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CLASSIFICATION AND EVOLUTION OF THE BIVALVIA: AN ANALYTICAL STUDY

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Thirty-seven superfamilies of Lamellibranchia (predominantly suspension-feeding) were graded according to their overall more primitive or more advanced structural condition, by tabulation based on two organ systems exhibiting progressive series of character-states (ctenidia, marginal pallial fusion). Commencing with the more primitive superfamilies, these were investigated in groups, recording the occurrence of those character-states that were especially relevant to the group in question. By this means the superfamilies were arranged in five clusters, and the structural characteristics of each cluster were clearly reported.

By these methods, and together with three superfamilies of Protobranchia, the Bivalvia are shown to comprise six clusters which have been arranged in the following classificatory system.

Subclass 1 Protobranchia
    Order 1 Nuculoida
    Order 2 Solemyoida
Subclass 2 Lamellibranchia
    Order 3 Pteriomorpha
    Order 4 Mesosyntheta
        Suborder Trigonioida
        Suborder Unionoida
    Order 5 Anomalodesmata
        Suborder Pholadomyoida
        Suborder Septibranchia
    Order 6 Gastropempta
        Suborder Veneroida
        Suborder Myoida

This classification is in general agreement with that adopted in the *Treatise on invertebrate palaeontology* (ed. R. C. Moore, University of Kansas Press, 1969–71) save for the following points.

(i) Four subclasses are suppressed, reasons given.

(ii) The superfamilies Crassatellacea, Carditacea and Leptonacea are transferred out of the Veneroida to join the Unionacea in an expanded suborder Unionoida.

This improved classification differs in a few respects from the taxonomic arrangement previously obtained by computer analysis (R. D. Purchon, *Phil. Trans. R. Soc. Lond.* B **284**, 425–436 (1978)) owing to additional information, and to more sensitive methods of analysis. The methods used provide clear reasons for the classification adopted, and permit easy adjustments to the classification if these are required after incorporation of any new information that may become available.

The principal attributes of the nuculoid protobranchs and of the subclass Lamellibranchia are compared and contrasted in tabular form.

A diagram, incorporating four hypothetical ancestral stages, illustrates the probable course of evolution in the class Bivalvia.

An appendix supplies five further tabulations demonstrating the relevance to classification of the structural variation within certain of the organ systems. Throughout these six tabulations a majority of the superfamilies exhibit uniformity in their associations.

INTRODUCTION

Cox (1960) has reviewed the numerous attempts to classify the Bivalvia over a period of two centuries since the publication of the tenth edition of the *Systema Naturae*, and the associated search for a primary taxobasis to be used for this purpose. The following short list of organ systems that have been used has been extracted from this review, in which the relevant literature is cited:

equality or inequality of the shell valves (Cuvier 1797);
the extent of marginal fusion of the mantle lobes (Lamarck 1801);
the adductor muscles and their scars (Lamarck 1812);
the foot (Gray 1821);
shell symmetry with respect to the substratum, and the presence or absence of a pallial sinus (D'Orbigny 1843–47);
hinge teeth (Neumayr 1884);
the ctenidia (Pelseneer 1889, 1891; Ridewood 1903);
ctenidial ciliation (Atkins 1936–38);
internal structure of the stomach (Purchon 1959).

Summarizing these, and other similar efforts, Cox observed drily that 'As any other organ or structure was made the subject of closer study, the claim was invariably made that this line of investigation, rather than any other, would lead to a natural classification' (Cox 1960, p. 68).

At a symposium organized by the Malacological Society of London, the status of the Protobranchia in the class Bivalvia was considered from various aspects including geological history, the ligament, feeding mechanisms, the stomach, and the digestive diverticula (Cox 1959; Owen 1959; Purchon 1959; Yonge 1959). It was generally concluded, from overwhelming evidence which is summarized in this paper, that the deposit-feeding Protobranchia on the one hand, and the predominantly suspension-feeding remainder of the Bivalvia on the other, should be assigned to two separate subclasses. This conclusion was endorsed in a recent computer analysis of a matrix of data on eight anatomical systems plus further information on the relationship of the bivalve with the substratum (Purchon 1978). Although in the *Treatise on invertebrate palaeontology* (Moore 1969–71) the Bivalvia were divided into six subclasses, it is now widely agreed that there are only two subclasses. These are the Protobranchia and the Lamellibranchia. It is important to emphasize the change in the meaning of the term 'Lamellibranchia', which used to be applied to the whole class, but which is now restricted to mean those bivalves with lamellar ctenidia plus the septibranch families Verticordiidae, Cuspidariidae and Poromyidae.

For almost 40 years I have used successively the classifications of Pelseneer (1906, 1911), that of Thiele (1935) and more recently the classification in the *Treatise on invertebrate palaeontology* (Moore 1969–71), but without gaining complete satisfaction from any of these. Thus it seems probable that two or more phylogenies may have evolved independently in parallel through the four (or five) structural and functional strata established by the classifications of Pelseneer. It is now agreed that ctenidial structure is an uncertain tool for the construction of a natural classification of the Bivalvia.

Thiele (1935) disregarded the great differences of ctenidial structure between the protobranchiate Stirps Nuculacea and the filibranchiate Stirps Arcacea, and grouped these in the Ordo Taxodonta on account of their hinge teeth. It is now accepted that the pseudoctenodont hinge teeth of Recent Arcacea are secondary (Cox 1959; Thomas 1978) and provide no indication of affinity with the Nuculoida. Pelseneer (1906) placed the filibranchiate Trigoniidae in the suborder Arcacea on account of ctenidial structure, while Thiele (1935) disregarded this and put the Trigoniidae with the eulamellibranchiate Unionacea, in the Schizodonta. The schizodont status of the Unionacea is questionable.

The *Treatise on invertebrate palaeontology* (Moore 1969–71) gives very satisfactory clustering of superfamilies, but the elevation of the Pteriomorpha, the Palaeoheterodonta, the Heterodonta and the Anomalodesmata to the grade of subclass is out of all proportion to the observed structural and functional differences between these taxa. It is interesting to note that Newell (1969, p. 213) said 'of the six subclasses [of Bivalvia] the Palaeotaxodonta and Pteriomorpha are considered by many to be natural, the other four are probably artificial'.

In no case is full supporting evidence provided for these classificatory systems, though the *Treatise on invertebrate palaeontology* does recognize the need for the coordination of data from different organ systems with this end in view. The present paper attempts to remedy this deficiency with a series of tabulations of character-states exhibited by many of the superfamilies within each cluster. It also offers a model of the probable course of evolution within the class Bivalvia, in a sequence of possibly unique evolutionary advances giving rise to the main taxonomic groups in the class, followed by minor adaptive radiations sometimes exhibiting developments in parallel within and between these groups. As compared with a previous study (Purchon 1978) an increased body of information has been used, and a serious attempt has been made to distinguish between complex evolutionary developments which are most unlikely to have occurred twice, and minor developments which might reasonably be expected to occur on a number of occasions. This combination of identifying clusters of superfamilies by deduction from tabulated information, with an admittedly subjective study of the probable course of evolutionary advance, is thought to be more sensitive than any previous study of the subject. It provides a method that permits easy revision whenever appropriate.

ANALYSIS OF THE DATA

In the computer study (Purchon 1978), data on the various character-states for each of eight organ systems were represented by appropriate numerals in table 1, as explained in the text. At some points in the table it was necessary to make a nil return, either owing to lack of information or to conflict of information from different taxa within one superfamily. These nil returns were recorded by use of different letters of the alphabet within any one vertical column, thus ensuring that nil returns were not scored as similarities. At that time it had not been possible to include information on the *nature* of the fusions of the mantle margins (as opposed to the *number* of these fusions), owing to some conflict in the mode of recording in the two principal scources of information (Yonge 1948, 1957). This difficulty has now been resolved (Yonge 1982) and it is now apparent that these two aspects of pallial fusion are broadly in agreement. Their correlation (table 1) has made it possible to define a new set of five character-states, which are substituted for those used in 1978. It has now been possible to record character-states in place of some of the nil returns in the study of 1978, and these will be recorded below for the relevant organ systems. Minor corrections have also been made in the matrix of data. It may be added that, since the two sets of information on pallial fusion are basically comparable, the

TABLE 1. CORRELATION BETWEEN THE NUMBER OF PALLIAL FUSIONS AND THE NATURE OF THESE MARGINAL FUSIONS

	no pallial fusions (1)	fusion of inner fold only (2)	fusion of inner and middle folds (3)	fusion of inner and middle folds and periostracal groove (4)
(4) two fusions; ventral fusion long		Chamacea	Veneracea Pholadacea Clavagellacea Pandoracea Pholadomyacea Gastrochaenacea	Myacea Poromyacea Hiatellacea
(3) two fusions; ventral fusion short		Cardiacea Tridacnacea Tellinacea Dreissenacea Arcticacea Glossacea Corbiculacea Lucinacea Gaimardiacea Cyamiacea	Solenacea	Mactracea
(2) one fusion		Leptonacea Carditacea Unionacea Crassatellacea		
(1) no pallial fusions	Arcacea Limopsacea Trigoniacea Mytilacea† Pteriacea Pectinacea Pinnacea Limacea Ostreacea† Anomiacea			

† In 1978 these two superfamilies were shown as having one pallial fusion, in recognition of a fusion involving the posterior ends of the ctenidia, but there is no direct fusion between left and right mantle lobes.

exercise conducted in 1978 is not invalidated by lacking the series of data on the *nature* of pallial fusion. Moreover, if the data on the nature of pallial fusion had been added to the matrix as an additional line of data, then the pallial system would have been over-weighted without good reason.

Since the Protobranchia have been distinguished as a separate subclass, and this is not disputed, the three protobranchiate superfamilies will not be subjected to further analysis here. The distinctions between the two subclasses of Bivalvia are specified in the Discussion.

Seven of the organ systems here under review are relevant only to very limited sectors in the Lamellibranchia, and only require brief comment.

The adductor muscles

Variation in the relative sizes of the anterior and posterior adductor muscles concerns four heteromyarian superfamilies including the unrelated Mytilacea and Dreissenacea, and six monomyarian superfamilies including the unrelated Ostreacea and Tridacnacea (Yonge 1953*a*, *b*; Yonge & Campbell 1968). The heteromyarian and monomyarian character states are certainly relevant to adaptive radiation within the Pteriomorpha, but offer no taxonomic aid elsewhere.

The pallial line and pallial sinus

In a majority of superfamilies, and especially in those that in other respects are regarded as primitive, the pallial line is entire, with no pallial sinus. A deep pallial sinus is restricted to nine superfamilies in which the siphonal process is long, and in most of which there is a habit of deep burrowing or deep boring. This character-state is not correlated in its occurrence with variations in hinge structure (heterodont or edentulous), or with stomach structure (stomach types IV or V), nor is it a diagnostic feature of any higher taxonomic group (Anomalodesmata or Myoida). This character-state is primarily useful for descriptive purposes in a narrow sector of the adaptive radiation of 'advanced' eulamellibranchs.

Byssal attachment

The byssus gland is a post-larval attachment organ which may, by neoteny, extend into adult life to give continuing attachment, and sometimes extensive modification of adult growth form. It is characteristic of the Pteriomorpha, but occurs sporadically among unrelated genera and families of Eulamellibranchia (see table 2).

Ctenidial ciliation

Eulaterofrontal cilia have been recorded in three superfamilies of Protobranchia, the Mytilacea, Ostreacea and 18 superfamilies of Eulamellibranchia (Atkins 1938). Presumably this was the primitive condition and these cilia were originally concerned with *cleaning* the ctenidial leaflets, and were subsequently adapted in most Lamellibranchia to collect minute food particles from suspension in the water. This proposition could be tested by scanning electron micrographs of protobranch gills, for powerful cleansing cilia would not require the delicate fringe of ciliary tips that have been seen, for example, in *Venus casina* (Owen 1978).

It would follow from this proposition that the lack of these cilia in the Microciliobranchia is a derived condition, probably achieved through *evolution by loss*, perhaps independently in several phylogenies. The Microciliobranchia as originally defined by Atkins (1938) comprised seven superfamilies (but probably also including the Limopsacea), but this was amended by the deletion of the Ostreacea (Purchon 1960*b*, 1978; Owen 1978). The very fine ciliary meshwork provided by the fringe of diverging ciliary tips on the eulaterofrontal cilia must cause considerable drag on the feeding and respiratory water current passing through the ctenidia, and this may have proved disadvantageous in these superfamilies. Alternatively, in some circumstances in sheltered waters and in the vicinity of gorgonians and sponges, the water may be calm and relatively free from minute suspended particles. In such circumstances the loss of the eulaterofrontal cilia might have been advantageous.

The Microciliobranchia, as amended, include the Arcacea, Pinnacea, Pteriacea, Pectinacea, Anomiacea, Limacea (and Limopsacea?). This assemblage differs from the Pteriomorpha and from the Gastrotriteia (Purchon 1959) in *excluding* the Mytilacea and Ostreacea, and also differs from the Gastrotriteia in *including* the Pectinacea, Anomiacea and Limacea. Within the Pteriomorpha adaptive radiation must be partly a mosaic; either the Microciliobranchia or the Gastrotriteia *must* be polyphyletic, and it is probably the former. Ciliation of the ctenidia cannot serve as a primary taxobasis for the class Bivalvia.

Shell structure

Detailed information on shell structure (Taylor *et al.* 1969, 1973) does not seem to clarify the phyletic affinities of superfamilies (Purchon 1978).

The ligament

The disposition of the component part of the ligament is dictated by the locations of the pallial epithelia that secrete them. The ligament is therefore subjected to constraints imposed by habitat and mode of life, and by the parameters of shell growth. A tangential growth component makes the ligament split anteriorly in the free-living infaunal *Glossus* as also in *Chama* which is attached to rocks by cementation (Owen 1953*a*, *b*; Yonge 1967). Thus the same constraint has comparable effects on ligamentary form even in very different circumstances, through convergence. It may be unsafe to use individual aspects of ligamentary structure in a search for affinities between superfamilies. Yonge (1978) concluded that the overall form of the ligament is a basic characteristic for each superfamily, but this offers little help in the clustering of superfamilies. The Crassatellacea and Carditacea share a common ligamentary structure, as also do the Pandoracea and Poromyacea (Yonge 1978; Yonge & Morton 1980).

Hinge dentition

Having excluded the Protobranchia (ctenodont), there remain four character-states, pseudoctenodont, schizodont, edentulous, and heterodont, which cannot be arranged in a natural series. The term 'schizodont' is of little use since its application to the superfamily Unionacea is dubious, and the hinge structures of the Trigoniacea and Unionacea have probably been acquired independently. The edentulous state may be primitive in some superfamilies, but may have been acquired in some through secondary simplification in response to the mode of life and habitat adopted, possibly with convergence in two or more superfamilies. The heterodont condition may be divided into the corbiculoid (= cyrenoid) and the lucinoid subtypes.

Two superfamilies for which nil returns had been entered in 1978 are now recorded as being edentulous, these being the Pteriacea and the Pectinacea. Finally, the Poromyacea are now recorded as edentulous, their weak hinge teeth being regarded as secondary manifestations not of heterodont origin.

In two of the three remaining organ systems the various character-states form a natural series, and the more advanced character-states can only have been attained by progression through earlier and more primitive states. These progressions are indicated by marginal arabic numerals in table 2. In the third organ system the various character-states cannot be so arranged.

Fusion of the mantle margins

Table 1 establishes the close correlation between two aspects of pallial fusion, and these have been combined into a single system with five character-states which is used in this paper (tables 2, A1 and A2). Information has now been obtained for the four superfamilies for which nil returns had been made in the review of 1978, that is, the Lucinacea, Leptonacea, Solenacea and Corbiculacea.

Ctenidial structure

The Protobranchia having been excluded from this part of the analysis, there remain four character-states, filibranch, pseudolamellibranch, eulamellibranch and septibranch.

TABLE 2. CORRELATION BETWEEN DEGREES OF FUSION OF THE MANTLE FOLDS AND CTENIDIAL STRUCTURE

(The numerals along each axis of the table indicate that in each of these organ systems the character states are arranged in a natural progression.)

	Filibranchia (1)	Pseudolamellibranchia (2)	Eulamellibranchia (3)	Septibranchia (4)
(5) two fusions, including periostracal groove			Hiatellacea† Myacea† Mactracea	Poromyacea
(4) two fusions, inner and middle folds			Clavagellacea Pholadacea Pandoracea† Pholadomyacea Gastrochaenacea Veneracea† Solenacea	
(3) two fusions, inner fold only			Corbiculacea† Glossacea† Arcticacea Tellinacea Tridacnacea† Cardiacea† Lucinacea Dreissenacea† Gaimardiacea Cyamiacea† Chamacea	
(2) one fusion, inner fold only			Leptonacea† Unionacea Crassatellacea Carditacea†	
(1) no pallial fusions	Trigoniacea Anomiacea† Pectinacea† Pteriacea† Mytilacea† Limopsacea† Arcacea†	Ostreacea Pinnacea† Limacea†		

† A functional byssus occurs in the adult state in at least some taxa in these superfamilies.

Stomach structure

Having excluded the Protobranchia (stomach type I), there remain four character-states which can be arranged in three series, types IV to III, types IV to V, and types IV to II. Information can now be given for six superfamilies for which nil returns had been made in 1978. This is due to new information gained concerning the Pholadomyacea and Leptonacea with stomachs of type IV. As regards the Lucinacea, Chamacea, Tellinacea and Corbiculacea in which some taxa possess a stomach of type IV owing to secondary modification, all are here assigned to stomach type V, by which these superfamilies are characterized (Purchon 1987).

It is of interest to ascertain the extent to which the last four organ systems here under consideration may have interacted in the adaptive radiation of the Lamellibranchia. This question has been approached by using the character-states of two organ systems at the same time to tabulate the constituent superfamilies. In this way each organ system has been compared with each of the others in 3+2+1 = 6 tabulations which collectively give a very convenient synoptic view of the major structural variations in the subclass. From a careful study of these six tables it became immediately clear that while each organ system may have had a certain appeal for use in classification, there is no question of selecting any one system as a taxobasis. All four organ systems are involved in the adaptive radiation, apparently operating to a considerable extent in harmony. It was also seen that several clusters of superfamilies had unbroken associations throughout these tabulations. These eight clusters, and another in the subclass Protobranchia, together embracing 24 out of a total of 39 superfamilies of Bivalvia, must obviously constitute nuclei for any higher taxonomic groupings within the class. These eight clusters of superfamilies are indicated by use of parentheses in table A 5. Of the six tabulations mentioned above, only one is portrayed here (table 2), the remainder being placed in an Appendix.

Having isolated the more primitive, deposit-feeding Protobranchia from the more advanced, suspension-feeding Lamellibranchia, we can now seek to identify the major taxonomic groupings within the latter. Table 2 has been so constructed that those superfamilies exhibiting primitive features appear at the bottom left of the table, whereas those with more advanced features appear at the top right of the table. The group of superfamilies possessing most primitive features includes the nine superfamilies in the Pteriomorpha plus the Trigoniacea. These are immediately separable from all other superfamilies by lacking any pallial fusions and by having filibranch or pseudolamellibranch ctenidia. In table 3 these 10 superfamilies, plus the Unionacea, are investigated as regards the possession of those features that characterize a *majority* of the Pteriomorpha.

Table 3 immediately establishes:

(i) the nine superfamilies in the Pteriomorpha comprise a natural assemblage as judged by the broad distribution through the group of the eight character-states used. These superfamilies constitute 'group 1' of the Lamellibranchia.

(ii) Notwithstanding the possession of filibranch ctenidia by the Trigoniacea, the two superfamilies of 'Schizodonta' are obviously independent from the Pteriomorpha.

(iii) Although the six superfamilies in the Gastrotriteia constitute a distinct phylogeny, as judged by their common possession of the very complex stomach of type III, there is no

Table 3. The distribution of eight character-states that are typical of a majority of the Pteriomorpha, in nine superfamilies of Pteriomorpha and two superfamilies of Schizodonta

	group 1										
	Arcacea	Limopsacea	Mytilacea	Pinnacea	Pteriacea	Ostreacea	Pectinacea	Anomiacea	Limacea	Trigoniacea	Unionacea
no pallial fusions	+	+	+	+	+	+	+	+	+	+	
posterior end of ctenidium lies free in mantle cavity	+	+		+	+		+	+	+	?	
ctenidia are filibranch	+	+	+		+		+	+		+	
ctenidial filaments lack eulaterofrontal cilia	+	+		+	+		+	+	+		
stomach is of type III	+	+	+	+	+	+					
major typhlosole and intestinal groove end near left pouch, not left caecum	+	+	+	+	+	+	+	+	+		
orifices of ducts from digestive gland are scattered or clustered, and do not open via deep embayments	+	+	+	+	+	+	+	+	+		
byssal attachment in at least some adults	+		+	+	+		+	+	+		
totals	8	7	6	7	8	4	7	7	6	2	0

justification for dividing the Pteriomorpha into two subordinate taxa on this, or any other, basis. The term 'Gastrotriteia' may remain as a convenient collective term for these six superfamilies, but at present serves no useful purpose in taxonomy.

(iv) The clear distinction between the Pteriomorpha and all the more advanced Lamellibranchia is based on relatively minor structural differences, which do not compare with the fundamental differences between the subclasses Protobranchia and Lamellibranchia. It is inescapable that the Pteriomorpha cannot be ranked as a subclass, but only as an order.

The distribution of the more primitive character states was next examined in the 'Schizodonta', together with three apparently primitive superfamilies of eulamellibranchs, and nine selected superfamilies of advanced eulamellibranchs as 'controls'. A few other character-states were included in the table to record known similarities between some of the superfamilies. The results (table 4) demonstrate a high degree of similarity among the two superfamilies of 'Schizodonta' and the primitive superfamilies Crassatellacea, Carditacea, and Leptonacea. In contrast, the 'Schizodonta' showed little similarity with any of the nine 'control' superfamilies. In support of these findings, it is interesting to note that Yonge (1969) recommends that the Crassatellacea and Carditacea should be united in one superfamily. Yonge also noted the close similarity between the ctenidial ciliation of *Cardita ventricosa* and that recorded for the Unionidae (not Unionacea) by Atkins (1937). I had myself noted that the ctenidial ciliation of *Beguina* (*Cardita*) *semiorbiculata* was the same as that of the Unionidae, that is, Atkins' type D, and had also noted a broad similarity between the posterior mantle margins of *B. semiorbiculata* and of *Anodonta* (unpublished observations from Singapore, 1950–60). These are the only hints as to the possible relationships of the Unionacea among the marine Bivalvia.

TABLE 4. THE DISTRIBUTION OF TEN CHARACTER-STATES, MOSTLY OF A PRIMITIVE NATURE, IN 14 SUPERFAMILIES OF BIVALVIA

(The first five superfamilies in the table are very similar, but differ markedly from the remaining nine superfamilies which were selected for use as 'controls'.)

	group 2													
	Trigoniacea	Unionacea	Crassatellacea	Carditacea	Leptonacea	Lucinacea	Chamacea	Cardiacea	Tellinacea	Pholadomyacea	Pandoracea	Clavagellacea	Gastrochaenacea	Hiatellacea
'schizodont' hinge teeth	+	(+)												
no pallial sinus	+	+	+	+	+	+	+	+						
one pallial fusion, inner fold only		+	+	+	+									
filibranch ctenidia	+													
stomach of type IV	+	+	+	+	+					+	+	+	+	+
duct orifices lie in deep embayments of stomach wall; no anterior sorting area in stomach	+	+	+	+	+	+	+	+	+	?			+	
major typhlosole and intestinal groove end external to the left caecum	+		+	+	+					+				+
posterior end of ctenidium lies free in the mantle cavity	+		+	?										
ctenidial ciliation of Atkins' type D, or very similar		+		+										
mantle isthmus divided into five lobes			+	+										
totals	7	5	7	7	5	2	2	2	1	2	1	1	2	2

(?) Examination of preserved specimens suggested that the posterior ends of the ctenidia are weakly attached to the inner surface of the mantle either by interlocking cilia or, less probably, by cuticular fusion in *Cardita variegata* and in *Beguina semiorbiculata* (Carditacea).

The five superfamilies that have been isolated by means of table 4 constitute 'group 2' of the Lamellibranchia.

Table 5 establishes that the Gastrochaenacea and the Hiatellacea show little similarity to the remainder. These two superfamilies are also very dissimilar from those in group 2 as defined in table 4, and are set aside for the present. The remaining four superfamilies in table 5 have several features in common and comprise group 3, the Anomalodesmata.

Table 5. The principal attributes of the remaining superfamilies with stomachs of type IV, together with the septibranch Poromyacea

	group 3					
	Pandoracea	Pholadomyacea	Clavagellacea	Poromyacea	Gastrochaenacea	Hiatellacea
hinge edentulous	+	+	+	+	+	
ligament with a lithodesma in some taxa	+			+		
Atkins' ctenidial type E	+	+	+	+		
simultaneous hermaphroditism	+	+	+	+		
byssal attachment in some taxa	+					+
fourth pallial aperture present	+	+	+			
stomach of type IV	+	+	+		+	+
taenioid muscle present in some taxa		+		+		
radial mantle glands present in some taxa	+	+		+		
totals	8	7	5	6	2	2

The distinction between group 3 and the remainder of the Lamellibranchia is assisted by reference to table 6, which records the distribution of stomachs of types III, IV and V. The original definition of stomach type V (Purchon 1960*a*) identifies 14 superfamilies of Gastropempta as listed in the top right hand box in the table. A more recent, exhaustive analysis of stomach structure establishes that the ending of the major typhlosole and intestinal groove within the stomach exhibits four alternative character-states (Purchon 1987). In condition D the left caecum is deeply penetrated by the major typhlosole and intestinal groove, and this condition is found in all 14 superfamilies mentioned above, and also in the Unionacea and Gastrochaenacea.

It is contended that in stomach type V the relationship between the intestinal groove and the ducts from the digestive diverticula that open into the stomach via the left and right caeca, is so remarkable that it cannot have evolved in more than one lineage. If this is correct it follows that all bivalve taxa possessing a stomach of type V must be related by descent from a common ancestry, and must therefore comprise a distinct phylogeny, the Gastropempta. It is not easy to decide whether the constituents of the Gastropempta are better indicated by the structure of the right caecum (Purchon 1960*a*), or by reference instead to that of the left caecum (Purchon 1987). This raises a question as to the correct taxonomic positions of the Unionacea and the Gastrochaenacea. Table 4 strongly suggests that the Unionacea are satisfactorily located in group 2. As for the Gastrochaenacea and the Hiatellacea, their appropriate taxonomic position will be considered at the next stage in the analysis. This caution is desirable in view of the known

Table 6. Stomachs of types III, IV and V as originally described (vertical columns) correlated with four different character-states in the termination of the major typhlosole and intestinal groove within the stomach (A, B, C, D)

(The characteristic distributions of sorting areas in stomachs of types IV and V are also shown. Taxonomic groups previously isolated by means of tables 3 and 4 are recorded in italic print.)

		stomach type III	stomach type IV	stomach type V	
termination of the major typhlosole and intestinal groove within the stomach	(D)		Gastrochaenacea ? ? ? *Unionacea*	Pholadacea Myacea Veneracea Solenacea Corbiculacea Glossacea Arcticacea	Dreissenacea Tellinacea Mactracea Tridacnacea Cardiacea Chamacea Lucinacea
	(C)	group 2	*Carditacea* *Crassatellacea* *Leptonacea* *Trigoniacea* Pholadomyacea Hiatellacea		
	(B)		Clavagellacea Pandoracea		
	(A)	six superfamilies of *Pteriomorpha*	three superfamilies of *Pteriomorpha*		
sorting area	1		common	scarce	
	3		common	nearly universal	
	6		scarce	nearly universal	
	8		common	common	

withdrawal of the major typhlosole from the right caecum in some species of *Donax* and *Chama* (Purchon 1958, 1960*a*).

Table 7 provides evidence supporting the separation of the remaining 16 superfamilies of bivalves into two groups of which group 4a including the Gastrochaenacea and Hiatellacea, corresponds exactly with the Myoida. The larger group 4b differs from the Veneroida (Adams & Adams 1856) only in the withdrawal of the superfamilies Leptonacea, Carditacea and Crassatellacea and their transference into group 2, together with the Trigoniacea and Unionacea.

To summarize, this analysis of the taxonomic groupings of 34 superfamilies of Lamellibranchia (= Filibranchia + Pseudolamellibranchia + Eulamellibranchia) has recognized five clusters of which group 1 (nine superfamilies), group 3 (four superfamilies), and group 4a (four superfamilies) correspond exactly with the contemporary compositions of the Pteriomorpha, the Anomalodesmata, and the Myoida, respectively. The two remaining groups introduce a change from present practice by transferring the relatively primitive superfamilies Leptonacea, Crassatellacea and Carditacea out of the Veneroida, and placing them with the Unionacea in an expanded Unionoida.

Table 7. The distribution of seven character-states in the Gastrochaenacea and Hiatellacea, previously considered, and in the 14 remaining ‘advanced’ superfamilies of bivalves

(The Gaimardiacea and Cyamiacea have not been considered. The Dreissenacea are not included in group 4a as the high score for this superfamily is partly attributable to convergence.)

	group 4a				group 4b											
	Gastrochaenacea	Hiatellacea	Myacea	Pholadacea	Lucinacea	Chamacea	Cardiacea	Tridacnacea	Mactracea	Solenacea	Tellinacea	Dreissenacea	Arcticacea	Glossacea	Corbiculacea	Veneracea
siphonal process long, with inhalant and exhalant siphons fused to their tips	+	+	+	+												
pallial sinus deep	+	+	+	+							+					+
hinge edentulous	+		+	+								+				
byssal attachment in the adult stage in some taxa		+	+				+	+				+			+	
two pallial fusions which include the periostracal groove		+	+						+							
stomach of type IV	+	+														
adductor scars heteromyarian	+											+				
totals	5	5	5	3	0	0	1	1	1	0	1	3	0	0	1	1

DISCUSSION

The Bivalvia comprise two subclasses, the deposit-feeding Protobranchia and the predominantly suspension-feeding Lamellibranchia. This independent status of the Protobranchia is widely accepted, but the great extent of the differences between the two subclasses is less well known. The differences may be summarized as follows.

Subclass I, Protobranchia Order Nuculoida	Subclass II, Lamellibranchia
The ctenidia are aspidobranch, and are primarily concerned in respiration.	The ctenidia are typically lamellibranchiate, and are primarily concerned in the collection of food particles from suspension in the supernatant water.
The labial palps possess palp proboscides which are extruded from the mantle cavity to probe in the sediment and collect food particles deposited there.	The labial palps do not possess palp proboscides; food particles collected from the inhalant water current are passed by the palps from the ctenidia to the mouth.
The 'style' is a soft amorphous secretion which lies in the wide, funnel-shaped proximal sector of the mid gut, and projects into the lumen of the stomach.	The crystalline style is a rod which lies in the slender proximal sector of the mid gut, being separated from the waste tract by two apposed typhlosoles. It projects into the stomach, rotating and stirring the stomach contents.
Digestion is exclusively extracellular, in the lumen of the stomach. Food particles are not admitted into the ducts and tubules of the digestive gland.	Digestion is partly extracellular in the lumen of the stomach and mid gut, but is also partly intracellular in the tubules of the digestive gland, the cells of which can phagocytose small particles.
The major typhlosole and intestinal groove do not pass forwards from the mid gut on to the floor of the stomach.	The major typhlosole and the intestinal groove extend forwards across the floor of the stomach. The major typhlosole typically arches over the intestinal groove, permitting removal of waste matter without interruption to gastric digestion.
The digestive diverticula open into the stomach by only three simple ducts.	The digestive diverticula open into the stomach by many ducts whose orifices may be scattered, clustered, or may open indirectly via one to three embayments of the stomach wall.
The main ducts from the digestive diverticula are much branched and are not ciliated, but have a brush border.	The main ducts from the digestive diverticula have a deep ciliated gutter in which the cilia beat outwards towards the stomach. The remainder of the duct wall is not ciliated, and here there is an inward counter-current carrying food matter towards the digestive tubules.
The secondary ducts are unbranched and are lined by cilia which reach to the centre of the duct.	The secondary ducts are short, unbranched, and are not ciliated.
Secretions from the digestive tubules are conveyed into the stomach, where only extracellular digestion occurs.	Some extracellular digestion occurs in the stomach by enzymes from the digestive diverticula as well as from the style. Additionally, digestive cells in the diverticula phagocytose and pinocytose material brought in via the counter current, and subject it to intracellular digestion.

The separation of these two subclasses of bivalves is not attributable to a primary taxobasis, but to a major sequence of events concerning more than one organ system, and resulting in the emergence of a new kind of biological model with enriched potential for exploiting new habitats and different modes of life. The magnitude of this development fully justifies recognition in the taxonomic hierarchy at the level of subclass. The above comparison has excluded consideration of the Solemyacea, which differ in important respects from the order

Nuculoida. In the Solemyacea the gut is secondarily simplified and is absent in one species of *Solemya* (Reid 1980). In the *Treatise on invertebrate palaeontology* (Moore 1969–71) the Solemyacea are treated as a second subclass of Protobranchia, but no detailed justification is offered for this view. It is here thought more appropriate to admit only one subclass of Protobranchia, with two orders, Nuculoida and Solemyoida. When sufficient evidence is forthcoming, a case could be presented for elevating the Solemyoida from order to subclass, but in our present state of knowledge such action would be premature. Moreover, if the Nuculoida and Solemyoida were to be recognized as separate subclasses, to what taxonomic rank should we elevate them jointly as Protobranchia? To treat the Protobranchia as a class would be absurd.

In the subclass Lamellibranchia, which are predominantly suspension feeders, three superfamilies have been excluded here: the Chlamydoconchacea which have been incorporated in the Leptonacea (Morton 1981*a*) and the Gaimardiacea and Cyamiacea, owing to lack of sufficient information. It has not been thought necessary to deal separately with three recently proposed new superfamilies, the Plicatulacea, Mesodesmatacea (Yonge 1975, and personal communication) and Thraciacea (Morton 1981*b*), for their taxonomic positions have not otherwise been affected by these suggestions. The proposed merging of the Crassatellacea and Carditacea into a single superfamily (Yonge 1969, 1978) has been noted, but both have been retained here as superfamilies, for convenience.

The remaining 34 superfamilies of Lamellibranchia have been arranged in five groups according to the possession of arrays of character states as specified in tables 2, 3, 4, 5 and 7. It is now necessary to consider the taxonomic status to be assigned to each of these groups of superfamilies. It is reiterated that there are no grounds for granting the status of subclass to any of these groups, which do not differ from each other to the same extent as do the Protobranchia and Lamellibranchia. It is not difficult to gain an understanding of the functional morphology of representatives of all these groups by dissection of a few specimens only, for they can all easily be equated with a common denominator such as *Anodonta*. The grades of order and suborder are sufficient for such cases.

Class Bivalvia
  Subclass I, Protobranchia
    Order 1, Nuculoida
      Superfamily 1 Nuculacea
      Superfamily 2 Nuculanacea
    Order 2, Solemyoida
      (Not discussed in this paper.)
      Superfamily 3 Solemyacea
  Subclass II, Lamellibranchia
    Order 3, Pteriomorpha

Principal characters as listed in tables 2 and 3. The composition of this order is exactly as given in the *Treatise*.

Superfamily 4 Arcacea
Superfamily 5 Limopsacea
Superfamily 6 Mytilacea
Superfamily 7 Pinnacea
Superfamily 8 Pteriacea

Superfamily 9 Ostreacea
Superfamily 10 Pectinacea
Superfamily 11 Anomiacea
Superfamily 12 Limacea

Order 4, Mesosyntheta (which signifies an intermediate condition with respect to pallial and to ctenidial fusions).

(Principal characters as listed in tables 2 and 4.)

Suborder Trigonioida
  Superfamily 13 Trigoniacea
Suborder Unionoida
  Superfamily 14 Unionacea
  Superfamily 15 Crassatellacea
  Superfamily 16 Carditacea
  Superfamily 17 Leptonacea

In the *Treatise*, the Unionacea and Trigoniacea are placed in different orders, and the three remaining superfamilies are assigned to a different subclass! The overall similarities in group 2 (table 4) belie the taxonomic distances given in the *Treatise* and warrant placing all five superfamilies in a single order. It is notable that many authorities associate the Trigoniacea and Unionacea, for example, Newell & Boyd (1975). However, the 'schizodont' condition in the Unionacea is a spurious similarity with the Trigoniacea and the latter should lie in a different suborder in recognition of its generally more primitive condition. Morris (1978) notes a close phylogenetic relationship between the Trigoniacea and the Crassatellacea.

Order 5, Anomalodesmata

Principal characters as listed in tables 2 and 5. The composition of superfamilies is as in the *Treatise*, where they are elevated to the order Pholadomyoida and subclass Anomalodesmata. Many classifications of the septibranchs are compared in a convenient tabulation by Allen & Morgan (1981), who place them in a suborder Septibranchia, order Anomalodesmata and subclass Lamellibranchia. This disposition is supported here.

Suborder Pholadomyoida
  Superfamily 18 Pandoracea
  Superfamily 19 Pholadomyacea
  Superfamily 20 Clavagellacea
Suborder Septibranchia
  Superfamily 21 Poromyacea

The Septibranchia merit recognition, at suborder level owing to their remarkable adaptations to a scavenging or carnivorous mode of life. Allen & Morgan (1981) separate the Septibranchia into two superfamilies, linking the Verticordiidae with the Poromyidae, and separating the Cuspidariidae from them. It seems strange that they should have chosen to name these superfamilies the Poromyoida and Cuspidaroida instead of using the conventional Poromyacea and Cuspidariacea.

Order 6, Gastropempta

Some difficulty is encountered as to the most appropriate nomenclature for this order. The heterodont condition is no longer confined to this order, since three heterodont superfamilies have been transferred to the suborder Unionoida. The term 'Gastropempta' is not ideal since it is troublesome to have to inspect the interior of the stomach of a Recent specimen, and the term cannot be applied to fossil material. Just as the heterodont condition is not applicable to various groups in the order Heterodonta, the Dreissenacea, Myacea, Gastrochaenacea and Pholadacea, which are secondarily edentulous, so also the gastropemptan condition is not applicable to the Gastrochaenacea and the Hiatellacea which exhibit stomachs of type IV, not type V. Table 6 indicates that the Gastrochaenacea might be correctly classified within the Gastropempta, and it is not impossible that both the Gastrochaenacea and the Hiatellacea have reverted from stomach type V to type IV as is known to have occurred in the Lucinidae, Thyasiridae and certain species of *Donax* and *Chama* (Purchon 1985). Since it is contended that the Gastropempta are of monophyletic origin, this is an important question regarding the integrity of the order Gastropempta.

Suborder Myoida
  Superfamily 22 Gastrochaenacea
  Superfamily 23 Hiatellacea
  Superfamily 24 Myacea
  Superfamily 25 Pholadacea
Suborder Veneroida

The composition of this group is the same as that for the order Veneroida listed in the *Treatise*, except for the transference of the superfamilies Leptonacea, Carditacea and Crassatellacea to the suborder Unionoida. It has not been possible to consider the taxonomic positions of the superfamilies Cyamiacea and Gaimardiacea, owing to lack of sufficient information, but as there is no reason to question their position in the Veneroida they are included in the following list of superfamilies.

Superfamily 26 Lucinacea
Superfamily 27 Chamacea
Superfamily 28 (Cyamiacea)
Superfamily 29 Cardiacea
Superfamily 30 Tridacnacea
Superfamily 31 Mactracea
Superfamily 32 Solenacea
Superfamily 33 Tellinacea
Superfamily 34 Dreissenacea
Superfamily 35 (Gaimardiacea)
Superfamily 36 Arcticacea
Superfamily 37 Glossacea
Superfamily 38 Corbiculacea
Superfamily 39 Veneracea

A few important changes have been made in this scheme of classification as compared with the results of the computer analysis (Purchon 1978, figure 1).

(i) Expansion of cluster 3 to form the suborder Unionoida, with the addition of the Leptonacea and Carditacea and with the deletion of the Lucinacea.

(ii) The merging of clusters 4 and 5 to form the suborder Veneroida, with the addition of the Lucinacea and the deletion of the Leptonacea and Carditacea.

(iii) The division of cluster 6 to form the order Anomalodesmata and the suborder Myoida, and with the addition of the Poromyacea to the former.

These improvements in judgement are attributable to the following changes.

(i) The acquisition of information that was not previously available for construction of the data matrix used in 1978.

(ii) The use of additional lines of data for restricted groups of superfamilies, in tables 3, 4, 5 and 7.

(iii) A change in policy as regards conflict of information for any one superfamily. Previously such a case was reported as a nil return. This is now thought to have been over-cautious and the *characteristic* condition has been recorded, conditions arising from a secondary simplification having been disregarded. Thus the reversion from a stomach of type V to type IV in some taxa in the Tellinacea, Chamacea and Lucinacea has been overlooked.

(iv) The present method of investigating the superfamilies in small groups has permitted the selection of suitable lines of data, and the omission of other lines of data which are seen to be irrelevant. This, with the additional lines of data mentioned in (ii), is clearly a more sensitive procedure.

The procedure adopted here is superior to the computer program previously used, because the data are no longer presented in cryptic form in a data matrix but in a form which is easy to read. The data can be amended in any way desired by addition, substitution, or deletion, in preparation for re-appraisal without recourse to any special technical facilities such as a computer. No difficulty should now be experienced in incorporating the results of new lines of research, for example, chromosome studies, or chromatography.

The proposed system of classification is better understood by reference to a diagrammatic representation of the probable sequence of functional advances in the adaptive radiation of the Bivalvia (figure 1). It is not possible to derive the Recent superfamilies of Bivalvia from any extant source, and four hypothetical ancestral stages are invoked to construct a sound evolutionary framework. In the account that follows, these four stages are described solely with respect to the advances made at each stage. The 'remote common ancestor' was a deposit-feeder with aspidobranch ctenidia and possibly with a dorsally hinged bivalve shell. As compared with this prototype, the nuculoid protobranchs (order 1) may have made important structural and functional advances, but these cannot be specified. The solemyoid protobranchs (order 2) may have advanced independently from the same origin, or may have diverged from a nuculoid ancestry.

'Hypothetical stage 1' provides a possible common origin for the filibranch superfamilies of the Pteriomorpha (order 3) and for the superfamily Trigoniacea in the order Mesosyntheta (order 4); this stage was a suspension-feeding, isomyarian bivalve stage with filibranch ctenidia, and with a stomach approximating to type IV. Evolving from this source, the Pteriomorpha (order 3) underwent a four-dimensional adaptive radiation involving: (i) extension of byssal attachment into adult life; (ii) modifications of the adductor muscles from isomyarian through heteromyarian, to monomyarian form; (iii) change of the ctenidia from filibranch to pseudolamellibranch; (iv) elaboration of the stomach from type IV to type III. This adaptive radiation exhibits elements of parallelism especially with respect to byssal attachment and to pseudolamellibranch ctenidia.

'Hypothetical stage 2' had heterodont dentition, one pallial fusion below the exhalant orifice, and eulamellibranch ctenidia. This stage contributed four superfamilies which joined with the

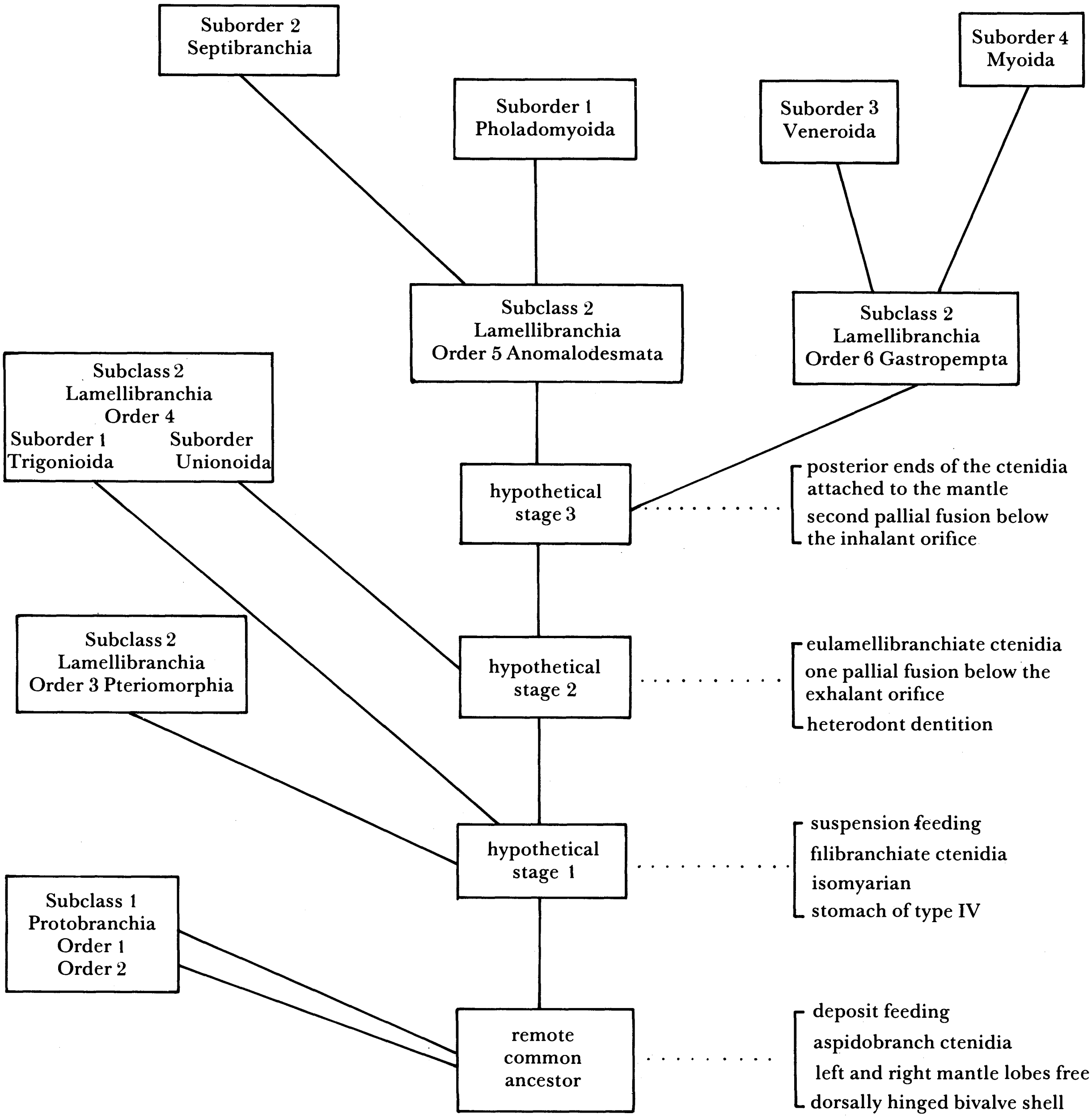

FIGURE 1. Diagrammatic representation of the probable evolutionary relationships of the two classes, six orders and six suborders in the class Bivalvia. The principal functional attributes of a remote common ancestor and of three hypothetical evolutionary stages are specified briefly.

filibranch Trigoniacea in the Mesosyntheta (order 4). While table 4 clearly demonstrates the close clustering of these five superfamilies, figure 1 indicates that the Trigoniacea diverged earlier from the remainder, and must therefore be assigned to a separate suborder. The order exhibits transition between the primitive, filibranch Pteriomorpha and the more advanced remainder of the Lamellibranchia as regards ctenidial interfilamentar tissue fusion, and the attachment of the posterior ends of the ctenidia, which are free in most lower forms. This last advance could have occurred independently in the Pteriomorpha (Mytilacea and Ostreacea), in the Unionoida (Carditacea, Unionacea and Leptonacea), as well as in all higher Lamellibranchia, and I am inclined to accept this as probable.

'Hypothetical stage 3' achieved two major advances; attachment of the posterior ends of the ctenidia, which may have occurred separately in some Pteriomorpha and some Unionoida; and a second pallial fusion separating the inhalant aperture posteriorly from the anteroventral pedal gape. After these advances the higher Lamellibranchia divided into two lineages giving the Anomalodesmata (order 5) and the Gastropempta (order 6), respectively. The Anomalodesmata retained the stomach of type IV, while the Gastropempta are marked by development of stomach type V.

The Anomalodesmata are edentulous, they exhibit simultaneous hermaphroditism, and Atkins' ctenidial type E (except for the septibranch families Poromyidae and Cuspidariidae), while some taxa possess a lithodesma, a taenioid muscle, and radial mantle glands (table 5, group 3). The Anomalodesmata are divided into two suborders in recognition of the extreme specialization of the Poromyacea to a carnivorous or scavenging mode of life.

The Gastropempta are a cluster 16 superfamilies (plus the Cyamiacea and Gaimardiacea whose stomach structure has not yet been determined) which evolved from 'hypothetical stage 3' by a monophyletic modification of the internal structure of the stomach (Purchon, 1987). There are two suborders, Myoida and Veneroida, of which the former possesses a long siphonal process with inhalant and exhalant siphons united to the tip, a deep pallial sinus, and with an edentulous hinge in some superfamilies. In two superfamilies the stomach is of type IV, possibly due to secondary simplification. The larger suborder Veneroida includes 14 superfamilies which have not been arranged in smaller clusters.

Fusion of the inhalant and exhalant siphon to their tips, forming a long, stout siphonal process, and inclusion of the periostracal groove in the pallial fusion, occur in both the Myoida and the Anomalodesmata, these being examples of parallel evolution in adaptation to the habit of deep burrowing.

As observed by Cox (1960, p. 67), 'Very seldom can it be demonstrated unambiguously that two taxa converge and unite when traced back in geological time. Either the record, even of marine invertebrates with hard parts readily preserved as fossils, is surprisingly incomplete or evolution was largely discontinuous'. This is certainly true at and above the level of superfamily, and the present study is necessarily limited to investigations of similarities which possibly include examples of parallelism or convergence; however, these can be deleted individually when they are detected.

If the events attributed to the four hypothetical ancestral stages (figure 1) truly reflect the course of evolution in the Bivalvia, then the classification, firmly based on structural similarities, is also a natural, phyletic classification. Starting from a deposit-feeding, protobranchiate origin, the evolutionary progression would have involved:

(i) development of suspension-feeding, with filibranch ctenidia, and a stomach of type IV;

(ii) improved suspension-feeding, with eulamellibranch ctenidia whose posterior ends are attached, a heterodont dentition, and a first pallial fusion forming a complete exhalant orifice;

(iii) further improvement to the control of suspension-feeding by a second pallial fusion, forming complete inhalant and exhalant orifices;

(iv) development of a stomach of type V, increasing control of ingestion of food particles within the digestive diverticula;

(v) development of the scavenging or carnivorous habit and colonizing nutritionally impoverished deep water marine deposits, by formation of a muscular septum of ctenidial origin, and a gizzard-like muscular stomach.

Each of these hypothetical stages is inferred from the component clusters in the array of recent superfamilies of bivalves: the Protobranchia, the Pteriomorpha, the Unionoida, Anomalodesmata, Gastropempta and Septibranchia respectively. Adaptive radiations occurred within each of these groups, in some cases re-enacting in parallel the advances listed above.

This paper is confined to analysis of the distribution of structural features, to the exclusion of phyletic considerations. Figure 1 is a flow diagram which makes no statement as to the number of phylogenies which may have passed independently through hypothetical stages 1, 2, and 3. It is now appropriate to test these findings in relation to those of Pojeta & Runnegar (1985). These authors interpret the earliest fossil bivalve genera, *Pojetaia* Jell and *Fordilla* Barrande, as the earliest representatives of the Palaeotaxodonta and Isofilibranchia, respectively. They are structurally similar and probably had a common ancestry. With respect to figure 1 they could lie in the *upper* part of the box 'remote common ancestor', leaving the lower part of the box available for an even more ancient ancestor which has not yet been found. *Pojetaia* represents the ancestry of the remainder of the Palaeotaxodonta, from which the Solemyoida diverged in the Ordovician. *Fordilla*, on the other hand, was probably ancestral to the remainder of the Isofilibranchia and the Anomalodesmata.

According to Pojeta & Runnegar (1985), whereas the Isofilibranchia gave rise to the Anomalodesmata in the Ordovician, the Palaeotaxodonta gave rise to the Heteroconchia also in the Ordovician, and the Pteriomorpha were an offshoot of the Heteroconchia. These propositions can be accommodated in figure 1 if we accept that two major phylogenies must have passed through hypothetical stages 1, 2, and 3. One of these lineages, originating from *Fordilla*, yielded the Anomalodesmata with its two suborders Pholadomyoida and Septibranchia. The other lineage, starting from *Pojetaia*, led to the subclass Protobranchia and to the Heteroconchia with its three component orders Pteriomorpha, Mesosyntheta and Gastropempta. In other words, although the Anomalodesmata and Gastropempta are seen in figure 1 to differ structurally only after hypothetical stage 3, their phylogenies had diverged substantially earlier.

SUMMARY

(i) The principal structural and functional differences between the Protobranchia and the remainder of the class are tabulated, and are evaluated as representing division of the class into two subclasses, the Protobranchia and the Lamellibranchia.

(ii) The various degrees of pallial fusion and of ctenidial structure are used to grade the superfamilies of Lamellibranchia as regards primitive, intermediate, or advanced condition. Variations in hinge dentition, and in stomach structure, are also used and in six tabulations twenty-two superfamilies are constant in their groupings, implying that these four organ systems are all important in the early stages of evolution in the Lamellibranchia.

(iii) The recent superfamilies of Lamellibranchia are sorted into clusters by means of a series of tabulations of character-states exhibited in the principal organ systems. These tabulations specify the typical, but not diagnostic, features of each cluster of superfamilies. Full supporting evidence is provided in a way which permits subsequent amendment, incorporation of new evidence, and re-evaluation without difficulty, should the need arise.

(iv) In the absence of phyletic evidence, this classification is necessarily based on features of structural and functional similarity, but a diagram including four hypothetical ancestral stages outlines the probable evolutionary sequence, with some parallelism in the later stages of adaptive radiation.

(v) The classification adopted here agrees closely with that used in the *Treatise on invertebrate palaeontology*, but differs in three important respects:

(*a*) within the Protobranchia the Solemyoida are downgraded from subclass to order, owing to lack of supporting evidence at present;

(*b*) within the Lamellibranchia three subclasses are suppressed because the differences among representative taxa are too trivial to justify so extreme a taxonomic distinction;

(*c*) the primitive Lamellibranchiate superfamilies Leptonacea, Crassatellacea, and Carditacea are transferred from the Veneroida into an enlarged suborder Unionoida.

(vi) The system of classification adopted here differs in various minor respects from the clustering obtained in an earlier computer analysis, and is regarded as more reliable owing to availability of additional information and to the adoption of more sensitive methods of analysis.

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APPENDIX

TABLE A 1. CORRELATION BETWEEN DEGREES OF FUSION OF THE MANTLE FOLDS, AND HINGE STRUCTURE

degree of fusion of pallial folds	pseudoctenodont	schizodont	edentulous	heterodont
(5) two fusions, including periostracal groove			Poromyacea Myacea	Hiatellacea Mactracea
(4) two fusions, inner and middle folds			Clavagellacea Pholadacea Pandoracea Pholadomyacea Gastrochaenacea	Veneracea Solenacea
(3) two fusions, inner fold only			Dreissenacea	Corbiculacea Glossacea Arcticacea Tellinacea Tridacnacea Cardiacea Lucinacea Gaimardiacea Cyamiacea Chamacea
(2) one fusion, inner fold only		(Unionacea)		Leptonacea Crassatellacea Carditacea
(1) no pallial fusions	Limopsacea Arcacea	Trigoniacea	Anomiacea Pectinacea Ostreacea Pinnacea Pteriacea Mytilacea Limacea	

TABLE A 2. CORRELATION BETWEEN DEGREES OF FUSION OF THE MANTLE FOLDS, AND THE TYPE OF STOMACH

degree of fusion of pallial folds	stomach type III	stomach type IV	stomach type V	stomach type II
(5) two fusions, including periostracal groove		Hiatellacea	Myacea Mactracea	Poromyacea
(4) two fusions, inner and middle folds		Clavagellacea Pandoracea Pholadomyacea Gastrochaenacea	Pholadacea Veneracea Solenacea	
(3) two fusions, inner fold only			Corbiculacea Glossacea Arcticacea Tellinacea Tridacnacea Cardiacea Lucinacea Dreissenacea Chamacea	
(2) one fusion, inner fold only		Leptonacea Unionacea Crassatellacea Carditacea		
(1) no pallial fusions	Ostreacea Pinnacea Pteriacea Mytilacea Limopsacea Arcacea	Trigoniacea Limacea Anomiacea Pectinacea		

TABLE A 3. CORRELATION BETWEEN CTENIDIAL STRUCTURE AND HINGE STRUCTURE

ctenidial structure	pseudoctenodont	schizodont	edentulous	heterodont
(4) septibranch			Poromyacea	
(3) eulamellibranch		(Unionacea)	Clavagellacea Pandoracea Pholadomyacea Gastrochaenacea Pholadacea Myacea Dreissenacea	Hiatellacea Veneracea Solenacea Corbiculacea Glossacea Arcticacea Tellinacea Tridacnacea Cardiacea Lucinacea Gaimardiacea Mactracea Cyamiacea Chamacea Leptonacea Crassatellacea Carditacea
(2) pseudolamellibranch			Ostreacea Pinnacea Limacea	
(1) filibranch	Limopsacea Arcacea	Trigoniacea	Anomiacea Pectinacea Pteriacea Mytilacea	

hinge structure

TABLE A 4. CORRELATION BETWEEN CTENIDIAL STRUCTURE AND STOMACH STRUCTURE

ctenidial structure	stomach type III	stomach type IV	stomach type V	stomach type II
(4) septibranch				Poromyacea
(3) eulamellibranch		Clavagellacea Pandoracea Pholadomyacea Gastrochaenacea Hiatellacea Leptonacea Unionacea Crassatellacea Carditacea	Veneracea Solenacea Pholadacea Myacea Mactracea Corbiculacea Glossacea Arcticacea Tellinacea Tridacnacea Cardiacea Lucinacea Chamacea Dreissenacea	
(2) pseudolamellibranch	Ostreacea Pinnacea	Limacea		
(1) filibranch	Pteriacea Mytilacea Limopsacea Arcacea	Trigoniacea		

Table A 5. Correlation between stomach types and hinge structure

(Brackets indicate eight groups of superfamilies which remain associated throughout tables 2, A1, A2, A3, A4 and A5. That is, within each of these groups the same character-states are found with respect to pallial fusion, ctenidial structure, hinge teeth, and stomach structure.)

stomach type II			Poromyacea	
stomach type V			Pholadacea Myacea Dreissenacea	Veneracea Solenacea]8 Corbiculacea Glossacea Arcticacea Tellinacea Tridacnacea Cardiacea Lucinacea]7 Mactracea Chamacea
stomach type IV		(Unionacea) Trigoniacea	Clavagellacea Pandoracea Pholadomyacea Gastrochaenacea]5 Limacea Anomiacea Pectinacea]4	Hiatellacea Crassatellacea Carditacea]6 Leptonacea
stomach type III	Limopsacea Arcacea]1		Ostreacea Pinnacea]3 Pteriacea Mytilacea]2	
	pseudoctenodont	schizodont	edentulous	heterodont

hinge structure