaria* in several important features, but resembles that of the venerid, *Gafrarium minimum*. Thus, the style sac and mid gut are conjoined and the minor typhlosole ends on the stomach wall close to the orifice of the mid gut. The gastric shield is relatively large and approaches closely to the margin of the style sac. The left pouch receives three ducts from the digestive gland, and a conspicuous beaded ridge passes out of the left pouch on to the stomach floor, just as in *G. minimum*. The left and right caeca are shallow and semicircular in shape; the major typhlosole and intestinal groove emerge from the mouth of the left pouch and end on the stomach floor nearby. A single duct from the digestive diverticula opens into the stomach on its right side, a little anterior to the right caecum. The dorsal hood is well developed, and bears two sorting areas on its anterior wall, but these are not the same two as in *M. arenaria*. Here, the anterior of the two sorting areas is a narrow strip which passes over the stomach roof close to the oesophageal orifice, and is probably comparable with the beaded ridge lying in front of the rejection tract in *M. arenaria*.

Pholadacea

Review of literature

Pholadidae (figure 15*g*, p. 254)	
Pholadinae, Jouannetiinae and Martesiinae	
Barnea candida (L., 1758)	(Purchon 1955*b*)
Barnea parva (Pennant, 1777)	(Graham 1949; Purchon 1955*b*)
Jouannetia cumingiana (Sowerby, 1849)	(Dinamani 1967)
Martesia striata (L., 1758)	(Purchon 1956*a*; Dinamani 1967)
Pholadidea loscombiana Turton, 1819	(Graham 1949; Purchon 1955*b*)
Pholas dactylus L., 1758	(Purchon 1955*b*)
Zirphaea crispata (L. 1758)	(Purchon 1955*b*)
Xylophaginae	
Xylophaga dorsalis Turton, 1822	(Purchon 1941)
Teredinidae (figure 15*e*)	
Bankia (*Xylotrya*) *gouldi* (Bartsch, 1908)	(Sigerfoos 1908)
Dicyathifer (*Teredo*) *manni* (Wright, 1866)	(Purchon 1960*a*)
Lyrodus pedicellatus (Quatrefages, 1849)	(Morton 1970)
Nausitora hedleyi Schepman, 1919	(Saraswathy & Nair 1971)
†*Psiloteredo amboinensis* Taki & Habe, 1945	(Purchon 1960*a*)
Teredo furcifera von Martens, 1894	(Saraswathy & Nair 1971)
Teredo navalis L., 1758	(Lazier 1924; Morton 1970; Purchon 1960*a*)
Teredora princesae (Sivickis, 1928)	(Saraswathy & Nair 1971)

With the exception of *Xylophaga dorsalis* there is a considerable measure of agreement in stomach structure among the other species of Pholadidae which have been investigated, and for which a common description can be provided. The oesophageal orifice is a transerve slit on the anteroventral face of the stomach, and beneath it there is typically a sorting area of vertical folds which direct particles away from the transverse sector of the intestinal groove. *P. loscombiana* is unusual in possessing a series of lobed papillae instead of this sorting area below the oesophageal orifice. These lobed papillae, which were not recorded by Graham (1949), are not dissimilar from those recorded in the Mactridae and Mesodesmatidae (Purchon 1960*a*). In *Z. crispata*, as also in *M. striata*, in addition to the sorting area below the oesophageal orifice there is a fleshy, lobed fold which crosses the face of the stomach anterior to the transverse sector of the intestinal groove. The style sac and mid gut open separately on the anteroventral floor of the stomach in all except *J. cumingiana*, in which the style sac and mid gut are fused basally and separate distally. An appendix to the stomach has been recorded in all except *Z. crispata*, *M. striata* and *J. cumingiana*. This appendix is judged to be homologous with the posterodorsal caecum of the Tellinacea, and with the wood-storing caecum of *X. dorsalis* and the Teredinidae. A grooved and ciliated area links the mouth of the appendix with that of the mid gut in some examples, for example, *B. candida*, and this is presumably instrumental in filling

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† This was only a provisional identification, owing to the lack of pallets. However, Turner (1966) reports that this species should be referred to *Spathoteredo obtusa* Sivickis. Since *Spathoteredo* has an elongated stomach the identification was faulty and the species I reported upon (Purchon 1960*a*) should only be referred to as 'a species of shipworm from Singapore'.

or emptying the appendix in which the products of boring are temporarily stored. The dorsal hood is well developed, typically with two sorting areas on its anterior face. The larger of these passes over the roof of the stomach on to its right side, where it discharges waste via a rejection tract into the intestinal groove. This, the 'posterior sorting area' is largest in *M. striata* and it is also large in *J. cumingiana*. The second sorting area of the dorsal hood has been recorded in fewer examples; in *P. loscombiana* it leads over the oesophageal orifice to the series of lobed papillae in much the same way as in the Mesodesmatidae. On the left anterior stomach floor there is a swelling which leads across the mouth of the left pouch, towards the orifice of the left caecum. In most cases this swelling is in the form of a series of large beads, but in *Z. crispata* it is a slender smooth flap which passes into the left caecum, and may be the origin of the major typhlosole.

The ducts from the digestive diverticula open into the stomach at no more than three sites, there being no independent duct orifices on the right side of the stomach. From two to four ducts enter the left pouch in *M. striata*, and as many as six in *Z. crispata*, but Dinamani (1967) found that no ducts enter the left pouch of *J. cumingiana*. There is an extensive sorting area on the floor and walls of the left pouch of *Z. crispata*.

There are major differences in the structure and organization of *Xylophaga* which justify the isolation of this genus in a separate family (Purchon 1941) or subfamily (Turner 1955). The alimentary canal of *X. dorsalis* has been investigated by general dissection and by serial sections, but the interior of the stomach has not been explored by dissection (Purchon 1941). The stomach of *Xylophaga* is a relatively large ovoid organ, a considerable part of its internal surface being protected by the gastric shield. The style sac and mid gut are separate, as in the majority of the Pholadidae. However, the style sac leaves the right posterior side of the stomach, whereas the mid gut leaves the stomach anteroventrally. The digestive diverticula open into the stomach anteroventrally by two broad openings which lie anterior to that of the mid gut. The stomach is dominated by the wood-storing caecum, a relatively huge U-shaped cylinder which arises from the right side of the stomach at the same level, but anterior to the orifice of the style sac. The opening from the stomach into the wood-storing caecum is on the posterior limb of the latter, on its concave surface a short distance from its posterior extremity. The interior of this caecum bears two conspicuous ridges enclosing a ciliated channel which presumably serves for movement of wood fragments into or out of the caecum.

Early studies on *Bankia gouldi* (Sigerfoos 1908) and on *Teredo navalis* (Lazier 1924) established the general organization of the alimentary canal in these examples of shipworms. Turner (1966), in her important survey and illustrated catalogue of the Teredinidae, reported her findings from dissections of preserved specimens of many species of shipworm, showing that the 13 known genera of shipworms can be arranged in three groups according to stomach types. In the first group the stomach is extremely simple in form, lacking all accessory pouches or caeca except the style sac, and lies at the posterior end of the visceral mass. This stomach type occurs only in the genus *Kuphus*, which is not reported upon here. The second type of stomach is globular and lies anterior to the posterior adductor muscle, and occurs in seven genera, including *Dicyathifer*, *Psiloteredo* and *Teredora*, briefly mentioned here. In the third type the stomach is elongated and extends far behind the posterior adductor muscle. This type is recorded in five genera, including *Teredo*, *Lyrodus* and *Nausitora* which are discussed in this paper.

It is easiest to start with those shipworms in which the stomach is globular and in which the general organization of the stomach conforms most closely with those previously described in this paper. Purchon (1960*a*)† studied two such examples, '*Psiloteredo amboinensis*' and '*Teredo manni*', with two figures of the stomach of the former. *Teredo manni* proves to be a synonym of *Dicyathifer manni* (Wright), as listed above. In *P. amboinensis*, as also in *D. manni*, a substantial prominence arises from the stomach floor in front of the crystalline style. Its anterior face is convex, and bears a lozenge-shaped raised sorting area which emerges from the mouth of the left pouch. This prominence appears to protect the base of the crystalline style from impact with material entering from the oesophagus. Morton (1970) figured a comparable structure in the elongated stomach of *Teredo navalis*, and it is possible that it is a characteristic of the stomach in the Teredinidae. The fragments of wood that are admitted into the stomach might otherwise erode the base of the exposed part of the style and so interfere with its functions. These wood fragments will either be admitted directly into the ducts leading to the special wood-digesting diverticula, or will pass first into the huge wood-storing caecum which is a special feature of the Teredinidae and of *Xylophaga* spp. The mid gut opens into the stomach separately from the style sac, and bears a large spherical expansion not far from its opening into the stomach. Within the expansion the major typhlosole is coiled or greatly dilated, and the structure probably functions as a valve controlling admission of waste matter into the mid gut. A comparable structure is present in *D. manni*, as also in *T. navalis* (Lazier 1924; Morton 1970). On the left anterior side of the stomach, below the mouth of the dorsal hood, the major typhlosole and intestinal groove enter and circumnavigate in turn three chambers, all of which receive several ducts from the digestive diverticula. The posteriormost chamber is invested by a saddle-shaped flare of the gastric shield, so it appears that this complex of three chambers has the attributes of both the left caecum and the left pouch! In contrast, in *D. manni* the major typhlosole and intestinal groove did not enter the left pouch, but penetrated deeply into a long slender left caecum and returned to terminate just outside its mouth, on the stomach floor. The dorsal hood is large, with thick fleshy folds on its anterior and posterior faces, and with a small sorting area on its anterior face. There is a well-developed sorting area on the right posterior stomach wall, from which waste matter passes into the intestinal groove. A sorting area of delicate folds directed towards the oesophageal orifice, in which the cilia beat away from the transverse sector of the intestinal groove, is directly comparable with similar sorting areas in various members of the Pholadidae.

Morton (1970) studied the elongated stomachs of *T. navalis* and of *Lyrodus pedicellatus*, and provided a detailed drawing of the interior of the stomach of the former. In some respects the stomach of *T. navalis* is comparable with that of *P. amboinensis*, for example, in the presence of a shield-shaped prominence on the anterior floor of the stomach, bearing a sorting area emerging from the left pouch, and protecting the base of the exposed part of the crystalline style. In *T. navalis*, as in *P. amboinensis*, relations between the major typhlosole and intestinal groove on the one hand and the left caecum and left pouch on the other, are atypical. The major typhlosole apparently enters the left pouch and sends flares into the five ducts from the digestive diverticula, a condition which has not been reported in any other bivalve. In addition, after circumnavigating the left caecum, the major typhlosole passes into the style sac and ends in a small diverticulum from the base of the style sac. This has not been recorded in any other bivalve. Another unique feature reported for *T. navalis* (Lazier 1924; Morton 1970) is the presence of a series of duct orifices (figure 15, G, WDG) on the left side of the major typhlosole,

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† See footnote on p. 256.

that is, on the left side of the major typhlosole where they are not protected by the scavenging action of the intestinal groove. Four of these ducts lie on the floor of the stomach, regularly spaced between the orifices of the left and right caeca. In both *T. navalis* and *L. pedicellatus* similar orifices also lie on the upper surface of the typhlosolar tongues which invade the left and right caeca. All these ducts lead to the special wood-digesting diverticula, and the special significance of their positions is that they are freed from the tyranny of the intestinal groove, and are able to receive fragments of wood which would otherwise be denied to them. It is this innovation, coupled with the development of a cellulase and hemicellulase, which permitted full exploitation of the wood-boring mode of life. As far as I am aware this has not yet been reported for other species of shipworm.

Lazier (1924) established that the stomach of *T. navalis* is elongated in the anteroposterior axis of the animal, and that it extends to almost half of the length of the visceral mass. It is extraordinary to find that the elongation of the stomach has been achieved by great extension of the anterior floor of the stomach in the *transverse* axis (morphologically) along the transverse sector of the major typhlosole and intestinal groove, between the orifices of the left and right caeca. This morphologically transverse extension has been accompanied by a backward movement along the right side of the stomach so that the orifice of the right caecum, and that of the mid gut, have been carried to the posterior end of the stomach, where they remain close together. The 'posterior sorting area' (Graham 1949) has been carried back along the right side of the stomach, as it extended, to the posterior end of the stomach where it remains close to the orifices of the right caecum and mid gut, and lies adjacent to the orifice of the wood-storing caecum. Morton (1970) reports that the 'normal' digestive diverticula. that is, those which are concerned with the intracellular digestion of minute particles derived from suspension in the sea water, communicate with the stomach by 'normal' ducts whose orifices lie in the left pouch, the left caecum and the right caecum. In contrast, the special wood-digesting diverticula are served by ducts whose orifices are unprotected by the intestinal groove, and lie on the surface of the typhlosolar tongues which invade the left and right caeca, and also lie on the floor of the stomach on the *left* side of the major typhlosole.

Saraswathy and Nair (1971) show that the stomachs of *Nausitora hedleyi* and *Teredo furcifera* are elongated, while that of *Teredora princesae* is globular. Their more detailed investigations of stomach structure are based on serial sections and are not always easy to evaluate.

Analysis

Valuable new evidence has been found concerning the destination of the major typhlosole and intestinal groove inside the stomach. Four different conditions have been recorded among filter-feeding bivalves.

(i) In association with the left pouch.
  (*a*) External to the pouch, in all Gastrotriteia, in the Pectinidae, and in *Sphaerium* (Pisidiidae, secondarily simplified as compared with the Corbiculidae).
  (*b*) Within the pouch, in the Limidae and Anomiidae. It is notable that the Gastrotriteia, together with the Pectinidae, Limidae and Anomiidae, constitute the Pteriomorpha.
(ii) On the left posterior stomach floor.
  (*a*) Near a posterior embayment receiving ducts from the digestive gland, in the Cleidothaeridae, Myochamidae, Pandoridae, and in *Cochlodesma* (Laternulidae).

(*b*) In the absence of the above embayment, close to the rim of the style sac, in the Lyonsiidae and Clavagellidae.

(iii) External to the left caecum.

In the Trigoniidae, Astartidae, Carditidae, Hiatellidae, Pholadomyidae, and in *Scintilla* (Erycinidae). *Scintilla* differs in this respect from members of the related Kelliidae.

(iv) Enters the left caecum and

(*a*) ends within the left caecum;

(*b*) forms a spiral coil within the left caecum;

(*c*) emerges and ends just outside the left caecum.

TABLE 3. THE ORIGIN OF THE MAJOR TYPHLOSOLE AND INTESTINAL GROOVE WITHIN THE STOMACH

(Brackets and dotted lines indicate family affinities.)

condition (iv) (*a*)	condition (iv) (*b*)	condition (iv) (*c*)	
Hyridellidae	Cardiidae	Cyprinidae	Isocardiidae
Mutelidae	Tridacnidae	Libitinidae	Corbiculidae
Unionidae	Mesodesmatidae.........	Mactridae	Gastrochaenidae
Lucinidae..............	Ungulinidae	Dreissenidae	Pholadidae
Donacidae	Tellinidae	Kelliidae	Teredinidae
Solecurtidae........	Semelidae	Solenidae	
Chamidae	Psammobiidae		
Myidae..............................	....	Aloididae	
	Veneridae..............	Petricolidae	
		Glaucomyidae	

No phyletic or classificatory significance attaches to the subdivisions of condition 4, because there are several instances where closely related families are assigned to different subdivisions.

In 'advanced' filter-feeding bivalves with stomachs of types IV and V the ducts from the digestive diverticula typically open into the stomach via three embayments, the left pouch, the left caecum and the right caecum. Ducts were recorded as entering the left pouch in a total of 44 families, the number of such ducts actually having been counted in 33 of these families. No relevant information was available for nine families. In a few examples it was observed that no ducts from the digestive diverticula entered the left pouch, and these came from eight families, all in the Gastrotetartica, namely the Astartidae, Crassatellidae, Pandoridae, Laternulidae, Lyonsiidae, Clavagellidae, Pholadomyidae and Parilimyidae. No such examples were found in the Gastropempta. There is no left pouch in three families of Protobranchia and three of Septibranchia. Some isolated ducts may open on the right side of the stomach independently from the right caecum, for example, a single duct orifice near the right caecum of *Anodonta cygnea* and of *Solen annandalei* but not in other closely related forms. This is of no significance for purposes of classification, but the occurrence of such isolated duct orifices is common in stomachs of type V and is infrequent in stomachs of type IV, for example, in the Unionidae, Carditidae, Hiatellidae, Gastrochaenidae, Laternulidae and Clavagellidae. Ducts leading to special wood-digesting diverticula in the Teredinidae lack the customary protection from the major typhlosole and intestinal groove. Some open within the left and right caeca, on the upper surface of the typhlosolar expanse, while others open independently on the stomach floor on the left side of the major typhlosole, as in *Teredo navalis* (Lazier 1928; Morton 1970) and *Psiloteredo amboinensis* (Purchon 1960).

Reid (1965) described three categories of sorting mechanism in the stomachs of bivalves, types A, B and C. Twelve different sorting areas of type A have been designated according to their location in the stomach, and their distribution throughout the families of bivalves has been tabulated. The numerical system is that used originally (Purchon 1957, 1958, 1960). These sorting areas may be arranged in two groups. Firstly those which are associated with the dorsal hood, numbers 3, 4, 5 and 8, of which number 3 may extend over the roof of the stomach and expand on its right side, while number 8 may pass over the oesophageal orifice and possibly join with number 7 lying below the oesophagus. Secondly those lying on the anterior floor of the stomach, and within the left pouch, numbers 1, 2, 6 and 7. The remainder, numbers 9, 10, 11 and 12, were only rarely encountered.

The two groups of bivalves differ markedly with respect to their predominant sorting areas (table 4). Although there are differences from family to family, almost all families in the Gastropempta exhibit sorting areas numbers 3 and 6 while number 1 is rare. In the Gastrotetartica sorting areas numbers 1, 3 and 8 are present in about equal numbers, but number 6 is relatively scarce. The subdivisions of the Gastrotetartica also differ markedly from the Gastropempta. Thus the Pectinidae, Limidae and Anomiidae lack sorting areas 3 and 7 and possess sorting area 1. The Anomalodesmata lack sorting area 6 and possess sorting area 1. The Schizodonta lack sorting areas 5 and 6 and most possess sorting area 1. There are too few examples in the Hiatellidae and Gastrochaenidae to justify comment, but the remaining five families differ in lacking sorting area 3 which is almost universal in the Gastropempta. This evidence does not prove the occurrence of two distinct phylogenies for the distribution of sorting areas within the stomach may be partly dependent on habitat and mode of life, but no conflicting evidence has been exposed.

Table 4. The distribution of sorting areas in the stomach in 24 families of Gastropempta and 20 families of Gastrotetartica

(There are fewer sorting areas in the latter group.)

	sorting areas												
group	1	2	3	4	5	6	7	8	9	10	11	12	total
Gastropempta													
number of families, 24	4	—	23	—	10	21	11	15	—	3	1	3	91
percentages	4	—	25	—	11	23	12	16	—	3	1	3	98
Gastrotetartica													
number of families, 20	12	—	12	3	4	6	9	13	1	—	—	—	60
percentages	20	—	20	5	7	10	15	22	2	—	—	—	101

The orifice of the oesophagus into the stomach is typically small, flattened dorsoventrally, and with tumid lips. In several taxa it is appreciably larger, circular, and widely open as in the Lucinidae, Thyasiridae, Ungulinidae, Clavagellidae, Septibranchia, and in *Limopsis*, *Enigmonia*, *Neotrigonia*, *Pholadomya* and *Parilimya*. This undoubtedly relates to the grade and quantity of sediment or other food admitted into the stomach. There is usually a ciliated pathway from the margin of the oesophageal orifice to the anterior face of the dorsal hood and this has been described either as a ridge or as a groove; in some taxa it has been figured as leaving the left corner of the oesophageal orifice, but in others as leaving the right corner. Such variation may be due to dissection technique, the degree of stretching of the anterior roof of the stomach, and the angle of incident light on the dissection. No taxonomic significance is ascribed to the variations recorded. A series of lobed papillae below or around the oesophageal

TABLE 5. THE DISTRIBUTION OF SORTING AREAS IN THE STOMACH IN 20 FAMILIES OF GASTROTETARTICA

(The principal subordinate groups individually differ from the Gastropempta.)

group	number of families	sorting areas 1	2	3	4	5	6	7	8	9	10	11	12	total
Pectinidae Limidae Anomiidae	3	3	—	—	3	1	2	—	1	—	—	—	—	10
Anomalodesmata	6	6	—	6	—	2	—	2	4	1	—	—	—	21
Schizodonta	4	3	—	4	—	—	—	1	4	—	—	—	—	12
Hiatellidae	1	—	—	1	—	—	1	1	1	—	—	—	—	4
Gastrochaenidae	1	—	—	1	—	—	—	—	1	—	—	—	—	2
remainder	5	—	—	—	—	1	3	5	2	—	—	—	—	11
all	20	12	—	12	3	4	6	9	13	1	—	—	—	60

orifice, in some cases grading above into a sorting area (SA^8) which passes into the dorsal hood, has been noted in the closely related Mactridae and Mesodesmatidae. It also occurs in the unrelated pholad, *Pholadidea loscombiana*.

Variations in the size and disposition of the gastric shield are without taxonomic significance. The gastric shield is associated with, or extended by, a cuticular sheath in nuculoid protobranchs, as also in *Limopsis*, the Verticordiidae, and the Cuspidariidae. The gastric shield is large in the Cardiidae, Tridacnidae, Isocardiidae, Ungulinidae, Hiatellidae, and in *Enigmonia*, *Montacuta* and *Pholadomya*. The enlarged gastric shield reaches the border of the style sac in the Limopsidae, Mactridae, Mesodesmatidae, Libitinidae, Aloididae and some of the Donacidae. In most of these the enlarged gastric shield may serve to protect the stomach wall from larger amounts or more coarse-grained sediment. This reason cannot be applicable to

TABLE 6. SEPARATION OF THE STYLE SAC FROM THE MID GUT IN VARIOUS LINEAGES OF BIVALVES

stomach type	style sac and mid gut separate distally but fused at the base	style sac and mid gut wholly separate	
		typical of family	exceptional cases
III			Mytilidae *Arcuatula elegans* *Musculista senhausia* *Mytela charruana*
IV	Kelliidae *Pseudopythina subsinuata*	Anomiidae Leptonacea	
		Mactridae	
	Solenidae *Solen annandalei*	Solenidae	
	Psammobiidae *Orbicularia orbiculata*	Donacidae	
		Dreissenidae	
V		Myidae	
	Pholadidae *Jouannetia cumingii*	Pholadidae	
	Tridacnidae Libitinidae *Fluviolanatus subtorta* Veneridae *Chione tiara*	Teredinidae	

Enigmonia which lives in a sheltered situation on the seaward fringe of mangrove associations where, even if there is occasional rough weather, the sediment is typically a very fine soft mud.

Among filter-feeding bivalves the crystalline style lies in a style sac, the lumen of which primitively communicates throughout its length with that of the mid gut, the communicating slit being guarded by the major and minor typhlosoles. This may permit the style to be contaminated by material from the mid gut, though this may serve a useful purpose in the retrieval of matter for exposure to a second cycle of digestion in the stomach and digestive diverticula. In more advanced conditions the distal end of the style sac, or even the entire style sac, is wholly separate from the mid gut (table 6). Contrasted conditions have been found in closely related taxa, the advanced condition must have evolved independently in various lineages, and such variation is of no taxonomic value.

Discussion

The stomach has only been investigated in a few members of the nuculoid Protobranchia, but it clearly differs in several important respects from those of the filter-feeding 'lamellibranch' bivalves. The differences include the absence of a firm crystalline style, and of any food-sorting caeca other than the dorsal hood, and the occurrence of only three ducts to the digestive diverticula. These ducts differ substantially in both structure and function (Owen 1956), as well as in number, from those of the filter-feeding bivalves. The acquisition of a filter-feeding habit by modifications of the ctenidia and the labial palps was accompanied by changes no less profound in the structure and organization of the stomach and digestive diverticula. The origin of the filter-feeding habit was a major evolutionary event which fully justifies the establishment of two subclasses for the nuculoid Protobranchia and for the filter-feeding 'lamellibranch' bivalves, respectively (Cox 1959; Owen 1959*a*; Purchon 1959, 1963; Yonge 1959*b*). (It is not possible to comment on the status of the Solemyacea, in which the stomach is much reduced, and in one of which there is no alimentary canal.) It is my firm conclusion that there is no justification for subdivision of the filter-feeding bivalves at the level of subclass, as has been done in the *Treatise on invertebrate palaeontology* (Moore 1969–1971). Analysis of the characteristic features of the principal taxonomic groups of the filter-feeding bivalves fails to reveal any single character, or any groupings of characters sufficiently important to apply at the level of subclass (Purchon 1978). Moreover Newell said 'of the six subclasses, the Palaeotaxodonta and Pteriomorpha are considered by many to be natural, the other four are probably artificial' (Newell 1969, p. 213).

With respect to the Bivalvia it is unfortunate that uniformity of policy and nomenclature is not yet achieved as between geologists and malacologists or as between usage in America and in Europe, even in the most basic features of classification. Thus Pojeta & Runnegar (1985) name the class 'Pelecypoda' and not 'Bivalvia' Linnaeus, and apply Palaeotaxodonta, Isofilibranchia, Anomalodesmata, Heteroconchia and Pteriomorpha as subclasses. Morton (1985) similarly treats the Anomalodesmata as a subclass. However, Allen (1985) divides the class Bivalvia into two subclasses, Protobranchia and Lamellibranchia, as is adopted here.

The search for a primary taxobasis on which to subdivide the group of nine families composing the Pteriomorpha (Moore 1969–1971) has been prolonged. The Pinnidae, Ostreidae and Limidae were separated as synaptorhabdic and not eleutherorhabdic (Ridewood 1903), or eulamellibranch and not filibranch (Pelseneer 1906). Subsequently Pelseneer (1911) recognized the Pseudolamellibranchia as intermediate between the Filibranchia and Eulamellibranchia and placed six families in this new group, the Vulsellidae (= Malleidae), Pteriidae, Pinnidae, Ostreidae, Pectinidae and Limidae. Thiele (1935) separated the Arcidae, Limopsidae and Glycymeridae, linking these three families with the Nuculacea on account of their taxodont hinge teeth. Atkins (1937), after an exhaustive survey of ctenidial ciliation, distinguished the Macrociliobranchia and Microciliobranchia according to the presence or absence of eulaterofrontal cilia on the ctenidial filaments. She placed the Mytilidae correctly in the former group, and the Ostreidae incorrectly in the latter group on the basis of the other criteria (Purchon 1960*b*; Owen 1978). For our present purpose the Microciliobranchia should lack both the Mytilidae and the Ostreidae. Among the Pteriomorpha the Mytilidae are unique in having a single pallial fusion, and in the Ostreidae the posterior ends of the ctenidia are attached to the mantle. The Pectinidae, Limidae and Anomiidae, with a stomach of type IV, were isolated from the remainder of the Pteriomorpha which have a stomach of type III (Purchon 1957*b*). Taylor *et al.* (1969, 1973) made an exhaustive study of 12 shell characters throughout the Bivalvia. The nine families of Pteriomorpha showed considerable variety and it is concluded that these shell characters, taken collectively, are not suitable for taxonomic purposes here.

As summarized in table 7, these findings are incompatible and it is necessary to select the most suitable taxobasis by a process of elimination. Ctenidial structure is unsuitable because there is a progression in five stages from filibranch to eulamellibranch, some taxa have representatives in more than one of these stages, and it is possible that two or more lineages may be evolving in parallel through these 'functional strata'. Moreover, there is no good reason why any one level should be selected as the break between a lower (more primitive) and a higher (more advanced) condition. Hinge structure is unsuitable as a taxobasis in this situation because the taxodont condition is a secondary development in the Arcacea and Limopsacea (Thomas 1978). Atkins' action in placing the Ostreacea in the Microciliobranchia, setting aside her own evidence on ciliation of their ctenidia, throws serious doubt on the value of ctenidial ciliation for taxonomic purposes. The possibility of separating both the Mytilidae (filibranch and heteromyarian) and the Ostreidae (eulamellibranch and monomyarian) has little to recommend it, owing to their possession of eulaterofrontal cilia. There remains only the possibility of recognizing the Gastrotriteia as a true, monophyletic assemblage. In view of data given below, on duct orifices and on the end of the major typhlosole, the Pteriomorpha stays unchanged.

Table 1 illustrates the evolutionary diversity that has been achieved within the Gastrotriteia, in so far as this concerns the structure of the stomach. The occurrence of a type B sorting mechanism (Reid 1965) necessarily implies that the Pteriidae and Mytilidae have a common ancestry, for the ciliated groove that links the apex of the typhlosolar tongue with the interior of the dorsal hood is most unlikely to have evolved independently in two or more lineages. It remains to be discovered whether a type B sorting mechanism occurs in any other family in the Gastrotriteia. The other variables noted could have developed independently in different lineages, and are best interpreted as the outcome of random diversification.

It was recognized at an early stage that stomach type IV could not be used safely as an indicator of phylogeny until after much more extensive observation and analysis of results, owing to the known occurrence of reversion from stomach type V to type IV in some species of *Donax* and *Chama*, and in the families Lucinidae and Thyasiridae, and possibly elsewhere. The results of such further studies are now available in tables 2, 3, 4, and 5. The distribution

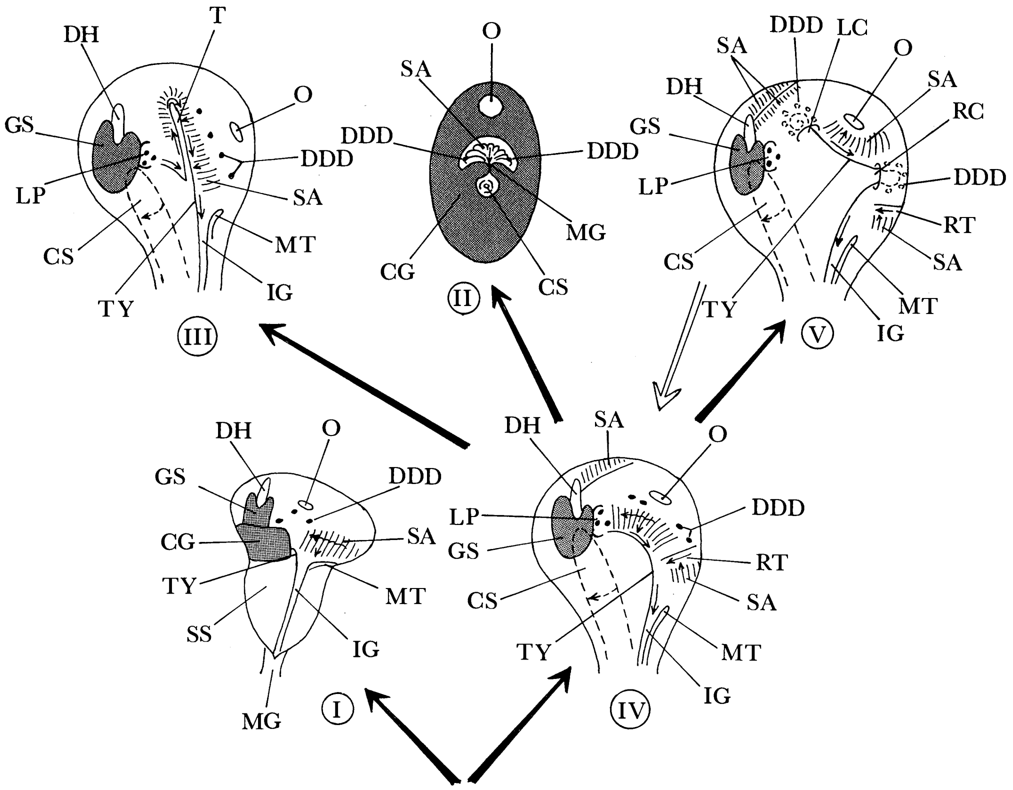

FIGURE 16. Basic structural features of stomach types I, II, III, IV and V in the class Bivalvia. Redrawn from Purchon (1959). I, Nuculoid Protobranchia; II, Septibranchia including the Verticordiidae; III, six superfamilies in the Pteriomorpha; V, Veneroida and Myoida; IV, The remainder of the Lamellibranchia. Solid arrows represent probable phyletic affinities among these types, while the hollow arrow signifies reversion to a stomach of type IV in the Lucinidae, Thyasiridae, and in certain species of *Tellina*, *Donax* and *Chama*.

Abbreviations in this figure only: T, tongue of major typhlosole; TY, major typhlosole; MT, minor typhlosole.

TABLE 7. ATYPICAL CHARACTER-STATES

(The atypical character-state is recorded in each vertical column. Ridewood recognized eight families of Eleutherorhabda and three of Synaptorhabda. Pelseneer first distinguished eight families of Filibranchia and three of Eulamellibranchia, but subsequently only five families of Filibranchia and six of Pseudolamellibranchia. Thiele emphasized the taxodont hinge structure of three families. Atkins (as amended by Purchon (1960)) placed the majority of these families in the Microciliobranchia, and only two in the Macrociliobranchia. Purchon recorded that the majority of these families had a stomach of type III, while three families had a stomach of type IV.)

family	Ridewood, (1903)	Pelseneer, (1906,	1911)	Thiele, (1935)	Atkins, (1937)	Purchon, (1956)
Arcidae				*	(amended)	
Limopsidae				*		
Glycymeridae				*		
Mytilidae					*	
Pinnidae	*	*	*			
Pteriidae			*			
Malleidae			*			
Ostreidae	*	*	*		*	
Pectinidae			*			*
Limidae	*	*	*			*
Anomiidae						*

of the various sorting areas in the stomach has a different pattern in stomachs of types IV and V. In stomachs of type V sorting areas 3 and 6 are almost universal, numbers 8, 7 and 5 are of decreasing frequency, while sorting area 1 is rare. In stomachs of type IV sorting areas 1, 3 and 8 are frequent, in about equal numbers, while sorting area 6 is uncommon. This evidence is consistent with the theory that these two stomach types characterize two distinct phylogenies (table 4). Examination of the distribution of sorting areas in the principal taxonomic groups having stomachs of type IV suggests that each of these subdivisions is similarly distinct from the Gastropempta, except perhaps for the Hiatellidae and Gastrochaenidae on which too little information is available (table 5). However, in eight superfamilies with stomachs of type IV there is no extensive sorting area on the anterior floor of the stomach (table 2) and it is expedient to reserve judgement as to whether the Gastrochaenacea has reverted from a stomach of type V.

Investigation of the mode of termination within the stomach of the major typhlosole and intestinal groove has been especially rewarding (table 3). Conditions 1a and 1b are deemed to be most primitive, and occur in all the Gastrotriteia, together with the Pectinidae, Limidae and Anomiidae. Conditions 2a and 2b are also seen as rather primitive, and occur in the Pandoracea and Clavagellacea. Condition 3 appears to be transitional, with the major typhlosole ending just outside the left caecum, and is found in six of the eight superfamilies with stomach type IV but which lack an extensive anteroventral sorting area. Finally the most advanced state is found in condition 4, in which the major typhlosole and intestinal groove penetrate the left caecum. This condition is found in two of the eight superfamilies just mentioned, the Unionacea and Gastrochaenacea, plus all taxa with a stomach of type V. This suggests either that these two superfamilies are in a transitional state, or alternatively that they may have reverted from stomach type V to type IV. The same may apply to the Leptonacea for although the major typhlosole ends just outside the left caecum in *Scintilla* (Galeommatidae) it enters the left caecum in *Pseudopythina* (Kelliidae). *Sphaerium* (Pisidiidae) is the only remaining exception, its major typhlosole ending outside the left pouch while in the related Corbiculidae it passes into the left caecum.

The locations of the orifices of ducts from the digestive diverticula closely support the data on the termination of the major typhlosole and intestinal groove. The most primitive condition is the presence of many ducts whose orifices are arranged in a curvilinear series on the anteroventral stomach floor (Arcidae and Limopsidae), or in a less regular series (Pteriidae, Vulsellidae and Mytilidae). In a more advanced condition fewer duct orifices are arranged in clusters (Pinnidae, Ostreidae, Limidae, Pectinidae and Anomiidae). These two conditions occur in the Filibranchia and Pseudolamellibranchia. Among the Eulamellibranchia the duct orifices are further concentrated and open into the stomach via three major embayments of the stomach wall, the left pouch, left caecum and right caecum, though some may open independently on the right side of the stomach. It is therefore suggested that the original definitions of stomach types should be extended as follows.

(i) Stomach type III. The major typhlosole ends external to the left pouch; there is no left caecum.

(ii) Stomach type IV. The major typhlosole ends either within the left pouch or just external to the left pouch, or external to the left caecum (if this is present); exceptionally it ends within the left caecum in the Unionacea, Leptonacea and Gastrochaenacea. There is a well developed sorting area on the anterior floor of the stomach, except in a group of eight superfamilies some of which may have reverted from stomach type V.

(iii) Stomach type V. The major typhlosole not only sends a semicircular or elongated flare into the right caecum, but also penetrates the left caecum either forming a simple loop within it and possibly emerging to end on the stomach floor just outside the left caecum, or alternatively forming a spiral within the left caecum and ending at the centre of the spiral.

Variation in the relations between the style sac and the mid gut are without taxonomic value since contrasted conditions have been found in closely related groups. Thus the style sac and mid gut are united in the Aloididae but separate in the Myidae; united in the majority of the Tellinacea, but separate in the Donacidae and in *Orbicularia* (Psammobiidae) (table 6).

No evidence has been found in the structure and organization of the stomach which would firmly support any phyletic groupings above the level of superfamily within the Gastropempta.

Some features of the stomachs of bivalves provide indications of affinity of greater or lesser utility. The posterodorsal caecum of the Tellinacea is homologous with the appendix found in many of the Pholadidae and with the wood-storing caecum of *Xylophaga* and of the Teredinidae. In living specimens of *Abra tenuis* it was seen to be contractile, pumping material out into the main cavity of the stomach and drawing further matter back from the stomach (Hughes 1977), and this is doubtless its typical function. A stomach appendix has also been found in the Mytilidae, for example, *Mytilus edulis*, *Modiolus metcalfei* and *Adula falcata*, in the Ostreidae, for example, *Ostrea edulis* and *O. forskali*, and in the Limidae. These are probably all examples of an archaic structure which may once have been widespread among bivalves. As such, it would have no value as an indicator of close phyletic affinity among these superfamilies and families (Reid 1965).

A curved flange on the floor of the stomach, lying posterior to and parallel with the major typhlosole, has been found in the Leptonacea, for example, *Galeomma paucistriata*, *Pseudopythina subsinuata* and *Scintilla hanleyi*, and also in some of the Tellinacea, for example, *Egeria radiata* and *Iphigenia brasiliensis* (Donacidae) and *Asaphis deflorata* and *Gari togata* (Psammobiidae). In view of the general lack of evidence of phyletic affinity between superfamilies, this fragment of information should not be dismissed too hastily as merely a matter of coincidence.

Attention is drawn to the group of similarities between the stomachs of *Glauconome rugosa* (Veneracea) and *Geloina ceylanica* (Corbiculacea) (figure 14*d*, *e*). *G. rugosa* had been transferred from the Solenacea to the Veneracea by Owen (1959*b*). These similarities include the shape of the gastric shield; the arc of duct orifices on the right side of the stomach; the blind pocket on the right posterior wall of the stomach, into which the posterior sorting area extends; the conspicuous forwardly projecting flap of the transverse sector of the major typhlosole; the large left pouch, from which a sorting area projects on to the stomach floor; the proximity of the left and right caeca, near the median line.

An interesting similarity between the stomachs of *Petricola pholadiformis* (Petricolidae) and *Trapezium sublaevigatum* (Libitinidae) may be attributable to comparable parameters of growth of the mantle/shell (Owen 1953*b*). In both cases the dorsal hood is pressed forwards so that it arches over the posterior end of the oesophagus, hiding the oesophageal orifice from view in a conventional dissection of the stomach by a mid-dorsal incision. The two walls of the dorsal hood, typically anterior and posterior, are here better described as ventral and dorsal, and the sorting areas which cover its ventral wall make a conspicuous contribution to the appearance of the interior of the stomach.

In a number of examples there is a transverse fleshy fold on the anterior floor of the stomach passing between the oesophageal orifice and the transverse sector of the major typhlosole, and passing up the right side of the stomach towards the mouth of the dorsal hood. Such a structure has been recorded in *Velesunio* (Hyridellidae), in *Donax faba* (Donacidae), in *Gari togata* and *Asaphis deflorata* (Psammobiidae), in *Dreissena* (Dreissenidae) and in *Zirphaea crispata* (Pholadidae). Apart from the Donacidae and Psammobiidae in the superfamily Tellinacea, these similarities must be regarded as coincidental, though the possibility that they are homologous structures cannot be excluded.

There is general similarity between the stomachs of *Anodonta* (Unionidae), *Velesunio* (Hyridellidae) and *Aspatharia* (Mutelidae), in addition to which there is a conical mound on the floor of the stomach in each of these genera, and this mound may be a diagnostic feature of the stomach in the Unionacea. In view of the long isolation of these families in Eurasia, Australia, and Africa, respectively, this emphasizes the stability of stomach structure in the Unionacea, and points to its potential for contributions to taxonomic enquiry.

It is now generally accepted that the Septibranchia (Cuspidariidae and Poromyidae) must have arisen from an anomalodesmatan ancestry close to the Verticordiidae. This view was originally based on studies of the muscular septum, which was judged to be of ctenidial origin. Purchon (1963*b*) had difficulty in envisaging the transition required from a ciliary microphagous suspension-feeding habit to a convulsive muscular scavenging and carnivorous feeding habit, while retaining feeding efficiency in the intermediate stages. However, Allen (1958*a*) showed that, with respect to the Lucinacea, the process of adaptation towards life in nutritionally impoverished marine deposits necessitated acceptance of all available food material. This was achieved by simplification and eventual loss of ciliary sorting mechanisms both in the mantle cavity and also in the stomach. In this way a carnivorous habit could have evolved via a facultative omnivorous stage. Studies on bivalve stomachs now support an anomalodesmatan origin of the Septibranchia. Allen & Turner (1974) and Bernard (1974) have recorded various degrees of specialization towards a carnivorous habit in the genera *Halicardia*, *Policordia* and *Lyonsiella*. In each of these genera less specialized species have a thinner muscle layer in the stomach wall, and a thinner scleroprotein lining within the stomach. They may possess a small major typhlosole and intestinal groove, a small folded sorting area, and a small dorsal hood, whereas all of these relics of a microphagous ancestry are lacking in the more highly specialized carnivorous species. The most striking evidence is supplied by *Parilimya* in which the stomach is in a state of transition from type IV to type II, and cannot be assigned to either of these types. The significance of this was not noted by Morton (1982).

The colonization of nutritionally impoverished sediments which has been described for the Lucinacea (Allen 1958*a*) has been carried further to achieve a carnivorous habit independently in two lineages which have developed different feeding strategies. In the Verticordiidae the food organisms are trapped by means of adhesive siphonal tentacles (Allen & Turner 1974), while in the Cuspidariidae the prey are captured by raptorial movements of the inhalant siphon (Reid & Reid 1974; Reid & Crosby 1980). Allen & Morgan (1981) recognize these two distinct lines of evolution among septibranchs by grouping the Verticordiidae and Poromyidae in the superfamily Poromyoida, and isolating the Cuspidariidae in the superfamily Cuspidaroida.

Purchon (1963*b*) distinguished the Protobranchia and Septibranchia, with few ducts from the digestive diverticula (Oligosyringia), from the filter-feeding remainder of the Bivalvia, which have many such ducts (Polysyringia). This distinction is not negated by the concentration of duct orifices especially in the Eulamellibranchia where these open via three embayments of the stomach wall, the left pouch, the left caecum and the right caecum. In some eulamellibranchs the stomach is greatly simplified, with only two or three large orifices leading to the digestive diverticula, for example, the Lucinidae, Thyasiridae, *Montacuta*, *Lasaea* and *Turtonia*. Two of these orifices are to be equated with the left and right caeca, that is, they are embayments and not ducts. In the Verticordiidae and Cuspidariidae it seems clear that there are two ducts, though it would be desirable to confirm this by histological investigation. If this is correct the term Oligosyringia is still applicable to the Septibranchia as a descriptive term, though not as a taxonomic category. Although Yonge (1928) had descrbed the ducts of septibranchs as being wide, this is open to question. Allen & Morgan (1981) said of *Cuspidaria obesa* 'The ducts are as short as they are wide (0.04 mm × 0.04 mm)'. A diameter of 0.04 mm corresponds with my own view that the ducts of *C. cuspidata* are *narrow*. Is it possible that the narrow ducts in the Verticordiidae and Cuspidariidae are derived from the relatively wide left and right caeca as a specialization towards the carnivorous habit, or could the oligosyringian condition be a primitive feature?

The genus *Chama* presents a problem which requires further investigation. *C. multisquamosa* was found to have a stomach of type IV, *C. lazarus* had a stomach of type V though this was somewhat abnormal, while *C. ?brassica* had a stomach of normal type V (Purchon 1958, 1960*a*, 1987 . Yonge (1967) stated that *Chama* is attached to the substratum by the left valve, while *Pseudochama* is attached by the right valve. Some species may attach by either valve so the distinction between *Chama* and *Pseudochama* is descriptive and not generic. However, in his samples of *Chama pellucida* and *Pseudochama exogyra* there was no such intraspecific variation. If this is also true for *C. lazarus* and *C. multisquamosa*, then these could be assigned to *Chama* and to *Pseudochama*, respectively. Unfortunately, owing to loss of personal records it has not been possible to check this detail for the specimens that were dissected in the original studies on these two species, nor do I have records of the sizes of the specimens dissected. The specimens of *C. ?brassica* reported upon here had a deep cup-shaped right shell valve which was attached to the substratum, so these specimens were *Pseudochama*. Further dissections of several species of *Chama*/*Pseudochama*, paying attention to the size of the specimen, and the valve of attachment, are needed to resolve this problem. Nevesskaya *et al.* (1971) adapted the original drawings of stomachs of bivalves by Purchon (1956*b*, 1957*b*, 1958, 1960*a*) into a series of standardized diagrams, assigning *C. multisquamosa* to *Pseudochama* and assigning *C. lazarus* to *Chama* without offering any justification. Their inclusion of the apparently abnormal stomach of *C. lazarus* seems decidedly uncritical, and they do not include any discussion of the subject. It seems unlikely that the type of stomach, IV or V, should be dependent upon whether a specimen of *Chama* should have attached by the left or by the right shell valve, but this could be investigated.

Summary

(i) This paper reviews the structure and ciliary sorting mechanisms within the stomach in 261 species, 157 genera, 68 families, and 37 superfamilies of bivalves. Detailed figures and descriptions are provided for six species which have not previously been studied in this respect.

(ii) Analysis of variations in structure within the stomach has permitted more detailed definitions of the five known types of bivalve stomach, with respect to the location in the stomach of the end of the major typhlosole and of the intestinal groove.

(iii) With only one exception, *Parilimya fragilis*, which exhibits a condition intermediate between stomach type IV and stomach type II, all species investigated have been assigned confidently to one or another of the five types of stomach described.

(iv) It is re-affirmed that stomach type IV represents survival of an ancestral condition from which stomach types II, III and V have diverged.

(v) Reversion from stomach type V to type IV has occurred in the Lucinidae and Thyasiridae, but not in the related Ungulinidae, and in a few species in the genera *Donax* (three), *Tellina* (one) and *Chama* (one), and may yet be confirmed in some other taxa. Apart from such reversions, stomach types I, II, III, IV and V are judged to characterize five independent phylogenies, the Gastroproteia, Gastrodeutera, Gastrotriteia, Gastrotetartica, and Gastropempta respectively.

(vi) The intermediate condition of the stomach in *Parilimya* provides further strong support for the conclusion that that Septibranchia arose from an anomalodesmatan source close to the Verticordiidae, that is, that stomach type II evolved from stomach type IV.

(vii) It is re-affirmed that the differences between the digestive systems of the deposit-feeding Protobranchia and the predominantly filter-feeding Lamellibranchia justifies the status of subclass for each of these two groups.

(viii) The subclass Protobranchia (= Gastroproteia) comprises the superfamilies Nuculacea, Nuculanacea and Solemyacea.

(ix) The subclass Lamellibranchia apparently comprises four phylogenies on the basis of stomach structure.

(*a*) Gastrotriteia, in which the major typhlosole bears a long, slender tongue which penetrates deeply into a food-sorting caecum, but which does not come into close association with any of the orifices of ducts from the digestive diverticula. There is no left caecum or right caecum. This group includes the Arcacea, Limopsacea, Mytilacea, Pinnacea, Pteriacea and Ostreacea.

(*b*) Gastrotetartica, in which the major typhlosole curves evenly across the stomach floor to the left; there is no typhlosolar tongue; the major typhlosole does not enter a right caecum, and in the majority of cases it does not enter a left caecum (exceptional cases marked by an asterisk). This group includes the Pectinacea, Limacea, Anomiacea, Pandoracea, and Clavagellacea. It possibly also includes the *Unionacea, Trigoniacea, Crassatellacea, Carditacea, *Leptonacea, Hiatellacea, *Gastrochaenacea and Pholadomyacea, though further evidence is desirable before any of these eight superfamilies can be assigned with confidence.

(*c*) Gastrodeutera, in which the stomach wall is highly muscularized and its greatly simplified interior is extensively lined by a scleroprotein sheath. This group comprises the Septibranchia (*sensu lato*) in the superfamily Poromyacea, with three families, Verticordiidae, Cuspidariidae and Poromyidae. Although derived from the Anomalodesmata these are structurally and functionally so different from other bivalves as to justify the same taxonomic status as the Gastrotetartica from which they arose.

(*d*) Gastropempta, in which the major typhlosole penetrates deeply into both the left caecum and the right caecum, coming into close association there with the orifices of many ducts from the digestive diverticula. This group comprises the Lucinacea, Chamacea, Cardiacea, Tridacnacea, Mactracea, Solenacea, Tellinacea, Dreissenacea, Arcticacea, Glossacea, Corbiculacea, Veneracea, Myacea and Pholadacea.

(x) Attention is drawn to the possibility that some stomach features might indicate affinity between taxa, for example, between the Leptonacea and the Tellinacea.

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KEY TO THE LETTERING ON THE FIGURES (1–15 only)

A	Appendix
AB	Apex of buttress
AC	Antechamber to the stomach (*Chama*)
ADH	Apex of dorsal hood
ATMT	Apex of the tongue of the major typhlosole
B	Buttress
BE	Broad transverse belt (*Chama*)
BPR	Backwardly directed process on floor of stomach
BU, BU′	Backwardly directed buttresses on left and right sides (*Pteria*)
C	Conical mound on stomach floor (*Aspatharia*; *Velesunio*)
CA	Ciliated area
CG	Chitinous girdle
CH	Chitin
CM	Circular muscle
CP	Convex prominence in front of crystalline style
CS	Crystalline style
CSH	Chitinous sheath
CSSMG	Combined style sac and mid gut
CUT, CUT′	Cut in tissues
DDD	Ducts from the digestive diverticula
DH	Dorsal hood
DHA	Anterior pocket of dorsal hood (*Chlamys*)
DHP	Posterior pocket of dorsal hood (*Chlamys*)
F	Flare of the rim of the major typhlosole
FSC	Food sorting caecum
GR, GR′	Groove

GS, GS′	Gastric shield
H	Elliptical hollow near left pouch (*Velesunio*)
HG	Hind gut
HGR	Hood groove
IG	Intestinal groove
IGF	Forwardly directed sector of intestinal groove
L	Lobe at orifice of style sac
LC	Left caecum
LD	Left duct
LP	Left pouch
LR	Longitudinal ridges
M	Mouth
MG	Mid gut
MIT	Minor typhlosole
MT	Major typhlosole
MT′	Transverse sector of the major typhlosole
O	Oesophageal orifice, or oesophagus
O′	Position of left side of oesophagus (*Pteria*)
OD	Orifice of secondary into primary ducts from the digestive diverticula
OGA	Opaque glandular area (*Trisidos*)
OIG	Origin of intestinal groove
OMG	Orifice of mid gut
OR	Opaque rim around margin of sorting area (*Chlamys*)
OSS	Orifice of style sac
P, P′	Deep pockets in right wall of stomach (*Aspatharia*)
PA	Swollen patch (*Chama*)
PAD	Swollen pad on right wall of stomach
PAP	Papillae
PL, PR	Pockets on the left and right sides of stomach, into which ducts from the digestive diverticula open (*Chlamys*)
PRB	Finger-like processes of buttress
R, R′	Ridge
RC	Right caecum
RD	Right duct
RE	Recess
RL	Row of lozenge-shaped elevations
RT	Rejection tract
SA	Sorting area
SA′	Sorting area seen by transparency
SF	Semicircular flange
SMB	Sorting mechanism of type B
SS	Style sac
SSR	Rim of style sac
ST	Stomach
SW	Swelling
T	'Tiara' on gastric shield
TMT, TMT′	Tongue of major typhlosole
TO	Tongue separating two conical pockets on stomach wall (*Aspatharia*)
TU	Row of tubercles (*Velesunio*)
TY	Typhlosole
V	Vestibule to stomach (*Chama*)
WDG	Orifices leading to wood-digesting diverticula
WSC	Wood-storing caecum
2, 4, 5	Numbers of orifices of ducts from digestive diverticula (*Chlamys*)