
An Analytical Approach to a Classification of the Bivalvia

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Phil. Trans. R. Soc. Lond. B 1978 **284**, 425-436

doi: 10.1098/rstb.1978.0079

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An analytical approach to a classification of the Bivalvia

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WITH AN APPENDIX BY G. CLARKE

A scheme of classification should depend on many organ systems, not on one. How should this be achieved, resolving conflict between different bodies of evidence? In the *Treatise on invertebrate paleontology* (vols N1–N3) special importance was apparently attached to *one* feature, the dentition. It is not clear how other criteria were integrated with this.

The anatomical features listed in diagnoses of superfamilies and higher taxa in the *Treatise* were tabulated in a few alternative character-states. Several of these features were rejected as lacking classificatory significance. Nine anatomical features were selected as potentially useful, some drawn from diagnoses in the *Treatise*, and others from reviews in literature. A matrix of data on the character-states for these nine anatomical features, for all 40 Recent superfamilies of Bivalvia, has been analysed by computer. This compared each superfamily in turn with all others, and clustered those superfamilies showing the highest percentage similarity of phenetic characters. Each cluster was assigned those characters common to all members of the group, and the clustering process was repeated. Each stage in clustering was reported in terms of percentage similarity, and a dendrogram was drawn by data plotter.

The investigation excluded variability below the superfamily, thus limiting confusion by convergence; unfortunately it also excluded information on phylogenetic relations between superfamilies (which could easily be added when available). The exclusively phenetic data are presented compactly in the dendrogram, which should be taken fully into account by anyone designing a phylogenetic classification.

The six clusters in the dendrogram correspond generally with the classification in the *Treatise*, which offers confidence in the methods used, but some changes are suggested. The procedure is objective, and can be repeated with suitable amendments, e.g. for correction of errors found, for exclusion of unsuitable data, and inclusion of newly acquired useful data.

It is suggested that the Bivalvia comprise only two subclasses, deposit-feeding proto-branchs and suspension-feeding lamellibranchs, thus recognizing the major functional differences between these contrasted life forms. The lamellibranchs can best be interpreted as a matrix of about 12 × 12 families which are evolving partly in parallel, and among which the taxonomic differences are of a lower degree.

1. INTRODUCTION

Ridewood (1903) divided the Class Bivalvia into three orders, Protobranchia, Eleutherorhabda and Synaptorhabda on the basis of ctenidial structure. He accepted that classificatory systems based on a single character must prove unsatisfactory; nevertheless he advocated comparable reviews of other organ systems and the formation of classificatory tables, based each on a single character, 'so that some future taxonomist might evaluate the compact and readily assimilable data, and arrive at the truth concerning the phylogenetic history of the class.'

In subsequent years further monographic studies have been made on the ciliation of ctenidial filaments by Atkins (1938), on the relation between the ctenidia and the labial palps (Stasek 1963), on the structure of the stomach (Purchon 1956, 1957, 1958, 1960*b*); and on the structure

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of the shell (Taylor, Kennedy & Hall 1969, 1973); Yonge has investigated mantle fusion (1948, 1957), and has reviewed the occurrence of a functional byssus throughout the class (1962).

Following the recommendation of Ridewood, a tabulation was made of different systems of classification with special reference to the Protobranchia, Filibranchia and Pseudolamellibranchia. Some of the entries concerned complete classificatory systems, rather than single organ systems as had been suggested by Ridewood. It became clear that it would be difficult 'to arrive at the truth concerning the phylogenetic history of the Lamellibranchia', owing to the lack of complete accord between different bodies of information (Purchon 1960*a*).

The *Treatise on invertebrate paleontology* (subsequently referred to as the *Treatise*) comes closer to Ridewood's recommendation in tabulating information on ctenidial structure, ctenidial ciliation, stomach type, association between the ctenidia and the labial palps, and on shell microstructure, for all extant superfamilies of bivalves (vol. N, p. 211); a small tabulation of data on ligaments is also provided. There is continuing sympathy, therefore, with the suggestion made so long ago by Ridewood, but it does not seem to have been put to serious test. How could this be done? If the data derived from two such studies are predominantly in agreement, how can one resolve the outstanding differences? If one is dealing with many such reviews the treatment of the conflicting evidence becomes increasingly difficult. Such difficulties could not be resolved by subjective decisions on the relative importance of different items of information.

Atkins (1938) faced such a problem with respect to her group 2, Microciliobranchia, which she described as the order Pseudolamellibranchia emended to include the suborders Arcacea (excluding the Trigoniidae) and Anomiacea. Purchon (1960*a*) concluded, from study of Atkins's text and tabulations, that she was driven to placing the Ostreacea in the group Microciliobranchia in defiance of her own evidence, 'from consideration of phylogenetic relationships, based on other characters'. Electron microscope studies by Owen & McCrae (1976) support the view that the Ostreacea should not have been assigned to the Microciliobranchia. Arising from this, it is emphasized that to meet Ridewood's recommendations any classification based on exhaustive study of a single organ system should draw exclusively on the evidence and should not be modified by other considerations.

2. THE DATA

This study concerns the interrelations of forty extant superfamilies of bivalves listed in the *Treatise*. The data have been drawn primarily from diagnoses of these superfamilies and higher taxonomic categories in the *Treatise*, and were recorded in one or another of a small number of alternative character-states. Where the information was not available, it was sometimes found in a monographic study of a relevant family or genus, in those superfamilies with very few and closely related constituents, e.g. the Tridacnacea, where the information so obtained could safely be regarded as characteristic of the superfamily as a whole.

It was found necessary to exclude descriptions of sculpture and shell shape, which could not easily be reduced to a number of simple alternative states. Where a character was variable within a superfamily, and where the information was unavailable, a NIL entry was recorded. Some additional columns of data were obtained from Atkins (1938); Taylor *et al.* (1969, 1973); Yonge (1962), and Purchon (1956, 1957, 1958, 1959, 1960*a, b*).

After the data had been tabulated, each column was considered in turn, excluding from further consideration those which were deemed unlikely to prove useful:

Shell symmetry: equivalve/inequivalve; equilateral/inequilateral.

Beaks: prosogyrous/orthogyrous/opisthogyrous.

Ligament: prosodetic/amphidetic/opisthodetic; external/internal; ali-/pari-/dupli-/multi-vincular; primary/secondary.

Trueman (1969, p. 62) considers the ligament to be unsuitable for use in classification because of its adaptive characters.

Closure of valves: complete/anterior gape/byssal gape/posterior gape.

Description of shell: presence of cardinal area; lunule; escutcheon; nymph.

Mantle fusion: types A, B, and C of Yonge (1948, 1957).

This very important category of information was excluded because of uncertainty how to score the information available for some superfamilies.

Siphons: simple orifices/short siphons/long separate siphons/long united siphons.

There was too much variation within some superfamilies.

Labial palps: the relation between the ctenidia and the palps, types 1, 2 and 3 of Stasek (1963).

This important information was not available for a sufficiently large number of superfamilies.

Exclusion of the above data by subjective decision is regretted, but any error in so doing could easily be rectified in the future, should this be desirable.

There remained nine columns of data which were considered 'useful' in the present context. These were given equal weighting, there being no good reason for doing otherwise. (There is no explicit weighting of characters in currently accepted systems of classification, but dentition was thought to be most satisfactory by Newell (1969, p. 49).) The alternative states for these nine characters are:

- (1) Hinge teeth: 1, ctenodont; 2, pseudo-ctenodont; 3, edentulous; 4 heterodont; 5 schizodont.
- (2) Adductor scars: 1, isomyarian; 2, heteromyarian with anterior adductor the larger; 3, heteromyarian, typical; 4, monomyarian; 5, abmyarian (both adductors lost).
- (3) Pallial sinus: 1, pallial line entire; 2, sinus weak; 3, sinus deep.
- (4) Pallial fusions: 0, no fusions; 1, one fusion below exhalant orifice; 2, two fusions, the second being below an anterior inhalant opening (found only in some of the Leptonacea); 3, two fusions, both posterior and short; 4, two fusions of which the anterior is long. Owing to the restricted occurrence of the fourth pallial orifice, this was not included.
- (5) relation with the substratum: 1, cementation; 2, byssal attachment in the adult stage in at least some examples; 3, no byssal attachment, but buried in substratum. In the Ostreacea a phase of byssal attachment in past history is presumed, though fossil evidence is lacking.
- (6) Ctenidial structure: 1, protobranch; 2, filibranch; 3, pseudolamellibranch; 4, eulamellibranch; 5, septibranch.
- (7) Ctenidial ciliation: 1, microciliobranchia; 2, macrociliobranchia. The Ostreacea are put in the Macrociliobranchia, owing to sustained criticisms of Atkins' dispositions.
- (8) Stomach structure: stomach types 1, 2, 3, 4 and 5.
- (9) Shell structure: eleven mutually exclusive groups, as discussed below:

Taylor *et al.* (1969, 1973) reviewed the structure of the shell and summarized their findings in a tabulation of twelve shell characters.

Examination of these data reveals that 26 superfamilies fall into eight groups, all members of any one group showing an *identical* array of 12 shell characters. Of the remaining 14 superfamilies, eight fall into three more groups, the members of any one of these groups having a high level of similarity of shell characters, but not an identical array. The outstanding six

superfamilies join one or other of these eleven primary clusters, at decreasing levels of similarity. The group containing the Anomiacea and Limacea extends to include first the Ostreacea and then the Pectinacea. The group comprising the Unionacea, Trigonacea and Pholadomyacea, joins with that containing the Pandoracea and Poromyacea, and these are then joined by the Clavagellacea and the Nuculacea. The three protobranchiate superfamilies are isolated from each other in this study.

The data on shell structure are here presented in a single column showing the eleven mutually exclusive groups of superfamilies.

TABLE 1. MAJOR ANATOMICAL VARIABLES

	hinge teeth	adductor scars	pallial sinus	number of pallial fusions	relation with substratum	type of ctenidium	ciliation of ctenidium	type of stomach	shell structure
1. Nuculacea	1	1	1	0	3	1	2	1	A
2. Nuculanacea	1	1	2	3	3	1	2	1	2
3. Solemyacea	3	2	A	A	3	1	2	A	10
4. Arcacea	2	1	1	0	2	2	1	3	5
5. Limopsacea	2	1	1	0	A	2	1	3	5
6. Mytilacea	3	3	1	1	2	2	2	3	9
7. Pinnacea	3	3	1	0	2	3	1	3	9
8. Pteriacea	A	4	1	0	2	2	1	3	9
9. Pectinacea	B	4	1	0	2	2	1	4	B
10. Anomiacea	3	4	1	0	2	2	1	4	1
11. Limacea	3	4	1	0	2	3	1	4	1
12. Ostreacea	3	4	E	1	2	3	2	3	C
13. Unionacea	5	1	1	1	3	4	2	4	7
14. Trigonacea	5	1	1	0	3	2	2	4	7
15. Lucinacea	4	1	1	B	3	4	2	B	11
16. Chamacea	4	1	1	4	1	4	A	C	5
17. Leptonacea	4	1	1	C	2	4	2	D	6
18. Chlamydoconchacea	3	5	B	1	B	4	B	E	D
19. Cyamiacea	4	1	1	1	2	4	C	F	2
20. Carditacea	4	A	1	1	2	4	D	4	5
21. Grassatellacea	4	1	1	1	3	4	2	4	11
22. Cardiacea	4	1	1	3	2	4	2	5	4
23. Tridacnacea	4	4	1	3	2	4	E	5	4
24. Mactracea	4	1	C	3	3	4	2	5	4
25. Solenacea	4	1	2	E	3	4	2	5	6
26. Tellinacea	4	1	3	3	3	4	2	G	3
27. Dreissenacea	3	3	1	3	2	4	2	5	4
28. Gaimardacea	4	1	1	3	3	4	F	H	2
29. Arcticacea	4	1	1	3	3	4	2	5	6
30. Glossacea	4	1	1	3	C	4	G	5	6
31. Corbiculacea	4	1	D	D	2	4	2	J	E
32. Veneracea	4	1	3	3	D	4	2	5	3
33. Myacea	3	B	3	4	E	4	2	5	6
34. Gastrochaenacea	3	3	3	4	3	4	2	4	6
35. Hiatellacea	4	1	3	4	2	4	2	4	10
36. Pholadacea	3	1	3	4	3	4	2	5	10
37. Pholadomyacea	3	1	3	4	3	4	H	K	7
38. Pandoracea	3	1	3	4	F	4	2	4	8
39. Poromyacea	4	1	2	3	3	5	J	2	8
40. Clavagellacea	3	5	3	4	3	4	K	4	F

The data described above for the nine different anatomical features are recorded as numerals in a tabulation prepared for analysis by computer (table 1). Within each vertical column NIL entries are recorded in a series of different letters, ensuring that these cannot be mistaken for comparable characters during the computer analysis.

3. THE ANALYSIS

A computer program in ALGOL, had been designed for study of phenetic similarities of bivalve genera (Purchon & Brown 1969), and had proved reasonably satisfactory, success having been limited chiefly by the small number of genera for which sufficient information had been available. This computer program was rewritten in FORTRAN and used after a minor amendment adapting it to the relatively small body of data being analysed. This ensured the same results regardless of the order in which the cards for the individual superfamilies were read in. The clustering process is of the 'single link' type, i.e. an additional superfamily joins a cluster of superfamilies if it shows the specified percentage similarity with at least *one* of the constituents of the cluster.

The program compared the data for each superfamily in turn with that for every other superfamily; it reported those two (or more) superfamilies with the closest resemblance to each other, the coefficient of resemblance being expressed as a percentage, and it combined these closely similar superfamilies into a primary cluster possessing the attributes common to all members of the cluster. The process was repeated with the reduced number of free superfamilies, thereby progressively reducing the number of these while increasing the sizes of some of the clusters.

The important features in the computer print-out are the constituents of the principal clusters, these superfamilies having a high proportion of anatomical features in common. These clusters report on phenetic resemblances and not upon phylogenetic relations, and these resemblances may derive in part from convergent evolution; this compactly presented phenetic evidence should not be disregarded when designing a phylogenetic classification. If convergence is suspected in a particular cluster, it should be possible to specify precisely which anatomical features are concerned. The data could then be edited to exclude the convergent items, and a fresh print-out would report on the consequences of the amendments.

It is emphasized that the later stages in clustering are of no significance, owing to the limited body of data presently available for analysis.

4. THE RESULTS

The computer print-out specifies all the data read in, permitting a check for accuracy; it records the sequence of clustering at specified levels of percentage similarity, and provides a dendrogram representation of the clusters. The relative positions of the constituents of a cluster can be rearranged in many alternative and equally satisfactory positions. For convenience in studying the dendrogram the constituent superfamilies have been arranged, so far as is possible, in the same order as that in the classification adopted in the *Treatise* (numbered from 1 to 40). Where the constituents of a cluster form a regular numerical series, the cluster conforms with accepted practice, unless the cluster crosses the barrier between two adjacent major taxa. Where the numerical series contains marked deviations from an arithmetic progression, there is a

appreciable difference from accepted practice. The *Treatise* organizes the superfamilies into 6 subclasses, and the dendrogram gives a small number of major clusters, with much similarity between the two (see figure 1).

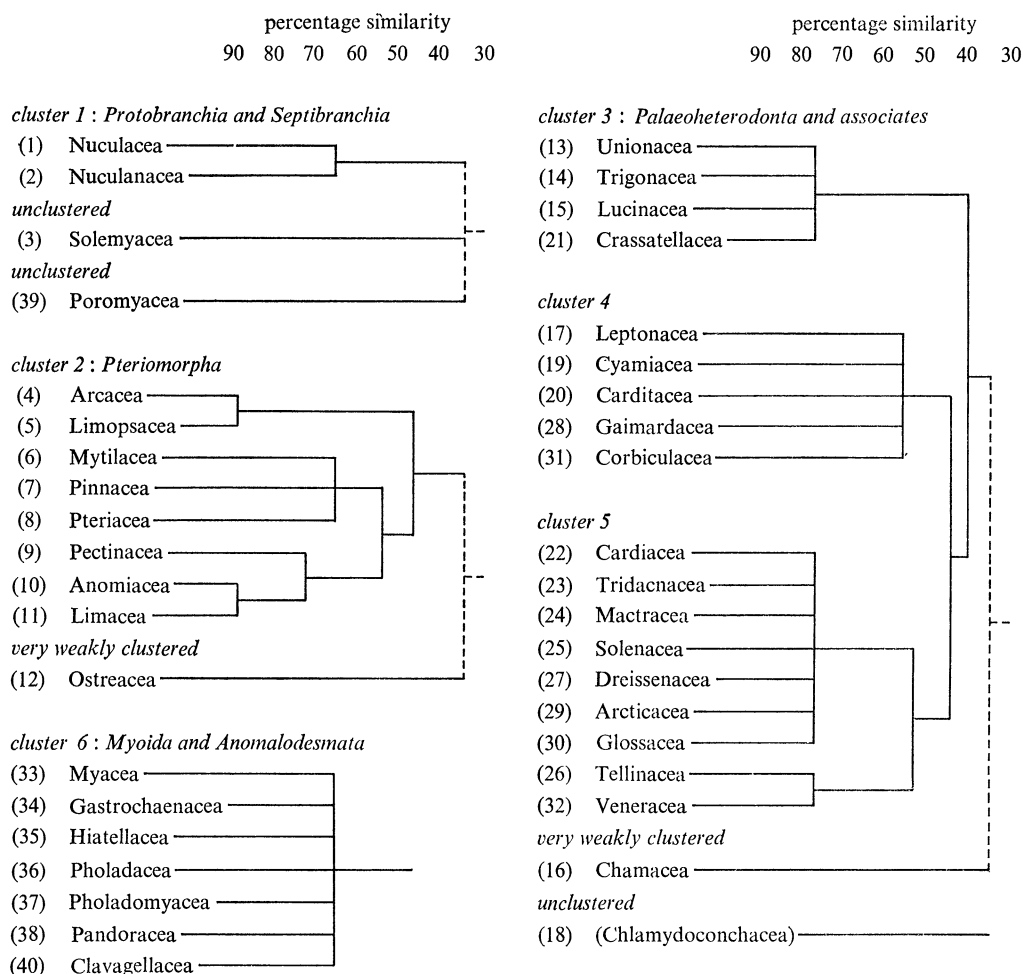


FIGURE 1. Dendrogram derived from phenetic characters of forty Recent superfamilies of Bivalvia, expressed in percentage similarity, showing six major clusters. The three clusters in the right hand column correspond with the Palaeoheterodonta and the Veneroida. Too little information was available regarding the Chlamydoconchacea. See the text for further discussion.

5. DISCUSSION

Both Cox (1960) and Newell (1969, p. 210) criticized 'single character' classifications, e.g. of Atkins (1938) and of Purchon (1963). While accepting this criticism, it remains desirable to pursue Ridewood's suggestion to develop classificatory tables, each based on detailed investigation of a single organ system, for cumulative use in taxonomy at some future time.

Newell (1969, p. 207), observed that 'the present outline of classification undertakes to synthesize and integrate the best features of the most widely used systems. It is neither basically new nor based on adequate morphologic and phylogenetic information'. To the present writer the diagnoses of superfamilies appear to be descriptive rather than diagnostic, and emphasis is apparently placed upon only one character, the dentition (Newell 1969, p. 49).

The present study, based on phenetic material investigates what information may have been used and how this might best be interpreted, and offers a method whereby newly available information could readily be assimilated. It would be desirable to find some way of incorporating relevant palaeontological information.

A major criticism of the present investigation could be that its results might be confused by widespread convergent evolution. Since the exercise is based upon diagnoses of superfamilies and higher categories this should exclude effects of adaptive radiation at a lower level, but with the loss of some information. How serious this loss of information may be is hard to tell.

The dendrogram supports the view offered in the *Treatise* (Newell 1969, pp. 52 and 215) that the Nuculacea and Nuculanacea comprise a homogeneous, natural group, the Nuculoida, from which the Solemyacea should be isolated. The fact that the differences between the Nuculoida and the Solemyacea are as great even as the differences between both of these groups and the wholly unrelated Poromyacea, is sufficient reason for regarding the Solemyacea as a second, independent lineage of protobranchs.

The nine superfamilies comprising the Pteriomorpha form a cluster conforming with accepted taxonomic practice save for the Ostreacea, which do not resemble the Pteriacea as closely as might have been expected from the classification in the *Treatise*. Cox (1960) thought that the Ostreacea possess a combination of characters which justify their separation from the pteriids and pectinids, a view which is supported by the phenetic dendrogram.

The Unionacea and Trigonacea are currently isolated from the Heterodonta in a subclass Palaeoheterodonta. The dendrogram indicates a high level of similarity between the Unionacea, Trigonacea and two superfamilies in the Heterodonta. Taylor *et al.* (1973) show identity of shell structure among the Unionacea, Trigonacea and Pholadomyacea. Atkins (1938) reported that only the Unionidae possessed ctenidia of type D, but it is now known that this type of ctenidium is shared with *Begonia semiorbiculata* in the Carditacea (unpublished personal observation). Pojeta & Runnegar (1974) state that many unionaceans have cardinal and lateral teeth. Cox (1960) thought that the Trigonacea should be separated from the Unionacea and placed in a separate order, while Newell (1969, pp. 52 and 215) said that 'the Palaeoheterodonta may be an artificial assemblage, the Trigonacea and Unionacea probably having arisen independently from an actinodont ancestry.' Thiele (1935) classified the Schizodonta (Unionacea and Trigonacea) as a suborder of Eulamellibranchia, although the Trigonacea are filibranchs. To conclude, it is suggested that the superfamilies Unionacea and Trigonacea should not be isolated in a subclass Palaeoheterodonta, but should be transferred into the subclass Heterodonta.

As regards the subclass Heterodonta, possibly enriched by addition of the Unionacea and Trigonacea, we have already considered the Lucinacea and Crassatellacea. Two further clusters, one of five superfamilies, and one of nine superfamilies, all fall within the order Veneroida, in harmony with the classification of the *Treatise*. Cox (1960) grouped the Chamacea in a distinct order of Heteroconchia, together with three fossil groups, implying that the Chamacea are not closely related to any other Recent eulamellibranchs. The isolated position of the Chamacea in the dendrogram supports that view. Not much weight should be attached to the manner of clustering of these groups, at 43% similarity; more information would clarify their relations, possibly throwing all into one large cluster, the Veneroida.

The last major cluster of the dendrogram includes all four superfamilies of the Myoida (Heterodonta), together with three superfamilies of Anomalodesmata, these seven superfamilies having clustered simultaneously at 66% similarity. Detailed examination of the nature of the

clustering within this group revealed nine pairings of superfamilies at an equally high level. Four of these lay between members of the Myoida, and five were between one superfamily of Myoida and one superfamily of Anomalodesmata. Thus the phenetic evidence opposes the isolation of the Anomalodesmata from the Myoida. Analysis of the data on shell structure (Taylor *et al.* 1973) shows a loose clustering of the Pandoracea and Poromyacea with the Clavagellacea, and with the Pholadomyacea, Unionacea and Trigonacea.

The reviews of the Lucinacea by Allen (1958) and the Verticordiidae by Allen & Turner (1974), establish how the septibranch condition could have arisen from that of an eulamellibranch, as regards both the ctenidium and the stomach. Adaptation for life in mud at successively greater depths on the sea floor will have involved living in water increasingly impoverished in microscopic suspended particles. The ctenidium would tend to lose sorting mechanisms, and everything entering the mantle cavity would be ingested regardless of size and quantity. The development of convulsive, muscular movements of the ctenidium/septum for respiratory/feeding purposes would not interfere with the simplified ciliary mechanisms. As in the Lucinacea, which are adapted to an infaunal life in impoverished circumstances, the stomach also would probably become simplified. It would become unnecessary to guard the entrances of the ducts of the digestive diverticula from access by very large particles, or by excessive quantities of fine particles. The stomach could therefore become simplified compared with that of a typical filter-feeding bivalve, by (1) reduction and loss of ridged and grooved ciliary sorting areas, (2) reduction in number and enlargement in size of the orifices of ducts leading to the digestive diverticula, and (3) withdrawal of the major typhlosole and the intestinal groove from proximity to these orifices. The resulting condition, from whatever structural origins, would tend towards a simplified stomach of type 4. Where the diet transferred primarily to small animals such as ostracods, copepods, etc., increase in extent of the gastric shield and development of muscles in the gastric wall could be expected, yielding instead a stomach of type 2, as in the septibranch *Cuspidaria*.

The fact that the septibranch condition may have arisen thus, from an eulamellibranch origin, and at a comparatively recent geological date, should not necessarily preclude the isolation of the septibranchs in a separate order, as recommended on anatomical grounds by Cox (1960).

The dendrogram indicates that the Poromyacea differ from all other superfamilies, being no less isolated on phenetic grounds than the Solemyacea. Serious consideration should be given to granting the same measure of taxonomic independence as that accorded to the Solemyacea.

(a) *Subdivision of the Bivalvia into subclasses*

At a symposium of the Malacological Society of London in 1959, three independent submissions emphasized a fundamental difference between the Protobranchia and the filter-feeding Lamellibranchia. It was concluded that this warranted the establishment of two subclasses of Bivalvia. The *Treatise* held this to be a retrograde decision in so far as one of these subclasses was to include the Nuculoida and Solemyoida. However, Cox (1960) recognized three subclasses, the Protobranchia (Pelseneer), including the Solemyacea, the Pteriomorpha (Beurlen) and the Heteroconchia (Hertwig).

This prompts me to ask: what is meant precisely by a subclass? Newell (1969, p. 213) says, 'the function of subclasses of Bivalvia is to provide a few major divisions for convenience in discussion and taxonomic sorting and ultimately to distinguish the trunk lines of phylogenetic

descent.' This definition does less than justice to the concept. Speaking as much as a zoologist as a malacologist, I consider that distinctions at the level of subclass should be reserved for major differences in structure and function. These might be provided *either* by a few diagnostic features of major importance *or* by a barrage of minor differences which are encountered at every turn. The former could be applied in comparing the Nuculoida and the filter-feeding Lamellibranchia, where there are fundamental differences in ctenidial structure and function, and also in the structure and functioning of the stomach and digestive diverticula (Owen 1959; Purchon 1959; Yonge 1959).

Turning to the filter-feeding Lamellibranchia, and concentrating upon those genera of which I have personal experience, I do not see those fundamental differences which I would expect to find at subclass level when comparing genera assigned variously to the subclasses Pteriomorpha, Palaeoheterodonta, Heterodonta, and Anomalodesmata. I cannot, from experience, envisage these as representing four contrasted kinds of animal. All, I feel, are variants on the same general theme, and should be assigned to the same subclass. I do not suspect any major discontinuity among lamellibranchs except, perhaps, for septibranchs, e.g. *Cuspidaria*. Leaving aside the question of the Solemyoida on which I cannot comment, the Bivalvia should be divided into two subclasses, one for Protobranchia and the other for filter-feeding Lamellibranchia.

It is interesting to note that Newell (1969, p. 213) said 'of the 6 subclasses, the Palaeotaxodonta and Pteriomorpha are considered by many to be natural, the other four are probably artificial.'

While recognizing the integrity of the Pteriomorpha, this could be recognized by ordinal status within a subclass Lamellibranchia. In view of affinities shown by the Recent Palaeoheterodonta, and also by the Anomalodesmata, both with constituents of the Heterodonta, further thought should be given as to how all these might be grouped at ordinal level.

Some attention should be paid to the discontinuities which separate taxa. Many species and genera are virtually unknown as living, functioning animals, and as new knowledge accumulates we are likely to find intermediate stages diminishing the differences between taxa. At this level taxonomic discontinuities are mere '*taxocrannies*'. At the other end of the scale the discontinuities are different. At the levels of phylum and class and, to a lesser extent at subclass, the animals are representatives of alternative kinds of biological model, each of which is designed to work in a particular way and under prescribed circumstances. The image of each biological model may be blurred by the adaptive radiation to which it may have given rise, but this should not alter the magnitude of the taxonomic discontinuity between one kind of biological model and another. Such a major discontinuity may be thought of as a *taxochasm*, which cannot be crossed. These are not technical terms, but colourful expressions which may assist our thinking. I see only one taxochasm here, that between the deposit-feeding protobranchs and the filter-feeding lamellibranchs.

(b) *Phases in evolution of bivalves*

The earliest deposit-feeding phase was probably confined to nutritious sediments, developing an adaptive radiation yielding two main products, the Nuculoida and the Solemyoida (figure 2a).

From these deposit-feeders there developed a nucleus of filter-feeding bivalves by structural and functional adaptations of the organs in the mantle cavity (figure 2b). This innovation exploited a new niche, utilizing nutrient-rich supernatant waters, and was so successful that it laid the foundations for all the filter-feeding lamellibranchs. This involved elaboration of the ctenidia, labial palps, and also the stomach (figure 2c). It should be emphasized that although

we can recognize strata which can be so arranged as to indicate a probable course of events in improving functional efficiency, we cannot preclude the possibility of a return to a simpler or more primitive condition, in some cases, through neoteny. This could have happened with respect to the ctenidia, and also to the interior of the stomach.

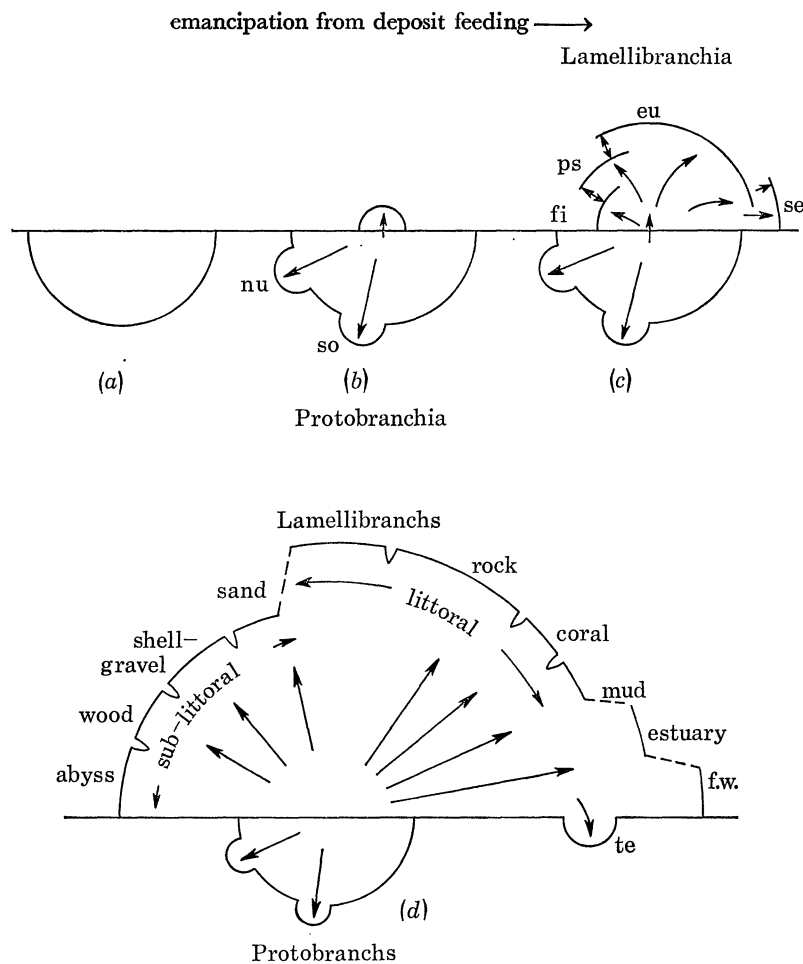


FIGURE 2. Diagram representing the main phases in the evolution of the Bivalvia. The horizontal line represents the interface between soil and water. (a) Ancestral occupation of a deposit-feeding niche. (b) Adaptive radiation of deposit-feeding protobranchs, with emergence of nuculoid (nu) and solemyoid (so) lineages. Origin of filter-feeding capability. (c) Development of a filter-feeding habit, with elaboration of ctenidia, starting with filibranch (fi), and passing through pseudolamellibranch (ps) to the advanced eulamellibranch (eu) condition. Two-way arrows signify the possibility of reversion at either of these points. Transition to septibranch (se), carnivorous or scavenging habit. Corollary changes occur in alimentary system. (d) Adaptive radiation among filter-feeding bivalves, exploiting all aquatic habitats, and all kinds of substratum: te, adoption of deposit feeding by a new method (Tellinacea).

The emergence of this new, filter-feeding model was a mega-evolutionary change: the stuff of which subclasses are made!

The newly created subclass was liberated from dependence upon the substratum as a source of food, and was free to explore all the environmental possibilities for exploitation of the filter-feeding habit (figure 2*d*). This involved a massive adaptive radiation, with neotenus use of the byssus – the larval organ of attachment – in many lineages, and with much parallel and convergent evolution.

We can now consider whether this whole process is exclusively attributable to a series of adaptive radiations, or whether there could also have been an as yet undetected mega-evolutionary element? Could there have been two, three, or four distinct phylogenies in the earliest formative stages of the filter-feeding bivalves? While this cannot be excluded, it has not yet been established. I envisage a matrix of evolving familial lineages, which might be represented by a multidimensional chess board, comprising up to 12×12 lineages. These lineages would have had much in common genetically, they would be responding to comparable environmental opportunities, and there would inevitably be parallelism and convergence. Some lineages might evolve rapidly in respect of ctenidial structure and function, and either rapidly or slowly as the case may be in respect of pallial fusion, etc. Advance in some respects would not preclude retention of some very primitive characters. With the elapse of time the matrix of phylogenies would suffer some losses through extinction, while some phylogenies would subdivide and produce clusters of families with obvious phyletic affinities.

Thanks are due to Mr Graham Clarke, of the Computer Unit, Chelsea College, who was responsible for adapting and running the computer program, and to Miss H. Haworth, Department of Zoology, Chelsea College, who kindly typed the manuscript of this paper.

The cards recording the computer program used, and the data in table 1, will be deposited in the library of the Mollusc Section of the British Museum (Natural History), Cromwell Road, London.

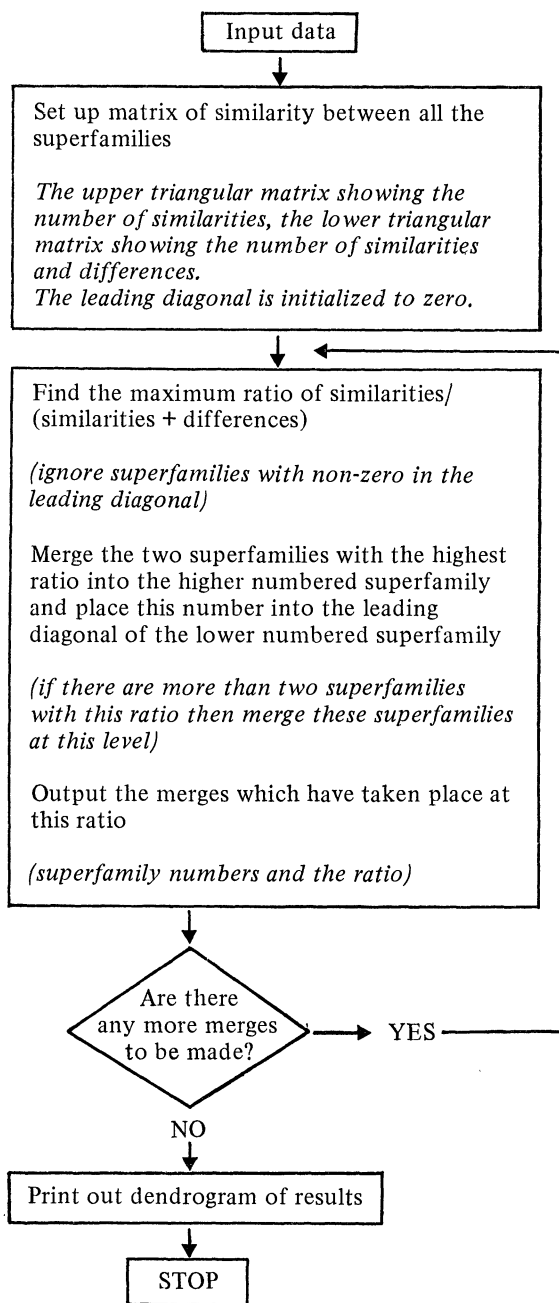
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APPENDIX: GENERAL FLOW CHART OF THE COMPUTER PROGRAM USED IN
THIS ANALYSIS, AND THE SIMILARITY MATRICES PRODUCED IN
COMPARING SIX SUPERFAMILIES

BY G. CLARKE

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9	Pectinacea	B4102214B
10	Anomiacea	341022141
6	Mytilacea	331122239
7	Pinnacea	331023139
8	Pteriacea	A41022139
11	Limacea	341023141

similarity matrix (i)

	9	10	6	7	8	11	
9	0	7	3	4	6	6	merge
10	9	0	4	5	6	8	10 & 11
6	9	9	0	6	5	3	at
7	9	9	9	0	6	6	88.89%
8	9	9	9	9	0	5	
11	9	9	9	9	9	0	

similarity matrix (ii)

0	*	3	4	6	13	
*	6	*	*	*	*	merge
9	*	0	6	5	7	9 & 11
9	*	9	0	6	11	at
9	*	9	9	0	11	72.67%
18	*	18	18	18	0	

similarity matrix (iii)

6	*	*	*	*	*	
*	6	*	*	*	*	merge
*	*	0	6	5	10	6 & 7
*	*	9	0	6	15	and
*	*	9	9	0	17	7 & 8
*	*	27	27	27	0	at 66.67%

similarity matrix (iv)

6	*	*	*	*	*	
*	6	*	*	*	*	merge
*	*	4	*	*	*	8 & 11
*	*	*	5	*	*	at
*	*	*	*	0	42	51.85%
*	*	*	*	81	0	

The data are the same as those in table 1 (note that once a superfamily has been merged into a higher numbered superfamily it cannot be merged again; thus it is irrelevant what happens to its results in the similarity matrix after it has been merged).