A Palaeontologist's View of Bivalve Phylogeny [and Discussion]

N. D. Newell, D. W. Boyd and R. M. C. Eagar

Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

A palaeontologist's view of bivalve phylogeny

By N. D. Newell† and D. W. Boyd‡

† *Department of Fossil and Living Invertebrates,*
The American Museum of Natural History, New York City, N.Y. 10024, *U.S.A.*
‡ *Department of Geology, University of Wyoming, Laramie, U.S.A.*

[Plate 1]

The fossil record of the Class Bivalvia is dominated by simple skeletons with relatively few characters, and induces much chance duplication of structure, mosaic evolution, parallelism, and convergence. Overall, there appears to have been a net increase in diversity that has not yet reached a limit. Considering the complex fluctuations in population size and selection pressures which characterized the history of many taxa, both the model of punctuated equilibrium and the Darwinian view of organic change as a slow, steady process seem simplistic.

Evolutionary trends, well documented in many pelecypod groups, include short-term, probably stochastic, repetition. Sustained trends are presumably products of sustained selection. Separate lineages commonly display similar sequences of morphological grades. In contrast to the vertebrates, many pelecypod superfamilies and orders are not clearly segregated into well defined adaptive zones.

Trivial differences separate marginal members of some higher categories suggesting that they originated as ordinary species of ancestral taxa preadapted to radiate into a variety of similar niches.

Strict cladistics and unweighted phenetics are inadequate guides to pelecypod phylogeny because they tend to ignore stratigraphic evidence. A more flexible evolutionary systematics is recommended that incorporates the chronological data of stratigraphy and palaeobiogeography.

Introduction

The title of this symposium, *Evolutionary systematics of the Bivalvia*, has stimulated us to discuss the pertinence of fossils in phylogenetic reconstruction and taxonomy. It is interesting that the contribution of fossils to biological classification, which seemed settled long ago, has come to the fore in spirited debates involving the whole subject of evolutionary systematics.

An outgrowth of the revival in the 1940s and 1950s of interest in evolution has been a search for an objective methodology, a guiding theory, for research in phylogeny and classification. The absence of any such coordinating strategy in the Bivalvia volumes of the *Treatise on invertebrate paleontology* (Moore (ed.) 1969–71) is apparent to all who use them. Production of these volumes required the efforts of a large team of specialists over a period of two decades. This work would have been greatly improved had a suitable phylogenetic theory been adopted by all participants at the inception of the project. Our purpose here is to review some characteristics of the fossil record of pelecypods and to consider basic premises in choosing an appropriate phylogenetic strategy for bivalve systematics.

In the past decade or so, three more or less overlapping theories of systematics have emerged: phenetics, cladistics and evolutionary systematics. In the current debates there is great emphasis on the importance of objectivity and a unified approach suitable for all organisms and

materials, fossil and living. These goals are, of course, desirable whenever they can be achieved without loss of information. Many of the discussants give little or no consideration to the fact that the materials to be studied – the raw data – are highly heterogeneous in quantity and quality, often necessitating special treatment. Many evolutionists unconsciously have in mind fossil vertebrates when they talk about the fossil record. But most of the record, even if we include plants, is made up of invertebrate skeletons with relatively few characters. Apart from this, the fossils of the different orders and classes of invertebrates are commonly structurally unique with few intergroup homologies. There is much chance duplication of structure, mosaic evolution of character complexes at varying rates and rampant convergence and parallelism.

DIVERSITY

A prime objective of biological classification is to render diversity manageable through grouping. How diverse are the bivalve molluscs? The *Treatise on invertebrate paleontology* recognizes more than 3000 subgenera, 500 genera and about 100 families, fossil and living. Only one-third of the genera and subgenera are still living, and a little over one-tenth are known thus far only in the living fauna. Boss (1971), after scaling down synonyms, estimates a few more than 6000 living species, and Raup (1976a) reports between 15000 and 16000 named fossil species. The ratio of five or six species per subgenus is about one-third the number expected for any species group stemming from purely random events (Anderson 1975). New discoveries have been appearing in the literature at a sustained rate of about 77 subgenera and genera per year and there is no present indication of slackening. We do not think that any deep biological significance should be inferred from these figures because the discovery and naming of species are themselves chance events. In common with other animal groups, the pelecypods display a broad spectrum of states of evolutionary plasticity ranging from those taxa which have hardly changed in hundreds of millions of years to others which evolved conspicuously in a few million years. Whether they are termed species or genera has been a matter of personal preference.

Most of the pelecypod record is marine rather than non-marine, and even in the most fossiliferous rocks this record is strongly biased by environmental facies. However, the class has a good Palaeozoic record and the representation improves as we ascend the geological scale. The quality of preservation varies with rock types but in general it gets better and the bivalves become more diverse as we approach the present. This phenomenon is typical of the major fossil groups, and has long been interpreted as evidence that biosphere diversity has been increasing with time. However, Raup (1976b) has suggested that the multiplication of taxa throughout the Phanerozoic may be an artefact of accessibility; a random, non-biological factor. The argument goes something like this: more rocks produce more specimens; given more specimens, an increased number of taxa should follow; but this would be strictly true only if the rocks were uniformly fossiliferous.

Using the same data as Raup, Sepkoski (1976) finds a fair correlation between diversity of marine benthos and the varying extent of the epicontinental seas through time, a conclusion already reached by many other investigators. The idea is similar to the island equilibrium theory of MacArthur & Wilson (1967): the larger the area of distribution, the greater the diversity of habitats and the lower the rates of extinction. A rough rule of thumb is said to be that a tenfold increase in area results in a doubling of the number of species at equilibrium

(Wilson & Willis 1975). To our view, however, the bivalve data show little in common with the computer simulation of rock volumes or areas of shallow seas. A more important source of increased diversity may be the fragmentation of provinces through geological time (Valentine 1973; Boucot 1976b).
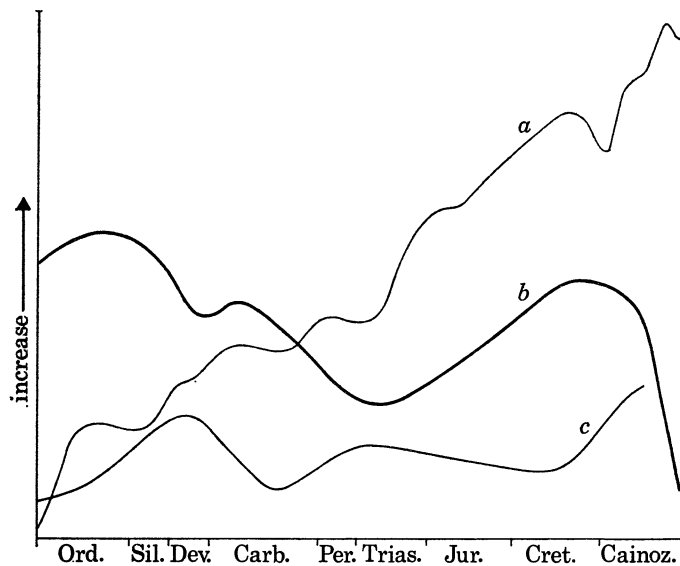

FIGURE 1. Bivalve diversity contrasted with changes in epicontinental seas and volumes of fossiliferous rocks: (a) Families, Bivalvia; (b) shallow seas, area; (c) rock volume. Shallow seas after Sepkoski 1976; rock volumes after Raup 1976b.

Biological diversity is usually attributed to the partitioning of available resources. Since these are obviously finite, it may be argued that niche subdivision must follow a logistic curve rising at first exponentially and then flattening out as ecological space becomes filled and equilibrium is reached. It is incredible that any group of organisms would radiate indefinitely, but the bivalves with all their limitations appear to go on and on. The primary radiation in the Ordovician followed a few major adaptive plans, but subsequent evolution has repeatedly subdivided these into more and more restricted biotic rôles. The pace of diversification increased after a sharp decline of the competing branchiopod–bryozoan community at the close of the Palaeozoic. Mass extinctions of genera and families at the boundaries of the Mesozoic era perturbed the trend but did not profoundly alter it. We interpret the evidence to indicate that the fossil record reflects a continuing real net increase in pelecypod diversity that has not yet reached a limit (figure 1).

EVOLUTIONARY MODES

The evolutionary systematics of bivalves received a salutary thrust in a new direction with Sir Arthur Trueman's work on Jurassic oysters of the genus *Gryphaea*, starting in 1922. This and Brinkmann's (1929) statistical study of evolution of the ammonite *Kosmoceras* set the stage not only for modern evolutionary palaeontology, but also for the new systematics and the synthetic theory of evolution which got under way about a decade later. Fossil collections came to be regarded as statistical samples of variable populations. Evolution of whole populations was seen to take place by means of persistent shifts in proportions of phenotypes.

Until the appearance of Simpson's *Tempo and mode in evolution* in 1944, and his *Major features of evolution*, in 1953, most palaeontologists assumed that evolution could be traced in successive fossil populations as gradual modifications *in situ* through fossiliferous strata of, say, a single faunal province. Simpson showed that uniform rates of evolution cannot be inferred from the fossil record; quite the contrary. He wrote of rapid evolution in small, therefore hard to discover, populations where morphology changed at rates many times faster than usual. Evolution was thought to be slow in large, far-flung populations. These ideas were an extension of Ernst Mayr's examples of geographic speciation in small isolated populations of living organisms (see, for example, Mayr 1942, 1963). More than any other person, Mayr demonstrated the overriding importance of peripheral isolates in producing diversity. He showed that detached fragments of populations even at the onset are not average samples of the parent population; furthermore, they have less variability and are subjected to different environmental stresses. Especially, they are much more reactive to inbreeding and to mutations than are large populations where new genetic effects are greatly diluted, much as a few drops of ink produce a dramatic change in a glass of water but are lost in a bathtub of water.

Thus the earliest history of a new lineage, when the founder population is small, tends to be missed in samples from the fossil record. This is the branching, or allopatric, phase in which parent and daughter populations become divided by some more or less effective barrier to gene flow. Since this model of geographic speciation has been abundantly demonstrated with living organisms, it has come to be widely accepted by biologists as a 'speciation event'.

Evolutionists since the time of Darwin have also envisaged gradual divergence (e.g. successional, or phyletic, evolution), after splitting, as an important mode of change. Palaeontologists especially, with the vast panorama of geological history in mind, have been impressed by successional evolutionary changes, but have given scant attention to the implications of population fragmentation, usually a geologically instantaneous event.

Eldredge & Gould (1972) challenged the usefulness of the idea of phyletic gradualism which, they argued, is ordinarily not required by the evidence. They view evolution as mainly a succession of quick events in small populations followed by relatively longer intervals of stability, *stasis*, after significant population expansion. Their concept, which they termed *punctuated equilibrium*, translates diagrammatically into a rectangular or stairstep pattern. This model, with its emphasis on phylogenetic branching, harmonizes with the cladistic theory of phylogenetic classification (Hennig 1966; Eldredge & Tattersall 1975). The condition of stasis in species for long spans of time has been documented in Upper Devonian and Jurassic clams by MacAlester (1962) and Hallam (1976).

If evolution requires a theory, then so does stasis. The internal regulatory system of living organisms, *homeostasis*, buffers them against predictable oscillations in the environment by providing physiological and other tolerances necessary for survival. Persistent environmental gradients, however, correlate nicely with geographic shifts in the homeostatic mechanisms, as illustrated by well documented species clines all over the world (see, for example, Schopf & Dutton 1976). Homeostasis does not insulate a population from mean changes in environmental parameters. From this we infer that the most plausible examples of stasis in the fossil record may be limited to eurytopic organisms represented in immense numbers and living in difficult but predictable environments characterized by wide seasonal oscillations.

We are not prepared to accept all reported stratigraphic ranges of species as examples of stasis. Some of the apparent stability, especially the shorter-ranging examples, may very well

be an artefact of the inflexibility of Linnaean nomenclature and the methods and objectives of biostratigraphy where species are regarded as indices to geological age and environment. The literature contains countless examples of palaeontological species that have been dissected and pruned in order to limit them to the smallest practicable stratigraphic units. Species that display appreciable vertical changes are either not allowed to continue under a single specific name or, if the changes are trivial, the extreme members of a chronocline frequently are informally designated as 'primitive' or 'advanced'. Most long-ranging pelecypod species have not been subjected to rigorous biometrical analysis. We may suspect that they have not evolved, but we cannot be sure.

There has been considerable discussion over the relative merits of the contrasting models of speciation. Which one is preferable: gradualism, or punctuated equilibrium? We suspect that they are really facets of a single complex process, usually not distinguishable in the fossil record. When we consider the environmental fluidity and resulting differentiation of any large geographic area over the total life span (millions of years) of a widespread species, it would appear to be highly probable that geographic races frequently evolve to species status through repeated isolation, reunification and hybridization. From this assumption, it would follow that speciation *in situ* is one consequence of environmental evolution. Large polytypic populations are fragmented by environmental changes and geographic races become founder populations of new species. Sylvester-Bradley (1977) has termed this comprehensive mode *reticulate speciation*, a useful innovation since the unqualified term 'speciation' does not suggest any particular model.

How does divergence take place during geographic isolation? Cladists tend to ignore this important question. When a geographic split takes place, the separated populations, small or large, will follow different evolutionary pathways, diverging *in situ* at rates inversely proportional to their numbers and proportional to selection pressures. Evolutionary change is rapid and gradual in now-living founder populations as phenotype frequencies shift through successive generations (Elton 1958). After genetic barriers are sufficiently developed in the divided populations they will not hybridize when they again come together (sympatric phase). The ensuing interspecific competition then will exert new selection pressures resulting in extinction of one, or character displacement in one or both. This means further evolutionary divergence within the shared territory. The options for change include convergence (mimicry) or further divergence (Grant 1972). If, after extended competition, one of the two closely related competing species becomes extinct (exclusion), the resulting release from competition may be expressed in further evolutionary modification in the surviving species. It is confusing to assign all of these evolutionary phenomena, as usually is done, to a single speciation 'event'. Every step in the sequence involves gradualism. The only genetic discontinuities are between lineages.

The Darwinian view of organic change as a steady, slow production of successional species fades when we consider the complex evolution of the Earth's crust and climate and the correlated unending ecological changes of wide, often global extent. Throughout these kaleidoscopic changes, local populations constantly fluctuate from small to large with frequent hybridization and changes in selection pressures. Thus, both models of punctuated equilibrium and phyletic gradualism seem to us too simplistic. We envision a spectrum of conditions among which the extremes are stasis in large, stable populations and rapid successional changes in small populations. The evolutionary changes characteristic of populations of immigrant pioneers illustrate divergence *in situ*, subsequent to splitting, through successive generations.

Each speciation event in an isolated population must produce an on-the-spot ancestor–descendant continuum. Intermediate rates of change probably characterize populations of intermediate size. The development of barriers (either geological or ecological) across any population initiates cladistic dichotomy and this is followed by successional divergence of the emerging lineages as described by Simpson (1953). In the fossil record there are many well documented examples of rapid evolution of whole new biogeographical provinces of large extent, among which may be cited the post-Miocene Panamic (Newman 1972) and Pontian faunas, and the Permian Paraná Basin of South America (Runnegar & Newell 1971). It is not possible to estimate the sizes of founder populations in these provinces, but there is no reason to doubt that the scores of divergent species and genera of pelecypods originated there in colonies of immigrants of considerable size.
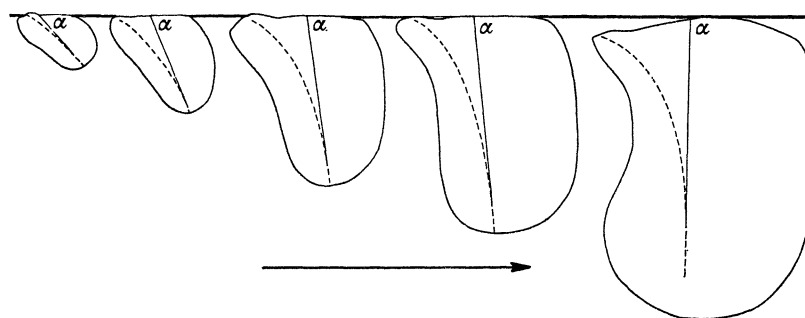

FIGURE 2. Trend in *Myalina* populations from the Midcontinent Pennsylvanian rocks of the United States spanning about 30 Ma (after Stanley 1972). The values of angle α and adult shell size are roughly allometric in both ontogeny and stratigraphic sequence. Such trends are common in Bivalvia.

TRENDS AND PHYLOGENETIC POLARITY

Early in the present century when Heisenberg was persuading scientists in many fields to modify their ideas about determinism in nature, palaeontologists were still busily documenting examples of what they called 'programme' evolution or 'orthogenesis'. Directional evolution was regarded as a heaven-sent gift to stratigraphers and it was no accident that the most striking examples of trends were rapidly evolving lineages of distinctive 'guide fossils'. The search for trends was a natural extension of the nineteenth century idea of evolution as a perfecting principle. Some examples of fossil trends have had to be rejected, but evolutionary trends do, indeed, exist in nature. Sustained trends are well documented in many groups of pelecypods (figure 2), and shorter term directional tendencies, often repetitive, sometimes apparently reversing, are common. Many of the shorter ones probably represent the binary options of plus or minus, more or less. But in every case they must harmonize with some available environment in order to continue. Sustained morphological trends must be adaptive to environmental trends.

Eldredge & Gould (1972), Stanley (1973) and Boucot (1976a) have made a case that the earliest ancestors in every lineage tended to be small and unspecialized compared with most of their descendants. After all, most of us are not unicellular microbes. If we accept this general axiom they say, then many, perhaps most, changes must have been in the direction of increasing size (with its allometric effects) and increasing complexity. This model alone, however, cannot account for adaptive advantages of increased size or complexity in individual

lineages. The fossil record does not consist of a spectrum of all conceivable conditions between primitiveness and specialization (figure 3). Increasing niche diversity must be correlated with narrowing specialization and improved efficiency as resources diminish. Trends must combine chance factors with environmental constraints.
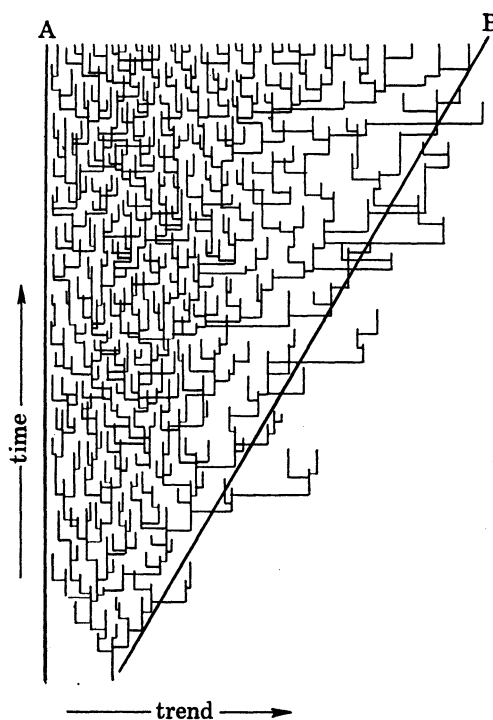

FIGURE 3. A theory of stochastic trends. Trellis pattern represents allopatric speciation 'events' (horizontal lines) alternating with intervals of 'stasis' (vertical lines). Ancestral animals tend to be smaller and relatively less specialized than their descendants. From this (boundary A) generalization most evolution would seem to be in the direction of increased size and/or narrower specialization (biomechanical limit B). (Adapted from Stanley 1973.)

Palaeontology is gradually falling into line with other sciences: chance is taking its place beside causality in the mechanics of evolution (Raup, Gould, Schopf & Simberloff 1973). Trends that have been adequately confirmed usually turn out to be irregular and winding if a mosaic of several characters is considered, comparable to a footpath across rough terrain. If the trend is based on only one character it may appear to be narrowly linear. In any case, trends must combine chance factors with the environmental guidance of natural selection. Separate clades frequently display parallel sequences of morphological grades shaped, evidently, by like selection of similar genotypes (figure 4). This phenomenon would be unknown save for its common occurrence in the fossil record.

HIGHER CATEGORIES

The method of classifying things in a hierarchy of increasingly comprehensive categories was adopted by Linnaeus who believed that he had discovered the divine plan of creation. The highest categories were those possessing a few generalized characters shared by all of their constituency. This phenetic system was based on overall similarities and was not directly concerned with genealogies.

The morphologic–phenetic hierarchy was taken by a few taxonomists to indicate that the basic structure of a taxon evolved first and later divided into the patterns of subordinate taxa down the line to the species; the big categories came first in time, eventually dividing up into the limbs and twigs of the phylogenetic tree. This view was expressed as recently as 1966 by Hennig, father of cladistics, whose phylogenetic scheme is supposed to be directly convertible into classification and again retrievable therefrom. But Linnean classification is two-dimensional and too inflexible to represent the three-dimensional patterns of phylogeny. Phylogenetic reconstructions in our view cannot be translated *in toto* into classifications by cladistics or by any other method. In systematic biology, the recognition of higher categories must be retrospective, coming after, not before, analysis of the constituent inferior groups of the hierarchy.
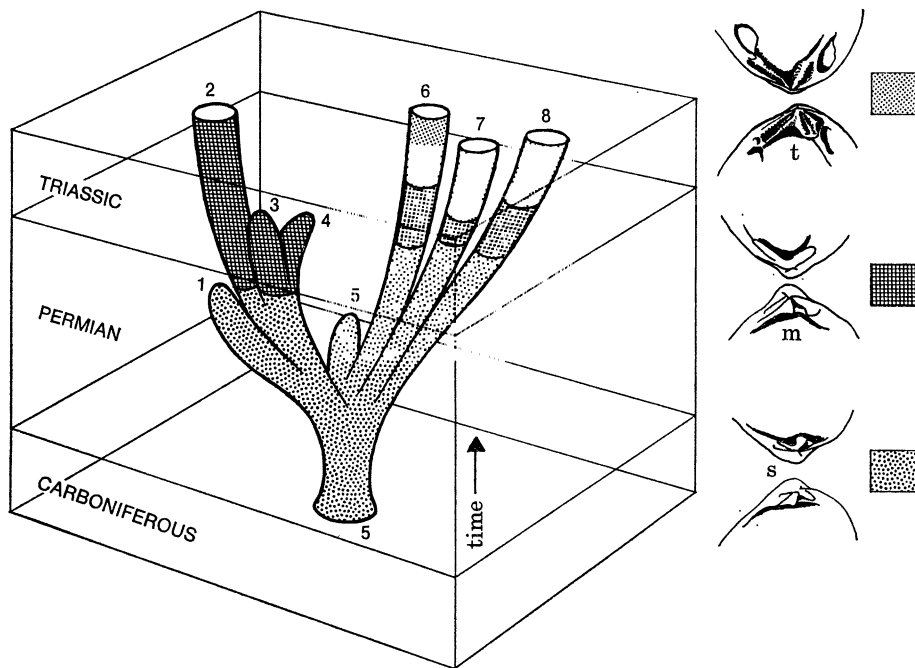

Figure 4. Parallelism in Trigoniacea, interpreted from the stratigraphic sequence of morphotypes: grades from the bottom up: (s) schizodian, (m) myophorian, (t) trigonian. Numbers 1–8 are separate families. (Data from Newell & Boyd 1975.)

Higher categories are higher because they are distinctive and comprehensive clusters. Usually, they had only one or a few of the group characteristics when they were arising. Many of the taxonomic categories of Bivalvia now in use were established as morphologic clusters, not necessarily evolutionary units, but they were thought to have some phylogenetic significance. The unfinished task is to determine just what that significance is and to bring together the most plausible genealogical lineages.

Simpson (1953) recognized a general correlation between higher categories of vertebrates and the adaptive zones they occupy. It is interesting that many of the higher categories of pelecypods are not clearly segregated into different adaptive zones. Bivalves of quite disparate structure frequently occupy the same habitat and they have the aspect of fulfilling similar ecological rôles. In any case, it is not now possible to provide adaptive explanations for the morphological differences among, say, all the superfamilies and orders of Bivalvia, although this can be done for a few. The problem deserves much more research.
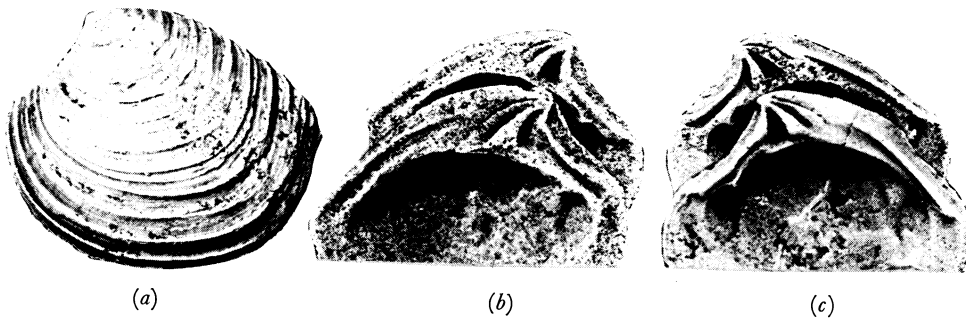
(a)　　　　(b)　　　　(c)

FIGURE 5. Mutant transposition of cardinal teeth in a Permian heterodont *Astartella auri*. (a) Left valve, magn. × 3; (b) left valves, magn. × 3; upper, normal; lower, transposed. Right valves, magn. × 4; upper, normal; lower, transposed. A new higher taxon which originate by such a mutation. (After Boyd & Newell 1968.)
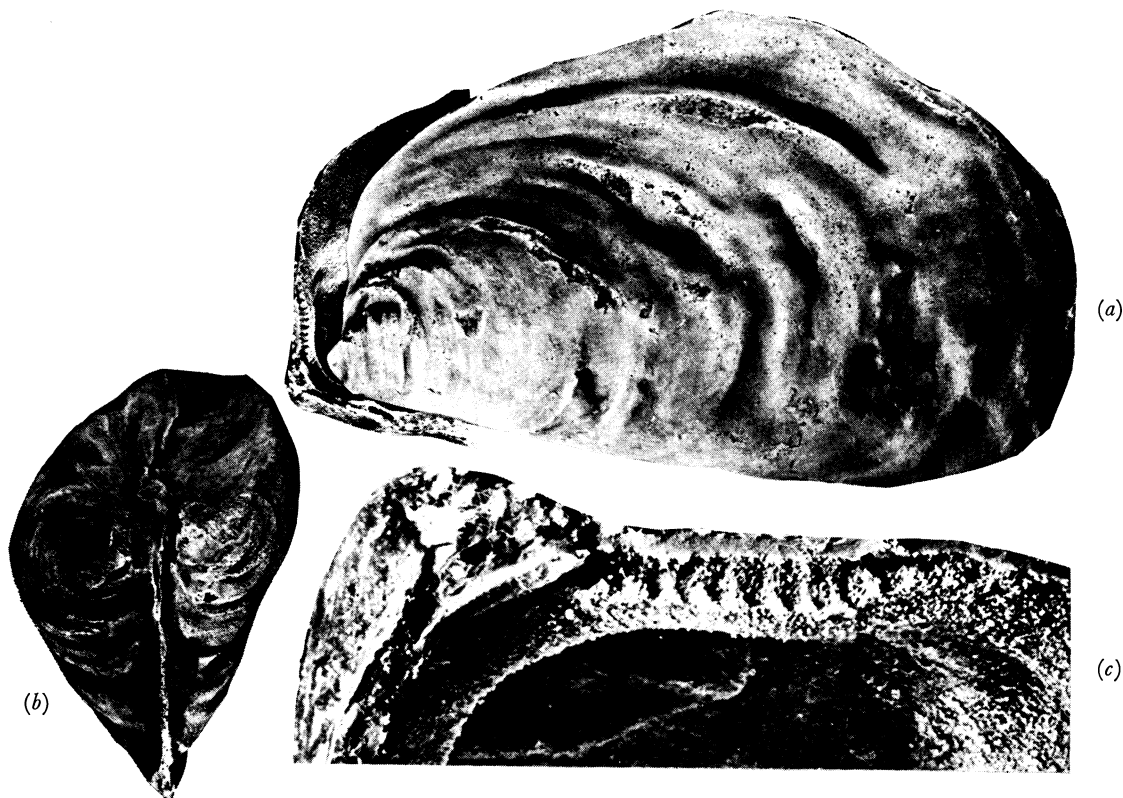

(a)

(b)

(c)

FIGURE 6. The oldest inoceramid, *Permoceramus brownei*, Permian of New South Wales, suddenly appears in a population of *Atomodesma*. The latter possesses a much more primitive ligament. It is suggested that the inoceramid grade is a mutant varient. Magnifications: (a) and (b), × ¾; (c) × 3¾. (After Browne & Newell 1966; see also Kauffman & Runnegar 1975.)

We suspect that all of the higher categories originated as ordinary species pre-adapted to radiate into a variety of not too dissimilar niches. They originated not as new higher categories but rather as ordinary species, the deviation points for new evolutionary directions. We shall now cite a few illustrations of the trivial differences that can separate marginal members of higher categories of pelecypods. Further divergence was achieved later.

In a series of stimulating papers, Pojeta & Runnegar (e.g. 1974) have been providing exciting new information about the probable origin of the Class Bivalvia. The lower Cambrian bivalve *Fordilla*, long regarded as a crustacean, now appears to be a pelecypod. It was probably derived from a monoplacophoran ancestor by way of the rostroconchs. Likely descendants of *Fordilla*, however, are unknown, and no presently acceptable pelecypod is known from the Middle and Upper Cambrian, an interval of around 40 Ma. *Fordilla* did not initiate any radiation of pelecypods. Could it be that the rostroconchs, or a common ancestor, gave rise to pelecypod-like molluscs more than once? Runnegar & Pojeta (1974) have made the interesting suggestion that *Fordilla* was so like certain rostroconchs that a single mutation eliminating the cap-shaped shell of a precocious larva would be sufficient to produce a flexible hinge, thus creating the dissoconch grade required by our definition of pelecypods. If so, might not a peripheral species, or even some individuals in a single variable population, be placed in one or the other class according to a single character difference?

Pelecypods frequently display mutant transposition of the cardinal teeth of the hinge affecting an appreciable percentage of individuals in a population (figure 5, plate 1). The result is a functional hinge unlike the usual dentition. Examples of transposed hinges are known in both heterodonts and palaeoheterodonts (Boyd & Newell 1968; Newell & Boyd 1975). We cannot cite an example of a new higher category formed in this way, but in view of the great emphasis placed on details of dentition, we do not doubt that such examples will be recognized as investigators critically examine the record with this problem in mind. Heterodont hinge teeth, ordinarily quite stable, are meristic characters and any change in the numbers of teeth tends to be abrupt from one category to another.

Another likely example of the production of a higher category by a small structural change, perhaps a single mutation, is the abrupt appearance of a member of the Inoceramidae (figure 6, plate 1) in a population of Permian pearl clams of the family Atomodesmidae. Kauffman & Runnegar (1975) have shown that a minor change in the ligament is the only really significant difference between the two families – that is, an advance from a simple alivincular to the multivincular ligament grade. This change was important only in retrospect. It became a permanent characteristic of a great host of Mesozoic clams.

The oysters and scallops resemble each other in many ways but they form two well defined groups of epibenthonic bivalves with long and distinguished histories back into the Palaeozoic (Newell & Boyd 1970). Some of the differences are apparent in fossils. In the scallops, the right valve is the obligate ventral valve. In the oysters it is the left valve that is invariably attached. Since the living attitude in both suborders has been constant as far back as we can trace them it evidently has a deeply rooted genetic basis. Early scallops had different ligaments and shell ultrastructure from modern ones; some characters changed markedly in mosaic while others remained primitive. We have suggested that the gryphaeids may have originated in a scallop affiliate, the pseudomonotids (figure 7), during the Triassic Period. A single mutation in a regulatory gene might have produced a precocious dissoconch with a tendency for re-supination. The foot, already vestigial in the scallops and confined to the right valve, would

have become useless if the animal became permanently inverted in the larval stage. If our hypothesis corresponds to reality, the transition from one suborder to another could have been accomplished within a few generations as the new mutation spread throughout the ancestral population.

As far as we can see, there was no shift in major adaptive zones in any of these examples. Instead, we postulate some correlated physiological improvement in efficiency in the advance from, for example, the pseudomonotid character state to the gryphaeid condition.
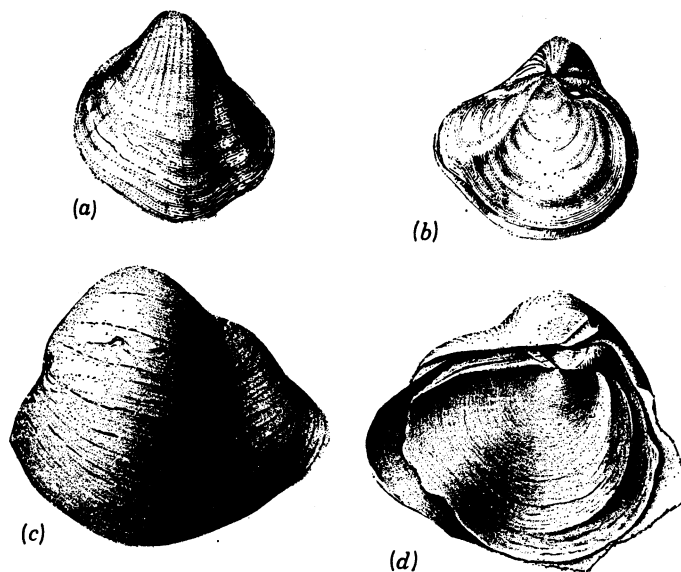

Figure 7. Origin of Gryphaeid oysters? (*a*, *b*) Palaeozoic *Pseudomonotis*, a byssate pectinacean, was usually cemented in adults by the flat right valve; (*c*, *d*) *Gryphaea*, an ostreacean, lacked a byssus, was cemented by the convex left valve. (Magn. approximately × 1.) (After Newell & Boyd 1970).

WHICH TAXONOMIC STRATEGY FOR THE BIVALVIA?

Cuvier, Lamarck, Haeckel and other great nineteenth century anatomists developed a phylogenetic tool based on comparisons of form and structure in organisms. This is now called phenetic analysis. It has been greatly improved by rigorous application of numerical methods (Sneath & Sokal 1973). The idea that organisms owe most of their similarities to shared homologous characteristics, that is to common descent, has become an axiom of evolutionary biology. This is still so, even though biochemical comparisons of proteins have shown that relationship sometimes does not exactly correlate with similarities. Mosaic evolution, convergence, and parallelism further disturb resemblances. The problem is to identify homologies correctly. In view of the fact that Linnaean classification was also based on similarities, it is not surprising that systematists after Darwin were basing their classifications on phylogenetic hypotheses derived from comparative anatomy.

Cladists believe that relationships are best interpreted in terms of the inferred number of branching steps in taxa of common ancestry – recency of splitting (Eldredge & Tattersall 1975). We do not doubt that the cladistic method is effective in determining the relative sequence of branching but alone it cannot provide a detailed chronology of evolution. Phenetics is blind to new adaptations, convergence, parallelism, and different rates of evolution in

different characters. These situations are ubiquitous in the fossil record. The two families Astartidae and Crassatellidae illustrate the importance of stratigraphic sequence in working out abrupt convergent changes in fossil clams. They are both still living, highly successful families that have been classed together in a single higher category (Crassatellacea) because of hinge resemblances. We have shown elsewhere (Boyd & Newell 1968) that highly probable ancestors are confidently identified in the Palaeozoic. Since the two lines are less similar in the Palaeozoic than subsequently, they became convergent in their later history (figure 8).
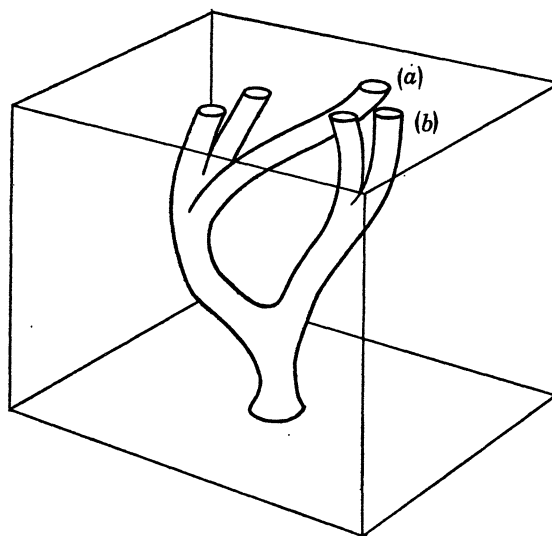

FIGURE 8. Convergence of Crassatellidae and Astartidae. These families ((*a*) and (*b*) respectively) are presently placed in a single superfamily but Palaeozoic ancestors are less similar than living examples. (Data from Boyd & Newell 1968.)

We do not regard either unweighted phenetics or strict cladistics as appropriate for pelecypod systematics. For fossils of few characters and a good record, such as the pelecypods, we favour the flexibility of evolutionary systematics, in the sense of Mayr (1974). First, a preliminary cladistic trial run may be made to determine, if possible, times of splitting of sister groups. Polarity is likely to be indicated by stratigraphic succession. For example, the crassatellid ligament area is divided by a tooth-like septum in Permian species but is undivided in younger representatives (Boyd & Newell 1968). Stratigraphic position is the only criterion for determining whether the septum is a primitive or a derived character.

It has long been axiomatic that primitive groups tend to outlive their more specialized descendants but derived members of a phyletic group rarely appear in the fossil record before the most primitive members. Ancientness and primitiveness are indeed correlated, but the correlation is not perfect. Fossil ranges provide minimum dates for origins and maximum dates for extinctions.

Many fossil species and genera are largely or wholly restricted to particular environmental facies and to particular palaeobiogeographical provinces. When the facts of distribution are substantially corroborated they also become part of the characteristics of fossils.

Our experience with the cladistic phase of analysis of pelecypods shows that it is difficult and insufficient, a conclusion also reached by Bretsky (1975). The next step should involve weighted multivariate analysis. It will show the frequency of association of characters, permitting clustering and arrangement of species and genera in a hierarchy. Putative ancestral

taxa will be incorporated in a phylogenetic tree that harmonizes all morphological and stratigraphic data. A similar conclusion has been independently reached by Engelmann & Wiley (1977) and by Szalay (1977). The most credible hypothesis will be one that is internally consistent with all sources of evidence. It will summarize what is believed to be the geological history of the studied lineages.

REFERENCES (Newell & Boyd)

Anderson, S. 1975 *Am. Mus. Novit.* **2584**, 1–9.

Boss, K. J. 1971 *Harvard Mus. Comp. Zool. occas. Pap. Mollusks* (Harvard) **3**, 1–135.

Boucot, A. J. 1976a *Nature, Lond.* **261**, 694–696.

Boucot, A. J. 1976b *J. Geol.* **84**, 731–735.

Boyd, D. W. & Newell, N. D. 1968 *Am. Mus. Novit.* **2328**, 1–52.

Bretsky, S. 1975 *Syst. Zool.* **24**, 113–119.

Brinkmann, R. 1929 *Abh. Ges. Wiss. Göttingen, math.-phys. Kl.*, **13** (4), 1–124.

Browne, I. A. & Newell, N. D. 1966 *Am. Mus. Novit.* **2252**, 1–10.

Eldridge, N. & Gould, S. J. 1972 In *Models in paleobiology* (ed. T. J. M. Schopf), pp. 82–115. San Francisco: Freeman, Cooper & Co.

Eldredge, N. & Tattersall, I. 1975 In *Approaches to primate paleobiology* **5**, 218–242.

Elton, C. S. 1958 *The ecology of invasions.* London: Methuen & Co.

Engelmann, G. F. & Wiley, E. O. 1977 *Zool. Syst.* **26**, 1–11.

Grant, P. R. 1972 *Biol. J. Linn. Soc.* **4**, 39–68.

Hallam, A. 1976 *Lethaia* **9**, 245–259.

Hennig, W. 1966 *Phylogenetic systematics.* Urbana, Illinois: University of Illinois Press.

Kauffman, E. G. & Runnegar, B. 1975 *J. Paleontol.* **4**, 23–51.

MacArthur, R. H. & Wilson, E. O. 1967 *The theory of island biogeography.* Princeton, N.J.: Princeton University Press.

Mayr, E. 1942 *Systematics and the origin of species.* New York: Columbia University Press.

Mayr, E. 1963 *Animal species and evolution.* Cambridge, Mass.: Belknap Press.

Mayr, E. 1974 *Z. Zool. Syst. Evol.-Forsch.* **12**, 128.

McAlester, A. L. 1962 *Bull. Peabody Mus. nat. Hist.* **16**, 1–88.

Moore, R. C. 1954 *Bull. Mus. comp. Zool., Harvard Univ.* **112**, 259–286.

Moore, R. C. (ed.) 1969–1971 *Treatise on invertebrate paleontology*, (*N*) *Mollusca Bivalvia*, vols 1–3. Lawrence, Kansas: University of Kansas.

Newell, N. D. & Boyd, D. W. 1970 *Bull. Am. Mus. nat. Hist.* **143**, 221–281.

Newell, N. D. & Boyd, D. W. 1975 *Bull. Am. Mus. nat. Hist.* **154**, 57–162.

Newman, W. A. 1972 *Bull. biol. Soc. Wash.* **2**, 247–259.

Pojeta, J. & Runnegar, B. 1974 *U.S. geol. Surv. prof. Pap.* **968**, 1–88.

Raup, D. M. 1976a *Paleobiology* **2**, 279–288.

Raup, D. M. 1976b *Paleobiology* **2**, 289–297.

Raup, D. M., Gould, S. J., Schopf, T. J. M. & Simberloff, D. S. 1973 *J. Geol.* **81**, 525–542.

Runnegar, B. & Newell, N. D. 1971 *Bull. Am. Mus. nat. Hist.* **146**, 1–66.

Runnegar, B. & Pojeta, J. 1974 *Science, N.Y.* **186**, 311–317.

Schopf, T. J. M. & Dutton, A. R. 1976 *Paleobiology* **2**, 255–264.

Sepkoski, J. J. 1976 *Paleobiology* **2**, 298–303.

Simpson, G. G. 1944 *Tempo and mode in evolution.* New York: Columbia University Press.

Simpson, G. G. 1953 *The major features of evolution.* New York: Columbia University Press.

Sneath, P. H. A. & Sokal, R. R. 1973 *Numerical taxonomy.* San Francisco: W. H. Freeman.

Stanley, S. M. 1972 *J. Paleont.* **44**, 165–212.

Stanley, S. M. 1973 *Evolution* **27**, 1–26.

Sylvester-Bradley, P. C. 1977 In *Concepts and methods in biostratigraphy* (eds E. G. Kauffman & J. E. Hazel), pp. 41–63. Stroudsburg, Pa.: Dowden, Hutchinson & Ross, Inc.

Szaley, F. S. 1977 *Syst. Zool.* **26**, 12–18.

Trueman, A. E. 1922 *Geol. Mag.* **59**, 256–268.

Valentine, J. W. 1973 *Science, N.Y.* **180**, 1078–1079.

Wilson, E. O. & Willis, E. O. 1975 In *Ecology and evolution of communities* (eds M. L. Cody & J. M. Diamond), pp. 522–534. Cambridge, Mass.: The Belknap Press.

Discussion

R. M. C. Eagar (*The Manchester Museum, The University, Manchester M*13 9*PL, U.K.*). Professor Newell's point, that the frequency of chance parallelism and convergence complicates phylogenetic analysis, is well demonstrated in Upper Carboniferous non-marine bivalves, although it is stressed that such analysis is not thereby prevented. A number of varieties of *Anthraconaia* spp. from the Hance measures of Kentucky, of very late Namurian or of earliest Westphalian age, may be matched with varieties of European *Anthraconauta* mainly of Westphalian D age, and of *Naiadites* of Westphalian A and C. Yet the varieties are all readily determinable generically when assemblages including them are examined. Determination is clear in spite of the fact that internal features of these shells are rarely seen and that variation within assemblages is characteristically wide.

Variation is particularly wide in *Carbonicola* of the British Pennines in measures of late Namurian to early Westphalian age, and in shell assemblages of faunas which, on the basis of several internal and external features, appear to have been ancestral to *Carbonicola* in upper Namurian (Kinderscoutian, R_{1c}) time, and which have been referred to the group of cf. *Sanguinolites* Hind *non* M'Coy (Eagar 1977 *Phil. Trans. R. Soc. Lond.* B, **280**, 535–570). The latter have many varieties which are externally identical with later *Carbonicola*. Recurrent morphological trends above the level of the genus, noted by Professor Newell, may be seen in the modal shapes of so-called invading faunas in cf. *Sanguinolites*, in *Carbonicola* and in much later assemblages referred to *Anthraconaia*. In invading faunas modes tend towards elongate shells with subparallel dorsal and ventral margins, short anterior ends and low obesities, which characterize typically silty to sandy sediments deposited under turbulent conditions in which there were phases of relatively rapid deposition. The bivalves tended to live with their inhalent apertures facing the prevalent current and with their long axes near the vertical. They show evidence of having risen vertically, thereby escaping burial by sedimentation from seaward moving deltaic lobes and bar fingers as the Pennine delta invaded their shallow-water marine palaeohabitats. By contrast, in the lower-energy conditions of lagoons and inter-distributary lakes, where mud bottoms prevailed and sedimentation was slow, shells were more oval, with longer anterior ends and higher obesities, and the bivalves tended to adopt a shallow burrowing or ploughing position on the substratum, or to lie with one or the other valve more or less flat upon it. This second trend, which is seen as the characteristic mode of established faunas, also appears above the generic level, but is especially typical of *Carbonicola*.
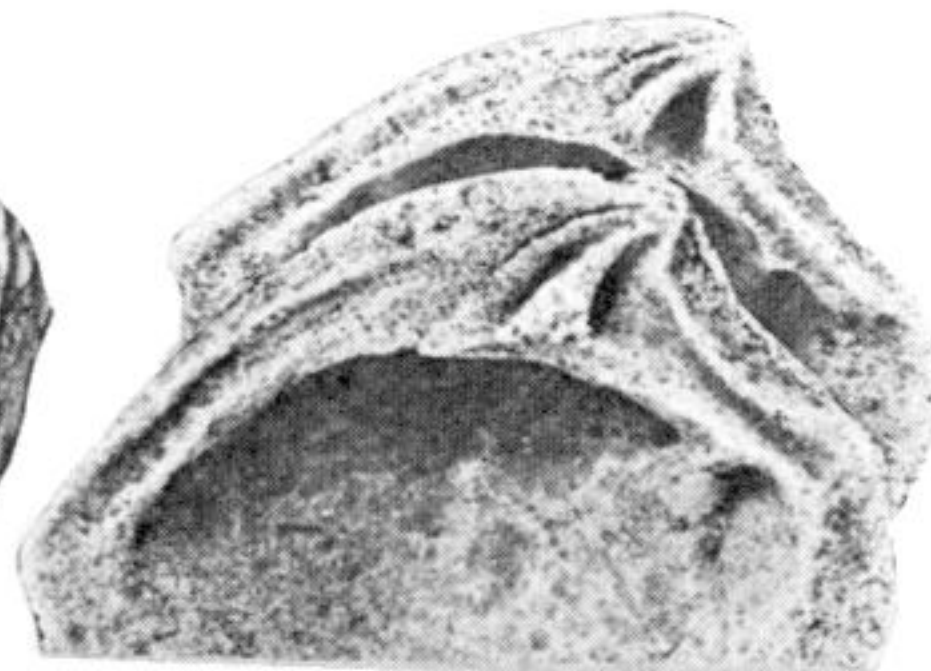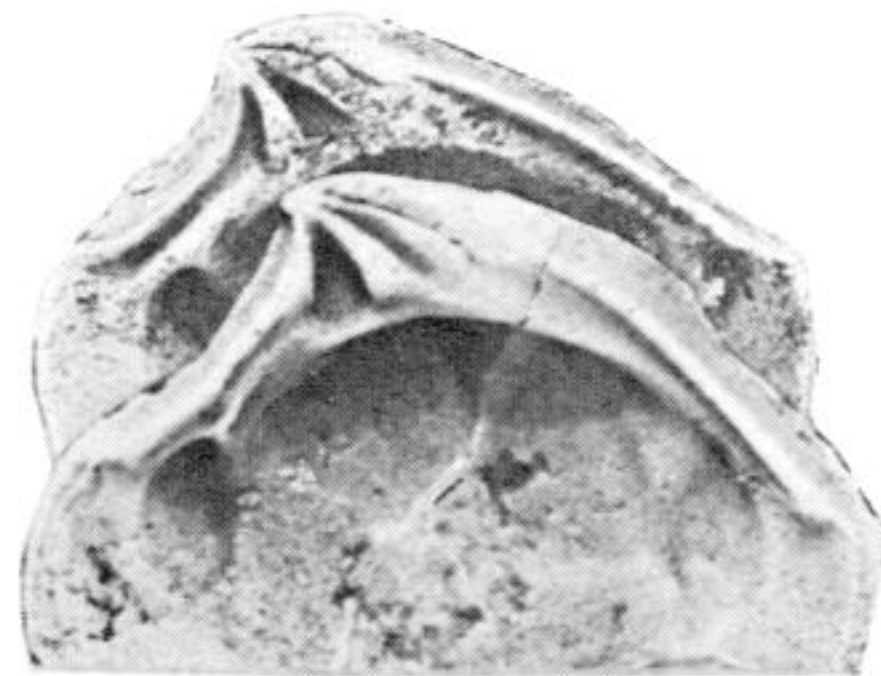
FIGURE 5. Mutant transposition of cardinal teeth in a Permian heterodont *Astartella auri*. (*a*) Left valve, magn. ×3; (*b*) left valves, magn. ×3; upper, normal; lower, transposed. Right valves, magn. ×4; upper, normal; lower, transposed. A new higher taxon which originate by such a mutation. (After Boyd & Newell 1968.)
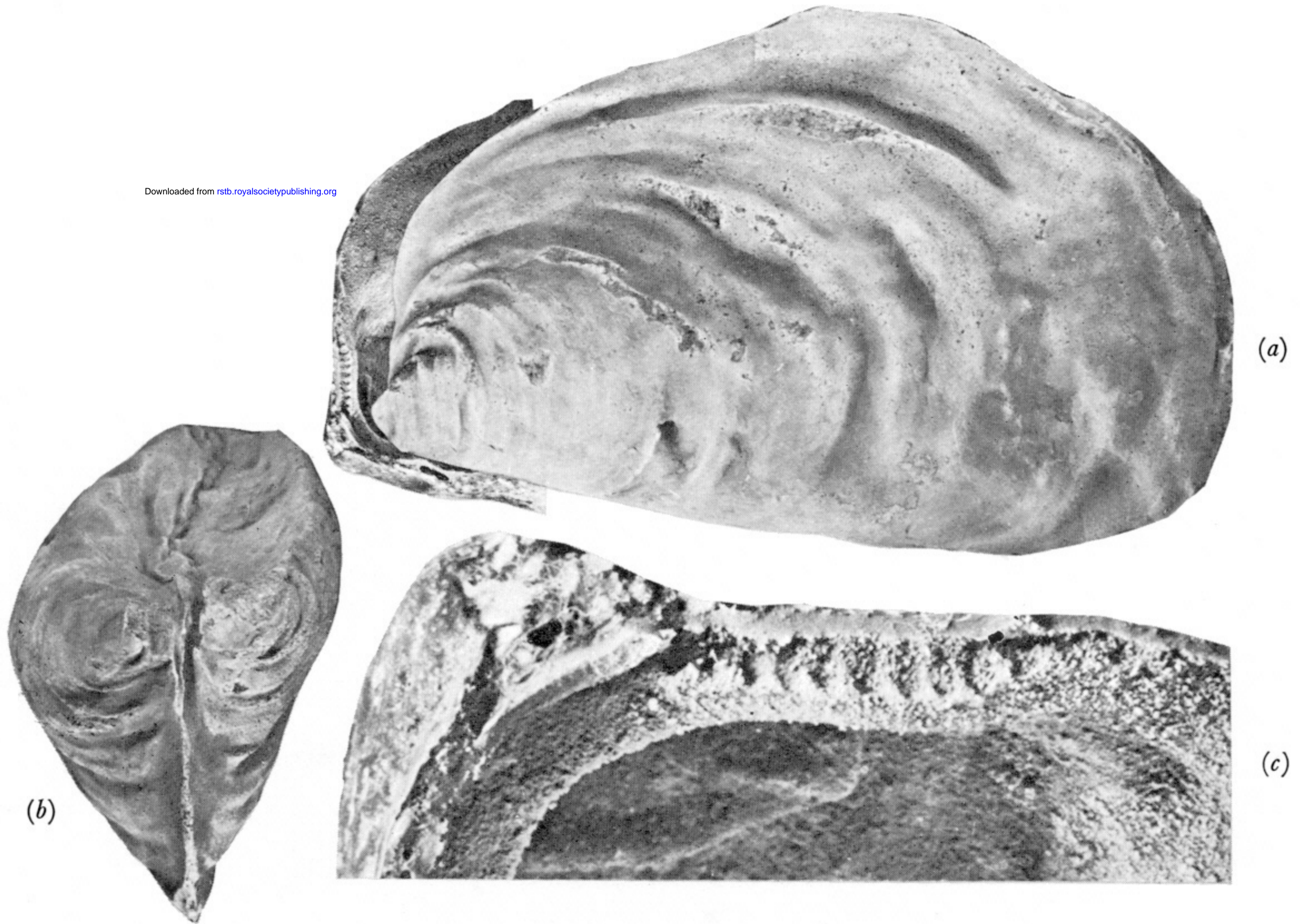
FIGURE 6. The oldest inoceramid, *Permoceramus brownei*, Permian of New South Wales, suddenly appears in a population of *Atomodesma*. The latter possesses a much more primitive ligament. It is suggested that the inoceramid grade is a mutant varient. Magnifications: (*a*) and (*b*), ×$\frac{3}{4}$; (*c*) ×$3\frac{3}{4}$. (After Browne & Newell 1966; see also Kauffman & Runnegar 1975.)