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Taxonomic concepts and superfluity in bivalve nomenclature

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Among the classes of invertebrate animals, the Bivalvia, with its extremely long fossil record and its preserved characters, which permit inferential anatomical reconstruction, comprises a group especially fit for phyletic analysis. Ideal for the investigation of the dynamics of speciation and the evolution of higher categories, bivalves represent a taxonomic unit whose systematics suffer from certain weaknesses. The relative narrowness of the anagenetic distances between lineages and the all-too-human tendency both to proliferate nomina and to elevate taxa partially obfuscate reality. The taxonomy of the Bivalvia is threatened by a cloying nomenclature both at specific and higher categorical levels.

Reappraisal of various, recently proposed, systematic arrangements and judicious application of Occam's Razor may allay the malaise of superfluity and promise the elaboration of a phyletically meaningful but somewhat simplified, utilitarian classification.

The bivalves comprise a group of invertebrate animals especially fit for phyletic analysis because of their extremely long fossil record and often well preserved shell characters, which frequently permit partial inferential anatomical reconstruction. Ideal for the investigation of the dynamics of speciation and the evolution of higher categories, bivalves represent a taxonomic unit which has received extensive attention. Cox (1960) admirably detailed the history of the classification of these animals, and Newell (1965) elaborated a systematic scheme which has been utilized in the most comprehensive treatment of bivalve taxonomic categories to the generic level. The early evolution of the class during the Palaeozoic and its possible phyletic linkages with other molluscan groups have received considerable attention recently, especially through the endeavours of Runnegar & Pojeta (1974).

Were generalizations to be made, it may be said that pelecypods have had a long, complicated fossil history, featuring a great deal of convergence, parallelism and mosaic evolution, that the principal lineages were established comparatively early, and that, not withstanding some remarkable adaptations, the phylogenesis of the group is characterized by a narrow conservatism. It appears to be probable that the group suffered severe constriction of its diversity at the Permo-Triassic interface (Nakazawa & Runnegar 1973) and that with a major adaptational shift concerning the effectiveness of infaunal filter-feeding including the development of siphons and the fusion of the mantle, it underwent a great radiation during the Mesozoic (Stanley 1968).

A further generalization concerns the taxonomy of the bivalves. The nomenclatorial problems are legion and seriously undermine the fundamental purposes of systems of classification which include the properties of information storage and retrieval as well as the more important aspects of predictive and explanatory biological theory. Some confusion has reigned virtually since Linnaeus established the heterogeneous Bivalvia, and today the available categorical schemata are perplexing and conflicting. The surfeit of nomenclature, both at specific and higher categorical levels, threatens to obfuscate phyletic reality.

The problem begins at the highest level. Although several nomina have been introduced for the class, Cox (1960) readily adopted the name Bivalvia and voiced the hope that alternatives be discarded. Discussing the matter further, Newell (1965) also proposed acceptance of the term Bivalvia. Thus, after considerable controversy and differing traditional, and sometimes almost nationalistic, usages, the term Bivalvia gained international, if not universal, currency. Today, however, with the discovery of the uniqueness of the bivalved Rostroconchia as well as the known occurrence of other bivalved animal groups in the Mollusca and the Arthropoda, certain workers have quietly advocated the return to the formal usage of Goldfuss's Pelecypoda (Pojeta 1971).

TABLE 1. SUPERGENERIC TAXA OF BIVALVES

Stoliczka (1871)		Dechaseaux (1952)	
orders	10	orders	2
families	45	suborders	3
subfamilies	41	families	70
Fischer (1887)		Korobkov (1954)	
orders	2	orders	6
suborders	14	suborders	3
families	69	superfamilies	30
		families	78
Dall (1895)		Newell (1965)	
orders	3	subclasses	6
(suborders)	11	orders	15
superfamilies	33	suborders	8
families	95	superfamilies	46
		families	159
Thiele (1934)		Nevesskaya et al. (1971)	
orders	3	superorders	3
suborders	4	orders	14
'stirps'	32	suborders	13
families	74	superfamilies	89
subfamilies	24	families	231

Next we are confronted by nomenclatorial superfluity. At the specific level I have previously pointed out that the bivalves, and for that matter most of the Mollusca, have been significantly over-named: there are now more nominal taxa than real species (Boss 1971). Probably fewer than 8000 living species of bivalves inhabit the marine and freshwater biotopes although many less critical estimates have suggested that there are over 20000 species. Vokes's (1967, p. 112) critical listing of bivalve genera includes both living and fossil taxa and totals over 9000 names. With the exception of all encompassing taxonomic revisions, a great reluctance to purge the system of unnecessary epithets is apparent. In fact, with the continued flourishing of researches based on geographically and stratigraphically restricted topics, the myopic trend has been to increase the burden of nomenclature rather than reduce it.

At the higher categorical levels we need only take note of the number and variety of available names discussed by Cox (1960) who mercifully omitted nomina suggested by Vest (1899), Gioli (1889) and Stenta (1908). Some designations at the higher categorical levels have been consigned to a deserved oblivion in the *Treatise on invertebrate paleontology*; others, of course, have arisen or been resurrected since then (Nevesskaya, Scarlato, Starobogatov & Ebersin 1971).

However, the superabundance of nomina is not the sole agent plaguing the taxonomy of the Bivalvia but there has been a constant readjustment, mostly upward, of named suprageneric

units into higher categorical ranks. By no means is this problem limited only to specialists in the class Bivalvia: the phenomenon is widespread, not only in animal taxonomy but in the botanical literature as well (Harris 1964).

The combined effects of nomenclatorial superfluity and the instability of the taxonomic schemata become readily apparent when several principal taxonomic treatments of the diversity of the Bivalvia are contrasted. Table 1 shows that over the last century the numbers of ordinal and familial level taxa have greatly increased. Although I have selected but eight principal treatises to elucidate this point, reference to Haas (1929–56), who has presented a more detailed listing, would confirm an even greater variance in usages. Not only the alteration of taxa from rank to rank but the introduction and multiplication of new nomina for various ranks seriously flaws the system of classification. Thus, while Stoliczka (1871) recognized but 45 bivalve families, the recent review by Nevesskaya et al. (1971) delineated 231. Similarly, the number of subclasses, orders, suborders and superfamilies differs from author to author and generally has increased throughout the years. Some authorities must be credited with having made serious efforts to utilize the earliest and phyletically most accurate epithet despite the lack of satisfactory regulations concerning the appropriateness or priority of such nomina in the International Code of Zoological Nomenclature.

What are some of the probable causes behind this plethora of nomina and confusing systematics? One ever present source which hampers the elaboration of valid, hopefully most accurate, phyletic schemes is in the assessment of taxonomically useful and meaningful taxobases. Several authorities have remarked on the inadvisability of establishing taxonomic hierarchies based on single-system analyses. Largely ignorant of the fossil record, and convinced of the greater importance of anatomical rather than conchological taxobases, malacologists have been especially blameworthy in elaborating classifications on unique animal features: the nature and number of adductor muscles (Lamarck 1807), the formation of siphons and their retractor musculatures (Orbigny 1843–7), the number and structure of the ctenidia (Pelseneer 1889, 1903; Ridewood 1903), the ciliation of the ctenidia (Atkins 1938) and the basic structure of the stomach (Purchon 1958, 1963). Palaeontologists, with greater knowledge of the actually phyletic history of the class, have usually been somewhat more successful (Dall 1895; Newell 1965; Pojeta 1971).

To establish more accurately, in this short contribution, the entire phylogeny of the Bivalvia would be more than presumptuous on my part and far beyond the scope of this discussion. However, I suggest that an appropriate model for the eventual reevaluation of the classification of these animals is embodied in a cladistic analysis of the matrices of taxobases. I have chosen the comparatively well studied Pandoracea with its six living families for a more or less formal, but herein abbreviated, cladistic analysis. Although systematics has been 'revolutionized' by the phylogenetic methodologies adumbrated by Hennig (1966), the formal adoption of systems based solely on sister-group branchings without taking into account the anagenesis of the lineages has received informed criticism (Mayr 1974). Actually the use of the cladistic method long antedates some of the recent philosophical (and vituperative) arguments.

What are the phyletic relations obtaining between the constituent families of the Pandoracea? Herein, an attempt will be made to identify primitive or derived characters, the plesiomorphous and apomorphous features in the Hennigian sense, at the various categorical levels. Many individual studies on the morphology of representative pandoracean species are fortunately available (Allen 1954, 1958; Ansell 1967; Boss & Merrill 1965; Burne 1920; Dall 1895; Deshayes

1844–8; Hancock 1853 a, b; Morse 1913, 1919; Morton 1973, 1974, 1976; Narchi 1968; Odhner 1917; Pelseneer 1891, 1911; Rosewater 1968; Tevesz 1975; Yonge 1952, 1976). Further, the long complex phyletic history of the Anomalodesmacea of which pandoraceans form a portion has recently been critically discussed (Runnegar 1974). There is some disagreement among authorities as to which families constitute the Pandoracea. M. Keen (in Cox 1969) and Nevesskaya *et al.* (1971) placed eight families in the group, namely Pandoridae, Cleidothaeridae, Margaritariidae, Periplomatidae, Laternulidae, Lyonsiidae, Myochamidae and Thraciidae. Runnegar (1974) removed the Margaritariidae, a generically monotypic, entirely fossil (Miocene) group to the allied Pholadomyidae as originally suggested by Vokes (1964) and added the Verticordiidae, a group which has now been shown to be allied to the Poromyacea (Allen & Turner 1974; Bernard 1974). I propose to discern cladistically the phylogenetic relations which obtain among the seven living families treated by M. Keen (in Cox 1969).

The following features are shared by the constituent families at the superfamilial level, a lineage represented by the ancestral laternulids in the Triassic: shell aragonitic, tri-layered, prismato-nacreous; hinge with opisthodetic external element and variously developed internal resilial element subtended by an accessory calcareous structure, the lithodesma; shell often invested with granules; animal siphonate, mantle fused ventrally except for antero-ventral pedal aperture, subsiphonal postero-ventral, so-called fourth pallial aperture, and posterior incurrent and excurrent siphons; foot provided with byssal groove; ctenidia consisting of ventrally pendant inner demibranch with both ascending and descending lamellae and of dorsally reflected outer demibranch with only descending lamellae; palp–ctenidial relation type III of Stasek; stomach of Purchon's type IV and Dinamani's type IIIB; animal reproductively hermaphroditic.

These features were identified by their being widely possessed by pandoracean families; however, some of these characters are symplesiomorphies for even higher categorical lineages and others have been lost or modified in certain families. Thus, the palp–ctenidial configuration is polyphyletically distributed among bivalves and the type II condition has been elaborated in the Lyonsiidae (Stasek 1963). Such a character as the prismato-nacreous shell was once possessed by the Thraciidae in the Cretaceous but subsequently was altered to a homogeneous condition (Taylor, Kennedy & Hall 1973). Similarly the functionally enigmatic fourth pallial aperture is retained in the thraciids, lyonsiids, myochamids and cleidothaerids but lost in the laternulids, pandorids, and possibly periplomatids. Other characters might well be included as pandoracean synapomorphs but insufficient data concerning their occurrences throughout the families preclude their present utility. For example, apparently the proteins of the shell matrix are characteristic; at least *Lyonsia* and *Periploma* share this similarity (Ghiselin, Degens, Spencer & Parker 1967).

The basic superfamilial lineage split into two constituent lines probably sometime during the Triassic (figure 1). Synapomorphic characters for the thraciid–laternulid–periplomatid lineage include elongate siphons, pallial sinus distinct and large, ventral pallial adductor muscles, ligaments supported by nymphal callosity or chondrophores. In contrast, the remaining four families share a nearly opposing matrix of derived characters: comparatively short siphons with a concomitant reduction or absence of a pallial sinus, and a sunken resilium which is not supported by specialized structures such as a chondrophore. From the first major dichotomy, the thraciids separated in the Jurassic; they eventually developed a homogeneous shell structure, with a weakly elaborated external opisthodetic ligament, supported bilaterally

with nymphal callosities and internally with a small narrowly curved digitiform lithodesma. The laternulids and periplomatids possess certain remarkable synapomorphies: resilium supported by a buttressed chondrophore, umbos uniquely fissured or cracked, lithodesma boomerang-shaped or subtrigonally arched. The periplomatids, characterized by naked, unsheathed siphons and rather inequivalve shell without marked anteroventral or posterior gapes, diverged from the earlier laternulid stock during the Cretaceous. Modern laternulids have elaborated several highly specialized features, including a large posterior gape to accomodate the united and sheathed siphons as well as a unique siphonal eye.
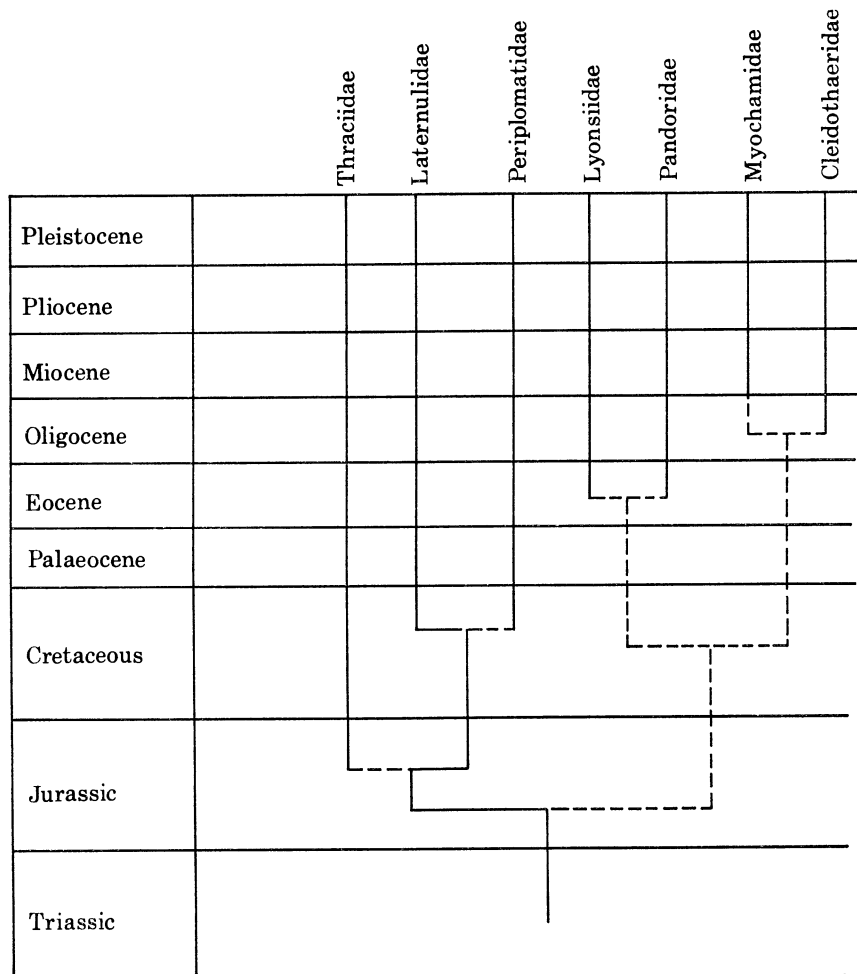

FIGURE 1. Cladogram showing phyletic relations among the families of the Pandoracea.

More than one possible phyletic arrangement might be suggested for the lyonsiid–pandorid–myochamid–cleidothaerid lineages (figure 2). Among the possibilities, pandorids might be more closely related to the lyonsiids (figure 2, cladogram 1) or to the myochamids and cleidothaerids (figure 2, cladogram 2). In the latter case, synapomorphies might include the heavier subsolid to solid shells with some degree of dorsal overlap found in pandorids and myochamids. Indeed, *Myadora* is frequently said to have a shell 'like *Pandora*'. However, careful comparison shows that the overlapping and inequality of the valves is completely opposite in the two genera. Further a closer phyletic relationship can be shown between lyonsiids and pandorids as indicated

by their sharing of traits such as simple shell shape, anterior position of umbos, rather deeply internalized, elongate resilium subtended by an elongate mesial lithodesma, a radially striped periostracum and, it has been suggested by Morgan & Allen (1976), such an arcane, little noticed, but possibly very important feature: odour.

The lyonsiids themselves may be distinguished by their elaboration of the type II palp–ctenidial configuration of Stasek, the presence of heavy dorsally fused periostracum connecting the valves and by the retention of a byssus in the adult stage with the concomitant development of a byssal retractor muscle. The pandorids have evolved several familially unique structures: a pallial line which consists of individualized muscular bundles, anterior and posterior pedal retractors which insert in the shell ventral to the adductor muscles, a reduction in size of the upturned outer hemidemibranch as well as a reduction in the number of plicae per filament in their heterorhabdic ctenidia. Additionally, the anteroventral pedal aperture is larger than in other pandoracean families to accomodate a larger and bilaterally compressed more active foot; the hinge is provided with blunt, irregular dentiform processes.
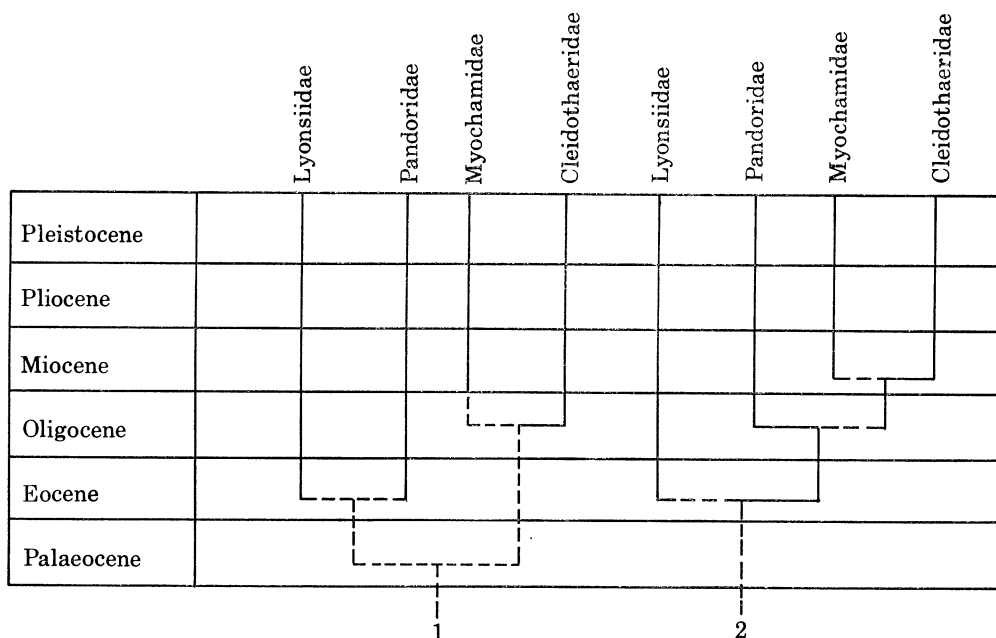

FIGURE 2. Cladograms showing possible phyletic relations among four families of the Pandoracea.

The myochamid–cleidothaerid lineage has few known synapomorphies, but the subtrigonally shaped young individuals suggest a close relationship between these rare groups (Odhner 1917). A curved, even coiled lithodesma subtends the alivincular resilium and there is a tendency to adopt the pleurothetic habit. The taxa are separable as adults by the cleidothaerid's having an elongate, arcuate anterior adductor muscle, the gill axis almost dorso-ventrally aligned, the siphons rather ventrally displaced, and a coiled lithodesma. Myochamids have simple, separate, posteriorly directed siphons, are free or attached, and the gill axis is gently inclined in an anterior–posterior direction.

As a number of contributors to this symposium have suggested, careful cladistic analysis will figure importantly in future research on the phylogeny of bivalves. Not only distinguishing between shared primitive and shared derived characters, the symplesiomorphies and synapo-

morphies, but also weighting of character-matrices, especially the identifying of complex synapomorphous features, will clarify certain problems in phylogeny. The pandoracean paradigm serves at once to illustrate the possibilities of the method and to suggest testing of the reliability of the delineated characters.

An appreciation of the phyletic distance between constituent taxa is usually not evident in cladograms. In fact, anagenetic divergence frequently goes unmentioned. However, in the example given here, a major evolutionary shift is exemplified by the cleidothaerid–myochamid lineage, most members of which have entered a new adaptive zone, the pleurothetic habit. The phyletic distance between the cleidothaerids and the myochamids is relatively narrow while that which separates the pandorids and the lyonsiids is much wider, reflected in the greater number of their different familial specializations. Similarly, the laternulids and periplomatids by their sharing of remarkably unique and complex structures – the buttressed chondrophores and fissured umbos are both unique features correlated to a novel mode of burrowing and the invasion of a new adaptive zone (Morton 1976) – are less phyletically divergent than their stem lineage is to the thraciids.

Subsequent to assessing phyletic relations and to recognizing real, natural taxa as represented in the accompanying cladograms, the taxonomist is confronted with the second principal process of classification: the ranking of taxa into meaningful categories. Ranking is fraught with subjectivity and is highly arbitrary. Possibly it has been the most important phenomenon subtending the variance in the categorical schemata suggested for the bivalves (table 1), and it too may be at the root of the problem of nomenclatorial superfluity, at least at supra-specific levels, in the taxonomy of these molluscs.

Perhaps as malacologists we should follow the example of the Society of Protozoologists and formulate a classificatory scheme for the Bivalvia somewhat simplified from that embodied in the *Treatise on invertebrate paleontology*. Such a classification could discard superfluous nomina, eliminate the distressing inflation in ranks and downgrade much of the hierarchical nomenclature to unusual, low-profile infra-categories such as those used in entomology (i.e. tribes, cohorts or phalanxes). Surely it is advisable that the most concerned scientific community elaborate some sort of stable categorical system which is at once comparatively simple, utilitarian and phyletically accurate.

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