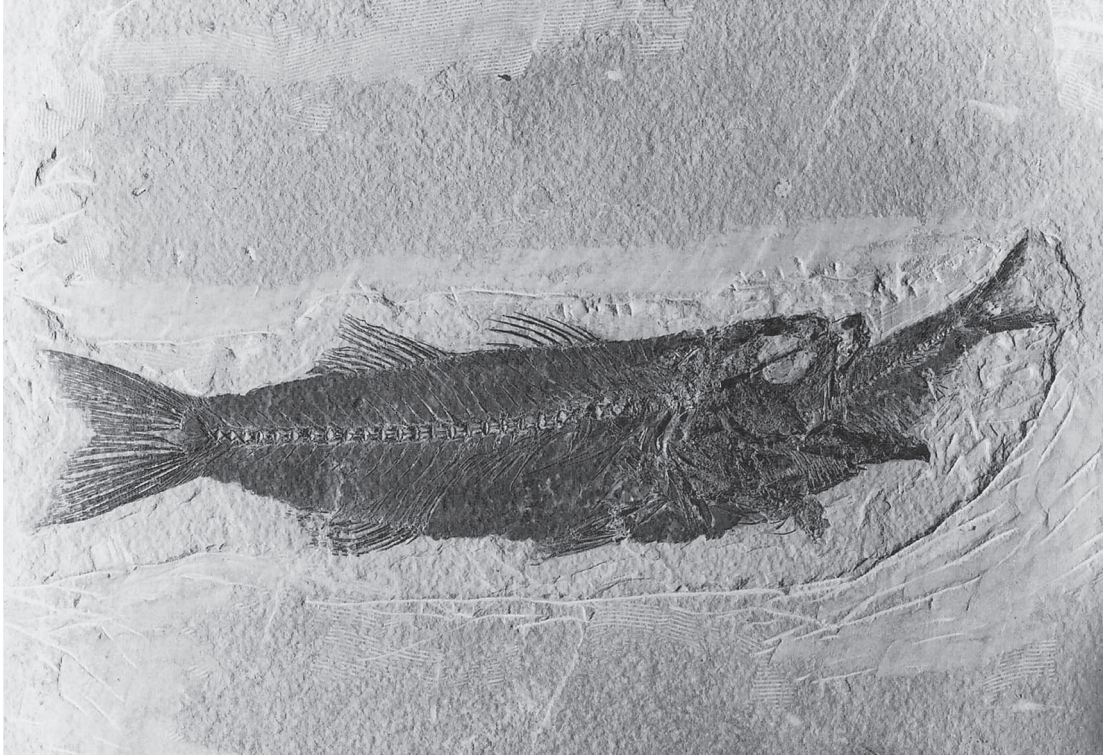


4

PALAEOECOLOGY



A percoid *Mioplosus labracoides* with a partially ingested small herring *Knightia eocaena* from the Eocene Green River Formation, $\times 0.4$. (From Grande, L. 1984. *Bulletin 63* (2nd edn). Geological Survey of Wyoming, with permission.)

4.1 Morphology

L. LUGAR

Introduction

Morphology is the science of describing and analysing form in animals and plants. For palaeobiologists the particular concern is to reconstruct the life form, habitat, ecological role, behaviour, and basic biology of fossil specimens that belong to taxa now extinct. The methodological questions that immediately confront the palaeomorphologist concern the intellectual tools that will reliably guide interpretation of form and function, especially when living specimens of related taxa do not exist. As with any morphological research, the palaeobiologist must describe or characterize the form of interest, set the boundaries of the structure to be analysed, form hypotheses about the function(s) of the feature in question, and determine what other elements of the fossil record are similar. The current upsurge in vigour of morphological research derives from advances of theory and methodology in all of these areas.

Morphological research on extant taxa can be central to interpreting the functions of fossil structures by providing well constructed models of structural systems that may give clues to the functioning of fossil organisms. Liem & Wake (*in* Hildebrand *et al.* 1985) classified current morphological research into two major approaches, the first asking questions about current function and the second about historical origin, transformation, and maintenance of morphological structures.

Experimental approaches to morphology

Experimental approaches can be used to investigate how structures work for living organisms in the environments in which they are presently found. The techniques used by researchers in this area — e.g. by Bramble & Wake, in a study (*in* Hildebrand *et al.* 1985) of the function of the lower tetrapod jaw in feeding — help to identify the elements of the skeleton or musculature involved, measure the forces they exert, and describe the way that these forces help effect food capture (Fig. 1).

Experimental approaches can also focus on specific mechanical problems faced by skeletal systems,

such as load bearing in structures that are subject to forces which may cause breakage. Such approaches attempt to determine how systems respond to the constraints or limitations on design imposed by forces generated in the environment. The development of new techniques, using equipment such as force transducers, strain gauges, and high speed filming, have improved the resolution and accuracy of measurements and have increased understanding of mechanical structures made of bone (Lauder 1981). The problems that these studies investigate — such as feeding at the air–water interface, or the use of filters in suspension feeding — are useful in palaeobiology as they address generalized problems about constraints or limitations that the environment places upon the functioning of organisms. Although none is directly applicable to fossils, these techniques can guide inquiry by illustrating the limits placed on function by the demands of the environment, and by exposing the assumptions underlying hypotheses of function. In this way they can help in the design of experimental methods that are applicable to fossils.

Palaeomorphologists can make physical models of fossil animals, and then experimentally test hypotheses about function and the adaptive qualities of structures of interest. Kingsolver & Koehl (1985), for example, constructed physical models of Palaeozoic insects and tested hypotheses about the possible uses of wings for gliding, thermoregulation, and stabilization during flight by placing these models in various regimes in a wind tunnel. They were able to differentiate between the relative effectiveness of long versus short wings for these properties, and to suggest that insect wings originally were subject to selection for thermodynamic qualities and only subsequently used for aerodynamically more stable movement (see also Section 1.9.1). A classic use of physical models in palaeobiology is Stanley's (1975) study of the effect of varying shell shape and surface texture on burrowing in bivalve molluscs.

Studies by Kontrovitz & Meyers (1988) on the eyes of ostracodes demonstrate an extremely efficient use by the eye of downwelling light in the water column. They were able to determine the

STRUCTURAL NETWORK

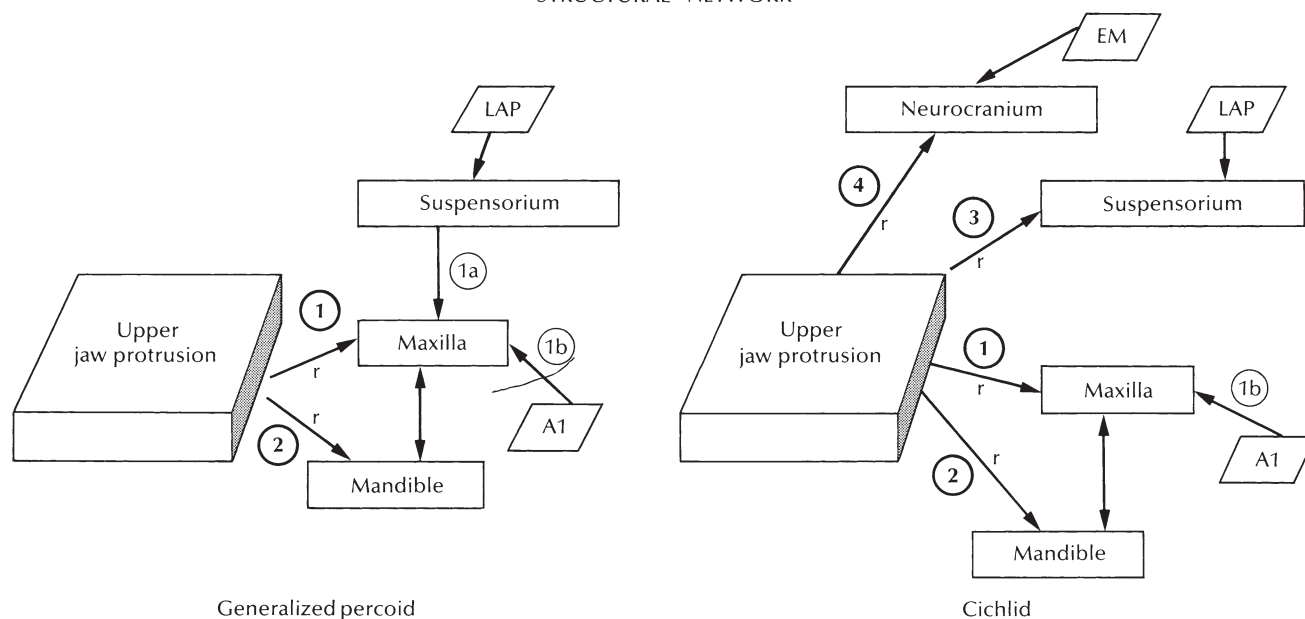


Fig. 1 Mechanical pathways which affect upper jaw protrusion in cichlid fish as compared with the generalized percoid. The research identified the morphological elements that are involved in the protrusion and illustrated the mechanical pathways controlling jaw movement, and the forces involved in this movement. In generalized percoids, two biomechanical pathways mediate upper jaw protrusion: mandibular depression and maxillary rotation (pathways 1 and 2). Suspensorial movement influences the upper jaw by an intermediary articulation with the maxilla (pathway 1a). In cichlid fishes, suspensorial movements can effect upper jaw protrusion independently of maxillary motion and the suspensorium has thus been mechanically *decoupled* from the maxilla (pathway 3). An additional mechanical pathway controlling upper jaw protrusion, neurocranial elevation by the epaxial muscles (EM), is also present. A consequence of the decoupling of suspensorial movement (elimination of pathway 1a) and the increase in number of kinematic pathways controlling the function of upper jaw protrusion is greatly increased functional versatility and increased diversity of jaw morphology in comparison to generalized percoid lineages. This example illustrates both decoupling of a primitive biomechanical link (pathway 1a), and a proliferation in the number of mechanical pathways controlling a function. Both modifications correlate with an increase in diversity of the structural network. A1 = part A1 of the adductor mandibulae muscle, LAP = levator arcus palatini muscle, r = realization of the function of upper jaw protrusion by the indicated pathway.

maximum water depth at which light could be distinguished from dark by the ostracode eye, based on physical equations and elements of eye morphology. This analysis can be extended to eye structures in fossils and, through the examination of fossil morphology, potentially can be used for palaeobathymetric determination and for estimating habitat light conditions.

This experimental approach corresponds to the equilibrium approach which, as characterized by Lauder (1981), assumes that the organisms studied are optimally designed for function in their present environment. Experimental approaches are widely used to reveal the biomechanical attributes of systems, and to determine current function. The demonstration that a structure helps an organism solve problems connected with its present mode of life is useful in establishing its 'adaptedness' in the original sense of well designed connection between

organism and environment (Fisher 1985; Section 2.9). However, demonstrating the present function of a structure does not necessarily establish the evolutionary adaptedness of the character, for it does not demonstrate that the structure was shaped by natural selection for its present function.

Theoretical criticisms of the equilibrium approach centre around difficulties in defining optimality, in choosing criterion scales whose maxima or minima provide a metric for discussion of optima, and in the existence of constraints of a historical nature that limit achievement of optima through natural selection (Lewontin 1987). Biologically oriented criticisms of optimality centre on the historical and genetic barriers to the potential realization of optimal form. Such barriers include possible lack of necessary genetic diversity in populations, constraints imposed by the requirement for a functional developmental architecture, and the disruptive ef-

fects of stochastic processes in evolution (Gould & Lewontin 1979). In addition, the realization that structures often have multiple functions, that function may change during the life of the individual, and that selection pressures may vary during ontogeny, has led to an increased understanding of the complexity of testing for adaptedness and optimality (see also Section 2.9).

Some workers have undertaken careful experimental designs that attempted to identify and evaluate the importance of various selective forces acting on a particular structure or pair of structures. Lowell (1987) used safety factor analysis to examine shell strength and foot tenacity of intertidal gastropod limpets, to identify the importance of selection for one factor on the achievement of effective performance in the other factor. Lowell's results indicated that two developmentally and functionally distinct structures, the foot and the shell, are quite closely coadapted in limpets from two separate gastropod subclasses (Lowell 1987). By examining mortality in the field in conjunction with safety factor analysis for these limpets, Lowell identified two potentially important selective pressures: lateral crushing forces generated by fish predators on tropical shores, and prying forces generated by crab and bird predators on both tropical and temperate shores. Although a crucial first step, demonstrating that a morphological structure functions particularly well under specific conditions does not establish conclusively that the structure contributes to differential survival and reproduction of that animal. Lowell's inferences about selective pressures on the limpets examined were strengthened by showing through field studies that there are predators active in the habitat capable of inflicting forces on the animals similar to the laboratory-generated forces. Lowell's study identified morphological features, such as a thickened aperture lip on the shell, which may be of use to the palaeontologist in examining the fossil record. However, even demonstrating that a feature is undergoing selection presently does not necessarily elucidate the origin and early evolution of that feature in a lineage. The equilibrium approach used by Lowell does not explain the origin and original forces shaping the basic limpet shell and aperture form, which appear in the fossil record in the Cambrian, well before the first occurrence of the hypothesized predators, and in a different habitat. Researchers interested in the origin and evolution of morphological features have developed methods to specifically address these questions.

Phylogenetic approaches to morphology

While some workers have focused on the role of natural selection in shaping morphology in response to functional requirements, others have explored the historical or phylogenetic approach — the *transformational approach* of Lauder (1981). Here the emphasis has been on understanding the intrinsic factors of structural evolution, within a well supported phylogenetic context. The transformational approach places features in nested sets within a monophyletic lineage and looks for generalized or emergent properties of functional systems (Lauder 1981). This allows the construction of testable hypotheses about historical patterns of change and about patterns of diversity involving terminal taxa.

One research programme for identifying intrinsic elements of design is to examine developmental processes. Evolution produces morphological change by varying particular features of the developmental pathways of organisms. Research has focused on several major classes of alteration of developmental processes. Changes in the time during development at which a process takes place, heterochrony, have been of central concern to morphological and evolutionary researchers (see Section 3.4). Alberch *et al.* (1979) developed a formal model for describing the effects of heterochronic changes in timing on the shape of animals. They identified the beginning and ending of growth of a feature, the rate of growth, and the size of the initial growth area, as being crucial to understanding the relationship between changes in developmental pathway and adult form. Some developmental biologists have begun to look at what Goodwin (1984) called *generative paradigms*. Here the emphasis is on describing developmental patterns arising from fields of embryonic tissue that specify elements of a structure, such as the developing limb of vertebrates (Fig. 2). There may be constraints (in a positive sense, i.e. focusing of direction or channelling of developmental possibilities) that arise from limitations on the possible alterations of specifications of patterns of developing limbs or other features (Goodwin 1984). The effect of theoretical advances in developmental studies has been to provide alternative hypotheses that explain patterns, such as the loss or gain of digits in lineages of tetrapods, and to provide new avenues for experimentation.

Within palaeobiology, the transformational approach can be used to order fossil taxa in nested sets, thereby elucidating structural patterns in the historical appearance of features. This ordering adds

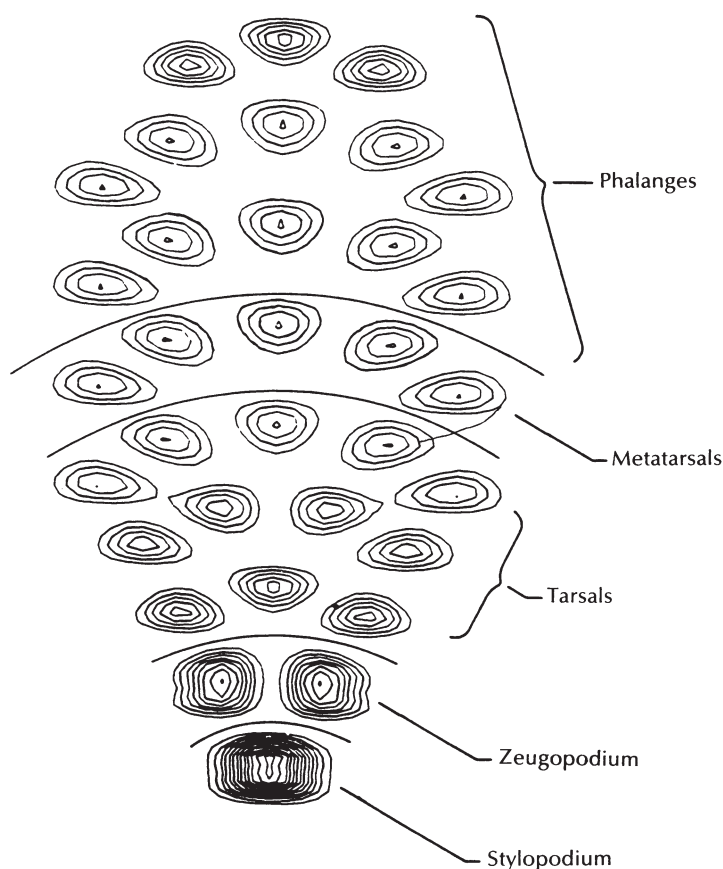


Fig. 2 The contour plots represent the solutions to field equations generated by a model of pattern formation for a hind limb with five digits. They demonstrate the possibility of generating specific descriptions of activity in limb buds which will describe patterns of organization and constraints on the possible forms which the bud can generate. (Reprinted by permission of John Wiley & Sons, Ltd, from *Evolutionary theory: paths to the future*, ed. J.W. Pollard, © 1984.)

precision to the imputation of homology, where a structure in a fossil taxon may be judged to share the known function in a Recent form due to proximity of relationship. Palaeobiological inquiry can add taxa to monophyletic evolutionary groups under study, which may provide new characters, characters in new complexes, or states not present in Recent taxa.

The uses of analogy in palaeobiology

For many organisms of interest to the palaeobiologist, no modern homologue is available. Indeed, one of the most interesting and challenging tasks in palaeobiology is the interpretation of the rich fossil record of forms having bizarre and unusual morphologies (Hickman 1988; Section 5.2.5). This study should be conducted not simply as a description of peculiar structures but also as a search for recurring patterns in 'fundamental attributes such as size, shape, symmetry, and ratios of surface area to volume' (Hickman 1988). When no modern homologues are available as guides to function or behaviour, analogy is invoked. Several conceptual tools have been developed within palaeontology to

increase the rigour and explanatory range of morphological research. These include the *paradigm method* of Rudwick (1964), Seilacher's *Konstruktionsmorphologie* (1973), *theoretical morphology* (e.g. Raup 1966), and the increased possibility for precision and analytical manipulation that comes from modern *morphometrics*.

The paradigm method. The paradigm method was elucidated by Rudwick (1964) as an attempt to formalize the use of analogy in explaining the function of a structure or element of structural design. The paradigm method is used to try to place the organism into an environment as a working machine. In Rudwick's formalization, the paradigm is the form of a structure that will most efficiently carry out the hypothesized function(s) of the biological structure of interest, provided that construction is of biological materials appropriate to the organisms being studied. The paradigm method is most useful when several functional hypotheses are being tested. Thus the application of the method proceeds by postulating several functions for a structure, specifying an optimally efficient form for each function, and examining the degree of resemblance between the

form possessed by the organism and those postulated by the researcher. The paradigmatic form with the closest fit to the real form may be judged to represent the actual function of the structure. The ideal forms that serve as the source of the analogy are usually chosen from classes of machine, such as pumps, levers, or bridges, for which mechanical engineering can be used to specify the optimal design for accomplishing a specific task.

The paradigm method has been criticized because it assumes optimality of design for the feature in question, and because it assumes only one function for a structure. It also uses chiefly mechanical analogies for function, thus ignoring other sources of insight such as architecture, communication systems, transportation systems, etc. (Hickman 1988). Further, although it can specify optimality of design in the ideal form, there are no rigorous criteria for the minimum resemblance between paradigm and organism needed to justify the imputed function (Signor 1982). However, Fisher (1985) has shown how the method can be translated into a problem in Bayesian inference, and he has also elucidated the use of tests of minimally sufficient or threshold conditions for achieving a particular functional effect. Further, if divergent hypotheses of function are made, with different ideal forms described, then observation may reveal which prediction of form is actually realized by the organism.

Constructional morphology. Konstruktionsmorphologie (or constructional morphology) was developed by Seilacher (1973); it enables the morphologist to speculate about function in a broad framework that takes into account both evolutionary history and ontogenetic problems. Seilacher cited three major factors that must be recognized in the analysis of form. These are: (1) the functional element (*Adaptiver Aspekt*); (2) the fabrication or architectural element (*Bautechnischer Aspekt*); and (3) the phylogenetic element (*Historischer Aspekt*). These factors summarize the action of various forces and constraints on the production of form. The functional element describes the action of natural selection in shaping a structure for efficient use. The fabrication element refers to the developmental patterns and processes that produce an individual organism. The phylogenetic element refers to the evolutionary history of a taxon. The interaction of these forces produces form, constrained by the limitations they impose. A primary goal of constructional morphology is the elucidation of the relative importance of these elements in the pro-

duction of specific forms. These categories have great value as a heuristic device for sharpening awareness in the researcher of 'what types of information prevail' in the production of a particular form (Hickman 1988).

When applied to particular systems, Seilacher's categories may be extended or modified to suit the needs of the system under analysis. Thus Hickman (1980) used phylogenetic, mechanical, ecological, programmatic, maturational, degenerative, and constructional factors in the analysis of form and function in the molluscan radula (a toothed tongue exhibiting substantial morphological variation). This expanded list of factors arises from the realization that certain aspects of morphology are best examined in a non-evolutionary context, so as to reveal important information about the production of form that might otherwise be obscured. The teeth of the molluscan radula, for example, are produced in a form that requires shaping by use before achieving the most effective functional form. A pencil, which comes from the factory in a form requiring modification before it can be used, provides an analogy.

Theoretical morphology. Theoretical morphology uses mathematical description of the parameters that control shape and its alteration to prescribe the domain of form that can result from transformations of the original specification. Raup (1966) used four parameters to establish the overall form open to conispiral shells. These four elements — the shape of the generating curve, the rate of expansion of that curve with respect to revolution about its axis, the position and orientation of the curve in relation to the axis, and the rate of translation around the axis — establish the basic morphospace for conispiral shells. By generating all possible outcomes of changes in these parameters, Raup analysed the use of form in molluscs in terms of which possibilities have been realized through the evolution of actual organisms. These areas of morphospace can be compared with those areas that are occupied. This allows hypotheses about function, or insights into structural or design constraints, to explain why certain forms have not evolved.

Morphometrics. The subject of morphometrics is developing very rapidly. The use of techniques such as the theta-rho analysis of Siegel & Benson (1982) to describe areas of shape that differ between two forms, while simultaneously identifying the areas that remain constant, have greatly improved

Plethodontidae

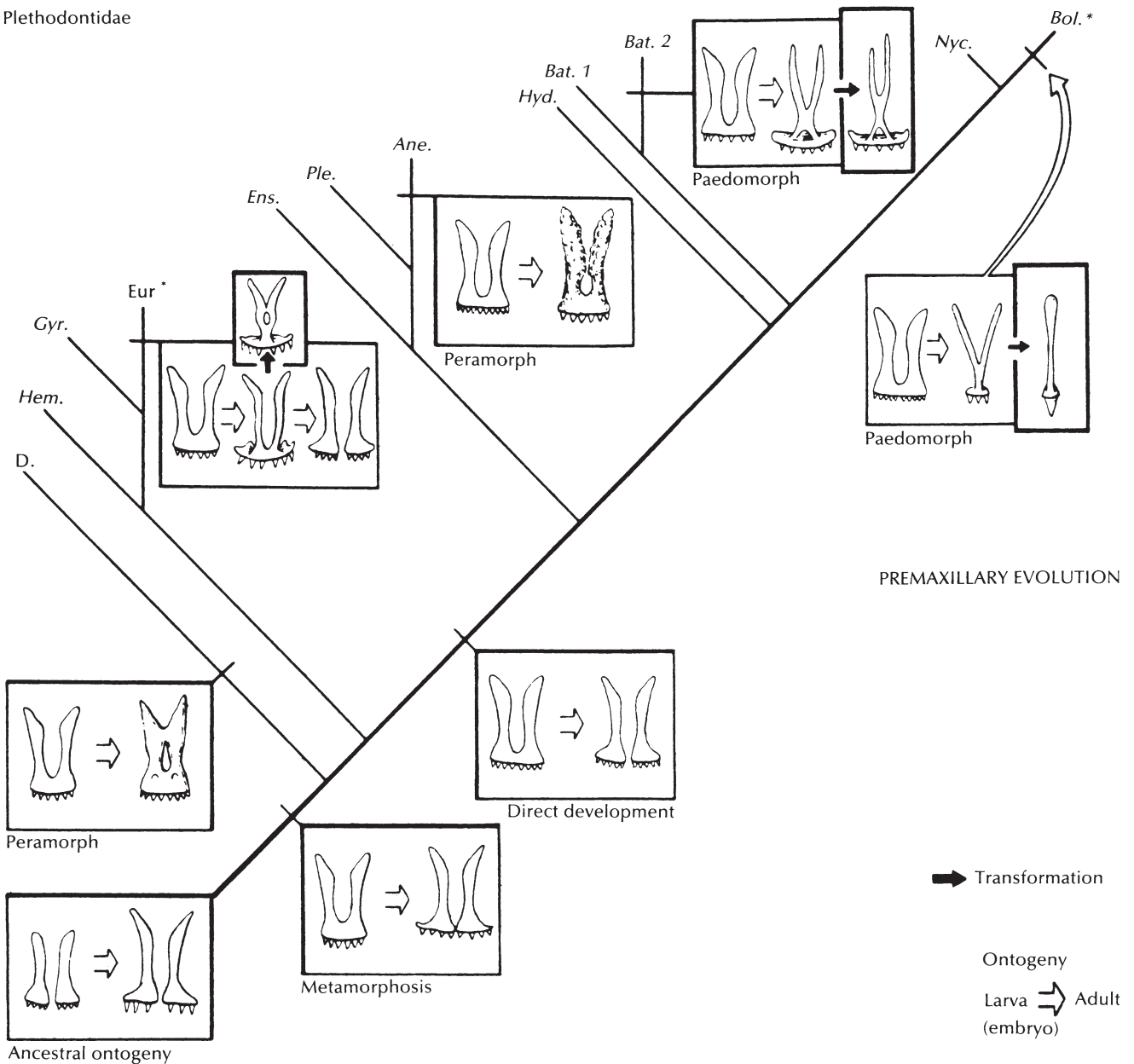


Fig. 3 The use of a phylogenetic hypothesis as the framework onto which the recurring forms of the pre-maxilla of plethodontid salamanders could be mapped illustrates the use of several lines of morphological evidence to elucidate an evolutionary question. The ancestral ontogeny is indicated at the base, with a bipartite premaxilla persisting throughout ontogeny (hollow arrow). Synapomorphies (Section 5.2.2) are indicated in boxes. Evolutionary transformations (solid arrow) occur within some of the synapomorphous states. The unipartite premaxilla typically divides during metamorphosis or early ontogeny, but evolutionary changes causing unipartite premaxillae to appear in adults have occurred at least five times, two by peramorphosis and two by paedomorphosis (Section 2.4). D = subfamily Desmognathinae, Hem. = *Hemidactylum*, Gyr. = *Gyrinophilus*, Eur.* = all members of the tribe Hemidactyliini except the two preceding genera, Ens. = *Enstatina*, Ple. = *Plethodon*, Ane. = *Aneides*, Hyd. = *Hydromantes*, Bat. 1 = *Batrachoseps campi* and *B. wright*, Bat. 2 = all remaining species of *Batrachoseps*, Nyc. = *Nyctanolis*; Bol.* = all members of the supergenus *Bolitoglossa* except *Nyctanolis*.

the ability of morphologists to study transformations of form during ontogeny and throughout evolutionary sequences. The use of computer-assisted methods of image capture, and of precise

measurements of such standard morphological determinations as lengths, widths, perimeters, and areas, has greatly increased the speed and accuracy with which measurements may be made and has

also speeded processes such as digitization to allow the compilation of larger databases (see Section 6.1).

Conclusions

The combination of several lines of approach to problems of evolutionary morphology seems likely to yield results that will make morphological research interesting to researchers in a wide array of fields, such as evolutionary biology, developmental biology, and ecology. Wake & Larson (1987) analysed the evolution of the skeletal and muscular elements of the autopodium, premaxilla, and feeding structure of plethodontid salamanders by using a combination of structural and neo-Darwinian approaches. They viewed individual development as a closed set of epigenetic transformations that could be used to predict a limited number of possible forms open to the organism, and they examined the production of these forms by using cladistic and populational genetic analysis of the history and population structure of natural populations. They were thereby able to identify design constraints on the salamander feeding structure, and illustrate its achievement in several living salamander genera (Fig. 3). They illustrated the frequent occurrence of heterochronic changes within the lineages examined and built up a hypothesis for the role of various forces affecting the morphology of plethodontid salamanders in the shaping of individuals and for the deployment of that shaping in evolutionary time.

Morphologists have a wide array of conceptual tools and experimental procedures available to them for the analysis of form, and the present flourishing of research into morphology reflects this. Evolutionary biology and palaeontology have continued to develop vigorously and an understanding of the ecological role, evolutionary history, and stratigraphic significance of fossil forms is still an area of active research. Thus morphology continues to play an important role in palaeobiology.

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4.2 Composition and Growth of Skeleton

B. RUNNEGAR

Introduction

Mineral skeletons appeared abruptly about 550 Ma in a great variety of different kinds of organisms. Prior to this time all living creatures used hydrostatic forces constrained by soft or flexible structures to shape their bodies. With the invention of mineralized skeletons, new types of body plans became possible and the conspicuous fossil record of the Phanerozoic began.

Many different kinds of amorphous or crystalline mineral compounds are formed biologically (Lowenstam 1981). These compounds are the building-blocks of rigid skeletons, but they also serve to rid cells of unwanted salts, to store useful elements (such as iron and phosphorus), and to act as components of sensory organs that are used for sight, balance, and navigation. In sizeable animals these functions are clearly discrete and are often performed by different kinds of biominerals. For example, some birds have phosphate endoskeletons, carbonate eggshells and gravity sensors, and a navigation system that depends in part upon magnetite.

The non-skeletal biominerals represent an insignificant volume of all but the smallest organisms. As a result, they are rarely fossilized and the history of biomineralization is largely the history of mineralized skeletal materials. These may be preserved in their original condition or be modified by the chemical and physical processes of diagenesis and metamorphism.

Nature of mineral skeletons

Nearly all of the mineral skeletons manufactured by living and fossil organisms are made from one or two common inorganic compounds: calcite (a rhombohedral form of CaCO_3), magnesian calcite (a solid solution of MgCO_3 in CaCO_3), aragonite (an orthorhombic form of CaCO_3 , normally having a small amount of SrCO_3 in solid solution), apatite (a family of compounds of the general formula $\text{Ca}_{10}(\text{PO}_4)_6(\text{OH},\text{F})$) and opal (hydrated silica with the general formula $[\text{SiO}_n \cdot \text{OH}_{(4-2n)}]_m$, where $n \leq 2$ and $m \gg n$). Each of these materials is readily available,

almost insoluble in water, and non-toxic, but each is also soft and brittle and most are relatively dense. How then are these substances used to make sizeable, strong, and light-weight skeletal structures, and when did these innovations first take place?

To a first approximation, most skeletons may be described as *stiffened walls*, *scaffolds*, or *shells*. Stiffened walls (such as the chicken eggshell) are mineralized all at once after they have been shaped by soft tissues, whereas shells are produced over a long period of time by incremental growth. Both kinds of structure may coexist in a single skeleton: the coiled conch of *Nautilus* is a classic shell but its internal septa are better described as stiffened walls. Similarly, the echinoid test is best modelled as a stiffened wall or 'Pneu' (Seilacher 1979), although its component plates display the incremental growth that is typical of shells. Scaffolds differ from both walls and shells in being static or dynamic structures formed of linear or planar subunits. The calcareous and siliceous spicular skeletons of sponges and the limbs and rib cages of vertebrates are scaffolds in this sense. They provide structural support but do not enclose the soft tissues and hence are of little use as armour.

In contrast, many skeletons are hollow structures in which organisms reside. These enclosures can be built in two main ways: either by assembling prefabricated modules in the shape required, or by growing the mineral inwards from a preformed substrate that surrounds the body. Both of these methods of construction have severe geometrical constraints.

Opaline silica has had limited potential as a skeletal material except in microscopic organisms (radiolarians, diatoms, silicoflagellates), because of its non-crystalline, glassy nature and intracellular mode of formation. In contrast, calcium compounds form anisotropic crystals that may be shaped and assembled in a variety of ways by habit-modifying macromolecules (Mann 1988). A few tiny organisms can make their skeletons from a small number of single crystals, but this method of construction is not available to sizeable organisms because large crystals are difficult to grow, mechanically weak, and unsuitable in shape. Most crystalline skeletons

are therefore composites of organic polymers interspersed with a mineral phase. These composite materials are better able to resist both plastic deformation and brittle fracture, and they have strengths that are much greater than those of either component alone.

Construction of carbonate skeletons

Almost two-thirds of the mineral skeletons formed by living and extinct groups of organisms are composed of the two common polymorphs of CaCO_3 , calcite and aragonite (see also Sections 1.4, 3.8.1). Alkaline earth elements with an ionic radius greater than about 0.1 nm form orthorhombic carbonates of the aragonite type and thus fit easily into the aragonite lattice. Those with ions smaller than Ca^{2+} (0.10 nm) form rhombohedral carbonates of the calcite type and also occur in solid solution in calcite. Thus aragonite commonly contains some Sr^{2+} (0.11 nm) but little Mg^{2+} (0.06 nm), whereas the converse is true for calcite. Only CaCO_3 can form both orthorhombic and rhombohedral polymorphs under conditions found at the surface of the Earth.

Synthetic calcite usually forms small rhombohedral crystals (Fig. 1) that correspond in shape to the three directions of perfect cleavage found in natural calcites. Similar rhombohedra often line cavities in carbonate rocks but more slowly deposited crystals can exhibit other forms. However, the normal habit of natural crystals of inorganic calcite is equidimensional or prismatic.

Aragonite crystals are almost invariably fibrous. Each fibre is pseudo-hexagonal in cross-section, being bounded laterally by four faces of one crystallographic form and two of another. The fibres are packed together into radial aggregates, so growth is slow perpendicular to the axis of the fibre and very fast at the tip. Thus, in simple inorganic systems aragonite is characterized by its fibrous habit and spherulitic growth (Fig. 2). Magnesian calcite also commonly forms fibrous crystals, possibly because the Mg^{2+} ion poisons the prism faces of the developing calcite crystals. For the same reason, the presence of Mg^{2+} may promote the formation of aragonite at the expense of calcite.

Single crystals of high-magnesian calcite are used as skeletal modules by calcareous sponges and echinoderms. In the echinoderm skeleton the intrinsic weakness of calcite is overcome by the formation of a higher order structure called *stereom*. In a sense, the echinoderm skeleton may be viewed as a two-phase cubic emulsion of mineral and living

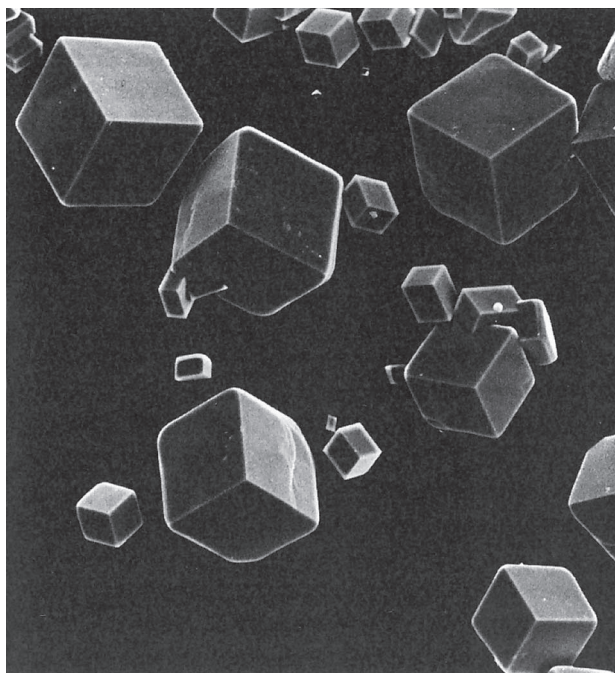


Fig. 1 Synthetic crystals of calcite (greatly magnified).

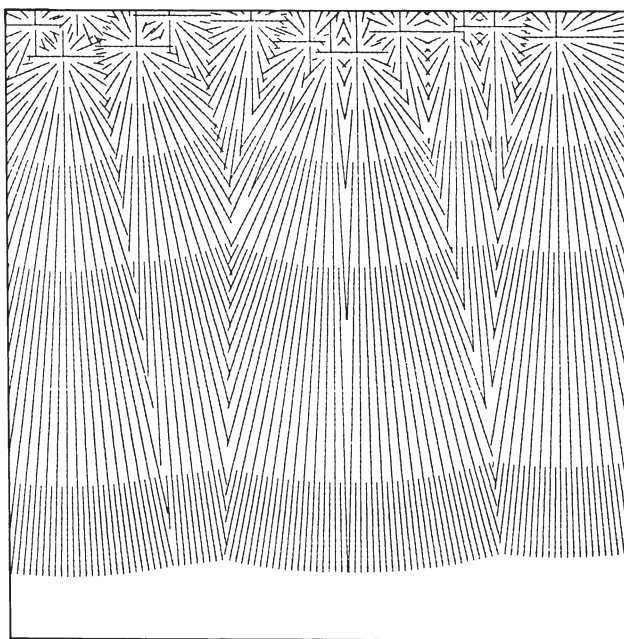


Fig. 2 Two-dimensional computer simulation of the spherulitic growth of aragonite fibres. The program allows equally spaced radial lines to grow from randomly distributed 'nucleation sites' until they intersect. (Program and simulation by F.A. Shaw.)

tissue. The interface between the two phases corresponds approximately to a surface of zero mean curvature, such as might be formed in a well shaken

mixture of equal parts of oil and water. The tissue-filled pores in the echinoderm stereom prevent fractures from propagating through the structure.

Some unicellular golden-brown algae manufacture articulated calcareous exoskeletons by prefabricating calcitic plates called *coccoliths* in intracellular vesicles. Each coccolith is composed of a number of calcite crystals assembled on an organic base-plate or scale in an organized way. The stereochemistry of the scale–mineral interface specifies the orientation of each calcite crystal needed to form the complete assembly. This requires the recognition of the trigonal symmetry of CO_3 groups within the calcite structure because the hexagonal array of calcium atoms carries insufficient information to specify a unique orientation of the crystal lattice. As a result, most coccoliths have an inherited right–left symmetry or *chirality* that is derived from the geometrical properties of calcite.

The ‘living fossil’ *Braarudosphaera bigelowi* is one of the most spectacular of all coccolith-bearing algae. It encysts within a regular dodecahedron formed of 12 equal-sized calcitic pentaliths (Fig. 3). Each pentalith is composed of five radial wedges that are single crystals of calcite set at approximately 72° ($360^\circ/5$) to each other. The fivefold symmetry of each pentalith is not derived directly from the crystallography of the mineral phase, but results from the fact that the 78° angles in the faces of calcite cleavage rhombohedra are almost a fifth of a circle.

Many of the hollow mineralized structures formed by organisms may, at least in principle, be regarded as shells. These are four-dimensional structures in that they are not formed all at once. Instead, growth occurs continuously or episodically for an extended period of time on linear margins or on previously formed surfaces. Most are scale-invariant objects that have the same proportions at all magnifications. The best-known example is the logarithmic spiral of the *Nautilus* shell, but most other shells, scales, tests, and teeth are built in a similar fashion. The ultimate strength of the construction depends both on its shape and upon the crack-stopping properties of its component materials.

In the simplest kinds of shells the mineral is nucleated on the surface of an enclosing membrane (epithec, periostracum) and it grows towards the living animal in an essentially inorganic fashion. If the mineral is aragonite, magnesian calcite, or apatite, the crystallites will normally be fibrous and the gross structure of the skeleton may consist of a series of spherulitic pseudoprisms (Fig. 4). Such pseudoprisms are moulded by surface forces rather

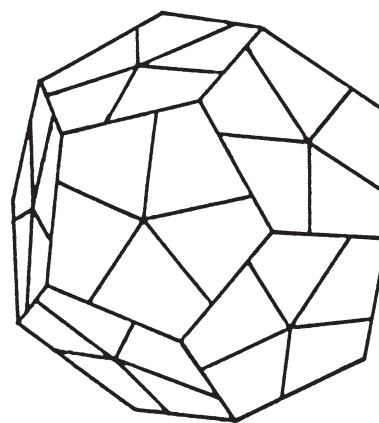


Fig. 3 The calcite coccosphere of the alga *Braarudosphaera bigelowi* is a regular dodecahedron composed of 12 pentaliths, each in turn made from five calcite crystals.

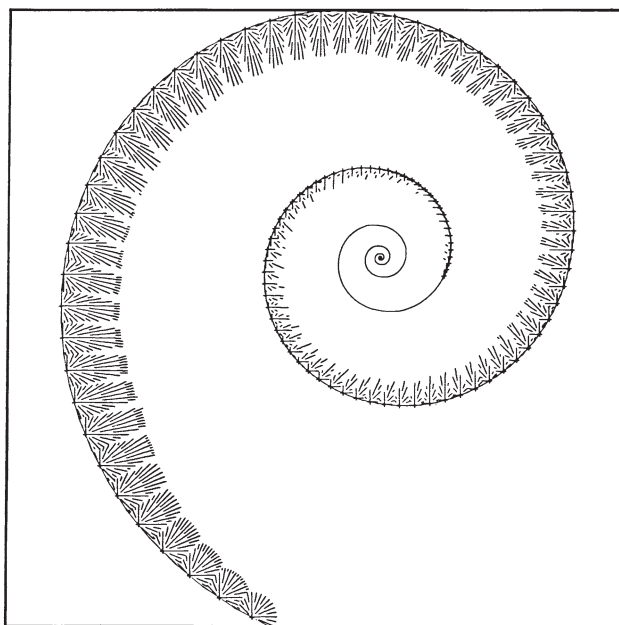


Fig. 4 Computer-drawn model of the growth of the outer layer of the *Nautilus* shell. Aragonite fibres represented by straight lines grow in from the periostracum (curved line) to form spherulites. (Program and simulation by F.A. Shaw.)

than chemical bonds, and they are found in both inorganic and unstructured biological deposits. They begin as hemispherical aggregates that may be nucleated at random on the inner surface of the enclosing membrane, and they grow competitively to achieve a uniform size and polygonal cross-section by obeying the rules of soap-bubble geometry. Spherulitic microstructures of this type are found, for example, in the walls and septa of coral

skeletons, in the outer layers of mollusc shells, and in vertebrate eggshells.

These simple fibrous microstructures are strong in compression but weak in tension because cracks easily penetrate the layers parallel to the fibres. This defect may be overcome by fibres inclined to the shell surface in one or more orientations, as in molluscan crossed-lamellar shell structure.

Another way of making stronger shells is to deposit the mineral in thin layers parallel to the shell surface. This method of construction requires a modification of the mineral crystallites to produce shapes that are rarely or never found in non-biological systems. Molluscan 'mother-of-pearl' (*nacre*) and its calcitic equivalents are good examples of such layered carbonates. The great strength of *nacre* allows *Nautilus* to inhabit depths of 500–600 m where the water pressure is about 60 pascals.

The spherulitic aragonitic prisms of the outer layer of the *Nautilus* shell present the {001} ends of innumerable fibres to the secreting surface of the mantle. The fundamental difference between the unmodified aragonite fibres and the flat crystals of the nacreous inner shell layers lies in a difference in habit not form. Both kinds of crystals are bounded by equivalent faces, but in *nacre* growth on {001} is very slow, whereas in the fibres it is very fast.

It seems likely that proteins rich in aspartic acid residues may be involved in limiting growth on {001} in aragonite and stereochemically comparable surfaces in calcite. Proteins of this kind have been isolated from the organic matrices of a great variety of skeletal carbonates. They are believed to occur as regular, two-dimensional networks (β -sheets), to bind calcium, and to have negatively charged amino acids spaced so as to match the arrays of calcium atoms in the surfaces of layered carbonates, such as *nacre* (Mann 1988). As the genes for these simple repetitive proteins could have arisen *de novo* on more than one occasion, it is likely that layered structures developed rapidly and convergently from primitive fibrous ones in a number of different lineages.

Other kinds of skeletons and the history of biomineralization

As a skeletal material, calcium phosphate has proved most successful as either dermal armour or internal support. As a result, most phosphate skeletons consist of a number of different parts (bones, teeth, sclerites, etc.) that may dissociate and disperse after death. Reconstruction of the whole skeleton, or more

generally the scleritome, presents particular problems for palaeontologists (Bengtson 1985).

Little is known about the mechanism of formation of phosphatic skeletons in animals other than vertebrates where the mineral is intimately associated with the proteins collagen and osteocalcin. There is increasing evidence that the γ -carboxyglutamic acid side chains of the osteocalcin molecule are responsible for the mineral–protein interaction, and that the role of collagen is to provide a structural framework. A similar situation appears to occur in mollusc shells where glycine-rich proteins that are insoluble in ethylenediaminetetraacetic acid (EDTA) seem to act as the foundation for EDTA-soluble proteins that are rich in aspartic acid residues (Mann 1988). In both cases the structural protein acts as the energy-dissipating component of the mineral-matrix composite in addition to providing a substrate for subsequent mineral growth. It is probable that a comparable organization is to be found in many other kinds of carbonate and phosphate skeletons.

Many kinds of skeletons may preserve historical information about the ontogeny of the owner and the conditions under which it lived, because they are continuously modified during life. Vermeij (1970) has made the distinction between permanent skeletons that are retained throughout postlarval life and transient skeletons that are shed periodically. The former may be secondarily remodelled by normal or pathogenic processes; the latter record snapshots of the ontogeny and are particularly characteristic of the Arthropoda.

Persistent incremental growth, as in tree trunks, shells, and open-rooted teeth, produces skeletons that may be viewed as continuous environmental recorders (Jones 1983). Successive variations in the thickness of growth increments have been used with varying degrees of success to estimate individual age and growth rates, analyse population structure, understand local environmental conditions, and provide empirical measures of past day length and other geophysical phenomena. Ontogenetic changes in the isotopic, elemental, and mineralogical composition of mollusc shells are increasingly being used for environmental analysis, as new analytical techniques allow the sample size to be reduced to growth increment scale.

The discovery that early phosphate or carbonate cements may have replicated the fine structure of skeletal minerals altered by subsequent diagenesis has provided new insights into the early history of biomineralization (Section 1.4). Almost all of the

known varieties of skeletal minerals and most of the different kinds of mineral skeletons appeared within a few tens of millions of years at the beginning of the Phanerozoic. Innovations such as molluscan nacre, echinoderm stereom, and the characteristic prismatic calcite of the shells of articulate brachiopods were being manufactured by at least the Middle Cambrian. Hardly any new types of skeletal materials were evolved after the Cambrian and the only kinds of mineral skeletons that appeared during the invasion of the land were the carbonate eggshells of snails and vertebrates. Thus, although new kinds of organisms began to build mineral skeletons in post-Cambrian time (corals, bryozoans, calcareous and siliceous plankton, etc.), they used pathways pioneered previously by cyanobacteria,

eukaryotic algae, animal-like protists, and a large number of metazoan phyla.

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4.3 Biomechanics

P. A. SELDEN

Introduction

Biomechanics is the application of mechanical principles to the study of organisms. In palaeontology, only recently have sufficient biomechanical studies accumulated to constitute a bibliography of the subject. These studies span almost the entire range of taxa; their objectives are usually functional morphological and commonly, but not necessarily, quantitative. Conversely, quantitative studies using mathematical or physical principles (e.g. growth form in Bryozoa or vision in trilobites) are not necessarily biomechanics. The major contribution which biomechanics makes to palaeontology is in testing hypotheses of functional morphology that are based on deduction from morphology or external factors, such as sediment, associated biota, or distribution. Biomechanics can be a powerful tool in hypothesis testing, but quantitative results, even on living organisms, must be interpreted with caution because of the inherent complexity of the natural world.

Undoubtedly the most important textbook on biomechanics is that by Alexander (1983) and his chapter headings are used here as a basis for

grouping examples of the uses of biomechanics in palaeontology.

Strength

An important branch of biomechanics investigates the structural design of organisms, and in particular the properties of the materials of which plants and animals are made (Wainwright *et al.* 1976). The common questions asked are about the strength of biological materials under stress, i.e. subject to a force, usually gravity, or a current flow in a static situation or during movement. There is considerable overlap here with *constructional morphology* (Section 4.1). Biological structural materials are usually complex, since they have to operate in a variety of mechanical environments and also perform other feats, like growing. They are mainly composites, good examples being wood, arthropod cuticle, and echinoderm stereom and stroma. Such materials are very resistant to fracture and other forms of failure because they combine both rigid and elastic materials, and laminates are used extensively for their crack-stopping properties. It is, of course, almost impossible to study the biomechanics of fossils

with soft skeletons. On the other hand, it may be as easy to investigate the mechanical properties of rigid, calcareous fossil skeletons as those of their living relatives.

As well as the building materials themselves, the architecture of plant and animal structures is extremely important for maximizing strength over energy expenditure. In general, tubes are as efficient as, but less costly than, solid beams, which is one reason why bones, arthropod limbs, bicycle frames, and many plant stems are hollow cylinders. There are optimum materials and designs, for example for cylinders required to support heavy, static loads, those which act as levers, and those which suffer heavy impacts. The principles of beam theory are relatively straightforward and have been used in a number of palaeontological analyses with enlightening (but perhaps not surprising) results.

As this point it is necessary to mention scaling (see McMahon & Bonner 1983). In many palaeobiomechanical studies either the aim of the work or a consequence of it involves consideration of a range of sizes of organisms. Dinosaurs are a good example. Large terrestrial animals must have disproportionately thicker limbs than their smaller relatives, or minimize the stresses involved in walking. The reason for this is that cross-sectional area of the limbs is proportional to [body weight]^{0.67} whilst the stresses due to gravity are proportional to [body weight]^{0.33}. *Apatosaurus* was probably quite capable of walking without the aid of water buoyancy, provided it did not indulge in acrobatics. Similarly, Dalingwater (see Briggs *et al.* in Rayner & Wootton 1991) investigated whether eurypterid arthropods (especially the large Carboniferous forms) could have walked on land, using living *Limulus* for comparison. *Limulus* can walk on land, even though it is an aquatic animal, but if the cuticle of the giant Carboniferous eurypterid *Hibbertopterus* had the same Young's modulus (a measure of elasticity) as that of *Limulus*, it is unlikely that the latter animal could have done so. A particular problem for arthropods on land is moulting; Dalingwater found that even a small *Limulus* is unable to support itself out of water in its soft, newly-formed cuticle. His calculations used simple expressions for buckling under static axial load, on the basis that if failure resulted under these conditions, then walking, with its associated greater, non-axial stresses, would be impossible.

Arthropod podomeres are hollow cylinders, the axial lumen housing the muscles which operate them, so the thickness (t) of cuticle cannot equal the

radius (r) of the cross-section ($r:t \neq 1$). This is another constraint on the size of terrestrial arthropods. In flying animals (Section 1.9) and swaying plant stems, the problem is less the result of weight and more that of failure by bending. Flight imposes a number of constraints, particularly on large animals like giant pterosaurs (*Quetzalcoatlus* from the Upper Cretaceous of Texas had a wingspan of 12 m, and was thus the largest flying creature ever). $r:t$ ratios below about eight give considerable strength against impact but are heavy. Where $r:t$ exceeds eight there is considerable weight saving, but brittle fracture is a problem, and buckling becomes a problem when $r:t$ exceeds 15. So how do large pterosaurs combine lightness with strength in their wing bones? (1) Their bones are laminated to lessen cracking under impact or load; (2) larger pterosaurs have higher $r:t$ ratios for lightness (the bone thickness is the same as in small ones but the lumen is wider); and (3) to prevent buckling, a number of devices (Fig. 1) are employed which effectively lower the $r:t$ ratio and produce strong 'T' sections without adding a significant weight of bone. Geological evidence shows that, not surprisingly, giant pterosaurs, like large birds, lived in open treeless surroundings where impact damage was minimized.

At the other extreme, low $r:t$ ratios are useful in situations where impacts are common. Kitchener (in Rayner & Wootton 1991) used beam theory to show that the $r:t$ ratio of the cross-section of the proximal part of Irish Elk antlers was far smaller than would be expected if the antlers were used for

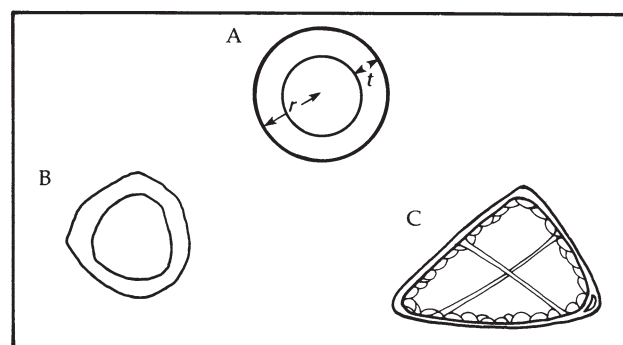


Fig. 1 A, Cross-section of a tube showing radius (r) and thickness (t); $r:t = 2.4$. B, Thick-walled section near base of Irish Elk antler; $r:t = 3$. C, Section of first phalanx of pterosaur, showing devices for combining strength and lightness: thin walls, triangular section with thickened corners (commonly hollow), struts, and spongy bone layer; $r:t = 11$. All are diagrammatic and not to scale.

display alone, and since antlers are shed annually they are a significant expense. Antlers of other Old World deer are used for fighting among males — vital for the breeding success of the species. The high $r:t$ ratio, together with the preferred orientation of osteons in the maximum impact direction of the proximal antler bone, is good evidence that fighting was the real function of Irish Elk antlers.

Force and energy

The force (in newtons) which Irish Elk antlers needed to withstand was that of an equal but opposing weight of stag colliding at the same rate of deceleration ($500 \text{ kg} \times 30 \text{ m/s}^2 = 15000 \text{ N}$ per antler). In this situation the force is maximum in the direction of motion of the deer. In a lever system, such as when muscles move a bone or an arthropod podomere, the resultant force is in a different direction to that of the muscle contraction. Alexander (1983, p. 5) gave an example of how some knowledge of the action of levers helps to explain the evolution of the mammalian jaw articulation from that of a primitive reptile. Claws (chelae) of crustaceans and chelicerates work in a manner similar to that of mammalian jaws. In a lever system, the ratio *resultant force:applied force* ($F_2:F_1$) is known as the mechanical advantage (MA), and $L_1:L_2$ is the velocity ratio (VR) (Fig. 2). A high MA or VR (i.e. close to 1) provides strong but slow movements; in contrast, a low MA or VR leads to weak but fast movements with the same power input. These simple relationships are useful for understanding the function of chelae or jaws in fossils, such as eurypterids (Selden 1984).

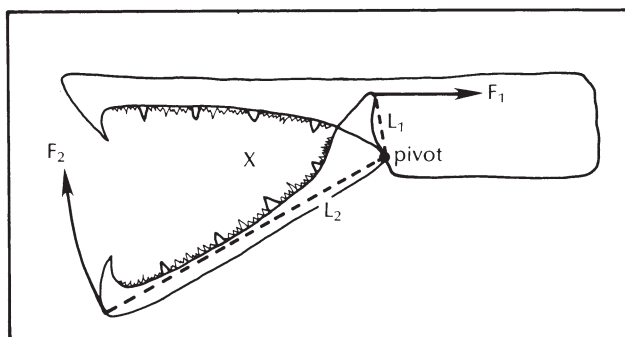


Fig. 2 Mechanics of cheliceral claw of a pterygotid eurypterid; VR ($L_1:L_2$) = 0.2 for tip of movable finger, therefore MA ($F_1:F_2$) is also low, and adapted for fast capture of prey. Prey inserted into claw at X could be sliced with high MA.

Similar principles apply to walking: long legs are good for fast running, short legs for strong pushing. The analysis of walking is complex (e.g. for arthropods see Briggs *et al.* in Rayner & Wootton 1991). For example, a surprising but useful source of information on the biomechanics of walking in fossils is their tracks. Stride length, and hence leg length, can be measured from footfalls. Alexander (1983, p. 35) used the concept of kinematic similarity, which allows extrapolation from the scale of a small animal to that of a dinosaur provided that their Froude numbers are the same. Froude number, like Reynolds number (see later), is a dimensionless quantity, u^2/gl , where u , g and l are a velocity, acceleration due to gravity, and a length respectively. Alexander calculated the speeds of some dinosaurs from Texas and found that the biped walked at *c.* 2.2 m/s while the quadruped strolled at *c.* 1 m/s; both are reasonable human walking speeds.

Pressure, density, and surface tension

Hydrostatic skeletons in plants and animals come under this heading, but the fossil record can tell us little about them. Surface tension may seem to be a phenomenon which cannot be studied easily in fossils, yet it is important wherever biological tissue encounters an air–water interface (e.g. in lungs). Alexander (1983, p. 176) discussed the importance of surface tension in the operation of plastrons in aquatic insects and mites; the surfaces of eurypterid respiratory organs resemble those of plastrons in morphology, but not in size, and therefore could not have worked in the same way.

Buoyancy is another hydrostatic phenomenon, and has been of interest to cephalopod palaeobiologists in particular. Fish and endocochleate (internal-shelled) cephalopods have nearly coincident centres of buoyancy and mass, which allows for accurate swimming and controlled manoeuvrability. This was probably true of the belemnites and some straight-shelled ectocochleates as well. The coiled ectocochleate nautiloids and ammonoids, on the other hand, had their centre of buoyancy above their centre of mass. This is inherently more stable when static, but jet thrust sets up a couple which rotates the animal, and a restoring moment is provided by the body mass when the thrust force subsides. A further disadvantage in the cephalopod model of a buoyant camerate shell, counterbalanced by solid or liquid ballast, is that it is costly in energy, both to secrete and to move, in contrast to the fish solution.

Motion in fluids

As soon as cephalopods start to move, they experience a variety of phenomena associated with motion in fluids. The dimensionless number describing kinematic similarity in fluid motion, equivalent to the Froude number where gravity is important, is the Reynolds number (Re). Two forces which act on objects moving through a fluid, and which are dependent on Re , are lift (L) and drag (D). These concepts are explained in Section 4.4. In biology, motion of a body through a fluid can initially be classified into *swimming* (in water) and *flying* (in air). Flight is discussed in Section 1.9; only swimming is reviewed here.

Jet propulsion is used extensively by cephalopods; water is drawn into the mantle cavity and then expelled rapidly through the funnel to push the body forward. Broadly speaking, the larger the mantle cavity, the greater the thrust which can be achieved and sustained; this is limited in ectocochleates by the size and buoyancy requirements of the shell. Endocochleates have no such restraint on the size of the mantle cavity. Progression consists of cycles of alternating propulsive jet thrusts (power stroke) and inhalation (recovery stroke). Such burst swimming may not be as inefficient as it appears, since it is common in fish, and bounding flight is efficient in small birds. Chamberlain (e.g. in Rayner & Wootton 1991) has analysed various aspects of swimming in ectocochleates; in particular, he showed how drag varies with changes in expansion rate, whorl shape, and position of whorls relative to the coiling axis. In general, involute oxycone shells have a lower drag coefficient (and hence were more efficient) than depressed cadicones. In some cases the amount of soft part protrusion has an effect on the drag, and fine ribbing can also reduce the drag coefficient significantly. Using experimental measurements of drag on fossil ammonite shells, calculations of body volumes, and comparison with the rotational moments experienced by living *Nautilus*, Chamberlain estimated the swimming speeds of these extinct animals. They were undoubtedly poor swimmers in comparison with modern fish.

Vertebrates and arthropods swim by one of two methods: axial or paraxial. The former method involves undulations of the body; it is predominant in fish, in which group direct comparison between living and fossil forms can be made. Paraxial locomotion is of more interest to palaeontologists because it was used by such extinct forms as eurypterids and plesiosaurs, and involves move-

ments of paired limbs to drive the body through the water. There are essentially two types of paraxial locomotion: drag-based rowing; and lift-based 'flying', so-called because the mechanical principles involved are the same as those in aerial flight (Section 1.9). In rowing, the paddles, with high drag, are moved backwards to propel the streamlined body forwards; during the recovery stroke, the paddles are feathered to reduce their drag. In subaqueous flight the flipper is moved up and down at right angles to the direction of body movement; the limb's hydrofoil cross-section produces a force, *lift*, which is directed forwards by rotating the flipper. Lift can be generated on both the up and down strokes, so that forward progression is continuous.

At Reynolds numbers below about 10^2 , viscous forces are important, so drag-based rowing mechanisms are used by small and/or slow swimmers. Above about $Re = 5 \times 10^3$, inertia dominates, so it is more efficient to fly, if possible. Eurypterids straddle this Re transition; small species undoubtedly rowed (Fig. 3B), but it seems most likely that the large (up to 2 m) pterygotids flew underwater. The biomechanics of eurypterid swimming was discussed by Selden (1984) and Briggs *et al.* (in Rayner & Wootton 1991). Using a simple rowing model, the maximum sustainable speed was calculated at 38 cm/s for a 16.5 cm long *Baltoeurypterus*, which conforms with extrapolations from the swimming speeds of water beetles. Estimates of Re at this velocity give approximately 2×10^4 , which is just into the range in which flying should be more efficient, so it is possible that swimming was normally slower than this, or that constructional morphology was a constraint. Morphology suggests that the paddles of *Baltoeurypterus* moved in phase, as in water boatmen (e.g. *Corixa*), a further example of burst swimming. Tilting of the oar blades would have produced lift for up, down, and sideways manoeuvrability.

Examples of living subaqueous fliers are penguins, and the Humpback Whale (*Megaptera*). Over the years, plesiosaurs have been visualized as either rowers or fliers, but recently, closer comparison has been made with the swimming of sea-lions. These animals generate thrust partly as lift when the flipper is moved downwards from a horizontally outstretched position at the start of the propulsive stroke, and partly as drag when it is then swept backwards to lie alongside the body at the end of the stroke. Recovery is passive and feathered, but some upward lift can be produced if required.

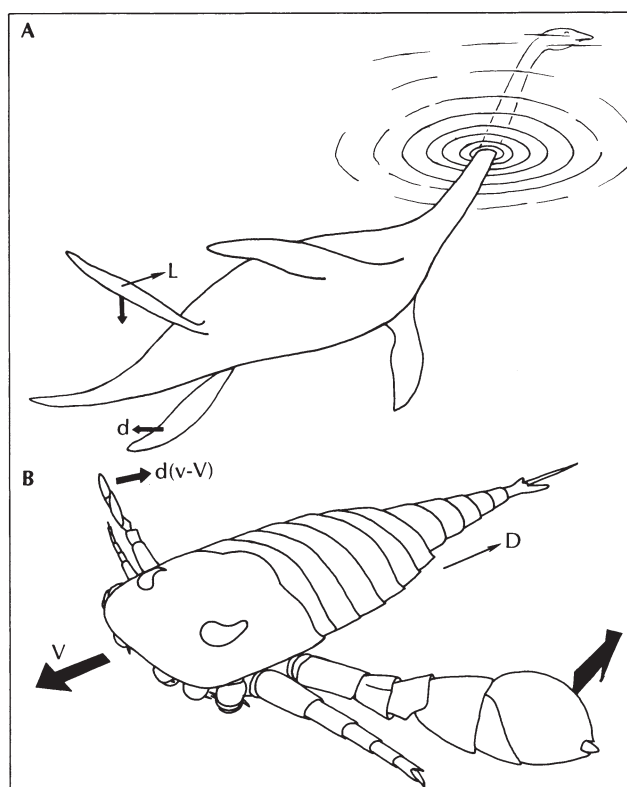


Fig. 3 A, Swimming mode of plesiosaur; right pelvic flipper on downward part of propulsive stroke, hydrofoil section gives lift (L) in forward direction; left pelvic flipper on backward thrust (drag) part of propulsive stroke; pectoral flippers on passive recovery stroke. B, The eurypterid *Baltoeurypterus* rowing, shown with oar blades half-way through propulsive stroke; D, d, and V, v are drag and velocity of body and limbs respectively.

In sea-lions, the pelvic limbs are used solely for manoeuvring, but in plesiosaurs with similar sized pectoral and pelvic limbs, propulsion was probably achieved by both pairs of limbs, working out of phase to produce continuous motion (Fig. 3A) (Frey and Riess in Rayner & Wootton 1991).

Conclusions

Biomechanics is a powerful tool in palaeontology, if used with care. The paucity of palaeobiomechanical studies to date may simply reflect a lack of appreciation of its possible applications, but as the studies reviewed here indicate, it has considerable potential for refining our interpretations of the palaeobiology of extinct animals.

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4.4 Hydrodynamics

M. LaBARBERA

Introduction

The field of fluid mechanics is classically divided into two subdisciplines: *hydrostatics* and *hydrodynamics*. Hydrostatics is concerned with the pressures and pressure variation within a fluid at rest, and the pressures exerted on immersed solid bodies. Hydrodynamics encompasses a much broader diversity of phenomena — the forces and flow patterns that result from relative motion between a fluid and

either a solid object or another fluid. Although hydrostatics is central to some aspects of geophysics (e.g. the concept of isostasy), its application to palaeontological problems has been largely limited to studies on shelled cephalopods, where it has illuminated the mechanisms of septal chamber emptying and (with empirical data and theory derived from solid mechanics) helped in estimating maximum depths for living or fossil forms.

Fundamentals

Two properties of a fluid are central to hydrodynamics, the fluid's *density* (ρ) and its *dynamic viscosity* (μ), a variable that relates the rate of shear in the fluid to the shear forces:

$$F = S\mu\theta/t, \quad (1)$$

where F is the shear force, S is the area parallel to the direction of shear, and θ/t is the rate of shear. Another variable, the *kinematic viscosity* (ν), is commonly referred to in the literature. Kinematic viscosity is merely the ratio of the dynamic viscosity to the density ($\nu = \mu/\rho$), a ratio (or its inverse) common in formulas of fluid dynamics. All references to 'viscosity' in the following discussion refer to dynamic viscosity. Note that both density and viscosity are functions of the temperature of the fluid, and that viscosity in particular is extremely sensitive to temperature; in experimental work it is vital that the fluid be at the relevant temperature or that appropriate corrections be made.

A basic assumption of fluid dynamics is the so-called '*no slip condition*', i.e. the fluid in immediate contact with any solid surface does not move with respect to the solid. Despite its counterintuitive nature, the no slip condition enjoys considerable experimental support and appears to be valid down to spatial scales of the order of the mean free path of the molecules in the fluid; the utility of this assumption lies in the fact that it implies that all shear is developed within the body of the fluid, allowing direct application of equation (1) or an often more convenient formulation:

$$\tau = \mu dU/dl, \quad (2)$$

where τ is the *shear stress* and dU/dl is the *velocity gradient*.

The conservation laws (mass, energy, momentum) of physics have their analogues in fluid mechanics, and proper application of these laws can simplify many experimental investigations (Vogel 1981). The conservation of energy relation in fluid mechanics, known as the *Bernoulli equation*, is of particular importance, since many suspension feeding animals apparently exploit it:

$$1/2\rho U^2 + P + \rho gh = \text{a constant}, \quad (3)$$

where U is velocity, P is pressure, g is acceleration due to gravity, and h is height above some baseline. This relationship must be used with some caution because it assumes that viscosity does not exist. Equation (3) should not be used across streamlines,

in regions of high shear, or for two widely separated points in the fluid, but generally gives robust qualitative predictions of the pressure differences between two points in a moving fluid.

Forces in flows

In fluid mechanics, it is irrelevant if an object moves through a stationary fluid or a fluid moves past a stationary object — the flow patterns and forces in virtually all cases are equivalent. Three major kinds of forces act (Fig. 1): (1) *drag*, a force parallel to the direction of motion which transfers momentum between the object and the fluid; (2) *lift*, a force acting perpendicular to the direction of motion (not necessarily upwards); and (3) *acceleration forces*, which act whenever the relative motion of the object and fluid changes (acceleration or deceleration).

Forces in fluid dynamics may ultimately be traced to two sources: shear forces arise from the viscosity of the fluid, while pressure forces arise from the fluid's density (although viscosity may be indirectly important in modifying flow patterns, thus changing the magnitude of the pressure forces). A convenient index to the relative importance of these two forces is the *Reynolds number* (Re):

$$Re = \rho UL/\mu \quad (4)$$

where U is velocity and L is some characteristic length of the object (usually the maximum dimension parallel to the flow). Re is a dimensionless index that can be viewed as the ratio of the inertial (pressure) forces to the viscous forces; it is central to all experimental modelling work, since equality of Reynolds numbers for a given shape implies identical flow patterns and equality of force coefficients (see below).

Any object moving at a uniform velocity with respect to a fluid experiences a drag force opposing its motion. At any Reynolds number, one source of drag is the shear of the fluid past the object; the magnitude of this drag is given by equations (1) and (2). Note that shear always implies a drag force; even the substrate and objects lying flush with the substrate experience a drag force. At low Reynolds numbers ($Re < 1$), almost all of the drag force arises from viscosity; drag on planktic and small benthic organisms is thus directly proportional to the wetted surface area of the organism and to the velocity of flow. A number of useful low Re drag formulas are given by Vogel (1981). At high Reynolds numbers ($Re > 500$) forces arising from the pressure differential between the front and rear of the object are

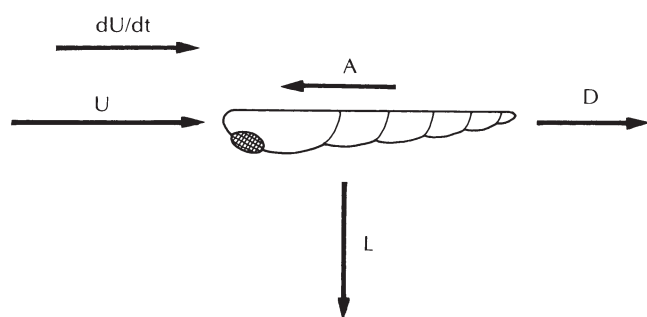


Fig. 1 A summary of the forces on an object immersed in a moving fluid. U = mainstream current velocity vector; dU/dt = acceleration of the object relative to the fluid, D = drag force on the object, L = lift force (shown acting downward to emphasize that lift need not act counter to gravity), and A = force arising from the acceleration reaction. If the relative speed of the object and fluid is constant, both dU/dt and A disappear.

the primary contributors to drag. In general,

$$D = \frac{1}{2}C_d\rho SU^2 \quad (5)$$

where D is the drag force and C_d is the *coefficient of drag*. The coefficient of drag is an empirical factor relating the shape of the object to the magnitude of drag. Note that C_d must be determined for each different shape and is valid over only a limited range of Reynolds numbers (see Vogel 1981). The definition of S in equation (5) depends on the context. In the engineering literature, S is usually the *frontal area* for bluff bodies (spheres, cylinders, etc.), the *total surface area* for streamlined bodies, the *planform* area for lifting bodies, or the two-thirds power of volume (dimensionally equivalent to an area) for airships. The last definition is becoming increasingly common in the biological literature since it scales drag to the volume of the organism. References in the biological and palaeontological literature often ignore these differing definitions of the relevant area and it is important to check carefully the definition used before experimental C_d values are compared to literature values. Also note that, despite many assertions in the literature, drag is proportional to velocity squared *only* at high Re .

At high Re , appropriate shapes may generate forces perpendicular to the flow (lift). The magnitude of the lift force is given by:

$$L = \frac{1}{2}C_l\rho SU^2 \quad (6)$$

where L is the lift force and C_l is the *coefficient of lift*. In equation (6), S is almost invariably the planform

area, although other definitions could be used if appropriate for the problem at hand.

Whenever an object accelerates or decelerates in a fluid, an additional force arises from the necessary acceleration of a volume of fluid in the opposite direction. This results in an increased effective mass of the object; the phenomenon is often referred to as the *acceleration reaction*. The magnitude of this force is given by:

$$F_a = (1 + \alpha)\rho V dU/dt \quad (7)$$

where α is the added mass coefficient (a dimensionless shape factor), V is the organism's volume, and dU/dt is the acceleration. Forces due to acceleration may either add to or subtract from drag forces; in general, the acceleration forces act to oppose changes in the relative speed of the object and fluid. For more information and a biological context, see Denny *et al.* (1985).

Experimental techniques

Except in the simplest cases, investigations into the hydrodynamics of fossils or sediments will involve some form of modelling. Such an approach is particularly attractive because it allows easy determination of the hydrodynamic significance of morphological features by modification of otherwise identical models. Relative motion between the model and the fluid may be produced using a towing tank, wind tunnel, or flow tank (flume); appropriate designs may be found in Vogel (1981) and Nowell & Jumars (1987). Information and references on techniques for mapping flow patterns, measuring flow velocities, and measuring flow-generated forces can be found in Vogel (1981). Methods for making models of fossils are strongly dependent on the specimens and available materials; no prescription is possible and investigators must depend on their own ingenuity. Models may be freely enlarged or reduced in size for experimental convenience *as long as the Reynolds number is held constant*. However, since identity of Reynolds numbers only guarantees that the force coefficients C_d and C_l (not the absolute forces) are identical, situations in which deformation of the specimen by hydrodynamic forces is an important consideration should preferably be modelled life size in the original fluid medium. (Such situations will generally pose considerable problems in the choice of modelling materials and should be avoided if possible.)

Applications

Studies of the hydrodynamics of living organisms that are potentially applicable to palaeontology are numerous and diverse; see Vogel (1981) for an introduction to the neontological literature. Palaeontological fluid dynamic studies are more limited in number, but are becoming increasingly common.

In the terrestrial environment, most work has focused on the aerodynamics of flying reptiles (e.g. Brower 1983) and the evolution of flight in birds and insects (Section 1.9); such studies have helped to clarify the significance of particular morphological features and the evolutionary pathways to aerial locomotion. Niklas' (1985) work on wind pollination in living and fossil plants is a particularly instructive example of the power of fluid mechanical analysis in palaeontological and evolutionary studies.

In the aquatic environment, the diversity of studies involving hydrodynamics is much greater. Locomotion tends to be the focus for much of the work, ranging from studies on molluscs (e.g. Chamberlain 1981) to arthropods (see Section 4.3), fish (Belles-Isles 1987), and reptiles (e.g. Godfrey 1984; Taylor 1987). Most such studies have used energetic arguments based on drag forces to explain evolutionary patterns; none has considered the possible importance of the acceleration reaction. A few studies have focused on the interactions between benthic animals, the sediment, and the hydrodynamic environment (e.g. Alexander 1984). The possible use of pressure differences implied by the Bernoulli equation to create or augment feeding currents has been studied in archaeocyathids and stromatoporoids (see Boyajian & LaBarbera 1987), and feeding currents have been reconstructed for fossil bryozoans (Fig. 2). Recently, several studies have attempted to relate the evolutionary history of particular groups to their hydrodynamics (e.g. McKinney 1986 and other references in that volume).

One attraction of hydrodynamic studies in palaeontology arises from the fact that the primary factors governing hydrodynamic relations — the external shape of the organism and the Reynolds number — can be determined relatively easily or estimated to a reasonable level of precision. The basic technology involved in experimental studies of organismal hydrodynamics is inexpensive, and the physical principles underlying such studies can be expected to be robust through geological time. However, as is the case in most of palaeobiology, some familiarity

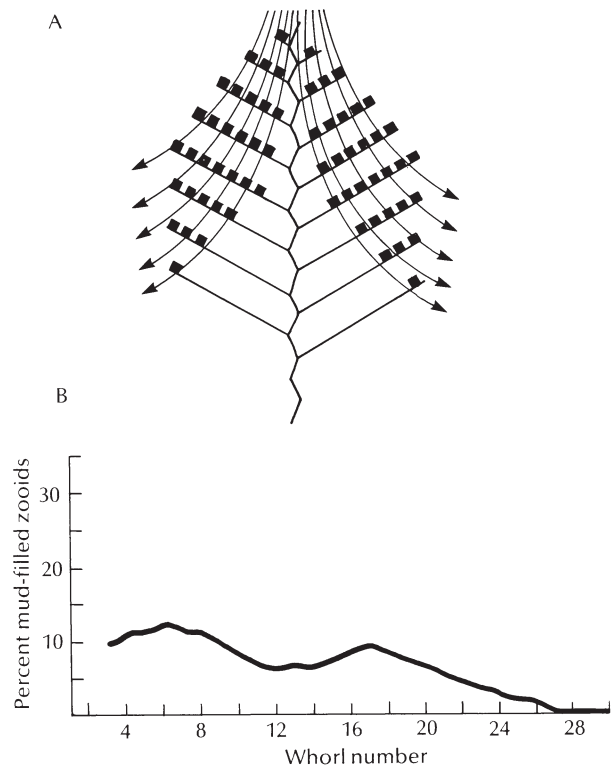


Fig. 2 A, Flow patterns of living *Bugula turrita*. B, Distribution of mud-filled zooids as a function of whorl number in fossil *Archimedes intermedius*. The line plotted in B is the moving average of five whorls for four nearly complete colonies. An interior stagnant region is prominent in living colonies of *Bugula*, and living polypides (dark squares) are largely restricted to the peripheral regions of the branches. Mud-filled zooids in *A. intermedius* are presumed to represent zooids abandoned during the life of the colony because they lay in regions of minimal water exchange. (After McKinney *et al.* 1986.)

with living descendants or analogues of the fossils is vital if mistakes are to be avoided.

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4.5 Populations

G. B. CURRY

Populations are groups of individuals from the same species which occupy a discrete geographical region. This apparently straightforward definition masks considerable complexity, especially in recognizing fossil populations that are subject to selective preservation and *post mortem* transportation. In some cases it has even proved difficult to apply this definition meaningfully to living organisms because the boundaries between adjacent populations are often fuzzy or even overlapping. Furthermore, the distribution of individuals within extant populations can be far from homogeneous, and mobile organisms which migrate from one population to another (or plants with wind- or animal-transported seeds) are a further complication. The heterogeneity of population structure has led ecologists to establish a hierarchical subdivision of populations into several *demes* (or local populations), each of which is composed of a variable number of family groups.

Such subdivisions are also difficult to apply to fossil populations, although there has been considerable progress in the use of computer reconstructions to investigate the structure of fossil populations. Computer studies (see also Section 6.1) are particularly helpful because population structure and dynamics are determined by the interplay of a large number of factors, the significance of which could be unravelled from computer simulations. From this type of analysis it became clear

that the structure of a population, as determined from size–frequency histograms, is primarily governed by the interplay between mortality rate and growth rate, although factors such as recruitment strategy and seasonal cessation of growth are also important (Craig & Oertel 1966). A major constraint for fossil populations is the difficulty of collecting a representative sample, which some authorities argue should number at least 1000 individuals (see discussion in Craig & Oertel 1966). In particular, many fossil populations lack juveniles, which are relatively fragile and hence much more susceptible to destruction and transportation.

Arguably the most important development in population studies during the last 20 years has been the advent of *genetic analyses* (Mayr 1970; Wright 1978; Hartl 1980; Ayala 1982). Such analyses are not possible for fossil populations at the present time (although new discoveries in molecular palaeontology may at some future date allow the utilization of fossil molecular data in population studies, at least at a crude level; Section 2.1). Nevertheless, the results of population genetics studies are of direct relevance for palaeontologists because they are beginning to reveal the fundamental features of populations and of their spatial and temporal behaviour.

The recent technological advances in genetics have provided a series of powerful new research

tools which can investigate the prodigious information stored in DNA, RNA, and proteins. Using such techniques it is possible to measure accurately molecular variability both between individuals of a single population and between different populations of a single species. The ability to quantify intra- and interpopulation variability is certainly a major step forward, and such data can be used to investigate how populations develop and evolve.

Geneticists define populations as communities of individuals which are linked by bonds of mating and parenthood, and hence share a common gene pool. This definition applies only to sexually reproducing populations, which are also known as *Mendelian populations* to distinguish them from those populations that are united by parenthood and a common gene pool but which reproduce asexually. Population genetics has become an active and often hotly debated branch of genetics.

Measurements of the extent of genetic variation between individuals of a population, known as *genetic distances*, allows the precise description of populations on the basis of their total genetic variability; this can be investigated over several generations, or directly contrasted with that of other populations, to provide information on population structure and dynamics. Population genetics is an inherently mathematical subject which can become very complex, both in terms of how genetic distances are calculated and how the resulting data are compiled, presented, and interpreted (Nei 1972; Nevo 1978).

The most precise (and hence most desirable) method of quantifying genetic variability is to determine the sequence of nucleotide bases in homologous regions of DNA or RNA. But direct sequencing is complex and extremely time-consuming, and was rarely a practical option at the time when interest in the genetics of populations was developing. Instead, population geneticists made use of several other techniques which yielded quick results and provided less accurate but still extremely useful estimates of genetic variability within individuals and populations.

By far the most widely used method of estimating genetic variability is *gel electrophoresis* of enzymes. This effectively detects DNA variability at 'second-hand', because enzymes are functional proteins produced from the coded information stored in DNA sequences. Individuals can contain one or more variants of a single enzyme, each of which is produced by different versions of a single gene (alleles) which have distinct nucleotide sequences. The dis-

covery that variants of a single enzyme, known as *allozymes*, could be distinguished using gel electrophoresis therefore provided geneticists with a convenient method of estimating genetic variability relatively quickly and with reasonable accuracy. Gel electrophoresis makes use of the different properties of allozymes in a direct electric field — both their direction and rate of migration varies according to their net electric charge and molecular size. Thus allozymes show up as discrete bands when subjected to gel electrophoresis (Fig. 1). To achieve a reasonable estimate of genetic variability, it is important that a sufficient number of randomly-chosen enzymes are investigated, and that a sufficiently large sample of individuals is measured from each population.

From the pattern of enzyme variability, as revealed by bands in gel electrophoresis, each individual can be described as *homozygous* (with only one allozyme) or *heterozygous* (two or more allozymes) for that particular coding gene locus (Fig. 1). The overall genetic variability of the population can then be expressed in terms of the number of polymorphic (i.e. heterozygous) loci (Table 1). In an attempt to standardize measurements of population polymorphism, geneticists had to decide on an arbitrary criterion to distinguish between polymorphic and non-polymorphic loci. Polymorphic loci are generally defined as those for which the dominant allele has a frequency of not more than 0.95. Thus in surveying 100 individuals from a single population for allozyme A or allozyme B, the gene locus coding for this particular enzyme would be considered polymorphic if 95 organisms had A and five had B, but it would be considered non-polymorphic if

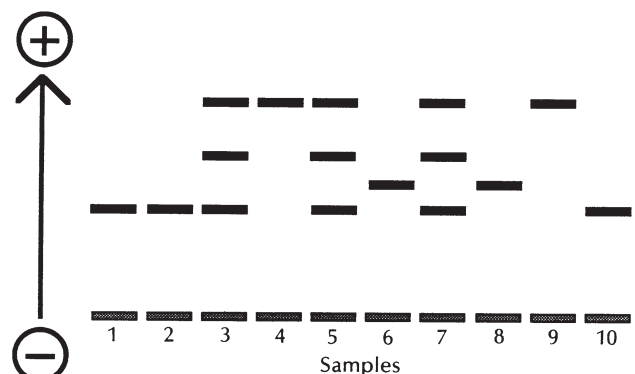


Fig. 1 Gel electrophoresis of allozymes determined for ten individuals. After separation in an electric current, specimens 1, 2, 4, 6, 8, 9, and 10 are seen to be homozygotes for this particular enzyme (i.e. only one band), while the rest are heterozygous (more than one band).

Table 1 Genetic variability in different groups.

Organism	Number of species	Loci studied	Polymorphism (%)	Heterozygosity (%)
Plants	17	16	26.4	4.6
Marine invertebrates	14	23	43.9	12.4
Flies	28	24	52.9	15.0
Wasps	6	15	24.3	6.2
Insects	4	18	53.1	15.1
Land snails	5	18	43.7	5.0
Fish	14	21	30.6	7.8
Amphibians	11	22	33.6	8.2
Reptiles	9	21	23.1	4.7
Birds	4	19	14.5	4.2
Mammals	30	28	20.6	5.1

96 individuals had A and only four had B. The overall genetic variability of the population can therefore be expressed as the proportion of polymorphic loci (Table 2), or simply *Polymorphism* (P).

Polymorphism is, however, an imprecise measure of genetic variation because it does not distinguish between loci which are only slightly polymorphic (for example with two or three alleles) and those which display extreme variability (e.g. with 20 or more alleles). Consequently, polymorphism alone is not considered a very useful measure of genetic variability, although it is often cited in the literature. A more widely used measure of population variability is *heterozygosity* (H), which is much more precise and does not depend on arbitrary determination of polymorphism. The heterozygosity of a population is measured by first determining the frequency of heterozygous individuals at each locus, and then averaging these frequencies over all loci (Table 3). Such determinations are limited by the ability of gel electrophoresis to detect mobility variations between allozymes, and almost certainly underestimates the total genetic variability present because allozymes with relatively similar net electric charge will not be resolved. In addition, allozyme

studies do not provide any information on the extent of nucleotide substitutions in non-coding regions of DNA (the introns, which can represent very large proportions of the genome), and hence electrophoresis is known to underestimate genetic variation at the enzyme level by an unknown amount.

Despite these problems, allozyme electrophoresis was rapidly adopted as the standard method for investigating population genetics, and many thousands of studies have been carried out since the technique was first described in 1966. Recent technological advances have now made it practicable to measure DNA variability directly, but such methods have not yet been as extensively applied, and the allozyme data remains unsurpassed in providing directly comparable population data on representatives of all the major life forms.

The major surprise from allozyme studies was the discovery that there is much more genetic variability in individuals and populations than had previously been suspected. In general, invertebrate animals have much more genetic variability than vertebrates, with the average heterozygosity among invertebrates being more than double that of the vertebrates (Table 1). Even the lower heterozygosity

Table 2 Calculation of average polymorphism in five populations.

Population	Number of loci		Polymorphism (P) %
	Polymorphic	Total	
1	19	30	63
2	15	30	50
3	14	30	47
4	18	30	60
5	17	30	57

Average = 55.4

Table 3 Calculation of average heterozygosity at ten loci.

Locus	Number of individuals		Heterozygosity (H) %
	Heterozygotes	Total	
1	56	100	56
2	16	100	16
3	28	100	28
4	0	100	0
5	8	100	5
6	41	100	41
7	6	100	6
8	21	100	21
9	3	100	3
10	12	100	12

Average = 18.8

levels represent an enormous amount of variability, considerably more than is needed to ensure that, with the exception of identical twins, all human beings, past, present, and future, will be genetically distinct. The vast amount of genetic data now accumulated demonstrates that the average interpopulation genetic distances are consistently smaller than, although overlapping with, the genetic distances between subspecies, species etc. (Fig. 2). In simple terms, such differentiation reflects the increasing degree and longevity of genetic isolation inherent in ascending the taxonomic hierarchy (White 1977; Templeton 1980).

More recently, a number of new and potentially more powerful methods of measuring genetic variability have become available. Mitochondrial DNA has particular significance for population studies because in many phyla it evolves much faster than

the nuclear DNA in the chromosomes, and hence offers a much more precise measure of relatively recent divergence events. Direct sequencing is now possible on a routine basis, but there are still considerable problems to be overcome in the interpretation of such data. The recognition of mutational 'hot-spots', where the DNA is subject to rapid substitutions, perhaps many times over at the same place, means that direct sequencing may not necessarily always be an ideal tool for the population geneticist, and indeed could be very misleading.

The importance of population genetics stems from the fact that populations are seen as fundamental units of evolution. The genotype (the total genetic content) of an individual is fixed from birth, but the overall population gene pool is dynamic and can change from generation to generation, thereby providing the variability on which evolutionary processes act.

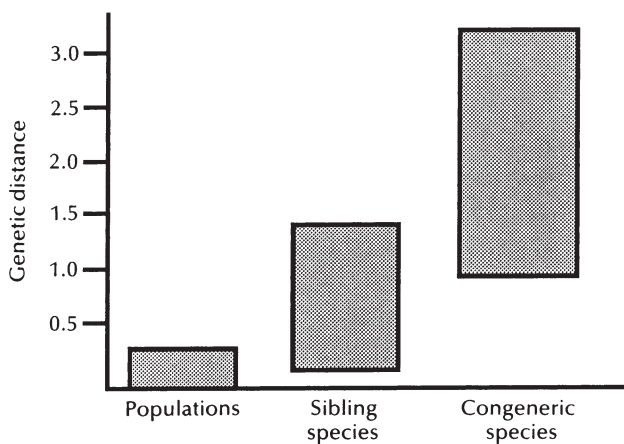


Fig. 2 Representation of the increasing ranges of genetic distances measured between populations, sibling species, and congeneric species. Data compiled from a large number of studies using gel electrophoresis of allozymes.

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4.6 Coloniality

B. R. ROSEN

Introduction

Colony has been used most consistently to refer to a population of a single species whose members have grown from one another but remained physically attached to each other. It follows that *coloniality* refers to the habit of living in colonies. Although there are other populations that have been called colonies, such as physical overgrowths (e.g. oysters, serpulids), sessile and mobile aggregations (e.g. barnacles, ophiuroids), and separate animals that live in functional or social systems (e.g. sea-bird colonies, fish and cephalopod shoals, ungulate flocks and herds), they are excluded here.

Although the above definition of coloniality is based on growth pattern, most organisms so defined are morphologically identifiable because they clearly consist of numerous similar colony members (like zooids or polyps). Thus, bryozoans and graptoloids are generally regarded as exclusively colonial, while Hydrozoa, anthozoan corals, and tunicates include numerous colonial representatives. Sponges are enigmatic because they have no obvious and consistent features that one might regard as colony members, and consequently are taken to be solitary by many workers. For a more complete phyletic survey, see Wilson (1975, p. 389).

Colonial organisms are entirely aquatic, mostly marine and sessile. Colonies are common on hard substrates, being especially important on reefs. Salps (Tunicata), siphonophores (Cnidaria), and graptoloids, however, are or were pelagic. Colonial organisms are amongst the largest and longest-lived of all organisms. Most possess mineralized skeletons (notably cnidarians and bryozoans) and collectively are represented throughout most of the Phanerozoic.

Palaeontological authors in Boardman *et al.* (1973) were influential in initiating much of the current

biological interest in coloniality, developing Beklemishev's ideas about integration in invertebrate colonies (see below). Ironically, however, palaeontologists cannot really answer many of the key questions from the study of fossils alone, and it is inevitable that the emphasis in coloniality studies has since become neobiological. This is clear from the contents of all the more recent multiauthor volumes in this field (Larwood & Rosen 1979; Jackson *et al.* 1985; Harper 1986; Harper *et al.* 1986). Even more ironically perhaps, the most important subsequent influence in this subject has come from outside zoology altogether, from what may seem the surprising source of plant population ecology (Harper 1977). For palaeontologists, the greatest scope for studying coloniality lies in investigations of patterns of form through time, form in different palaeoenvironments, and inferences of colony growth patterns (*astogeny*) from fossil collections at different growth stages.

Clonal growth and form

Two aspects of growth and form, *clonoteny* and *iteration* respectively, provide the most precise framework to date for discussing and investigating colonies (Table 1) (and also permit sponges to be considered colonial in particular instances). Clonal life histories are extremely varied. The kinds of physically continuous colonies typified by cnidarians and bryozoans have grown by the bodily retention of clonal individuals (*clonoteny*), though many of these same organisms can also initiate new colonies by shedding their clonal offspring (*clonopary*), either passively (e.g. through colony breakage and partial mortality) or as part of an inherited growth pattern. Clonal organisms can often fuse too, and this represents a non-clonotenuous component of colony building (though it is likely

Table 1 Criteria and terminology of coloniality.

	Body plan <i>unitary</i> (non-iterative, non-modular, non-colonial, <i>solitary</i>)	Body plan <i>iterative</i> (consisting of <i>iterative units</i> or <i>modules</i> derived from each other by continuous growth and attached to each other)
Life history		
		Colonies (in the sense of having iterative form only)
Aclonal — offspring by sexual reproduction only	One zygote develops into one unitary organism One level of physical individuality e.g. humans (except identical twins)	One zygote develops into one iterative organism Two levels of physical individuality: 1 Iterative units, e.g. zooids 2 Colonies e.g. most trees, graptoloids, siphonophores and (<i>by default</i>) all iterative organisms without known clonal habit
		Colonies (in the sense of being clonotenous, hence iterative in form)
Clonal — offspring by sexual reproduction <i>and</i> cloning	All clones shed (<i>clonopary</i> , <i>iteropary</i> , <i>fission</i>) by parent One zygote develops into one clonal lineage (<i>genet</i>) of numerous genetically identical unitary ramets Two levels of physical individuality: 1 Ramets 2 Genets e.g. <i>Amoeba</i> , some flatworms, <i>Hydra</i> , many sea anemones, some solitary corals like <i>Fungia</i> ; also aphids, water fleas and rotifers (<i>by parthenogenesis</i>)	Some clones shed (<i>clonopary</i> , <i>iteropary</i> , <i>fission</i>) and some retained (<i>clonoteny</i>) by parent One zygote develops into one clonal lineage (<i>genet</i>) of numerous genetically identical iterative ramets Three levels of physical individuality: 1 Iterative units, e.g. zooids 2 Ramets = colonies 3 Genets e.g. many hydrozoans and octocorals, colonial corals, tapeworms, some polychaetes, some bryozoans, tunicates, salps, strawberry plants

Notes: (1) In practice, different authors' definitions vary slightly; (2) there is some transition between the two concepts of coloniality on the right hand side because some iterative-only organisms (upper right) are occasionally clonoparous; (3) in the case of iterative-and-clonotenous colonies (lower right), new ramets might be unitary at the outset and become iterative, or be iterative at the outset; and (4) *Modules* is meant here in Harper's sense — see text.

that only members of the same infraspecific clonal strain can do this). In bulk terms, it is not the main colony-building process. In fossils it is sometimes difficult to distinguish fusion from *post mortem* overgrowth.

Although aggregations were excluded (above) from colonies, the members of many organisms that live in close populations or societies are also clonoparous, or have life histories in which at least some members are produced parthenogenetically (e.g. aphids) or from unfertilized eggs (e.g. male honey bees). In this respect, populations of these organisms have been likened to colonies within

which the physical connections between members are virtual rather than real.

Cloning must also be seen in the wider context of reproduction and dispersion. In many sessile clonoparous organisms, clones may remain close to their parents, while other organisms show combinations of cloning patterns that include both clonotenous colonies as well as a clonoparously produced vagile phase (e.g. the cnidarian medusa). Even the larval phase in Cnidaria, generally zygotic in origin, can be produced clonoparously by some taxa. Thus clonal organisms can variously allocate resources to growth of existing individuals, production of clonal

offspring (which can either be shed or retained by the parent growth), or to sexual reproduction.

A remarkable consequence of this is that, whereas in non-clonal organisms a single zygote generally produces a single individual, in a clonal organism it is represented by two or more physical levels of individuality, all genetically identical (Table 1). The whole single-zygote population unit is a *genet*, which consists of clonoparously produced units (*ramets*). Ramets in different organisms can be solitary or colonial. Within colonies, units may have different forms and functions (*polymorphs*, as in siphonophores, many bryozoans (Fig. 1), and hydrozoans). Clearly, the simple ecological concept of an individual as it applies to non-colonial organisms is inadequate for colonial organisms. Not only are there several levels of individuality to consider but also the dynamic relationships between them.

The basic demographic parameters of births, deaths, immigrants, and emigrants used for non-colonial organisms can be applied on all these levels.

On one level, a colony's growth can be studied by treating its within-colony individuals as a population (*metapopulation*) and applying standard demographic concepts (e.g. number and colony location of births and deaths of different kinds of zooids through time). On another level, an ecological survey based on coral heads (i.e. whole colonies) uses ramets as its individual units.

At both the ramet and genet level, the number of intracolony individuals, as well as number of ramets themselves, appears to increase indefinitely through time, the main exception being organisms whose colonies have determinate growth (e.g. many pelagic forms, such as graptoloids). While their within-colony individuals may senesce and perish, there is usually a turnover in their population, with a net increase. Colonies (ramets) themselves often show no obvious signs of senescence and the genets of many clonal organisms seem to be virtually immortal. It follows that fecundity (the potential for sexual reproduction) of a clonal organism increases,

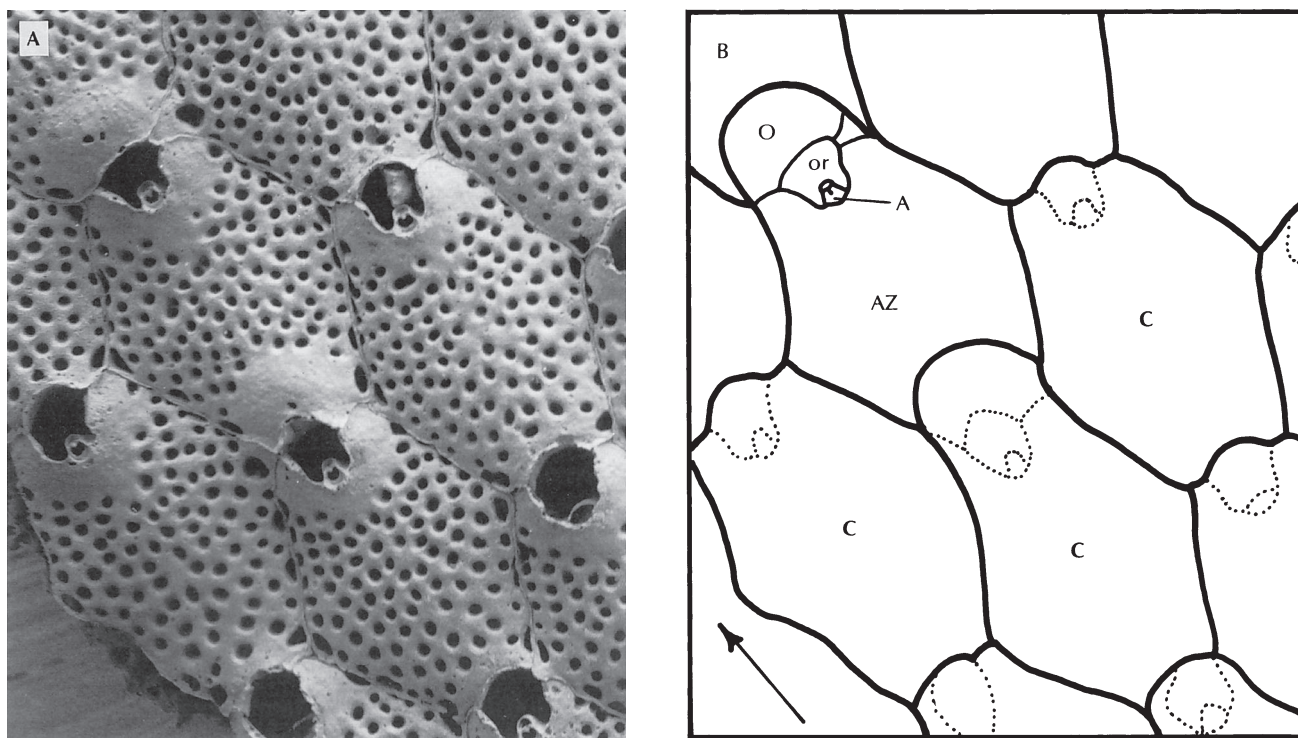


Fig. 1 A, Scanning electron micrograph ($\times 36$) of the skeleton of a cheilostome bryozoan colony, *Smittina exertaviculata* Rogick; BM(NH) D53488, subfossil, McMurdo, Antarctica, showing polymorphic iterative units grouped into cormidia ($\times 36$).

(Photograph courtesy of P.D. Taylor.) B, Key to colony organization in A. Each kind of polymorph (A,AZ,O) is seen here in its zooecial (skeletal) part only. In the living animal, each corresponds to a different kind of zooid or zooidally-derived structure. A = avicularium (?defensive role) within orifice of autozooeum, AZ = autozooeal frontal wall with pores (autozooid has feeding function), O = ovicell (brood chamber), or = autozooidal orifice, C = cormidium. Arrow gives direction of growth (from proximal to distal). Ovicells and avicularia are not present throughout colony. Although ovicells function with respect to the adjacent proximal autozooid, they may originate from either this or the adjacent distal zooid.

generally exponentially, with the age of both ramets and genets, in distinct contrast with non-clonal organisms, whose potential (i.e. for a given zygotic individual) usually peaks and then declines. As a result of all these traits, as well as the possible occurrence of colony fusion, it is clear that the standard working concepts of population biology — individuals, births, deaths, age, senescence, fecundity, and size — together with the relationships between them, as widely understood for non-clonal organisms, do not apply in the same way, if at all, to clonal (hence colonial) organisms.

Individuals, iteration, and modularity

Although the most satisfactory concept of a colony is based on clonal features, the simplest practical way of identifying a colony is on the occurrence within it of numerous similar intracolony individuals, like zooids (Fig. 1). This is straightforward if these individuals closely resemble a solitary counterpart. The polyps of cnidarian colonies, for example, can be compared directly with solitary cnidarians like *Hydra* or sea anemones. This approach encounters difficulties, however, when the supposed colony individuals do not clearly resemble known solitary counterparts. For instance, a colonial coral whose corallite walls are incomplete or absent effectively consists of a multi-mouthed (*cerberoid*) body sharing one coelenteric cavity. On their own, these mouths do not represent a plausible solitary organism. Are cerberoid corals 'individuals' with many mouths, or 'colonies' of mouths with one coelenteron? In the case of sponges, we do not have a recognizable body plan at all — just repeated functional features like aquiferous units, or anatomical units like cells and spicules. This problem of identifying colony individuals is also highlighted by polymorphism. The spinozooids of some bryozoans for example, differ very much from the basic bryozoan body plan. Polymorphic groups of individuals are also frequently organized in higher level intercommunicating systems (*cormidia*) of great functional importance which are themselves repeated (Fig. 1). Do these cormidia represent the colony individuals or do the zooids?

While clonoteny provides the most theoretically satisfactory criterion of coloniality, recognition of a clonal habit is not usually possible without long term observations. For fossil organisms, cloning must remain an inference. In most of the examples (above) where the criterion of identifying a clear intracolony individual is a problem, it can be

circumvented by using Harper's (1977) alternative criterion of *iteration* (Table 1), derived largely from botany. Harper refers to all iterative features (above the cell level) as *modules*, though the word actually has several other older botanical meanings within his broader concept. For the sake of space and clarity here, it is more satisfactory to call them *iterative units*.

In practice, many living iterative organisms are also clonoparous, but the two phenomena are certainly not identical. Trees are iterative, but (horticultural cuttings aside) only a few are clonoparous. Pelagic iterative organisms show only a limited capacity for clonopary: isolated zooids of physonectid siphonophores, for example, cannot produce new colonies, and evidence for cloning in graptoloids is confined to only a few taxa. Conversely, there are many organisms (Table 1, lower left) that are clonoparous but *unitary* (not iterative), though this point partly depends on choice of iterative unit, since the concept of iteration is deliberately broad. The distinction between iteration and cloning is also palaeontologically useful because although coloniality-*sensu*-clonoteny can only be *inferred* in a fossil, coloniality-*sensu*-iteration can easily be *observed*. The idea of iterative units, however, can lead to triviality or over-enthusiastic application. Tentacles, zooids, cormidia, or branches in a coelenterate colony might all be designated iterative units depending on relevance to a particular problem, but on many biological considerations zooids would be the primary choice.

Ecological significance

Since unitary and non-clonal organisms exist and flourish as abundantly as iterative and clonal organisms, it is impossible to state absolute benefits of coloniality. It appears to confer advantages for particular organisms in particular environments (e.g. corals on reefs). Most ecological scenarios concerning coloniality originate from size considerations. Assuming that every organism has mechanical constraints on the ultimate size of its body plan, mainly arising from changing ratios of surface area : volume, then one (but *not* the only) escape from these constraints is iteration. Presumably iteration developed in those (mostly lower) organisms that already possessed the ability to clone or to regenerate. Their consequent ability to grow very large seems to have enabled them to occupy substrate or the space above it, or both, more effectively than their unitary counterparts. It also improved their chances

of surviving adverse events. Diversity of colony form can be interpreted as different ways of obtaining resources and of responding to otherwise unfavourable circumstances like heavy wave action, muddy substrates, and intense grazing.

For the large number of colonial organisms that are also fixed to the substrate, iteration provides a form of mobile behaviour. Although adverse conditions may kill off parts of a colony, other parts survive and, in effect, escape. Storms, and sudden increases in wave and current action damage whole stands of iterative organisms, but their broken pieces are often swept into sheltered places and survive. Ramets and iterative units are often destroyed, yet the genotype survives.

Another behavioural consequence of iteration is the ability to grow in a particular direction, or to develop more of one kind of specialized zooidal polymorph than another, in response to particular environmental events or gradients. Iterative organisms characteristically show great intraspecific plasticity of colony form, some of it in response to different conditions. Iteration appears to confer great flexibility on how a colonial organism fills its occupied spatial envelope. This in turn reflects the capacity of colonial organisms to vary the ecologically significant relationships between their biomass, surface area, actual colony volume, and their spatial envelope (though not necessarily within a single colony or taxon). *Phalanx* growths (sheets and mounds) can blanket a substrate to the exclusion of other benthos, and take maximum advantage of locally favourable conditions, whereas *guerilla* growths (runners, often branching or anastomosing) can occupy a broader spatial envelope on a given substrate much more quickly, circumvent hostile neighbours, and rapidly find the most suitable sites (*spatial refuges*) in very patchy microenvironments (see also Section 4.9).

The ability of some iterative organisms to grow much further away from their substrate than a single body plan allows, even from a small densely-occupied area, gives access to better or different conditions from those closer to the substrate (e.g. food bearing currents, clearer water). Typical of such forms are mounds, plates, and especially branching forms like trees. Tree-like forms share some of the features of *guerillas* in three dimensions, because they can forage, explore, or circumvent habitat features. Although branching is one of the most common modes of clonotenuous colony increase (e.g. corallites in rugose corals), it also arises at higher organizational levels, as in the zooidal groups

that make up the branches of ramose tabulate and scleractinian corals.

Growth and plasticity in iterative organisms can be explored in terms of three parameters:

- 1 An inherited growth plan (*architectural model*) which is topologically constant (i.e. always has the same definitive qualitative growth plan). To judge from tropical trees, there is only a surprisingly small number of realized models (Hallé *et al.* 1978).
- 2 Quantitative modifications to this pattern (e.g. branching angle), which may be phenotypic or environmentally induced, or both.
- 3 Reiteration of the whole architectural model (e.g. in response to a traumatic event).

Pelagic iterative organisms like siphonophores, salps, and graptoloids differ in many respects from sessile iterative organisms, especially in their reduced plasticity and clonopary, and in having determinate growth form. Nevertheless, iteration can again be interpreted in terms of size, with enhanced resource capture, more effective swimming and floating, and better chances of surviving predatory attack compared with unitary forms.

Functional significance

Iteration is usually associated with various levels of integration between units. This commonly includes sharing of resources, intercommunication for defensive retraction of zooids, co-operation in capturing and consuming resources (including prey that are much larger than the iterative units), and maintenance of colony form following damage. Unfortunately, because these dynamic aspects of integration are not observable in fossils, they can only be inferred — mainly on indirect skeletal evidence such as presence of interconnecting structures between zooids and loss of morphological distinctness ('identity') of zooids. Nevertheless, W.N. Beklemishev's idea (further developed by Boardman *et al.* 1973) that integration becomes more complete as colonial organisms evolve has been a great influence and has so far proved to be a reasonable hypothesis, even on these skeletal grounds alone (but see Mackie in Harper *et al.* 1986).

A related widespread feature of colonial organisms, best seen in hydrozoans, siphonophores, and bryozoans, is the division of functions between their polymorphic iterative units (e.g. reproduction, prey capture, larval brooding, swimming, and maintenance of colony-wide feeding currents), analogous to the role of organs in a unitary animal (Fig. 1).

So complete is this organizational and functional integration in some organisms that authors have referred to them as 'superorganisms'.

Evolutionary significance

The ability of colonial-*sensu*-clonal organisms to exist as numerous separate ramets within a single genotype, and for their genets to grow indefinitely in space and time, represents a highly developed alternative to: (1) sexual reproduction for initiating new individuals, albeit of the same genotype; and (2) the customarily cited advantages of genetic heterogeneity (i.e. as derived from sexual reproduction). On the other hand, the vast numbers of sexually mature iterative units present within a single genet at any one time suggests that these organisms have retained this as an important option. So far, however, these observations have not so much generated satisfying explanations as cast doubts on the validity of current textbook generalizations about populations, genetics, dispersion, selection, and evolution, since these are almost entirely based on unitary, non-clonal organisms.

One idea is that if potential habitats for colonization are not environmentally heterogeneous or unstable, there is no clear benefit in having genetically diverse progeny. As large numbers of iterative units within sessile colonial organisms are often also fertile, however, high fecundity seems to offer an alternative in the event of a significant environmental disturbance. This would be important for those species (such as reef corals) whose main vagile phase is a sexually produced larva. It may be that genetic turnover, and hence evolutionary rates, should be slower in clonal compared with asexual organisms, but Jackson and Coates' comparison (*in* Harper *et al.* 1986) of their respective geological longevities has revealed no clear difference.

One reason for this similarity may be that, although it is reasonable to assume that ramets within a single genet are genetically identical, a genet overall can be so long-lived that genetic variants (and hence evolutionary novelties) could conceivably arise even without sexual reproduction,

appearing gradually within the ramet-lineage of a single genet (i.e. mitotically). An additional relevant factor that increases this possibility is that, whereas in unitary organisms gametogenesis is localized within a single body, and is under central control (genetically and physiologically) within that body, gametogenesis in clonal organisms continues indefinitely in time and space without any evident central control (i.e. between ramets of a single genet). Suppose any such spontaneous genetic variants were also subject to environmental selection, and were even to find their way into gametes and so be passed on to other generations of genets?

Clonal organisms have yet to be properly incorporated in models of evolution by natural selection (van Valen 1987). It seems that, for at least some colonial organisms, even the possibility of Lamarckian factors in their evolution cannot be ruled out.

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4.7 Stromatolites

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Introduction

Stromatolites are organosedimentary structures produced by the sediment trapping, binding, and/or precipitation activity of photosynthetic microorganisms, principally cyanobacteria (blue-green algae). Most fossil stromatolites are found preserved as limestone or dolostone in the form of laminated domical and columnar structures, centimetres to metres in size. Other types of constructions are also grouped with stromatolites: (1) planar to wavy laminated stratiform structures, the so-called cryptogalaminites; (2) unlaminated to poorly laminated loaf- to mound-shaped structures with a macroscopic clotted fabric, called thrombolites; (3) globular, unattached structures called oncolites that have incompletely enveloping laminae; and (4) Recent unlithified microbially accreted sedimentary structures of various geometries, termed microbial mats or algal mats. Occasionally, ancient stromatolites, composed partially or entirely of chert, are found to contain fossilized microbes that commonly resemble cyanobacteria (Figs 1, 2).

Fossilized prokaryotes and stromatolites are the oldest fossils known on Earth (see Section 1.2). Sequences c. 3500 Ma in Western Australia and South Africa have yielded surprisingly well developed stromatolites. However, stromatolites are rare in the Archaean (3800–2500 Ma), with less than 20 occurrences known. During the Proterozoic (2500–c. 570 Ma), stromatolites became very abundant and diverse. They are the most conspicuous fossils discovered from this eon. Several Proterozoic columnar stromatolites are morphologically distinctive enough to merit taxonomic description, and some appear to have restricted time ranges (Section 2.13.1). Stromatolites waned in diversity and abundance during the transition into the Phanerozoic and became comparatively minor marine fossils for the remainder of geological time. During the Late Cambrian and Early Ordovician, they underwent a slight resurgence and became locally abundant. Although most stromatolites are from marine or presumed marine sequences, non-marine stromatolites are found in strata as old as Late Archaean. Stromatolites are rather common in Cenozoic non-marine

deposits. Today, stromatolites, although rare, are forming in a wide variety of marine and non-marine environments that include shallow subtidal (normal marine to hypersaline waters) to supratidal settings, lakes, streams, and thermal springs.

Stromatolites provide a variety of environmental and ecological evidence, as follows: (1) their presence indicates the activity of photosynthetic microbes. For the Early Archaean, stromatolites are important indicators of the presence of microbiologically complex life; (2) they indicate deposition



Fig. 1 Silicified columnar-branching stromatolite from the c. 2000 Ma, Gunflint Iron Formation, Canada, $\times 1.1$.

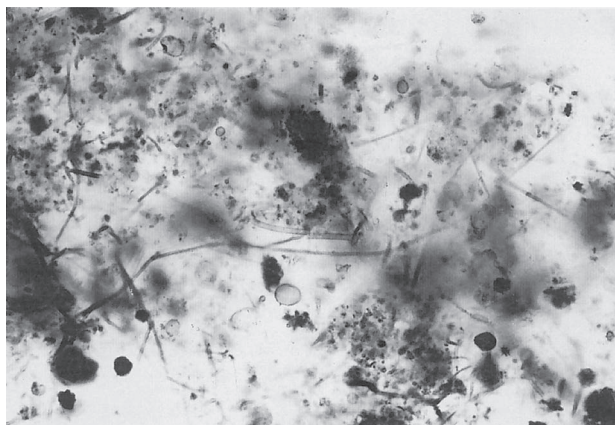


Fig. 2 Photomicrograph of filamentous and coccoidal cyanobacterial microfossils in Gunflint stromatolite from Fig. 1, $\times 380$.

under permanently or intermittently aqueous conditions; (3) they indicate deposition in shallow environments, within the photic zone. Unfortunately, without diagnostic sedimentary structures, stromatolites cannot provide a more precise indicator of permanently submerged or periodically exposed settings; (4) the presence and direction of currents can be determined by the shapes of domical and columnar stromatolites. They commonly elongate and oversteepen toward the direction of sediment supply or current (Fig. 3); (5) oncolites are useful indicators of agitation in marine settings; and (6) some Proterozoic and a few Cambrian stromatolites (in particular, columnar, columnar-branching, and conical stromatolites) are useful in biostratigraphy.

Recent stromatolites

Although not abundant today, stromatolites are forming in a variety of environments (Figs 3, 4). They are known from such non-marine settings as streams, lakes, thermal springs and even refrigerated environments like the frozen lakes of Antarctica. In marine environments, their distribution ranges from subtidal to supratidal and from hypersaline to normal marine. Cyanobacteria are the dominant micro-organisms involved in stromatolite construction; however, other photosynthetic microbes, including diatoms, green algae, red algae, and chloroflexacean bacteria, contribute to accretion. The micro-organisms that build stromatolites are organized into complex communities consisting of a few to several tens of species. A common theme among the modern occurrences of stromatolites from all environments is the sharply reduced activity of epifaunal, grazing, and burrowing animals, and macro-algae and plants, caused by one or several ecological factors: elevated salinity or alkalinity, periodic desiccation, elevated temperatures, precipitation of mineral matter during growth (this creates hard, indurated substrates), and strong currents or wave action. One of the major problems facing the use of Recent stromatolites in the interpretation of ancient forms is that no modern analogues have yet been discovered corresponding to the large number of columnar and columnar branching shapes found in the Proterozoic.

Ancient stromatolites

Fundamental differences exist between the pre-Phanerozoic, the Phanerozoic, and the Recent. The most significant differences with respect to stro-



Fig. 3 Modern subtidal columnar stromatolites off Lee Stocking Island, Bahamas. They are oversteepened and lean in the direction of current and sediment supply.



Fig. 4 Modern domical and columnar stromatolites from the intertidal zone of Hamelin Pool, Shark Bay, Western Australia.

matolites are as follows: (1) animals do not appear in the fossil record until ≤ 650 Ma; (2) eukaryotes do not appear in the fossil record until c. 1500 Ma. Thus, the possible influences of algae, other protists, or even fungi on stromatolites could not have been expressed until the Middle and Late Proterozoic. There is no suggestion that these early eukaryotes directly affected stromatolites; (3) prior to 2300 Ma, the Earth was essentially anoxic. Oxygen levels were probably very low for the remainder of Early Proterozoic time. During the Middle and Late Proterozoic, oxygen levels gradually increased, so that by the latest Proterozoic (≤ 650 Ma, metazoan respiration could have been supported; (4) shallow marine, carbonate accumulating environments (environments where stromatolites have thrived) were

different in the pre-Phanerozoic. The dominant carbonate sediment was lime mud with relatively few sand-sized or coarser carbonate grains available. During the Phanerozoic, carbonate secreting invertebrates and algae produced abundant coarse-grained sediment that was readily available in agitated environments; and (5) although morphologically similar to modern stromatolite builders, the microbes that built pre-Phanerozoic stromatolites might have been phenotypically different for some characteristics as well as genotypically different from extant microbes.

The Archaean. Archaean stromatolites are rare; the number of localities known with convincing examples is less than 20. The stromatolites are relatively simple, exhibiting what could be termed a 'generalized' morphology. They are typically stratiform, domical, and columnar-layered, shapes common throughout the fossil record. Columnar, columnar-branching (with simple branching patterns), and conical stromatolites are rare. The complex varieties known from the Proterozoic, such as complexly branching columnar stromatolites, are unknown. Environments in which Archaean stromatolites formed included permanently submerged to periodically exposed marine settings, as well as lacustrine to fluvial settings. The rarity of Archaean stromatolites is probably due not to the lack of suitable microbiological constructors, but to the tectonic-sedimentary environments of greenstone belts in which relatively stable, shallow-water, low sediment-input environments were rare.

The presence of 3500 Ma, early Archaean stromatolites in two greenstone belts, one in Western Australia (Walter *et al.* 1980) and the other in South Africa (Byerly *et al.* 1986), argues convincingly that microbes had already evolved the phenotypic attributes necessary for stromatolite construction. Although not morphologically complex, the stromatolites are nevertheless well laminated and range in shape from undulatory, stratiform structures to domical structures (Fig. 5); some of the stromatolites have a pseudocolumnar and columnar-layered organization, and all are morphologically very similar to Proterozoic and Phanerozoic examples. Filamentous and coccoid microfossils have been discovered in chert from strata near the stromatolites in both regions (e.g. Awramik *et al.* 1988). At the Western Australian site, most of the filaments occur within thinner, dark laminae of wavy laminated, light-dark laminar couplets, and they are commonly oriented parallel to the lamination — an organization that

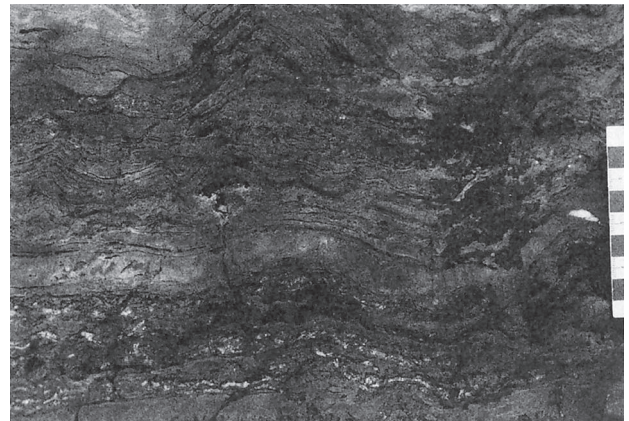


Fig. 5 Wavy laminated to domical stromatolites from the Early Archaean Warrawoona Group, Western Australia. Scale in cm.

suggests stratiform stromatolitic laminae. The South African filamentous microfossils coat grains but are not found in a laminated fabric suggestive of stromatolitic activity. Unfortunately, no microfossils have yet been found in the more convincing stromatolite morphologies.

The occurrence of stromatolites in such ancient rocks has great palaeobiological significance. The construction of a stromatolite requires metabolically, behaviourally, and morphologically sophisticated microbes that interact with a complex of environmental factors. The following phenotypic attributes of prokaryotes are suggested to have evolved by Early Archaean time (and are considered to be general requirements for stromatolite-building microbes regardless of their age): (1) the builder must be benthic throughout most or all of its life cycle. For this to be the case, the microbe has to be denser than the fluid medium and/or develop a means of attachment, like the extracellular gel (sheaths and envelopes) found in today's stromatolite-building microbes; (2) the microbes must have the ability to trap and/or bind sediment. Sediment incorporation by the growing microbes is required for most stromatolites. Trapping of sediment is a result of the microbes' growth habit, e.g. cyanobacteria with erect filaments can trap sediment grains between the filaments. Binding can occur with the growth, movement, and extracellular secretions of the microbes. The mucilaginous extracellular secretions help to glue together sediment grains and the microbes; and (3) the benthic organisms must be able to maintain a position at or near the sediment-fluid interface. The photosynthetic physiology is the key solution to this requirement. In addition to sunlight acting as the catalyst for

chemical reactions, it also provides the stimulus for tropisms and taxes. Photosynthetic microbes that build stromatolites orient themselves positively with respect to sunlight (phototropism) and many move toward sunlight (phototaxis). Thus by 3500 Ma, microbial evolution was already well advanced.

By Late Archaean time, stromatolites had become more common. Large-scale cratonization occurred during the geological transition from the Archaean to the Proterozoic. This produced relatively stable, shallow marine platforms along the edges of continents. Cratonization began first in Western Australia and southern Africa. As it continued into the Early Proterozoic, the area open to colonization by stromatolite-building cyanobacteria increased significantly.

The Proterozoic. During this 2000 million year interval of geological time, stromatolites achieved their greatest abundance, the acme of their diversity, and dominated the fossil record. There are numerous unique geometrical arrangements of stromatolite laminae, columns, and branches in the Proterozoic. Analysis of stromatolites (first by Soviet geologists) led to the recognition that certain types of stromatolites can be used as index fossils for Proterozoic and Cambrian strata. Unlike most Phanerozoic and Archaean stromatolites, Proterozoic stromatolites are often given binomial names. By Early Proterozoic time, stromatolites appear to have expanded into all their major habitable ecological zones, except for ice-covered regions (stromatolites, however, are associated with late Proterozoic glacial deposits).

By the end of Early Proterozoic time (1600 Ma), all the basic stromatolite architectures had appeared: stratiform, domical, nodular, columnar, columnar-layered, columnar-branching, conical, and conical-branching, along with oncolites and possibly thrombolites. Studies of the palaeomicrobiology of the c. 2000 Ma Gunflint Iron Formation in Canada indicate that all classes and orders of modern cyanobacteria had evolved. Columnar, conical, and columnar-branching stromatolites underwent substantial morphological elaboration and taxonomic diversification during the Middle and Late Proterozoic (1600–800 Ma) (Awramik 1971). This diversification reached its peak around 1000 Ma (Walter & Heys 1985). Columnar and columnar-branching stromatolites are the forms that best illustrate this increase in diversity and the morphological complexity that was achieved by stromato-

lites (Fig. 6). High diversity was maintained in the early and middle parts of the Late Proterozoic; however, diversity began to drop sharply c. 680 Ma. Columnar-branching stromatolites and conical stromatolites were rare by Early Cambrian time. This decrease in diversity and abundance was probably due to the evolution of grazing metazoans which inhibited the formation of microbial mats, and to burrowing metazoans which destroyed the characteristic fabric of microbially accreted sediments. Meiofauna might have played a major role in the decrease.

The Phanerozoic. The evolution and radiation of Metazoa greatly reduced the abundance and diversity of stromatolites in marine Phanerozoic sequences. Representatives of the group *Conophyton* (a distinctive conical stromatolite with peculiarities of laminae in the axial zone) are no longer found; elaborately branched columnar stromatolites are rare, as are most other columnar-branching stromatolites; domical and columnar stromatolites and oncolites occur and are occasionally locally abundant. Thrombolites (stromatolites that lack lamination and have a macroscopic clotted fabric) became important in the Early Palaeozoic.

In addition to the well developed vertical burrows and bioturbated sediments that first appeared in the Early Cambrian, a second eukaryote-induced factor further stressed stromatolite-building microbial communities: the widespread appearance of coarse bioclastic sediment (Pratt 1982). The evolution of calcium carbonate biomineralization by animals and protists in the Early Cambrian, and the radiation of these organisms, produced significant amounts of bioclastic material, much of it larger than micrite (the dominant carbonate grain size in the



Fig. 6 Middle Proterozoic columnar-branching stromatolite *Baicalia cf. rara* from Liaoning Peninsula, China.

Proterozoic and Archaean). Cyanobacteria are not well adapted to trap and bind coarse-grained material (Awramik & Riding 1988). It is probable that algal eukaryotes combined with cyanobacteria to produce some stromatolites, in particular those composed of silt-sized or larger sediments. Fine-grained stromatolites, nevertheless, continued to occur and probably dominated the marine Phanerozoic record of stromatolites.

The Cambrian and Early Ordovician were times of continued stromatolite activity, albeit at reduced levels. Columnar stromatolites, some with branches, domical and stratiform stromatolites, and oncolites were well represented. Microbially bound sediment, at times recognizable by macroscopic stromatolitic laminated fabrics, is an important component of Early Cambrian archaeocyathan bioherms (Rowland & Gangloff 1988). Some thrombolites, which were most abundant during the Cambro-Ordovician, along with laminated stromatolites, built reefs in the Late Cambrian and Early Ordovician. Oncolites were locally abundant, possibly at levels that exceeded those of the Archaean, Proterozoic, and Late Phanerozoic. Unlike the Proterozoic, when the subtidal realm was the primary site for stromatolite growth, from the Cambrian onward a proportionally large number of stromatolites (in particular those with a stratiform, wavy laminated, and domical morphology) formed in intertidal settings.

During the remainder of Phanerozoic time the abundance and diversity of stromatolites became further reduced. A third eukaryote-induced inhibition probably brought this about: the Early–Middle Ordovician diversification and radiation of benthic eukaryotic organisms. These metazoans and algae outcompeted stromatolite-building cyanobacteria for suitable substrates. Nevertheless, stromatolites are not uncommon contributors to reefs and other organic build-ups. In the Late Devonian and Late Permian, for example, reef-like structures composed primarily of stromatolites are known. Stratiform to low dome-shaped stromatolites are not uncommon in intertidal carbonate deposits. The further diversification of benthic green and red algae (for which there are good fossil records) and other algae during the Mesozoic probably further inhibited stromatolite formation.

The Phanerozoic non-marine stromatolite record, in particular for the Cenozoic (Fig. 7), is moderately well developed (Monty 1973). Most non-marine stromatolites appear to have formed primarily as a result of the precipitation of calcium carbonate on and within the microbial mat; allochthonous



Fig. 7 Pleistocene non-marine stromatolites and oncolites from the Koobi Fora Formation, Lake Turkana region, Kenya.

sediment incorporation was a relatively minor phenomenon. Because of the ephemeral nature of fluvial and lacustrine environments and their general unlikelihood of being preserved for long periods of geological time, the non-marine stromatolite record is comparatively poor. All manner of structures occur: columns, branching columns, conical structures, stratiform constructions, domes, and oncolites. Except for the oncolites, most of the constructions are smaller (centimetres in scale) than their marine counterparts (centimetres–metres in scale). Oncolites, on the other hand, are well represented by decimetre-sized examples. These large oncolites, however, are usually compound structures with the top side of the encapsulation characterized by small domes, columns, and branching columns, while the underside contains smooth–wavy laminated, occasionally pseudocolumnar layers. The upper side of the oncolite is commonly thicker. Unlike most of the marine oncolites, which formed as a result of the alternation of mobile and stationary conditions, many non-marine oncolites formed *in situ*.

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4.8 Reefs and Carbonate Build-ups

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Introduction

Definition has always been a prominent issue in reef studies, at the heart of which has been the struggle to integrate two perspectives, one based on modern and the other on fossil structures. Although modern reefs provide important insights into processes, they can be misleading as gross analogues because of the way in which they have been affected by Quaternary glacioeustatic events — events that cannot be assumed to have applied to all reefs and build-ups throughout the geological record. It is appropriate here to be pragmatic and accept, *de facto*, all features that have been regarded as reefs and build-ups to date (Scholle *et al.* 1983; James & Macintyre 1985; Scoffin 1987). While no simple definition unites them all, there is a logical (if sometimes indirect) thread that connects them. For a succinct discussion of reef types, see James & Macintyre (1985, p. 22). Fig. 1 summarizes the principal organic contributors to reefs and build-ups through geological time.

Criteria mentioned in most reef definitions include one or more of the following: *organic framework*, *raised relief*, *wave resistance*, *photic zone restriction*, and *tropical (or warm water) distribution*. In practice, the only structures that can be *observed* to fulfil all these criteria are modern tropical coral reefs. All other structures that have been regarded as reefs and build-ups, past or present, usually show (or have been interpreted as showing) *either* evidence of framework, *or* raised relief, *or* both. Generally, if any distinction between reefs and

build-ups is made at all, reefs are usually thought of as showing evidence of framework as well as relief ('ecological reefs' (Fig. 2B)), whereas build-ups can also be used for relief structures without (observable) framework. Criteria other than framework and relief have come to be regarded as secondary, and may or may not be met in the identification of a particular reef or build-up.

However, even this simple approach leaves problems. Various fossil structures have come to be called reefs simply because their features *seem* to include framework or relief, in the absence of clear evidence to the contrary. Moreover, the search for Recent analogues of all the different fossil structures now included in reefs and build-ups has generated interest in Recent biogenic structures other than tropical coral reefs, notably deep- and cold-water coral banks, lithoherms, and carbonate mounds (Cairns & Stanley 1981; Mullins *et al.* 1981; Scholle *et al.* 1983; James & Macintyre 1985). These have also become part of the broad notion of reefs and build-ups.

Principal reef criteria

Framework. The consensus is that framework (Fig. 3) consists of three biogenic components: (1) closely packed, primary *in situ* accumulations or intergrowths of rigid macro-organisms (typically corals, branching coralline algae, rudistid bivalves, stromatoporoids) further bound together by (2) a secondary framework of *in situ* encrusting and

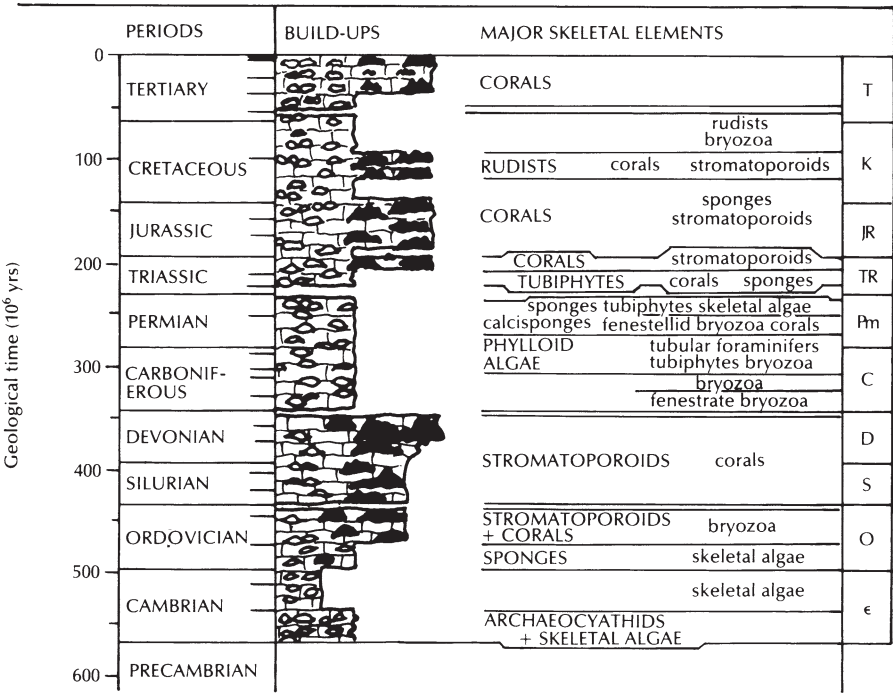


Fig. 1 Idealized stratigraphic column showing major organic contributors to reefs and build-ups through the Phanerozoic. Block symbols represent framework structures, and open symbols represent structures without framework ('reef mounds'). Gaps indicate times when there appear to have been no framework structures, and times when there were no build-ups at all. Note that many authors would regard skeletal algae as being similar in importance to corals in the Tertiary. (After James in Scholle *et al.* 1983, by permission from the American Association of Petroleum Geologists.)

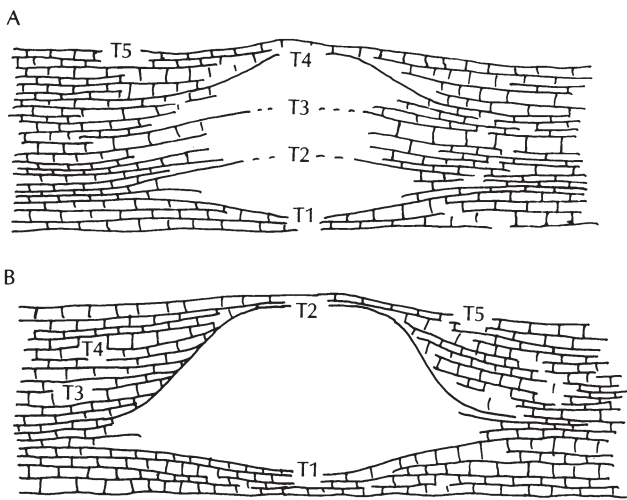


Fig. 2 Schematic difference between A, a stratigraphic reef and B, an ecological reef. Successive time planes are indicated by 'T' symbols. Stratigraphic reefs may also contain ecological phases, as in the lowest and uppermost reefal units in A. (After James in Scholle *et al.* 1983, by permission from the American Association of Petroleum Geologists.)

cementing organisms (typically coralline algae, bryozoans, and encrusting foraminifera and sheet-like corals); and (3) infilling material, trapped within this rigid structure, consisting of sediment whose origins may be from either the framework itself or beyond it. There are also numerous infilling organ-

isms, usually smaller than the main framework contributors, both encrusting and free-living, many of them (*coelobites*) occupying caves, cavities, and overhangs (*cryptic habitats*). Much sediment infill is also postlithification.

This rigid framework model, however, is an idealized end-member of a whole spectrum of 'frameworks'. Different processes of sedimentation and preservation result in an intergradation of prominence between the above three framework components. Large branching or mound-like organisms may be sparse or absent, leaving encrusting and cementing organisms like coralline algae to build up structures on their own (Bosence 1983; Scholle *et al.* 1983), as in the largely algal Bermuda cup reefs. Encrusters can also bind sediment ranging in grain size from fine mud and silt (as in stromatolites) to cobbles of broken, worn, and transported material, or other accumulations of biogenic clasts like rhodoliths. If the clastic material consists of large, relatively unworn coral fragments, it may be hard to distinguish the finally preserved rock from a true *in situ* framework of macro-organisms. At another extreme (and probably more abundant than the idealized framework model), dense stands or accumulations of organisms can occur without any apparent binding organisms, e.g. the coral beds of the British Carboniferous and many facies of rudistid reefs. In the case of lithoherms, early diagenesis has a significant constructional role not

unlike a framework built by organic encrusters, but in this case, primary structure consists almost entirely of sediment; the organic component consists of secondary colonizers.

While a true framework is usually considered to be a relatively permanent feature, frameworks of non-rigid organisms are also very important as constructive agents, although they usually break down before preservation. Structures of this kind, built up by sediment-trapping marine grasses, occur in the inshore areas of the Florida Keys (Scholle *et al.* 1983; James & Macintyre 1985, Bosence *et al.* 1985). Delicate branching corals, crinoids, and organisms whose preservable skeletal elements are held together by soft tissues (such as many sponges and octocorals) can also have a similar sediment-trapping role, but usually break down into fragments and spicules before preservation. The environment of such non-rigid frameworks is generally less favourable to cementing organisms than that of rigid frameworks, so the resulting rock contains large amounts of sediment in relation to primary organisms. Even with rigid frameworks, however, the final proportion of framework in the resulting rock can be surprisingly reduced to shadowy remnants where they have suffered extensive *in situ* contemporaneous destruction by boring organisms (such as endolithic algae, clionid sponges, and various bivalves). Diagenetic processes can also destroy framework.

Thus the concept of framework, like that of reefs, has become broad, and takes into account both frameworks that are preserved and those that are not. The end-product may be a structure with relief but no apparent framework, a framework with raised relief, or a framework without true relief (i.e. a laterally developed *in situ* growth or biostrome). There are also relief-features to consider that may never have had any framework at all, as discussed next.

Relief. For fossil build-ups, the identification of relief is usually an inference derived from the observation of a facies discontinuity that marks the limits, ideally, of a bioconstructional formation. Relief is inferred if this discontinuity has a mound- or ridge-like geometry, and (in theory at least) it results from the ability of framework organisms to maintain net growth against the agents of destruction and transport. In many cases, moreover, it is difficult to conceive what other primary sedimentary process could cause the commonly observed steepness of sedimentary dips. Problems arise from

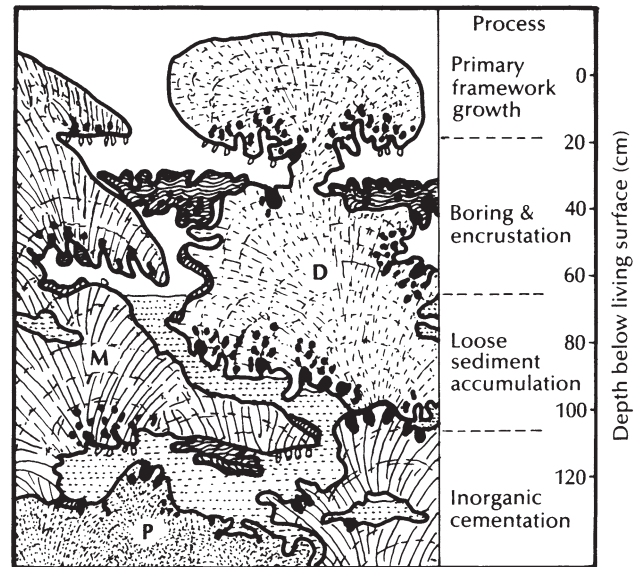


Fig. 3 Vertical cross-section through part of a Bermuda lagoonal patch reef, showing framework structure and internal processes. Capital letter symbols indicate primary framework of scleractinian corals, here consisting of three genera (D, *Diploria*; M, *Montastrea*; P, *Porites*). Secondary framework (laminated pattern) consists of coralline algae above, Bryozoa in middle cavities, and *Agaricia* coral in lower cavity. The encrusting foraminiferan, *Homotrema*, lines undersides of overhangs. Sediment infill is shown by horizontal stipple. Bioerosion is denoted in black: mainly by bivalves like *Lithophaga* (larger holes) and clionid sponges (smaller holes); not to scale. (After Scoffin 1987.)

this, however:

- 1 Some of the relief and its flank-slope steepness may be due to antecedent structure (Fig. 4, and discussed below).
- 2 There are relief features that contain no clear framework. This might be because framework has not been preserved, or because the build-ups were shaped primarily by contemporaneous hydrodynamic factors or early diagenesis. (Such features can also be colonized by organisms as they grow, giving the illusion of framework.)
- 3 Postlithification erosion can 'create' or enhance primary relief. It is not always easy to distinguish a discontinuity surface which is due to stratigraphical disconformity from a syndepositional interface between framework and flanking facies, especially when identification of framework is uncertain. Similarly, the present-day surface of land erosion can also 'create' reef-like relief in ancient deposits, and this is not easy to distinguish from the exhumation of ancient syndepositional features. Although emphasis has been placed on the recognition of talus blocks to infer syndepositional relief,

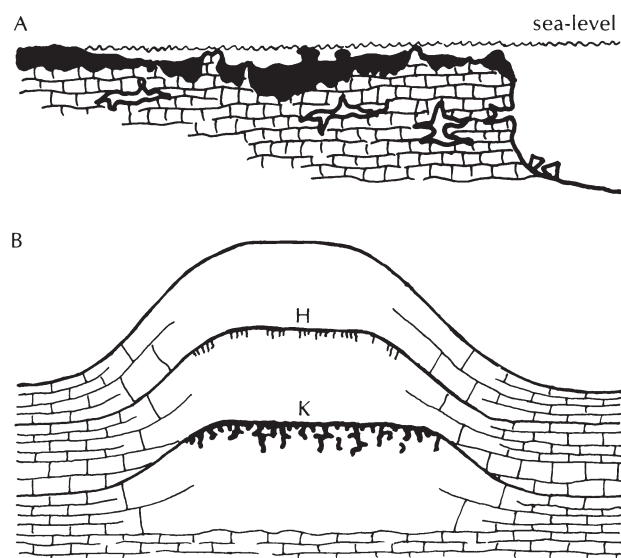


Fig. 4 Composite structure and antecedent surfaces as factors in reef relief (not to scale). A, Recent model showing Holocene reef growth as a veneer, 0–10 m thick (black), overlying disconformity in karst-eroded, pre-Holocene reef limestones. (After Braithwaite 1987.) B, Fossil reef structure composed of a stacked series of reef phases separated by discontinuities; lower discontinuity (K) is a karstic erosion surface, while upper discontinuity (H) is a hardground. (After James & Macintyre 1985.)

this kind of evidence can be misleading. Blocks at the foot of modern deep fore-reef slopes in the Caribbean, previously taken to be modern and syndepositional, might well be residuals derived from subaerial erosion of older reef limestones during pre-Holocene low sea-level stands. Many ancient talus deposits might therefore have originated in analogous fashion. Better knowledge of Pleistocene–Holocene karstic phenomena and the erosional history of modern reef complexes (below) has stimulated a search for intraformational palaeo-karstic surfaces in fossil build-ups (Fig. 4). This has revealed that at least part of the apparently contemporaneous relief of some supposed build-ups may actually be due to cyclical alternation of deposition of prograding carbonates with emergence and karstic erosion.

4 Another possible cause of 'pseudo-relief' is that of sharp syndepositional interfaces between different communities and facies. Where the relative lateral extent of these interfaces persists, waxing and waning through time, a mound-like geometry can develop, although at the time of deposition, one facies may not have projected significantly more than another above the sea floor ('stratigraphic

reefs': Fig. 2A). Other postdepositional factors, such as diagenesis and relative compaction, may also account for 'pseudo-relief' or exaggerate primary relief.

Even in modern environments, reef relief, though readily observed, is not a simple phenomenon. It is certainly not always attributable to framework or sediment-trapping organisms. Hydrodynamic influence can be as important as the direct role of organisms, or more so, as in the growth of columnar stromatolites, and in the linear carbonate mud mounds of Florida Bay (now regarded as partial analogues of Carboniferous Waulsortian reefs; Bridges & Chapman 1988).

A great deal of apparent relief, moreover, can be ascribed to underlying, antecedent topography (Fig. 4). This is now beyond doubt for most modern coral reefs, for which glacioeustatic events have been especially important. Shallow drilling and radiometric dating show that in both scale and detailed topography, much of their relief still matches the dissected and cavernous morphology of pre-existing platforms formed by underlying, older reef limestones. These were evidently exposed subaerially during glacioeustatic regressions, especially during the last 140 000 years, and subjected to karstic erosion. Since then, the Holocene transgression has drowned the resulting topographies, and renewed modern growth has contributed only a veneer (varying from a few centimetres to about 10 m or more) which often scarcely masks these older features (Fig. 4A). Recognition of this took a surprisingly long time and was hindered by: (1) the lithological similarity between modern and older limestones; and (2) the fact that some of the older limestones were prograded to approximately the same sea-level as today, so the uppermost features of modern reefs are in fact partly contemporary and partly fossil.

Implications of this for the study of fossil reefs are as follows: (1) they may similarly have been affected by intraformational, erosional histories (Fig. 4B) that are not immediately obvious and might still be unrecognized; and (2) the most informative modern analogue for fossil reefs is not the gross structure and relief of modern reefs, since this is usually a composite of numerous phases which may go back to the Early Tertiary or before. Rather, it is the Holocene veneer alone that provides the most direct clues for a single phase reef-growth model. However, even this has limitations as a general case for the fossil record, because it represents a relatively short term response to transgressive conditions. It

must be adapted to take account of the probable effects of static or regressive sea-levels, as well as different rates of sea-level change and the vertical component of any tectonic movement that affected the foundations.

Even without eustatic influence in the history of a build-up, the ecological preference of many benthic organisms for sea-floor highs (like submarine horsts, scarps, and volcanoes), as well as the greater rates of carbonate deposition on such features, points to a general likelihood of an antecedent factor in almost any carbonate complex.

In order to relate relief in fossil build-ups to that of modern reefs, physical scale must also be considered. Many modern coral reefs are extensive complex structures many kilometres across with a whole mosaic of carbonate facies. True framework is highly localized, not necessarily at the seaward rim of such complexes, and usually accounts for much less surface area and volume than bioclastic sediments, oolites (e.g. Bahamas), and evaporites. This facies complexity appears to reflect immaturity, because Holocene submergence and growth recovery has been so recent, and this is another constraint to be considered in using modern reefs as fossil analogues.

Although some fossil build-ups are also seen as complexes (e.g. the Devonian of the Canning Basin), many are defined purely with respect to a local outcrop of a framework or relief feature, perhaps only metres across (e.g. the Silurian of the British Wenlock). The best analogues for such structures are not complete reef complexes like modern atolls, which are tens of kilometres across, nor even platform reefs like those of the Australian Great Barrier Reef complex, but rather the separate small-scale constructional features within these carbonate systems. The lagoonal patch reefs of Bermuda, which are just one of a whole range of features within its atoll-like complex, are much more comparable in scale and structure to reefs of the British Wenlock.

Similarly, there is confusion of scale in the use of 'lagoon' in reef studies, which might denote anything from the shallow (less than 5 m) sheet of water that covers many modern reef flats, to the large and relatively deep (up to 70 m or more) areas that lie within atoll rims or between barrier reef complexes and their mainland. It follows that 'fore-reef' and 'back-reef' concepts also have various meanings. It is probably best to think of reef relief as a fractal phenomenon — similar topographic patterns repeated within themselves on different scales (e.g. compare atolls, faros, and microatolls).

Other criteria

Remaining criteria are secondary, often introduced in support of a particular reef interpretation. Although such criteria apply to modern coral reefs, there also exist modern bioconstructional features and other possible analogues of ancient build-ups that occur: (1) below wave base; (2) below the photic zone; (3) in deep and cold water; and (4) in high latitudes. Many kinds of largely algal build-up, sometimes combined with bryozoans, occur in temperate latitudes, and there exists a whole suite of different deep- and cold-water coral banks (Cairns & Stanley 1981; Mullins *et al.* 1981; Bosence 1983; Scholle *et al.* 1983; James & Macintyre 1985; Scoffin 1987).

Common arguments for inferring wave influence are: (1) relief as an indication of wave resistance; and (2) zonation of communities as a response to sharp environmental gradients caused by the breakwater-like effect of a positive feature close to sea-level. But relief is equivocal evidence, as already discussed, and zonation can occur in deeper-water structures. Conversely, modern small surface patch reefs of a size comparable to many fossil build-ups are often too small to show either real zonation or any clear fore-reef and back-reef differences. In view of the popular use of reefs and build-ups as palaeoclimatic and palaeogeographical indicators, it is therefore also worth noting that their occurrence (defined broadly) in the geological record is not a reliable reflection of temperature, climate, latitude, water depth, or wave energy, even when corals or algae are prominent.

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4.9 Encrusters

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Introduction

Encrusting animals and plants are important colonizers of marine hard substrata today (Jackson 1983), and are well represented in the Phanerozoic fossil record. Interest in modern encrusters is linked both to their commercial importance as foulers of man-made structures (e.g. ship's hulls and offshore oil platforms), and to the fact that encrusting communities on artificial settlement panels are excellent subjects for studies of competition and ecological succession. Encrusters are also attractive subjects for palaeoecological studies because they retain their original spatial relationships to the substratum and to one another, thus allowing the inference of life orientations and interactions. Furthermore, the substrata used by encrusters are often discrete and of a size suitable for collection in the field and transportation back to the laboratory for detailed study.

Communities living on hard substrata are usually dominated by sessile organisms which include *endobionts* (boring into the substratum) and *epibionts* (attaching to the surface of the substratum). The epibionts comprise organically-attached (e.g. pedically-attached brachiopods, bysally-attached bivalves) and cemented forms. Many organisms have cemented bases or holdfasts which anchor more extensive erect parts (e.g. crinoids, arborescent bryozoans). However, the term 'encruster' is here restricted to organisms of low profile which are cemented to the substratum across a large part of their basal surfaces. Organisms cementing to small substrata which they quickly outgrow to rest freely on the sea bed (e.g. gryphaeate oysters, many

stromatoporoids) are excluded from this definition of encrusters, although, as with erect organisms, they may intergrade with typical encrusters.

Encrusting animals are characteristically suspension feeders, capturing particulate food from the water column. Being sessile as adults, they are dependent for colonization on a free-swimming larval stage. Those individuals whose larvae settle successfully and survive immediate post-settlement mortality are termed *recruits*.

Taxonomic composition and morphology of encrusters

The following groups generally dominate modern encrusting biotas: algae, foraminifera, sponges, coelenterates, bryozoans, brachiopods, bivalves, serpulid polychaetes, ascidian tunicates, and barnacles. Apart from ascidians, all of these groups contain at least some species with mineralized skeletons, and therefore have good preservation potential. Even soft-bodied encrusters are occasionally preserved as fossils by *bioimmuration*, i.e. when overgrown by other encrusters and left as natural moulds on their undersides.

It is useful to classify encrusting animals according to aspects of their growth and form that determine how they use and compete for substratum space. A fundamental distinction is between solitary and colonial forms. Solitary forms typically grow to a fixed size and shape (determinate growth), whereas colonial forms, which grow by the asexual budding of modular units (zooids), are often highly irregular in size and shape (indeterminate growth), may suffer partial mortality (death of some but

not all zooids in the colony), and undergo fission into several parts or fusion with other colonies (Section 4.6).

Encrusters commonly found as fossils are shown in Fig. 1. Solitary encrusters fall into two main morphological groups: forms with a subcircular outline shape which grow centrifugally from an encompassing growing zone, and linear forms which grow in straight, curved, or spirally coiled lines from an apical growing zone. Subcircular forms are often bivalved or multiplated, and are well equipped to defend their margins against lateral overgrowth by other encrusters. Many linear forms can change growth direction and 'migrate' significantly across the substratum, but they have poorly defended flanks which are vulnerable to lateral overgrowth.

Colonial encrusters also fall into two main morphological groups (Jackson 1979): *sheets* (Fig. 2A), which are 'two-dimensional' colonies, with closely-packed zooids, which spread across the substratum by zooidal budding from an encompassing growing zone; and *runners* (Fig. 2B), which are 'one-

dimensional', branching colonies which grow by budding zooids from numerous growth tips. Sheet-like colonies are highly committed to defending and winning substratum space from other encrusters (*confrontational* or *phalanx* strategy). Runners, by contrast, are vulnerable to lateral overgrowth, but distribute their zooids across wide areas of the substratum (*fugitive* or *guerilla* strategy); this enables them to locate patches of substratum (*spatial refuges*) where the probability of mortality is lower and in which some zooids may survive (see also Section 4.6).

Points to note in the geological history of encrusters (Fig. 1) are the major radiation of encrusters in the Ordovician, the scarcity of encrusters in the Late Palaeozoic, and the Mesozoic radiation of the modern encrusting biota, with the late appearance of acorn barnacles.

Encruster-substratum relationships

Modern communities of encrusters are best known from intertidal and shallow subtidal habitats, and

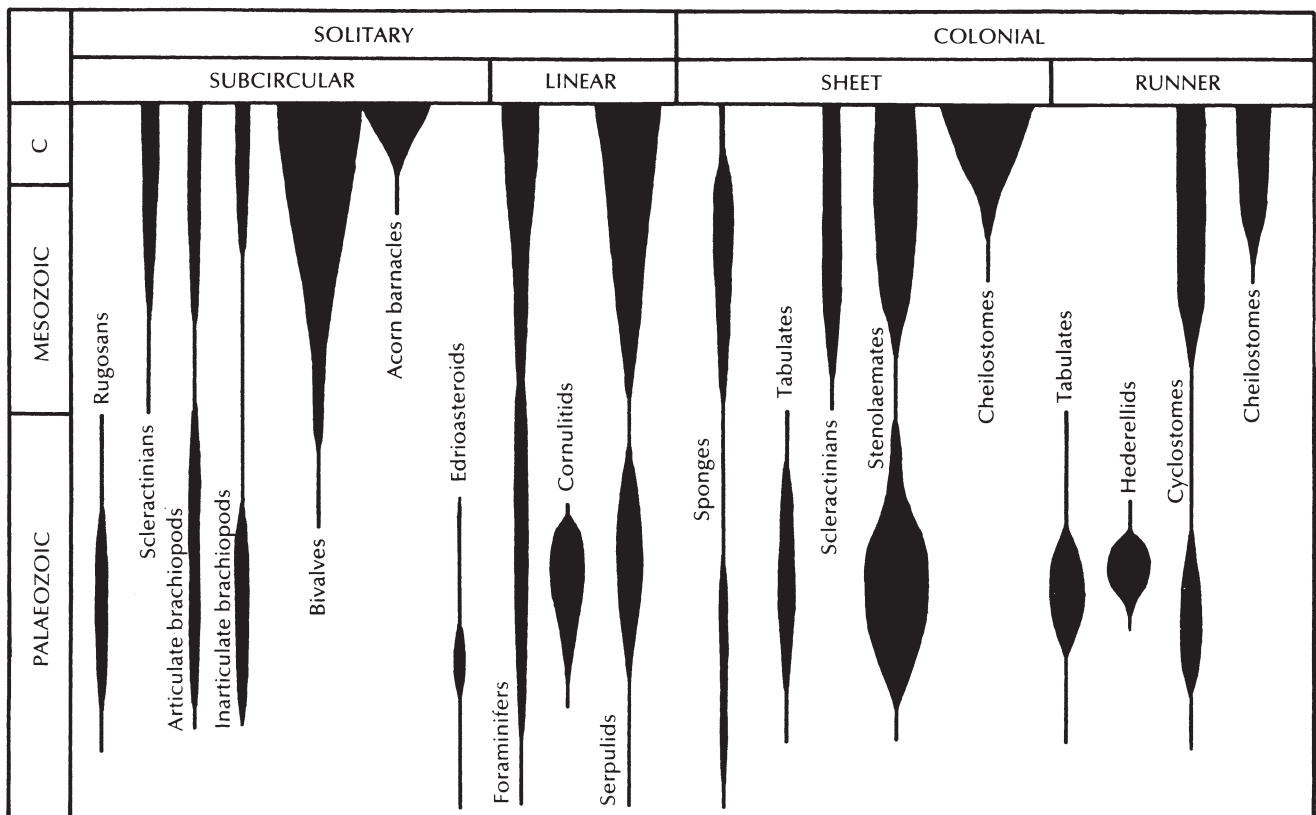


Fig. 1 Stratigraphic distribution and morphological classification of the principal taxonomic groups of encrusting animals represented in the fossil record. Line thickness gives a very approximate indication of the importance of each group in encrusting assemblages. The category 'stenolaemates' includes encrusting cyclostome, cystoporate, and trepostome bryozoans.

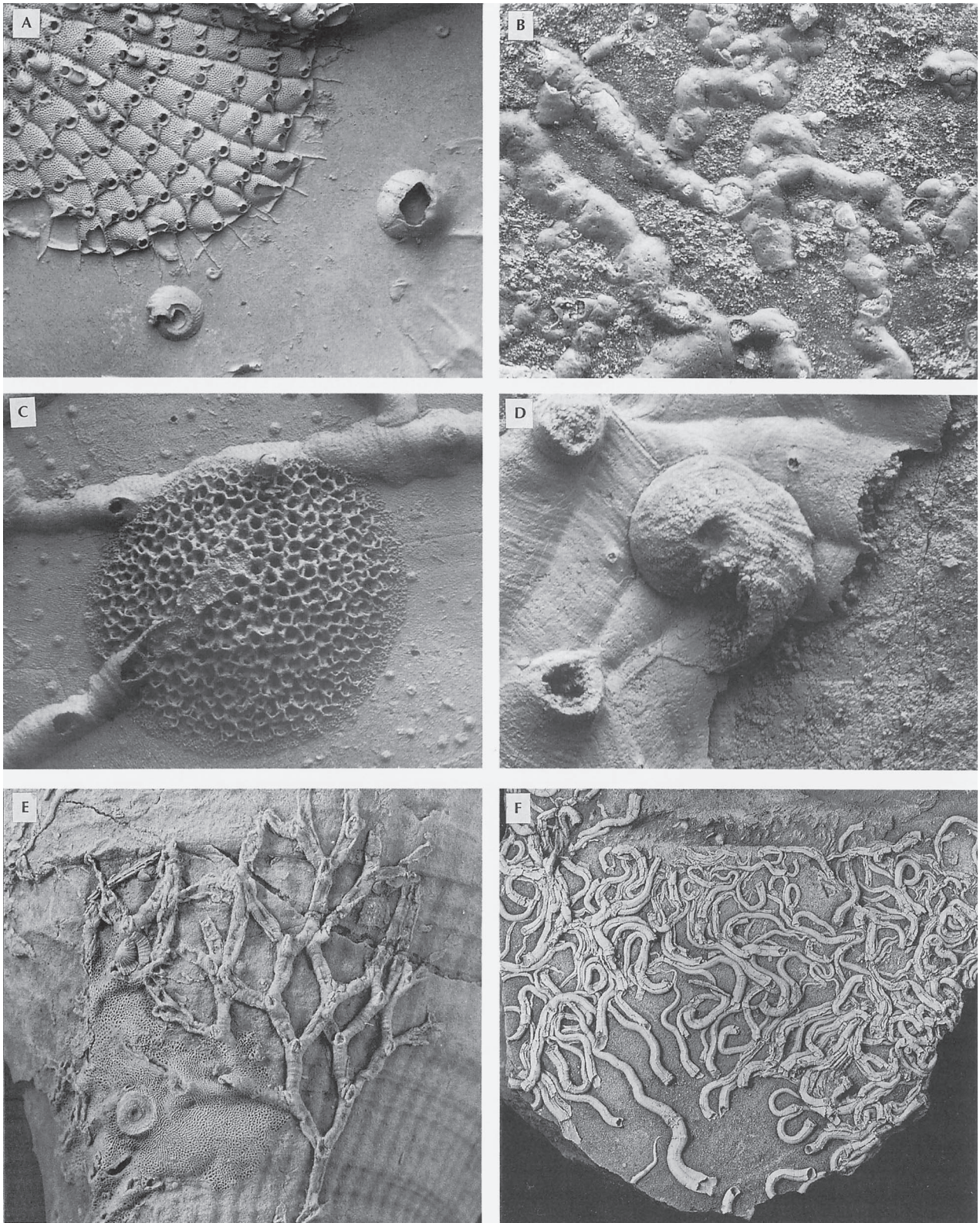


Fig. 2 Encrusting animals and their interactions. A, Sheet-like cheilostome bryozoan *Schizoporella* growing towards a polychaete tube *Spirorbis* and a small barnacle; Recent, Adriatic Sea ($\times 10$). B, Linear growth-form in encrusting foraminifers *Nubeculinella*; Upper Jurassic, Normandy, France ($\times 42$). C, Reciprocal overgrowth between a sheet-like sponge and a runner-like cyclostome bryozoan; the upper part of the sponge is overgrowing the branch flanks of the bryozoan, but a branch of the bryozoan is overgrowing the sponge at the bottom left; Upper Cretaceous, Norfolk, U.K. ($\times 14$). D, *Spirorbis* fouling the surface of the cyclostome bryozoan *Sagenella*; Silurian, Gotland, Sweden ($\times 57$). E, Runner-like tabulate *Aulopora*, partly overgrown by the basal holdfast of a cryptostome bryozoan, encrusting the epitheca of a solitary rugose coral; Silurian, Gotland, Sweden ($\times 3$). F, Dense encrustation of serpulid polychaetes on a cobble; Middle Jurassic, Gloucestershire, U.K. ($\times 1.4$).

include communities attached to rocks, shells and skeletons of living and dead animals, macroalgae, and artificial substrata (e.g. pier pilings). Organisms which attach to living plants are termed *epiphytes*; those attached to living animals are termed *epizoans*. Epiphytic communities of nearshore macroalgae have been extensively studied, but macroalgal epiphytes have yet to be recognized in the fossil record. Epizoid communities can be found at the present day on a wide variety of hosts, particularly sessile animals (e.g. large epifaunal bivalves, undersides of corals). Colonization by epizoans can be advantageous or disadvantageous to the host animal. For example, some Recent bivalves gain from the camouflage provided by epizoans, but it has been shown that certain epizoans increase drag and therefore the probability of dislodgement. The term 'epizoan' should be applied only to encrusters whose hosts were alive at the time of encrustation, although inference of life association can be extremely difficult in fossils (one of the few reliable criteria is epizoan-induced modification of host growth pattern; Section 4.14).

Encrusted skeletal substrata are very common in the fossil record and range from intact, *in situ* skeletons of probable living hosts, to fragmented, transported, and *remanié* skeletal debris. The condition of encrusted substrata can provide useful information on depositional environments, particularly on the occurrence of episodic sedimentation and reworking. Among studied hard substrata are: Palaeozoic stromatoporoids, which frequently harbour encrusting biotas on the cryptic undersides of their coenostea; cavities in reefs occupied by *coelobionts*; and Cenozoic molluscan shell gravels in which the concave inner surfaces of bivalves may be particularly well encrusted. In environments normally hostile to epibenthos, as in some muddy deposits, the rare substrata provided by the shells and bones of nektonic animals (e.g. cephalopods, marine reptiles) constitute important *habitat islands* for sessile species which often form dense encrustations.

Abiotic substrata for encrusting organisms range from rocky shorelines to hardgrounds, pebbles and cobbles, and even coarse sandy sediments. Colonization of ancient rocky shorelines has seldom been recognized, but a good example occurs in the Upper Cretaceous of Sweden where Surlyk & Christensen (1974) described zonation in encrusted boulders of Precambrian gneiss. Hardgrounds formed by early lithification of carbonate sediments are better known as substrata for encrusters (Palmer 1982).

Hardground morphology determines the types of habitats they provide. Upper surfaces may be planar or hummocky, and the hardground can be undercut, broken-up, or penetrated by burrows excavated before the sediment was lithified. Hummocky Ordovician hardgrounds commonly lack encrusters on the hummocks but are colonized by bryozoans and other encrusters between the hummocks. Undercut and burrowed hardgrounds commonly show a polarization of encrusters between exposed upper surfaces and cryptic undersides or burrow walls. Trends through the Phanerozoic in hardground assemblages have been towards: (1) greater diversity of cryptic inhabitants of hardgrounds; (2) replacement of encrusters on hardground surfaces by borers; and (3) an increase in the proportion of encrusters with exoskeletons. These trends may reflect the increasing influence of grazing predators.

Clasts of widely ranging size and derived from various sources (including broken-up hardgrounds, and exhumed concretions — 'hiatus concretions') frequently support encrusting biotas. While the surfaces of cobbles and pebbles in high energy environments may be very stressful habitats, cavities and vacated borings in these clasts can act as important refuges for encrusters. On the microscopic scale, the larvae of many encrusters preferentially settle in cracks and crevices (*rugophilic* behaviour).

Encrusters of *in situ* substrata may be found to exhibit orientated growth, e.g. the commissures of encrusting bivalves and brachiopods often point downslope, presumably allowing unwanted particles to be more easily expelled.

Competition, aggregation, succession, and disturbance

Living space is often a limiting resource which is actively competed for by organisms inhabiting hard substrata today. Even when free space appears to be present (as in most fossil assemblages), the chance juxtaposition of encrusters may cause interference competition. A great deal of research has been published on spatial competition among living encrusters (see Buss 1986), and there is much controversy about its influence on community composition relative to such factors as composition of the larval pool, disturbance, and predation. Encrusters compete for space by overgrowing the margins (lateral overgrowth) or settling on the surfaces (fouling) of other encrusters, by releasing toxic chemicals, or by prising competitors off the sub-

stratum. Settlement panel studies have shown a decrease in spatial competitive ability from ascidians to sponges, to bryozoans, to serpulids and barnacles. However, details of spatial interactions in specific communities can be very complex, and rarely is there a simple competitive hierarchy (i.e. species A overgrows B, and both A and B overgrow C, etc.). Overgrowth interactions between pairs of species can be *intransitive* (i.e. species A sometimes overgrows B, but sometimes B overgrows A), *reciprocal* overgrowth (Fig. 2C) may occur between individuals (i.e. individual A overgrows B along part of their contact, but B overgrows A elsewhere), and growth of both competitors may cease at their contact (*stand-off*). Such interactions are better expressed in the form of a competitive network. Overgrowth does not always result in mortality; colonial animals typically survive overgrowth of some of their zooids (Section 4.6), and overgrowth of exoskeletons may leave the feeding parts of some organisms free to function (*epizoism*).

Certain morphological features correlate with success in spatial competition. Sheet-like colonies and subcircular solitary encrusters have well defended margins and can often overgrow runner-like colonies and linear solitary encrusters. Other attributes which can aid overgrowth include large body size (especially thickness, increased by the frontal budding of zooids in some colonial encrusters), rapid growth rate, spinosity, and the ability to raise margins above the substratum or to redirect growth to encounter competitors 'head-on'. Many organisms strongly resist fouling of their surfaces by larvae, and may therefore pre-empt substratum space if they are able to recruit early and grow rapidly.

The study of spatial competition in fossil assemblages is hampered by time-averaging; determining whether the encrusters lived contemporaneously can be a major problem. Superimposition of individual A on individual B can mean either: A succeeded B in time and overgrew B's dead skeleton; or A competed successfully for space with B. Only when reciprocal overgrowth is observed (Fig. 2C), or competitor-induced modification of skeletal morphology can be inferred, is it possible to demonstrate that the individuals were contemporaneous. Nevertheless, spatial competition among ancient encrusters clearly did occur, both by lateral overgrowth and fouling (Fig. 2D), and was apparently very similar to that among modern encrusters, although often involving very different groups of organisms (see Taylor 1984). As in the Recent, sheet-

like colonies generally overgrew runner-like colonies.

Aggregation of conspecifics (Fig. 2F) is a common feature of encrusters (e.g. barnacles, spirorbid serpulids). The mechanisms by which aggregation is achieved vary and include selective settlement of larvae close to adult conspecifics (gregarious behaviour) and differential mortality of settlers. Among the demonstrated or suggested advantages of aggregation are greater probability of outbreeding, increased success in interspecific competition for space, and enhanced feeding ability.

Temporal changes in the composition of encrusting biotas on settlement panels have been widely investigated. Classic models of ecological succession which were developed for terrestrial vegetation view early colonizers as 'paving the way' for later colonizers by modifying the habitat. However, many encrusters inhibit later colonizers, and succession often depends more on the lifespans of individual species, with long-lived species replacing short-lived species through time, and also on their spatial competitive abilities. An initial increase in species diversity can be reversed in later stages if one or a few competitively dominant species are present. In some communities (e.g. cryptic coral reef habitats) there is an overall tendency for solitary species to be replaced by colonial encrusters, but in others (e.g. temperate shallow subtidal habitats) the reverse sequence is found. Of relevance to palaeobiological studies is the increasing proportion of non-fossilizable soft-bodied encrusters found during succession in a tropical cryptic community (Rasmussen & Brett 1985).

Disturbance can be an important factor in the development of encrusting communities. Agents of disturbance include grazing predators (especially echinoids), sediment scour, and overturning of substrata by currents and mobile animals. In general, disturbance 'arrests' succession by preventing superior spatial competitors from achieving dominance. Macroinvertebrate grazers, for example, allow grazer-resistant but competitively subordinate algae to flourish on some hard substrata. Osman (1977) found that rocks of intermediate size (1–10 dm²) supported the highest diversities of encrusters because they were disturbed by wave currents too often to prevent their domination by species of high competitive rank but too seldom to prevent their colonization by a large number of species.

An Ordovician cobble-dwelling biota of encrusters provides a good example of how succession

may have been affected by disturbance (Wilson 1985). Stabilized cobbles became dominated by the sheet-like bryozoan *Amplexopora*, which overgrew all other encrusters, whereas periodically disturbed cobbles developed high diversity assemblages because *Amplexopora* had insufficient time to overgrow the other encrusting species. Bioerosion as a form of disturbance is evident on many post-Palaeozoic substrata that are marked by the grazing traces of echinoids (*Gnathichnus*) and of gastropods and chitons (*Radulichnus*).

Future studies of fossil encrusters promise to progress beyond the description of individual assemblages to comparative studies of assemblages through time which may shed light both on long-term ecological changes, and on possible coevolution between competitors for substratum space.

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4.10 Reconstructing Ancient Plant Communities

A. C. SCOTT

Introduction

Terrestrial vegetation comprises a diversity of plant communities, the majority of which live in erosional rather than depositional areas. In addition, during the life cycles of the constituent plants, organs such as leaves and seeds are shed and may be transported, buried, and preserved far from the growth site. Different plant parts may behave in various ways during transport by wind or water, and decay rates may also vary, depending on their original plant chemical composition (Scott & Collinson 1983; Ferguson 1985) (Fig. 1). Consequently, the reconstruction of ancient plant communities from fossil assemblages is fraught with hazards. One major problem is a general lack of knowledge of whole plants; relatively few have been reconstructed in

total, combining roots, stems, leaves, and fertile organs.

There are several approaches to fossil plant ecology, both biological and geological. Detailed morphological and anatomical studies of plant fossils can yield ecologically significant data concerning form or life habit. For example, a thick cuticle may imply a xeromorphic (dry) habitat, while specialized cells in roots may indicate life in a waterlogged environment. Geological observations may distinguish *in situ* vegetation from drifted plant assemblages. In order to use this geological data, methods of qualitative and quantitative data collection should be carefully considered (Scott & Collinson 1983). The plants have undergone transport, deposition, and diagenesis before collection, and a series of interpretive steps must be taken

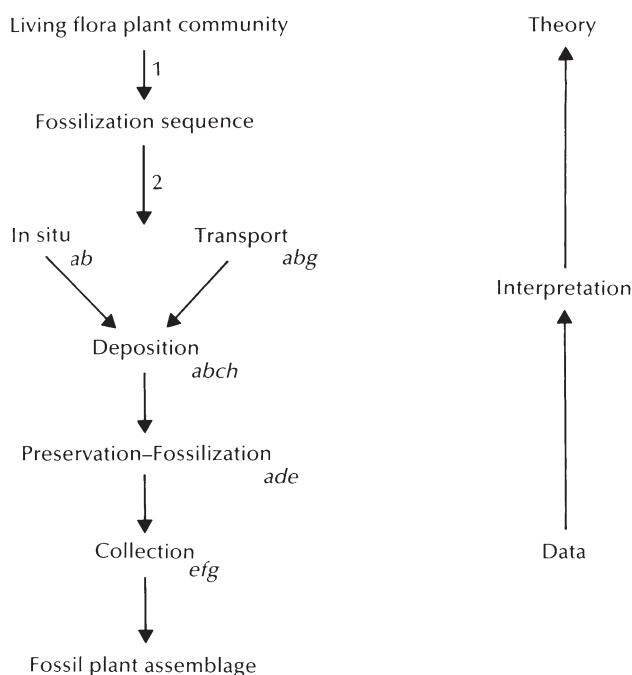


Fig. 1 Problems in relating fossil plant assemblages to contemporaneous plant communities. Initiators of the fossilization sequence (on some or all of the plants in a community): 1, internal factors, such as organ abscission, organ shedding, disease, and resistance of plant organ to decay. 2, external factors, such as animal destruction, storms, floods, land subsidence, climatic change, erosion, other natural catastrophies (e.g. forest fires), and proximity to site of transport. Key factors controlling fossil plant assemblages (affecting some or all of the plants in the fossilization sequence): destructive mechanisms, such as (a) decay, (b) mechanical break-up, (c) immediate post-depositional reworking, (d) diagenesis, (e) weathering, and (f) collecting bias; and interference, such as (g) sorting, and (h) additions from other communities. (From Scott 1977.)

before hypotheses of plant communities are formulated (Fig. 1).

In situ and drifted plant assemblages

Important data come from the study of *in situ* vegetation, but even here the plants preserved may be highly selected. Two types of *in situ* plant assemblages are generally encountered: fossil forests and peats (coals). Upright trunks occur widely both geographically and stratigraphically; well known examples include the Tertiary forests in Yellowstone National Park, U.S.A. and the Purbeck fossil forests in southern England. In both cases the trees comprise only trunks preserved as silica permineralizations or petrifications; leaves or reproductive

structures are not usually found attached, and generally only the bases of the trunks survive. Similarly, few non-arborescent plants are preserved; herbaceous forms are especially poorly represented because they decay quickly. More diverse assemblages are preserved in peats and coals but they represent specialized wetland floras (Broadhead 1986). Only a selection of the original plant community is preserved, because of selective decay during the peat-forming process. Only if permineralization (Section 3.10) took place early in peat formation is a more complete community preserved, e.g. the Rhynie Chert from the Lower Devonian of Scotland and Upper Carboniferous coal balls of Europe and North America. Studies of coal balls from several levels through coal seams have allowed the identification of numerous plant communities. Such data, together with considerations of reproductive structures (particularly of the lycopods) have generated hypotheses concerning the relative water table during peat formation.

The interpretation of drifted plant assemblages is even more difficult. Plants become incorporated into the sedimentary record in a variety of ways. Leaves, branches, and fertile organs may be naturally abscised or broken from the plant by storms or fire. These fragments may be carried by wind and if they reach water may be transported into a depositional environment. Most plant material decays before reaching water, or during transport. Of the original plant community, only a small number of species may survive and be represented by a restricted number of parts (Spicer 1989). Obviously plants living near water have a greater chance of being represented, but even then much depends on differential decay, e.g. conifer needles with thick cuticles survive transport and deposition more easily than herbaceous plants (such as grasses) which decay where they grow. The fossil record is very biased toward wetland plants, which are more resistant to decay. Many assemblages, however, represent plant litter incorporated into rapidly deposited sediment following storms and floods (Fig. 2).

Our interpretations of fossil plant assemblages have benefited much from taphonomic studies of Recent material, including studies on the modern analogues of ancient depositional settings, such as deltas and lakes (Spicer 1989; Scheihing & Pfefferkorn 1984; Collinson 1988). Plant assemblages found in various sedimentary settings have been compared to the surrounding vegetation. In addition, experimental studies of decay, break-up, transport, settling

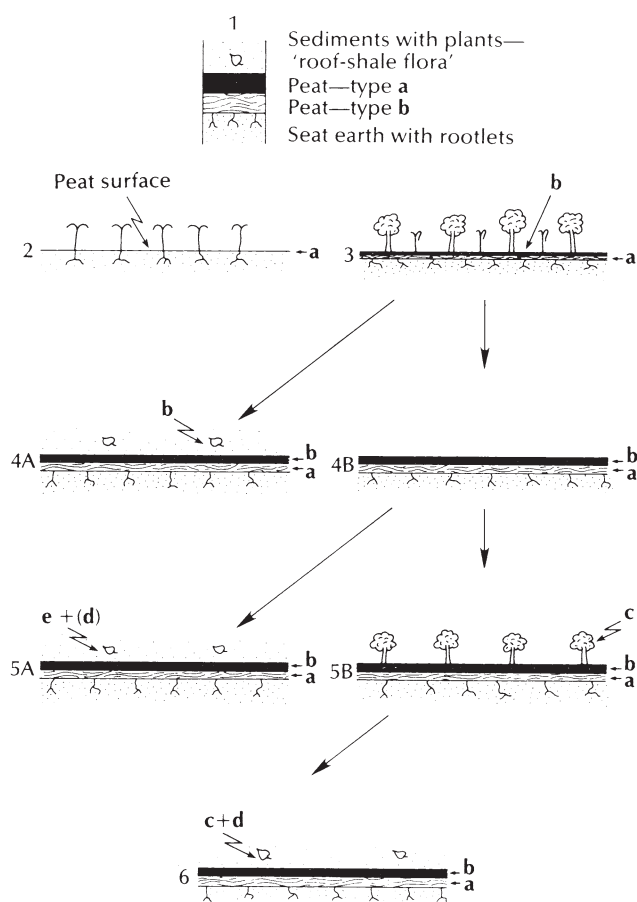


Fig. 2 Relationships of peat-forming floras to 'roof shale' floras. 1, A typical section showing peat (coal) of two types underlain by seat earth and overlain by sediment incorporating plants; alternative ways of forming such a sequence are illustrated in 2–6. 2, Colonization of sediment surface by peat-forming community *a*. Initial formation of seat earth (soil) and deposition of peat. 3, Vegetational succession with colonization by peat-forming community *b*, giving rise to a different peat type. 4A, Subsidence or rise in watertable over peat surface, thus halting plant growth; area flooded and sediment deposited, so incorporating plant fragments from peat-forming community *b*. 4B, Changing conditions cause peat formation to stop and plants of community *b* to die. 5A, Area now flooded and sediment deposited, resulting in incorporation of plant fragments derived from outside the area (from community *e* and possibly *d*). 5B, Peat surface colonized by plants of community *c* but conditions not good for peat formation. 6, Area flooded and sediment deposited, thereby not only incorporating plants from community *c* but also bringing in plant fragments from outside area (e.g. from community *d*). (After Scott & Collinson 1983.)

rates, and preservation have emphasized that only a small proportion of the original vegetation, derived from several sources, may become fossilized.

Much data may be obtained from the enclosing sediments. Facies studies aid interpretation of the depositional environment and provide data concerning the transport history. Identification of storm layers and of the mixing of plant material from different sources is important, but is often difficult to achieve. Layer by layer collecting and recording of plant material is of major value (Scott & Collinson 1983).

Even after burial there is potential for further alteration, with decay by bacteria and fungi continuing and causing further selection. However, when the organic material of the plant decays, an impression may be left. Early permineralization by pyrite, calcite, or silica may lead to anatomical preservation (Section 3.10). Compaction after burial may cause two originally separated plant organs to become closely associated. Equally, two successive layers of plant remains may have had quite different origins and histories (Fig. 2). Despite these problems there are several approaches to the study of fossil plant ecology, including field observations, laboratory, and experimental studies.

Field and laboratory data gathering

Data collection in the field is of prime importance. This may be quantitative (such as percentage cover or volume), semiquantitative, or qualitative (present/absent, common–abundant, etc.). The data may be handled in several different ways: presented purely in tabular form or, e.g., as histograms, or handled statistically using a variety of techniques (including principal component analysis, discriminant analysis, or correspondence analysis). Whatever collecting method is chosen, bed by bed recording is essential, as is the recording of detailed sedimentological data. The methods employed, such as the use of quadrats, will depend on the type of exposure and a consideration of what is to be achieved. Bulk collections are advisable. Interpretation of sedimentological data is equally important and may concern process, depositional environment, and transport history of the plants. Taphonomic studies are also necessary, including an analysis of size and the type of organ present, potential preservational bias, and the occurrence, for example, of charcoal (Scott & Collinson 1983; Broadhead 1986).

In the laboratory the methods used depend on the type of preservation. Where plant assemblages comprise mainly leaf compressions, simple splitting of the rock may suffice. Where abundant small

plant organs (such as fruits and seeds) occur, disaggregation of the sediment and sieving may be required. Where permineralizations occur (such as in limestones and other lithified rocks) beds must be cut into slabs and peeled. Comparing data from these three types of deposit can be difficult. Experimental studies of transport (involving a flume) or compression can yield data significant for the interpretation of the assemblage. Only when all these studies are complete should a vegetational reconstruction be attempted.

The ecology of ancient plant communities

Reconstruction of whole plants is a major problem and depends on finding connections between plant parts. Common associations may only reflect sedimentological criteria but, if anatomical features are also shared, may prove acceptable evidence. Many reconstructions of ancient vegetation contain poorly reconstructed plants based on unsatisfactory evidence (Collinson & Scott 1987). There are relatively few fully reconstructed plant species, although a general idea of what others looked like is known.

Reconstructing the ecology of ancient plant communities is difficult and opinions differ amongst specialists on how far it is possible to go. Vegetation has been reconstructed not only from *in situ* plant assemblages but also from fossil soils and drifted assemblages. Guiding principles must be: (1) collect accurate data; (2) interpret the data, knowing its limitations; and (3) finally produce a hypothesis concerning the plant communities. The acquisition of new data may, therefore, necessitate the development of new hypotheses.

In some cases (such as peats or coals), successive changes in vegetation can be established. Plant communities have often been used to interpret climatic regimes and both short- and long-term change in climate (Section 4.19.1). Changes in peat-forming vegetation in the Upper Carboniferous coals of North America appear to reflect long-term climatic cycles, such as a drying from the Westphalian to the Stephanian, and a change of dominant vegetation from arborescent lycopods to tree-ferns. Abrupt changes in plant communities, as occur at the Cretaceous–Tertiary Boundary, have been used to support the idea of catastrophic events. Major changes in plant communities through time may also reflect important evolutionary innovations and the ability of plants to inhabit new environments, e.g. the evolution of leaves, the tree habit,

and the seed (see also Sections 1.8.2, 1.10, 1.11; Collinson & Scott 1987).

Plant communities should not be considered in isolation. From the time of the earliest plant communities there is evidence of animal–plant interactions (Section 1.8.2). Most involved arthropods, at least until the Late Carboniferous when vertebrates first exploited plants as a major food source (Scott *et al.* 1985). From the Mesozoic and Tertiary comes diverse evidence for animal–plant interactions, the most significant being that between insects and flowering plants. This unique relationship and the development of diverse pollination vectors was one of the main reasons for the success of angiosperms (Section 1.10). Likewise there is a close link between the evolution of grasslands and vertebrate grazers in the Late Tertiary (Section 1.11; Friis *et al.* 1987).

Our knowledge of ancient plant communities is very limited but recent developments, especially in studies of plant taphonomy, will encourage rapid progress in this field.

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4.11 Trace Fossils

S. G. PEMBERTON, R. W. FREY & T. D. A. SAUNDERS

Trace fossils (or ichnofossils) are biologically produced sedimentary structures that include tracks, trails, burrows, borings, faecal pellets, and other traces made by organisms. Excluded are markings that do not reflect a behavioural function, such as those that result from the rolling or drifting of dead animals (Fig. 1). Owing to their nature, trace fossils can be considered as both palaeontological and sedimentological entities, thereby bridging the gap between the two main subdisciplines in sedimentary geology. Recent summaries dealing with general ichnological principles can be found in publications by Frey (1975), Frey & Seilacher (1980), Ekdale *et al.* (1984), and Frey & Pemberton (1984, 1985).

Classification of trace fossils

Unique classification schemes have been developed in order to decipher trace fossils because they represent behaviour rather than actual body remains. Historically, trace fossils have been classified in descriptive, preservational, taxonomic, and behavioural terms. Of these, the behavioural (or ethological) scheme is by far the most important; the behavioural record of benthic organisms is dictated and modified by prevailing environmental parameters.

Ekdale *et al.* (1984) recognized seven basic categories of behaviour: resting traces (*cubichnia*), locomotion traces (*repichnia*), dwelling structures

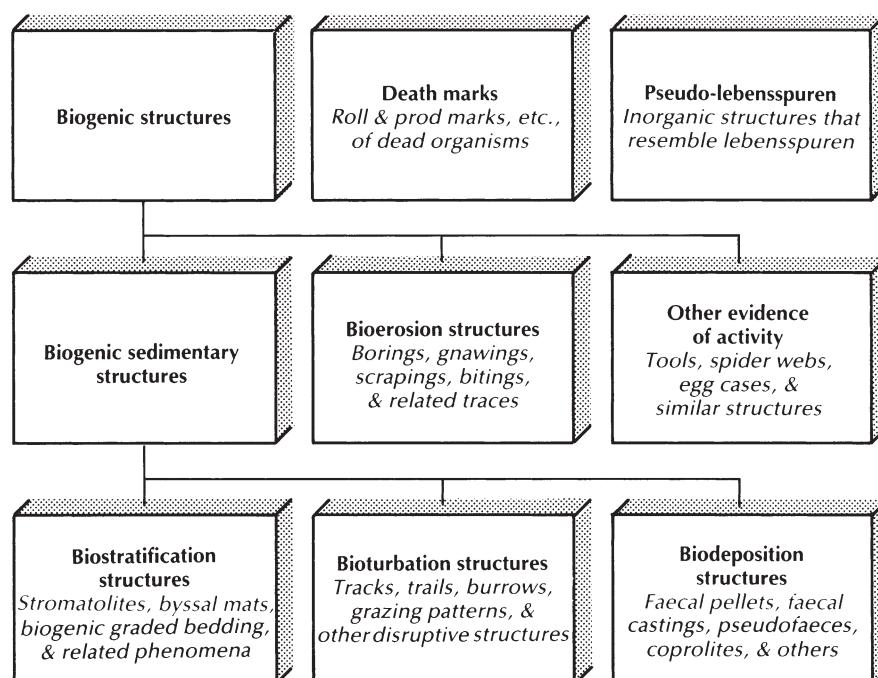


Fig. 1 Major relationships among biogenic structures. Trace fossils *sensu stricto* include only those structures which: (1) reflect behaviour by live organisms; and (2) correspond somehow to the anatomy of the tracemaker. Thus excluded are biostratification structures, as well as 'death marks' and 'pseudo-lebensspuren'. (After Frey & Pemberton 1984, by permission from the Geological Association of Canada; Frey & Pemberton 1985.)

(*domichnia*), grazing traces (*pascichnia*), feeding burrows (*fodinichnia*), farming systems (*agricchnia*), and escape traces (*fugichnia*). Such fundamental behavioural patterns, although genetically controlled, are not phylogenetically restricted. These basic ethological categories, for the most part, have persisted throughout the Phanerozoic. Individual tracemakers have evolved but basic behaviour essentially has not. For example, deposit feeders are preadapted to quiescent environments where deposited foodstuffs are most abundant, therefore they do not fare well in turbulent-water settings. The opposite is true of suspension feeders. Similarly, locomotion traces can be preserved only under a strict set of environmental conditions. This ability to discern behavioural trends of benthic organisms represented in the rock record greatly facilitates environmental interpretations.

The conceptual framework of ichnology

The importance of ichnology to the fields of stratigraphy, palaeontology, and sedimentology stems from the following characteristics displayed by trace fossils: (1) *long temporal range* — which facilitates palaeontological comparisons of rocks differing in age; (2) *narrow facies range* — which reflects similar responses by organisms to given sets of palaeoecological parameters; (3) *no secondary displacement* — trace fossils generally cannot be transported or reworked; (4) *occurrence in otherwise unfossiliferous rocks* — trace fossils are generally enhanced by diagenetic processes that destroy body fossils; and (5) *creation by non-preserved soft-bodied biota* — many ichnofossils represent organisms that generally are not preserved because they lack hard parts; such organisms, in many environments, represent the greatest biomass.

Significance of ichnology

Whether on local or regional scales, trace fossils are potentially capable of yielding substantial amounts of palaeontological, palaeoecological, and sedimentological information (Table 1). In general terms, the more significant kinds of information that can be gleaned from the ichnofauna include: (1) diversity, activity patterns, and the fossil record of 'non-preserved' organisms; (2) spatial correlation and structural attitude of 'unfossiliferous rocks'; (3) production, alteration, and consolidation of sediment textures and fabrics; (4) facies and facies sequences; and (5) such intangibles as bathymetry (Section

4.19.5), rates of deposition and erosion, oxygen levels (Section 4.19.4), salinity (Section 4.19.3), and substrate coherence and stability (Frey & Seilacher, 1980).

The ichnofacies concept

Perhaps the essence of trace fossil research involves the grouping of characteristic ichnofossils into recurring ichnofacies. This concept, developed by Adolf Seilacher in the nineteen-fifties and nineteen-sixties, was based originally on the fact that many of the parameters that control the distribution of tracemakers tend to change progressively with increased water depth (Section 4.19.5). Nine recurring ichnofacies have been recognized, each named for a representative ichnogenus (Fig. 2): *Scoyenia*, *Trypanites*, *Teredolites*, *Glossifungites*, *Psilonichnus*, *Skolithos*, *Cruziana*, *Zoophycos*, and *Nereites*. These trace fossil associations reflect adaptations of tracemaking organisms to numerous environmental factors such as substrate consistency, food supply, hydrodynamic energy level, salinity, and oxygen levels (Frey & Pemberton 1984). The traces in the non-marine assemblage (*Scoyenia*) are general and in need of revision; the marine softground ichnofacies (*Psilonichnus*, *Skolithos*, *Cruziana*, *Zoophycos*, and *Nereites*) are distributed according to numerous environmental parameters; the traces in the firmground (*Glossifungites*), wood-ground (*Teredolites*), and hardground (*Trypanites*) ichnofacies are distributed on the basis of substrate type and consistency.

Representative occurrences of the various ichnofacies are summarized below. However, each may appear in other settings, as dictated by characteristic sets of recurrent environmental parameters. From the standpoint of ecological requirements of trace-making organisms, for example, certain intertidal backbarrier environments are not all that different from certain subtidal forebarrier environments and may contain virtually identical suites of lebensspuren.

The *Scoyenia* ichnofacies (Fig. 3) is a very generalized association of trace fossils, found typically in continental red beds. However, prospects for the recognition of additional non-marine ichnofacies remain encouraging. For example, Ekdale *et al.* (1984) and Frey & Pemberton (1987) noted that distinct suites of trace fossils characterize aeolian dunes, fluvial overbank, palaeosol, and lake environments.

The *Psilonichnus* ichnofacies (Fig. 4) is associated

Table 1 Major contributions of ichnology to sedimentary geology. Relative importance (indicated by number of Xs) refers to the relative worth of that information in contemporary sedimentary geology. (After Frey & Seilacher 1980.)

Disciplines and components	Geological setting	
	Modern	Ancient
1 Palaeontology		
(a) Fossil record of soft bodied animals	X	XXX
(b) Patterns of activity by benthic organisms	XX	XXX
(c) Diversity of fossil assemblages	XX	XX
(d) Evolution of metazoans and of behaviour	X	XXX
2 Stratigraphy		
(a) Biostratigraphy of 'unfossiliferous' rocks	—	XX
(b) Correlation by marker beds	—	X
(c) Structural attitude of beds	—	X
(d) Structural deformation of sediments	—	X
3 Sedimentology		
(a) Production of sediment by boring organisms	XX	—
(b) Consolidation of sediment by suspension feeders	XX	X
(c) Alteration of grains by sediment-ingesting animals	X	—
(d) Sediment reworking		
(i) Destruction of initial fabrics and sedimentary structures	X	XXX
(ii) Construction of new fabrics and sedimentary structures	X	XXX
4 Depositional environments and palaeoecology		
(a) Specific adaptations and behaviour of individual genera or species of organisms	XXX	X
(b) Facies and facies successions	X	XXX
(c) Bathymetry	X	XXX
(d) Temperature and salinity	X	XX
(e) Depositional history		
(i) Rates of deposition	X	XX
(ii) Amounts of sediment deposited or eroded	X	XX
(f) Aeration of water and sediments	XX	XX
(g) Substrate coherence and stability	X	XX
(h) Current direction	X	X
5 Consolidation of sediments		
(a) Initial history of lithification	—	XX
(b) Measures of compaction	—	X
(c) Early diagenesis	—	XX
(d) Secondary mineralization	—	XX

with supralittoral–upper littoral, moderate–low energy marine and/or aeolian conditions typically found in beach to backshore to dune environments. The trace fossils are characterized by: (1) vertical shafts, ranging from small structures, some with bulbous basal cells, to larger, irregularly J-, Y-, or U-shaped dwelling structures; (2) invertebrate and vertebrate crawling and foraging traces; (3) vertebrate tracks and coprolites; (4) low density and diversity; (5) invertebrates — mostly predators or scavengers; and (6) vertebrates — mostly predators or herbivores.

The *Skolithos* ichnofacies (Fig. 5) is generally associated with high energy, sandy, shallow-marine environments. The trace fossils are characterized by: (1) predominantly vertical, cylindrical and U-shaped burrows; (2) few horizontal structures; (3) few structures produced by mobile organisms; (4) low diversity, although individual forms may be abundant; and (5) mostly dwelling burrows constructed by suspension feeders.

The *Cruziana* ichnofacies (Fig. 6) usually is associated with infralittoral–shallow circalittoral marine substrates below fairweather wave base and

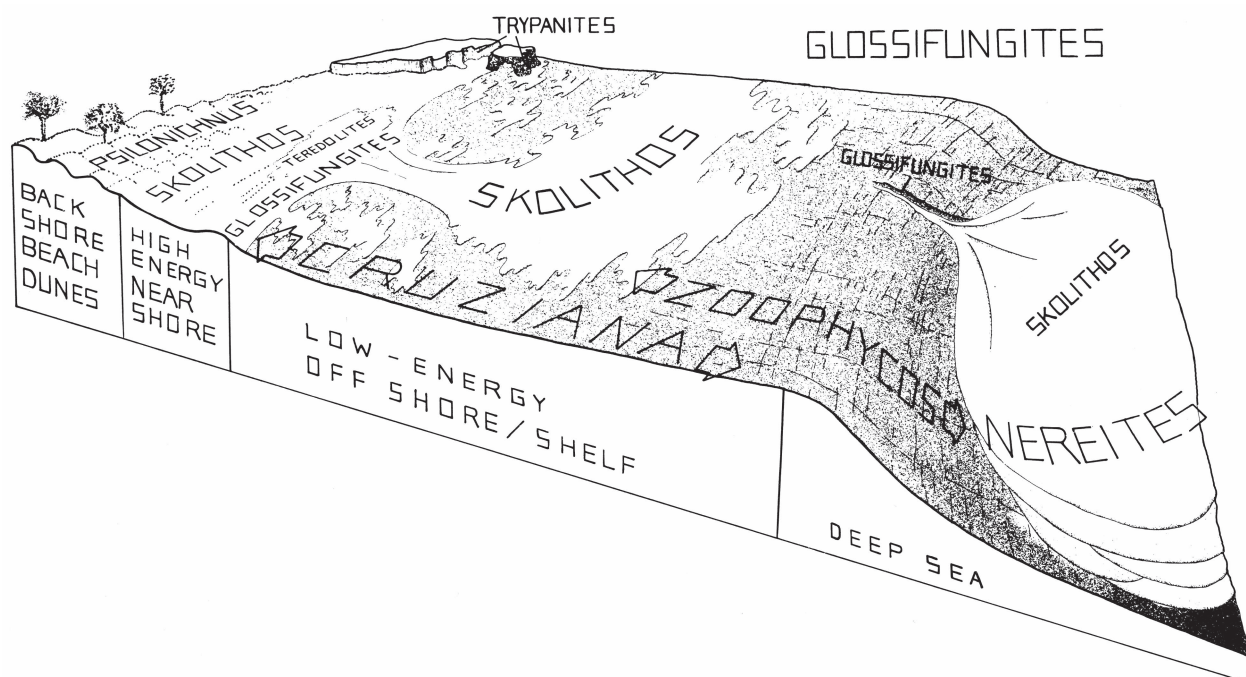


Fig. 2 Schematic diagram illustrating the general distribution of the nine recurring ichnofacies. The softground ichnofacies are generally distributed according to numerous ecological parameters which may be replicated in more than one environmental setting. For instance, the *Skolithos* ichnofacies is found not only in shallow, high energy substrates but also in offshore storm sands and submarine fans. Of the remaining ichnofacies three are substrate controlled, with the *Trypanites* ichnofacies in fully lithified substrates, the *Glossifungites* ichnofacies in semi-consolidated substrates, and the *Teredolites* ichnofacies in xylic substrates. These suites will occur wherever the requisite substrate is found; for example, the *Glossifungites* ichnofacies can be associated with exhumed muds in the shoreface or along the sides of submarine canyons.

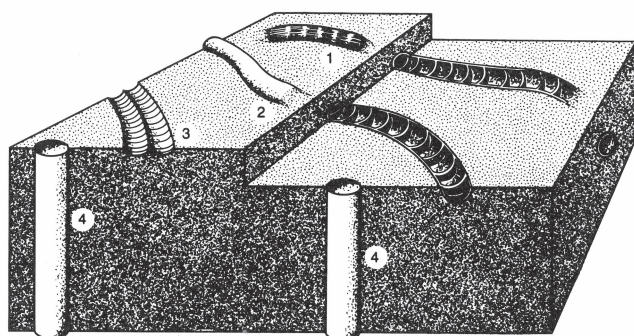


Fig. 3 Trace fossil association considered to be indicative of the *Scoyenia* ichnofacies *sensu stricto*. 1 = *Scoyenia*, 2 = *Ancorichnus*, 3 = *Cruziana*, including the '*Isopodichnus*' of various authors, 4 = *Skolithos*. (After Frey & Pemberton 1984, by permission from the Geological Association of Canada.)

above storm wave base. The trace fossils are characterized by: (1) a mixed association of vertical, inclined, and horizontal structures; (2) presence of traces constructed by mobile organisms; (3) generally high diversity and abundance; and (4) mostly feeding and grazing structures constructed by deposit feeders.

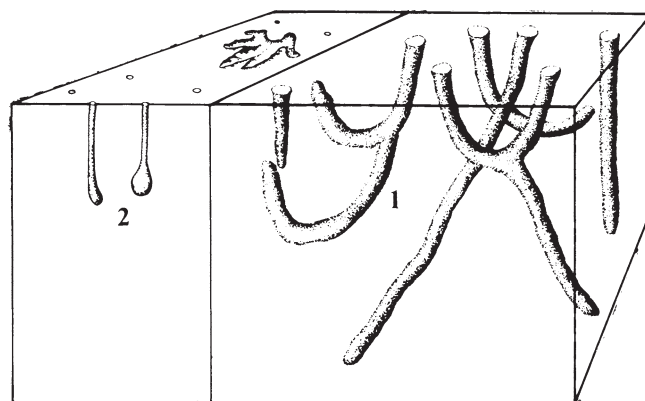


Fig. 4 Trace fossil association characteristic of the *Pylonichnus* ichnofacies. 1 = *Pylonichnus*, 2 = *Macanopsis*.

The *Zoophycos* ichnofacies (Fig. 7) ideally is found in circalittoral–bathyal, quiet-water marine muds or muddy sands; below storm wave base to fairly deep water; in areas free of turbidity flows and subject to oxygen deficiencies. The trace fossils are characterized by: (1) low diversity, but individual traces may be abundant; (2) grazing and feeding

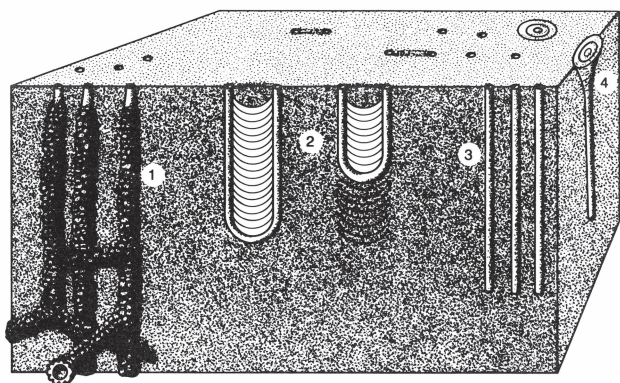


Fig. 5 Trace fossil association characteristic of the *Skolithos* ichnofacies. 1 = *Ophiomorpha*, 2 = *Diplocraterion*, 3 = *Skolithos*, 4 = *Monocraterion*. (After Frey & Pemberton 1984, by permission from the Geological Association of Canada.)

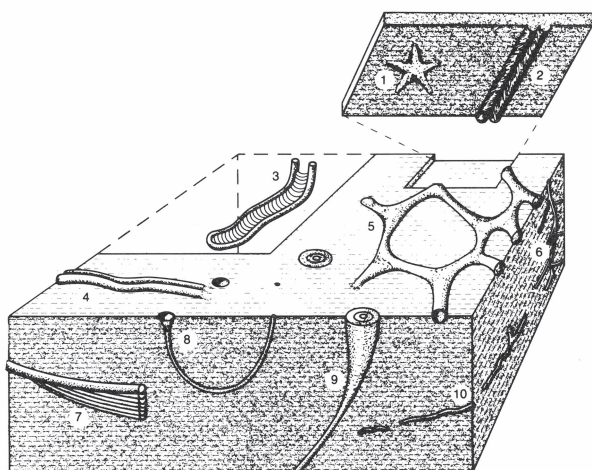


Fig. 6 Diverse trace fossil association characteristic of the *Cruziana* ichnofacies. 1 = *Asteriacites*, 2 = *Cruziana*, 3 = *Rhizocorallium*, 4 = *Aulichnites*, 5 = *Thalassinoides*, 6 = *Chondrites*, 7 = *Teichichnus*, 8 = *Arenicolites*, 9 = *Rosselia*, 10 = *Planolites*. (After Frey & Pemberton 1984, by permission from the Geological Association of Canada.)

structures produced by deposit feeders; and (3) horizontal to gently inclined spreiten structures.

The *Nereites* ichnofacies (Fig. 8) typically is associated with bathyal–abyssal, low energy, oxygenated marine environments subject to periodic turbidity flows. The trace fossils are characterized by: (1) high diversity but low abundance; (2) complex horizontal grazing traces and patterned feeding-dwelling structures; (3) numerous crawling-grazing traces and sinuous faecal castings; and (4) structures produced by deposit feeders, scavengers, or harvesters.

The remaining three ichnofacies are specialized, substrate-controlled and, environmentally, very

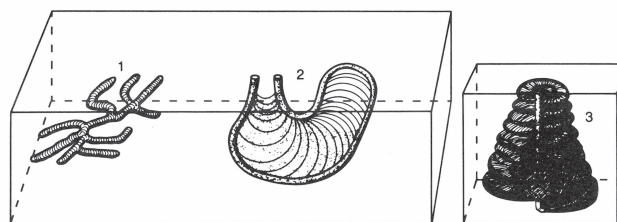


Fig. 7 Restricted trace fossil association characteristic of the *Zoophycos* ichnofacies. 1 = *Phycosiphon*, 2 = *Zoophycos*, 3 = *Spirophyton*.

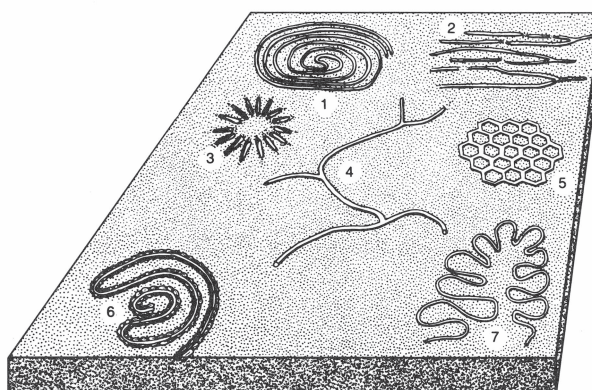


Fig. 8 Trace fossil association characteristic of the *Nereites* ichnofacies. 1 = *Spirorhaphe*, 2 = *Urohelminthoida*, 3 = *Lorenzina*, 4 = *Megagraption*, 5 = *Paleodictyon*, 6 = *Nereites*, 7 = *Cosmorhophe*. (After Frey & Pemberton 1984, by permission from the Geological Association of Canada.)

general in scope. The *Glossifungites* ichnofacies (Fig. 9) develops in firm but unlithified substrates (i.e. dewatered muds). Such substrates can dewater as a result of burial and are made available to trace-makers if exhumed by later erosion. Exhumation can occur in shallow-water environments as a result of coastal erosion processes or from submarine channels cutting through previously deposited sediments. Such horizons may be critical in the evolving concept of *sequence stratigraphy*.

The *Trypanites* ichnofacies (Fig. 10) characterizes fully lithified marine substrates such as hardgrounds, reefs, rocky coasts, unconformities, and other kinds of omission surfaces. The *Teredolites* ichnofacies (Fig. 11), on the other hand, encompasses a characteristic assemblage of borings in marine xylic (woody) substrates. These differ from lithic substrates in three main ways: (1) they may be flexible instead of rigid; (2) they are composed of combustible material instead of mineral matter; and (3) they are readily biodegradable. Such differences indicate that the means by which, as well as the reason for which, these two types of substrates are

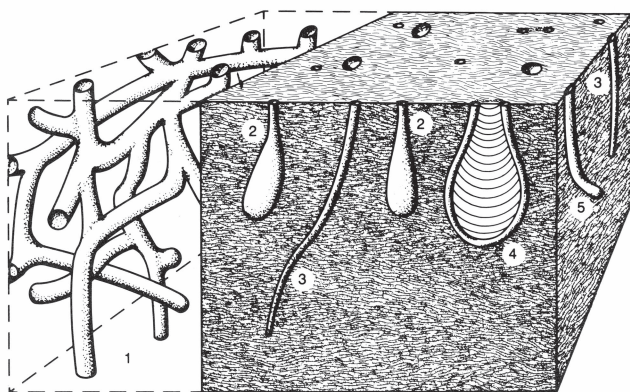


Fig. 9 Trace fossil association characteristic of the *Glossifungites* ichnofacies. 1 = *Thalassinoides* or *Spongeliomorpha*, 2 = *Gastrochaenolites*, 3 = *Skolithos*, 4 = *Diplocraterion*, 5 = *Psilonichnus*. (After Frey & Pemberton 1984, by permission from the Geological Association of Canada.)

penetrated are different. Again, such assemblages will be of considerable importance in defining sequence and parasequence boundaries.

Palaeobiological implications

Trace fossils record the activities of benthic organisms, many of which are soft-bodied and are not readily preserved. This 'less preservable group' includes entire phyla (such as the nemerteans, nematodes, nematomorphs, annelids, sipunculans, echiurans, pogonophores, priapulans, phoronids, and enteropneusts) or classes (i.e. anthozoans, aplacophorans, holothuroids, and demosponges). Many of these lineages are diverse (i.e. at present there are 18 000 extant species of annelids, 15 000 species of nematodes, 900 species of nemerteans, and 320 species of sipunculans) and many are known to have originated at the start of the Phanerozoic. For example, annelids, echiurans, pogonophores, priapulans, phoronids, and enteropneusts are known from deposits as old as Cambrian. Traditionally, however, palaeontologists have relegated such groups to 'minor phyla' status and have ignored them in: (1) the analysis of diversity trends through time (Sections 1.6, 2.7); (2) the taphonomic implications of the 'incomplete fossil record' (Section 3.12); (3) the evolution of infaunal suspension and deposit feeders (Section 1.7.1); and (4) the interpretation of population strategies.

Although the phylogenetic relationships of trace fossils are difficult to establish, careful analysis of circumstantial evidence can yield convincing and important interpretations (Osgood *in* Frey 1975).

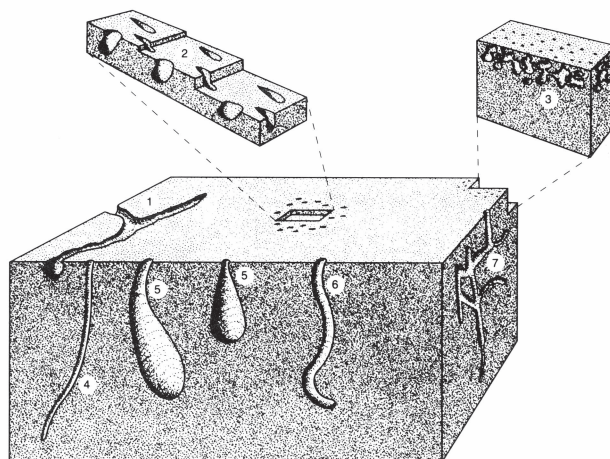


Fig. 10 Trace fossil association characteristic of the *Trypanites* ichnofacies. 1 = echinoid grooves, 2 = *Rogerella*, 3 = *Entobia*, 4 = *Trypanites*, 5 = *Gastrochaenolites*, 6 = *Trypanites*, 7 = polychaete boring. (After Frey & Pemberton 1984; by permission from the Geological Association of Canada.)

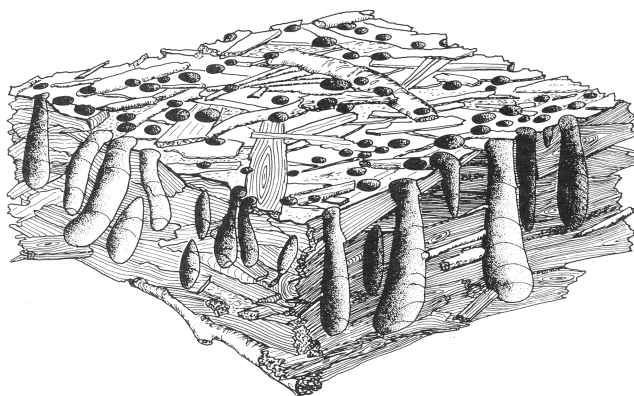


Fig. 11 Trace fossil association characteristic of the *Teredolites* ichnofacies, dominated by *Teredolites*. (After Bromley *et al.* in Miller *et al.* 1984.)

Palaeoecology and environmental reconstructions

The concept of functional morphology, a basic premise employed by ecologists and palaeoecologists in environmental reconstructions, is equally applicable to ichnology. In fact, ichnofossils are unique in that they represent not only the morphology and ethology of the tracemaking organism but also the physical characteristics of the substrate; they are closely linked to the environmental conditions prevailing at the time of their construction. Frey & Seilacher (1980) re-emphasized that such variables as bathymetry, temperature and

salinity (Section 4.19), rates of sediment deposition, amounts of sediment deposited or eroded, aeration of water and sediment, and substrate coherence and stability have a profound effect on resultant ichnofossil morphologies and hence can be used in the determination of original biological, ethological, and sedimentological conditions. Rhoads (*in* Frey 1975) stated that one of the most important variables controlling the distribution of bottom-dwelling organisms is the nature of the substratum, such as grain-size distribution, organic content, bottom compaction, and sedimentation rate. In lithified deposits, sediment grain size and organic content are directly observable; however, bottom hardness and sedimentation rate can best be approximated using trace fossils (Rhoads *in* Frey, 1975). Size or composition of sediment grains in many instances is less important than the geotechnical properties of the substrate. Details of the palaeoecological significance of trace fossils were summarized in publications by Frey (1975), Ekdale *et al.* (1984), Ekdale (1985), and Frey & Pemberton (1985).

The application of ichnology to palaeoenvironmental analysis goes far beyond the mere establishment of gross or archetypal ichnofacies. For instance, shallow-water, coastal marine environments comprise a multitude of sedimentological regimes, which are subject to large fluctuations in many physical parameters. In order to fully comprehend the depositional history of such zones in the rock record, it is imperative to have some reliable means of differentiating subtle changes in these physical characteristics. Detailed investigations of many of these coastal marine zones in Georgia have shown the value of utilizing biogenic sedimentary structures (in concert with physical sedimentary structures) in delineating them (Frey & Pemberton 1987). The application of these studies in deciphering palaeoenvironments has also proved significant (Miller *et al.* 1984; Curran 1985).

Similarly, the use of ichnofossils in the interpretation of freshwater deposits is becoming increasingly important. Reviews by Chamberlain (*in* Frey 1975) and Ekdale *et al.* (1984) stressed the abundance and diversity of tracemaking organisms in freshwater environments and emphasized their potential importance in palaeoenvironmental reconstructions. Distinct differences in ichnofossil types and abundance have been reported from a wide range of freshwater–terrestrial environments, in both ancient and recent settings (Ekdale *et al.* 1984).

Recently, marginal marine environments (including tidal channels, estuaries, bays, shallow lagoons,

and delta plains) have been recognized with more frequency in the rock record. Such environments characteristically display steep salinity gradients which, when combined with corresponding changes in temperature, turbulence, and oxygen content, result in a physiologically stressful environment for numerous groups of organisms. The typical trace fossil suite in such environments reflects these stresses and is characterized by: (1) low diversity; (2) ichnotaxa which represent an impoverished marine assemblage rather than a true mixture of marine and freshwater forms; (3) a dominance of morphologically simple structures constructed by trophic generalists; and (4) a mixture of elements which are common to both the *Skolithos* and *Cruziana* ichnofacies.

One of ichnology's greatest strengths, the bridging of sedimentology and palaeontology, in some ways can be its greatest liability. Sedimentologists tend to use a strict uniformitarian approach to palaeoenvironmental interpretation and rely heavily on modern analogues. Palaeontologists, on the other hand, must temper their observations in the light of organic evolution. Although trace fossils can be considered as biogenic sedimentary structures and are difficult to classify phylogenetically, they are constructed by biological entities and are thus subjected to evolutionary trends. For example, occurrences of well developed terrestrial trace fossil assemblages are much more prevalent in post-Palaeocene rocks. This development corresponds to the evolutionary explosion of the insects brought on by the diversification of the angiosperms in the Late Cretaceous (Section 1.10). Prior to this time terrestrial substrates may not have been as extensively bioturbated due to a paucity of tracemakers. Likewise, patterned grazing traces, which characterize deep-sea sediments, show a trend toward fuller organization through most of the Phanerozoic. This trend may be related to the evolution of more efficient foraging strategies (Frey & Seilacher 1980). For these reasons, palaeoenvironmental interpretations based on trace fossils must be considered not in strict uniformitarian terms, but rather, in actualistic ones.

Equally important, unique, quantitative environmental indicators are indeed rare in the geological record, and ichnology is no exception (Frey & Seilacher 1980). However, trace fossils can supply a wealth of environmental information that cannot be obtained in any other way and which should not be ignored. Their potential usefulness is accentuated when fully integrated with other (chemical, physi-

cal, and ethological) lines of evidence. Combined studies of physical and biogenic sedimentary structures constitute a powerful approach to facies analysis.

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4.12 Evidence for Diet

J. E. POLLARD

Introduction

The diet of ancient organisms may be deduced from a variety of direct and indirect evidence from body fossils and trace fossils. Direct evidence comes from the discovery of ingested prey in a predator's skeleton and the analysis of gut contents or coprolites (fossil faeces). Regurgitates or rejected prey with bite marks indicating predation, or trace fossils reflecting grazing, rasping, or highly patterned feeding activity, are major categories of indirect evidence. More generalized information on diet may be derived from functional analysis of specialized feeding organs, such as appendages in arthropods, radulae in gastropods or cephalopods, and teeth and jaws in vertebrates. Such structures are usually interpreted by analogy with living animals, e.g. the use of modern dental analogues to deduce the diet of fossil mammals.

Feeding habits — general type of diet

Many fossil invertebrates show adaptation of their

hard parts to specialized feeding — either as primary consumers of suspended or benthic detritus, or as carnivores (usually predators; see also Section 4.13). Arthropods lacking grasping or feeding appendages, such as trilobites, are interpreted as detritus feeders, producing the furrow feeding traces *Cruziana*. However, some trilobites, like *Olenoides* in the Cambrian Burgess Shale, may have used leg spines to tear soft-bodied prey. Carnivorous arthropods frequently possess specialized grasping, tearing, or crushing appendages, whether active predators like *Sidneyia* from the Burgess Shale (Conway Morris 1986) or scavenging decapod crustaceans, probably crabs, which cut open body chambers of eleganticeratid ammonites as they lay on their sides on the Jurassic sea floor (Lehmann 1981). The gastropod radula has been used by pateliform types in algal grazing on hard substrates at least since the Cretaceous, and by carnivorous forms to bore into bivalve shells (Bishop 1975).

Most vertebrates have toothed jaws. The shape of the tooth is closely related to its function or to the type of food it must prepare for digestion. In general

terms, piercing teeth are cone shaped; shearing or cutting teeth are long and blade like; crushing teeth are low, flat and button shaped; grinding teeth often have complex cusping patterns and a continuous growth or replacement mechanism. The arrangement of teeth types in the jaw is also an indication of diet.

Although correlation of dentition and diet is best known among mammals, it also provides major insights into the feeding habits and diet of fossil sharks and marine and terrestrial reptiles of the Late Palaeozoic and Mesozoic eras. Nectic hunting sharks (e.g. *Carcharodon megalodon*, Miocene) possess the familiar triangular sharks' tooth, while benthic sharks and rays (e.g. *Ptychodus*, Cretaceous) feeding on shelled invertebrates have button-shaped crushing teeth. Marine reptiles have diverse specialized dentitions which can sometimes be related to diet, as indicated by gastric contents or bite marks on prey. The placodonts of Permian seas were highly specialized predators on shelled invertebrates, with anterior chisel-like nipping teeth and flat crushing teeth in the rear of the jaws and on the palate (Fig. 1). Permian bivalves are known with crescentic chips removed from the edge of the shell, perhaps resulting from such predation (Bishop 1975). Selective diets among Jurassic ichthyosaurs are reflected by the piercing teeth in fish-eating forms and the loss of teeth in late Jurassic cephalopod eating ophthalmosaurs. These diets are confirmed by gastric contents (see below). Similar dietary preferences can also be recognized among Jurassic plesiosaurs; these predators retained their teeth, specializing as small headed, long necked fish-eating 'plesiosaurids' and large headed, short necked 'pliosaurids' which ate other marine reptiles and cephalopods (Norman 1985). These diets are confirmed by stomach contents, which usually contain gastroliths (stomach stones) to aid the digestive breakdown of prey. In the Late Cretaceous the marine predaceous mososaurs developed several dietary specializations: fish eaters can be recognized from stomach contents; cephalopod eaters even preyed on ammonites, as indicated by specimens of the Cretaceous *Pachydiscus* bitten up to 16 times (Bishop 1975); a probable shellfish eater (*Globidens*) possessed rather flattened placodont-like teeth.

Dinosaurs show a remarkable range of dietary specializations (Norman 1985). Carnivorous dinosaurs include coelurosaurs with small, sharply pointed teeth and weak jaw mechanics, ornithomimosaurs which lacked teeth, and large carnosaurs with tearing claws and serrated dagger-like teeth.

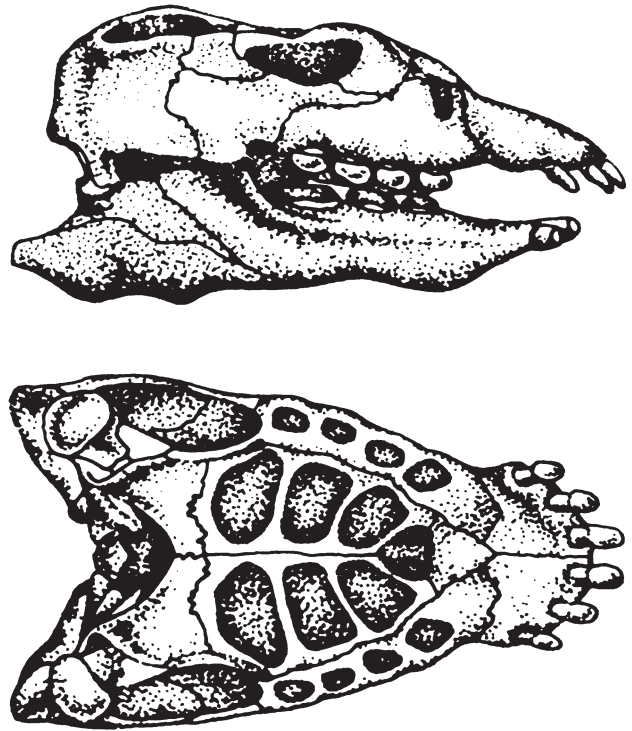


Fig. 1 Skull of a placodont reptile (*Placodus*) with anterior nipping teeth, and cheek and palatal crushing teeth, suggesting that the animal fed on shelled invertebrates, probably brachiopods or bivalves. Original skull about 0.25 m long. (After Bishop 1975.)

Stomach contents of coelurosaurs (*Coelophysus*, Triassic) show that some were cannibalistic on their own young, while others (e.g. *Compsognathus*, Jurassic of Solnhofen) were fast, agile hunters, preying on contemporary running ground lizards (*Bavarisaurus*). There has been considerable debate about the diet of the toothless ornithomimosaurs, including suggestions that they were insectivorous, shrimp eaters, frugivores, or omnivores. Bite marks preserved on large Jurassic sauropod vertebrae correspond with the size and spacing of the teeth of *Allosaurus*, a contemporary carnosaur. A fish-eating diet has been suggested for the carnivorous dinosaur *Baryonyx*, recently discovered in the Cretaceous rocks of Surrey, on account of its elongate jaws with numerous teeth and scales of *Lepidotes* preserved within the rib cage.

Dentition and jaw mechanisms indicate two distinct feeding habits among herbivorous dinosaurs. Those with unspecialized chisel or peg shaped teeth, such as sauropods, stegosaurs, and ankylosaurs, are believed to have simply stripped off vegetation, which was swallowed whole into a capacious stomach where it was pounded by gastroliths and

slowly digested, as shown by preserved stomach residues. Iguanodonts, hadrosaurs, and ceratopsian dinosaurs had a horny beak at the front of the mouth and a battery of grinding teeth at the rear. These teeth were continually replaced and, although the jaws were capable only of up and down movement, the tooth battery produced a very efficient oblique mill to grind up food prior to swallowing. Gastric contents of late Cretaceous 'mummified' hadrosaurs in western Canada contain conifer needles, twigs, and seeds, as well as angiosperm fragments, but lacked gastroliths. This supports the suggestion that these dominant Cretaceous herbivores had evolved a feeding mechanism capable of coping with a diet of tough conifers and angiosperms, rather than the softer vegetation of Bennettitales, cycads, or seed ferns exploited in the Jurassic sauropod-stegosaur type of feeding.

Ingestion—digestion of food — regurgitates and gastric residues

The most direct evidence for diet is where food remains are preserved within the body of the host before becoming unrecognizable through the digestive process. Such remains are often termed *pre-coprolite* and may be preserved as regurgitates, gut contents, gastric contents, or intestinal residues.

Regurgitates, which differ from gut contents in being preserved remote from the producer, and from coprolites in lacking a phosphatic matrix, are an important source of dietary information. Modern birds regurgitate pellets which are very distinctive as to producer and so to predator–prey relationships (Bishop 1975). Fossil regurgitates composed of bivalve shell debris (*Myalina*), probably produced by sharks, have been recognized in Carboniferous shales, and in Cretaceous carbonates composed of shell debris of *Inoceramus* (bivalve) or claws of the crustacean *Callianassa* (Bishop 1975). Regurgitates can be dispersed by currents during sedimentation and so may introduce an unrecognized bias into the fossil record.

In the Middle Cambrian Burgess Shale (Section 3.11.2), gut contents are known from several animals, both predators at the top of the food chain and some infaunal deposit feeders, the primary consumers. The predatory arthropod *Sidneyia* frequently has gut contents composed of ostracodes, small trilobites, hyolithids, and fragmented inarticulate brachiopods. Another predator on hyolithids and inarticulate brachiopods was the priapulid worm *Ottoia*, which swallowed its prey

whole and at times was cannibalistic. The annelid worm *Burgessochaeta* has gut contents of sediment, sometimes formed into faecal pellets, suggesting that it was an infaunal deposit feeder. This evidence of diet from gastric contents and its correlation with functional morphology (see above) has enabled the trophic web of the Burgess Shale community to be reconstructed in considerable detail (Conway Morris 1986; Section 4.16).

Gut contents are also important in the analysis of plant–arthropod relationships in Carboniferous coal swamps. Specimens of the large myriapod *Arthropleura armata* with gut contents of lycopod wood, and of an early insect with abundant spores in the gut, demonstrate the development of a phytophagous diet among arthropods by the Late Carboniferous. This is further supported by coprolites from coal balls (see below).

Several Jurassic Lagerstätten in Europe preserve gastric residues which shed light on the diets of ammonites. Liassic ammonites *Arnioceras* and *Hildoceras* are preserved with gastric remains of foraminifera, ostracods, and the jaws of juvenile ammonites in their body chambers. A specimen of *Physoderoceras* has gastric contents composed of arm and calyx fragments of the free swimming crinoid *Saccocoma*, which is also a major component of the coprolite *Lumbricaria* from the contemporaneous Solnhofen Limestone (Section 3.11.7). Such evidence suggested to Lehmann (1981) that ammonites may have been benthic scavengers rather than active predators.

Several predatory fish have been fossilized with their prey only partly swallowed, e.g. *Caturus* in the Solnhofen Limestone (Jurassic) and a perch (*Mioplosus*) partly ingesting a herring (*Knightia*) from the Eocene Green River Formation of Wyoming (see p. 305; Bishop 1975).

Occasionally, gastric contents are sufficiently well preserved to enable detailed analyses of diet, feeding habits, and the trophic web among the vertebrate fauna to be established. A hybodont shark from the Jurassic Posidonia Shale of Holzmaden, West Germany (Section 3.11.6), has a mass of over 100 belemnite rostra preserved between its pectoral fins (Fig. 2). Ichthyosaurs from the same formation mostly have dibranchiate cephalopod hooklets in their stomach contents, although fish remains (*Dapedius*, *Leptolepis*, *Ptycholepis*, and *Pachycomus*) also occur and a complex food web has been established. Lower Liassic shales at Lyme Regis have also produced some remarkable specimens. One young ichthyosaur found in the nineteen-sixties

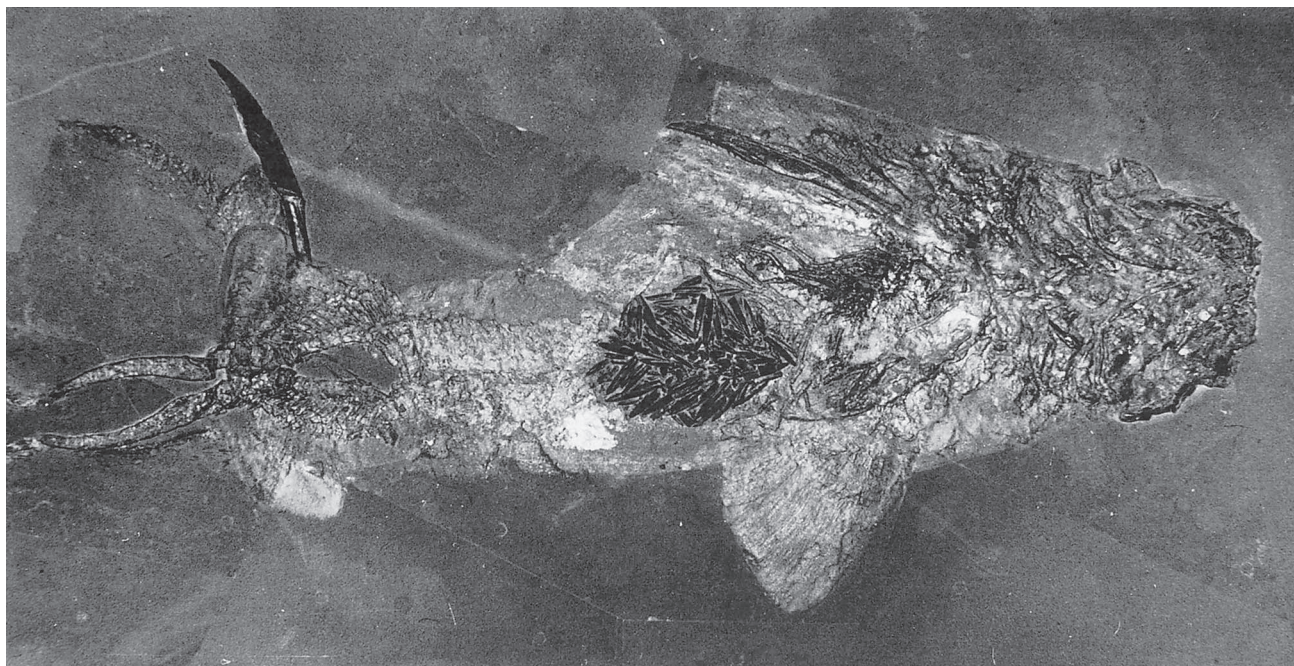


Fig. 2 Dorso-ventrally compressed skeleton and body outline of hybodont shark *Hybodus* with gastric residue of many belemnite rostra preserved between its pectoral fins. Posidonia Shales, Lower Jurassic; Holzmaden, West Germany. Original specimen about 2 m long. (From Stuttgart Museum für Naturkunde.)

has a gastric mass of cephalopod hooklets (estimated at $478\,000 \pm 53\%$) representing a consumption of between 760 and 2430 individual cephalopods (Pollard 1968). This estimate compares closely with the remains of between 2000 and 14 000 squids recovered from the stomachs of recent sperm whales (Pollard 1968). Although these cephalopod hooklets appear to belong to belemnites, the rostra are absent, unlike in the hybodont shark from Holzmaden (Fig. 2). It appears that only the head and arms of these belemnites were swallowed after the body with rostrum had been bitten off and regurgitated.

The Eocene oil shale deposit of Grube Messel, West Germany (Section 3.11.8) has yielded some remarkable stomach contents of mammals, including bats and early horses. The bats fed on nocturnal Lepidoptera and therefore suggest that these aerial predators had developed an ultrasonic location system as far back as Eocene times. The early horse *Palaeotherium* has gastric contents of leaves and fruit, proving that it browsed on forest vegetation (as inferred from dentition 70 years ago), and thus had quite a different diet from more recent grass eating horses. Pollen analyses of the gastric contents of late Pleistocene Siberian mammoths show that they fed mostly on grass. The state of ripeness of the

grass seeds indicate that the mammoths usually died at the beginning of the summer. The complete pollen spectra from these gastric contents show that they inhabited steppes and open tundra with a warmer climate than Siberia today.

Defecated food remains — faecal pellets and coprolites

Careful analysis of size and form, macroscopic contents, microfauna and microflora, mineralogy, and geochemistry of coprolites has provided dietary information on organisms ranging from Palaeozoic terrestrial invertebrates to prehistoric man.

Faecal material produced by invertebrates is usually in the form of discrete pellets (microcoprolites) or more rarely strings, representing unbroken discharge. Faecal pellets vary greatly in size, form, composition, and nature of the invertebrate producer (see Moore in Häntzschel *et al.* 1968), but two broad categories are of particular interest in the fossil record: those of early terrestrial herbivores and marine substrate feeders. Burrows in a late Ordovician palaeosol in Pennsylvania are packed with ferruginous faecal pellets believed to have been produced by the earliest known terrestrial

arthropods. Coprolites from the Upper Carboniferous shales and coal-balls contain lycopod cuticle remains and spores. Distinct size groupings of these coprolites suggest that they were possibly produced by soil mites (30–60 μm), Collembola (100–700 μm) and millipedes (greater than 1 mm). Borings in Pennsylvanian fern stems or cordaitan wood are packed with coprolites, while coprolites containing undigested fragments of leaf cuticle have been found associated with *Glossopteris* leaves with insect eaten edges in Carbo-Permian deposits in India. Such coprolite evidence suggests that detritus feeding soil arthropods existed as early as the Late Ordovician, and that diverse feeding mechanisms and diets had developed among phytophagous arthropods by Late Palaeozoic times.

Faecal pellets produced by substrate feeding invertebrates frequently have distinctive shapes or occur in association with particular burrows or trails. Strings of sausage-like faecal pellets, *Tomaculum*, are common in both Ordovician and Westphalian marine shales; in Mesozoic carbonate sediments, burrows like *Rhizocorallium* (Muschelkalk, Triassic) or *Thalassinoides* (Great Oolite, Jurassic) are frequently stuffed with pellets. The faecal pellets in thalassinoid systems are often the distinctive form *Favreina* with ten internal, crescent-shaped longitudinal canals, and were probably produced by deposit feeding shrimps like *Eryon* or *Glyphaea*, which inhabited the burrow systems.

Most vertebrate coprolites are composed of calcium phosphate or more rarely organic matter, and are frequently replaced by siderite, limonite, or silica during diagenesis (Häntzschel *et al.* 1968). They were produced predominantly by carnivorous predators, but the great variety of size and shape (and an insufficient knowledge base for the faeces of recent animals) makes assignment to specific producers difficult. Spiral coprolites (Fig. 3) frequently possess delicate surface markings believed to result from the intestinal membranes of their producers. They have been regarded therefore as infillings of spiral intestines (*enterospirae*; Fig. 3) rather than defecated coprolites. However, recent observations on living sharks has shown that the spiral form can be retained on discharge into the colon from the spiral intestine, so that they are probably truly *cololitic*–*coprolitic* in origin. These distinctive coprolites were produced by a range of fish groups with spiral intestinal valves, including agnathans, actinopterygians, dipnoans, and coelacanth (Fig. 3G, H, *Macropoma mantelli*, Chalk, Upper Cretaceous). Most commonly, however, they



Fig. 3 Coprolites and 'cololite'. A, Spiral intestine of dogfish (*Scylliorhinus*) injected with Roman cement; vascular structure (still apparent in desiccated membrane) resembles impressions on surfaces of many coprolites. B–F, Spiral coprolites from the Lias, Lyme Regis, Dorset. B shows spiral folding, vascular markings, and dark included fish scales of *Pholidophorus limbatus* (enlarged as C₁, C₂). D, transverse section of a coprolite showing spiral folding and sections of embedded fish scales. G, H, Spiral folded coprolites from the Chalk Marl, near Lewes, Sussex. G, pattern of spiral folds and vascular markings produces a resemblance to a 'larch cone'. H, longitudinal section of spiral coprolite. (All from Buckland 1836.)

were probably produced by chondrichthyans, sharks, or rays (Fig. 3A–F).

Coprolites from Cretaceous non-marine sediments are frequently assigned to terrestrial reptile producers, often dinosaurs or crocodilians. The abundant phosphatic coprolites found in the Wealden sediments at Bernissart, Belgium, associated with *Iguanodon* skeletons, were at first assigned

to that dinosaur (Bertrand *in* Häntzschel *et al.* 1968). However, their phosphatic nature and content of vertebrate bones suggests that the producer was a predator, not a browsing herbivore like *Iguanodon* (Norman 1985) and the associated crocodiles seem more likely producers (see Bertrand; Abel; Casier; all *in* Häntzschel *et al.* 1968). Although some very large coprolites (up to 0.29 m long) may have a dinosaur origin, as yet no undoubted coprolites of herbivorous dinosaurs have been described. By contrast, crocodile coprolites are frequently recognized and analysed, especially from Late Cretaceous and Eocene non-marine sediments of North America. Two broad diets seem to be represented, piscivorous forms which fed on the Gar Pike *Lepisosteus* and more omnivorous forms which defecated fish bones, reptile scales, seeds, and leaves of plants (especially the water plant *Salvinia*). Pollen analysed from phosphatic coprolites appears to have been ingested with drinking water or silt swallowed while scavenging, and it reveals more information about the habitat of the producer than the diet.

Although mammal coprolites occur fairly widely in Cenozoic sediments, those of Pleistocene or post-glacial mammals have received most attention. In his classic work on Pleistocene cave deposits Buckland (1823) described an unusual substance 'album graecum' from cave earths associated with mammal bones. He identified this as being the coprolite of cave hyaenas, composed of digested bone and complementary to the dietary evidence provided by fragmented mammal bones with hyaena tooth marks in the same deposits. Subsequent workers have recognized coprolites produced by rodents, cave bears, and other mammals in Pleistocene cave deposits (Häntzschel *et al.* 1968).

Desiccated coprolites of both Late Pleistocene ground sloths and prehistoric humans in North America have yielded much detailed information on diet and contemporary environments. Coprolites from cave shelters in New Mexico and Arizona

(dated as 40 000–11 000 BP) show that ground sloths fed on a vegetation of juniper woodlands and montane conifers, which still persist in the area today. Assessments of the energy, fibre, and nutrient values of the diet of these ground sloths has failed to explain their extinction (at about 11 000 BP) as a result of climatic change or dietary stress; human predation remains a likely cause. Coprolites have been used for the past two decades as a means of determining ancient human diet. For example, they showed that the diet of the inhabitants of Tamaulipas, Mexico (7000–1700 BC), was largely vegetarian, but also included mice, snakes, lizards, grasshoppers, and perhaps other insects; and that the diet of ancient inhabitants of Peru (2500–1200 BC) was entirely vegetarian (Callen *in* Häntzschel *et al.* 1968).

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4.13 Predation

4.13.1 Marine

C. E. BRETT

Introduction

Predation, the killing and consumption of animals for food, is of fundamental importance in controlling diversity and abundance of organisms in modern marine environments. Predation was probably also critical in shaping longer term trends in adaptation; Vermeij (1977, 1987) has documented an evolutionary 'arms race' between marine shelled organisms and their predators through Phanerozoic time. Co-evolution between organisms and their predators has led to an intensification of the struggle for existence and increased complexity of organisms through time, which Vermeij refers to as *escalation*.

Predators form the apex of the biomass pyramid in any given community, and are commonly designated as first, second, or third order, depending on whether they feed primarily on herbivores or on other carnivores.

Predator–prey interactions are normally considered to represent dependent coactions, and a considerable theory has been developed based on the assumption that population sizes of predator and prey are mutually dependent. Indeed, certain terrestrial community studies appear to document a dependency of predators on specific prey. However, it has also been argued that much predation, particularly amongst marine organisms, is of a non-specific and opportunistic nature. In this case, the impact of predation on a particular prey species, and vice versa, may be less significant.

Modes of predation

The act of predation involves several phases (Bishop 1975): *search*, *capture*, *penetration*, *ingestion*, *digestion*, and *defecation*. The penetration and ingestion phases can be combined under the heading of *subjugation*. Vermeij (1987) further subdivided the modes of subjugation employed by durophagous marine predators into five categories. *Whole animal ingestion* involves swallowing the entire body of the prey animal and generally leaves no distinct marks

upon the prey skeleton. In the process of *insertion and extraction*, the predator penetrates the skeleton of the prey and removes flesh through the aperture, again without damaging the skeleton. These modes of predation are not generally reflected in the hard part morphology of predators and thus are not identifiable in the fossil record. Some predators kill their victims by grasping them and *transporting* them into environments in which they cannot survive, e.g. in the case of shore birds which commonly transport marine molluscs into subaerial environments where they feed upon them. The chances of detecting this mode of predation in the fossil record are slim.

Preingestive breakage and *drilling* both leave direct trace fossil evidence in the form of bite or crush marks and circular to parabolic bore holes. Both of these modes of predation have been the subject of several recent studies (for reviews see Vermeij 1987). Many predators break or puncture the shells of their victims prior to ingestion, using a variety of tools. Several marine molluscs employ a form of forced entry to break or separate the valves or plates of their prey. For example, the gastropod *Acanthina* utilizes a sharp spine on its shell's outer lip to break apart the plates of barnacles; whelks of the genus *Busycon* use the sharp outer lip of their shell to chip and pry at the valve margins of bivalves. Cephalopods also possess chitinous or calcified beaks for biting or crushing prey. A wide variety of marine vertebrates, both living and fossil, utilize blunt pavement teeth to crush hard-shelled prey; these include rays, ptyctodonts, placodonts, and various marine sharks. Most sharks, as well as fossil mosasaurs, use sharp teeth to pierce or fracture the shells of their prey. In the process, they may leave distinctive bite marks, such as divots or rows of holes in those shells (Fig. 1A–D). Crustaceans use three distinct strategies to break the shells of their prey, and in the process also produce distinctive traces. The shells may be crushed between the opposed surfaces of claws. Peeling involves the piece by piece breakage of the outer margin of gastropod shells by crabs (Fig. 1C) until the flesh of the organism becomes accessible to the predator. Still other crustaceans, primarily stomatopods, crush the shells of their prey by pounding them with blunt, expanded segments of their maxillipeds.

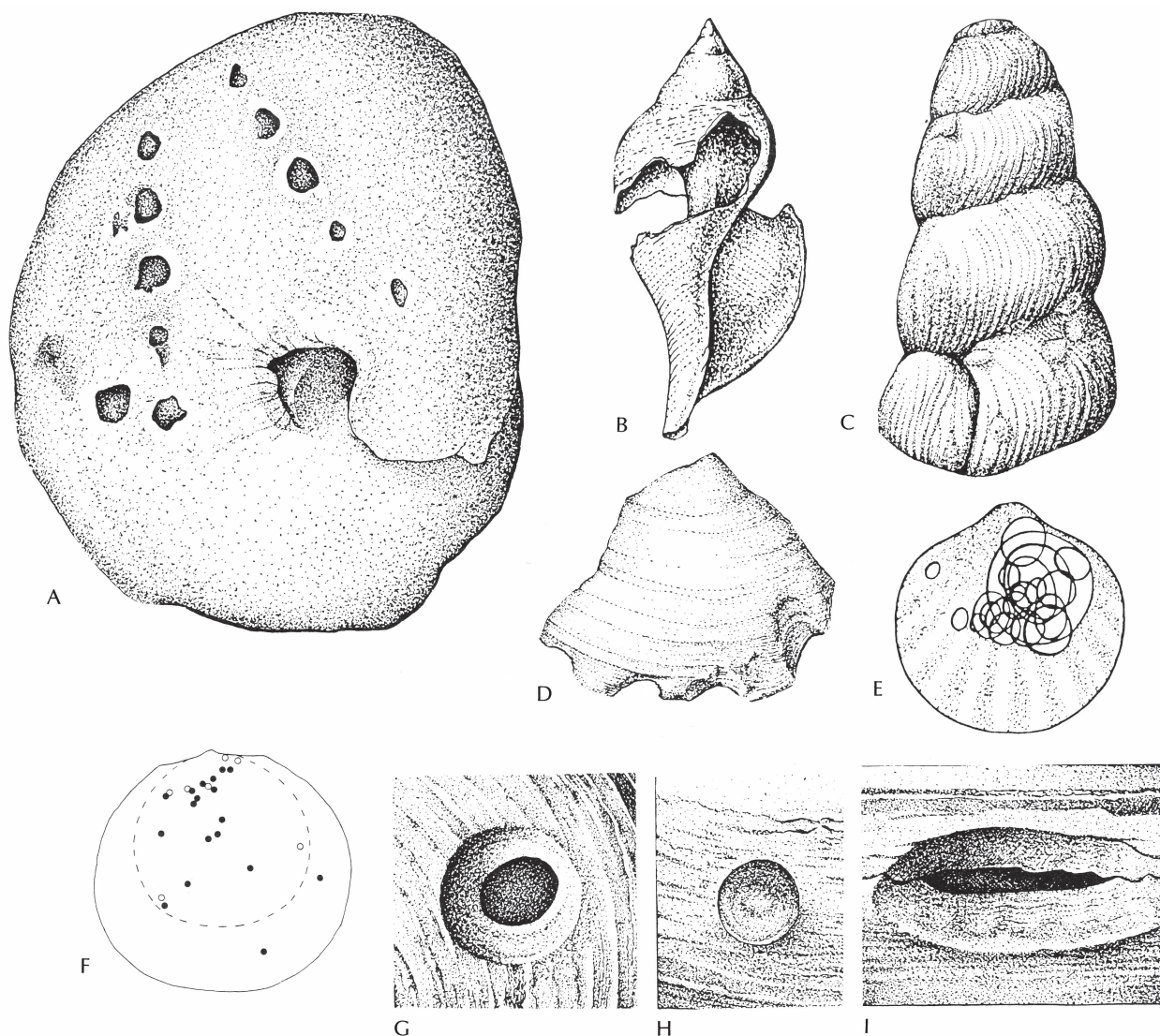


Fig. 1 Fossil evidence of predation. A, Cretaceous ammonite *Placenticerus* displaying rows of punctures apparently made by the teeth of a mosasaur, $\times 0.6$. B, Recent gastropod shell exhibiting peeling damage inflicted by the predatory crab *Calappa*, $\times 1$. C, Devonian gastropod *Palaeozygopleura* with a healed, scalloped fracture of the outer lip, probably resulting from a failed attempt at lip-peeling by a predator, $\times 5$. D, Permian bivalve with crescentic breakage along valve margin, probably the result of fish predation, $\times 1$. E, Diagram showing locations of most frequent drilling on Recent bivalves from the Nile Delta; note selective positioning of boreholes near umbo. F, Diagram illustrating positions of complete (black) and incomplete (white) boreholes in the Devonian brachiopod *Rhipidomella*; note concentration near umbo. G–I, Recent gastropod boreholes in bivalve shells. G, complete borehole of *Natica severa*; note bevelled outer edge and change from circular (outer) to elliptical openings, $\times 6$. H, incomplete borehole of *Polinices duplicatus*; note presence of raised boss at centre of view, $\times 6$. I, boring of *Murex fulvescens* on the commissure of a bivalve shell, $\times 6$.

Figures redrawn from photographs as follows: A, Kauffman & Kesling 1960; B, Bishop 1975; C, Brett & Cottrell 1982; D, Boyd & Newell 1972; E, Reymont 1971; F, Smith *et al.* 1985; G–I, after Carriker & Yochelson 1968.

Drilling is a specialized mode of predation, largely restricted to marine molluscs, including both gastropods and cephalopods. These organisms leave very distinctive drilling traces, referred to the ichnogenus *Oichnus* (Fig. 1G–I), that provide direct records of successful predation. The boring procedure involves secretion of unknown acids by an accessory boring

organ and mechanical abrasion by the denticles of the radula. The entire process is relatively slow, requiring from 5 to 100 hours for completion. Consequently, normally only a single hole is drilled per shell, although rarely one or more incomplete holes may be observed and there are instances of holes being produced in unoccupied shells. As a whole,

gastropod predatory boreholes can be distinguished from other types of borings in that they are circular in outline, penetrate the prey shell perpendicular to the shell, are parabolic or cylindrical in cross-section, and normally range from about 0.5 mm to 3.0 mm in diameter. Hole size is generally related to the size of the gastropod predator. Modern drilling gastropods are rather highly prey selective, favouring certain species of bivalves. They also show preferential positioning of the bore hole, most commonly near the centre of the prey shell (Fig. 1E, F). However, some *Polynices* and many muricids actually drill shells along the commissure (Fig. 1I). Naticid drill holes tend to be regularly parabolic in cross-section and, when incomplete, display a raised boss in the centre of the floor (Fig. 1H). Muricid gastropods, on the other hand, produce holes that are cylindrical in outline, tend to be more randomly distributed on the shells, and do not show a raised boss when incomplete. A third group of gastropods, the cassids (helmet shells), produce circular holes in echinoid tests.

Cephalopods drill primarily for the purpose of paralysing their prey. The hole is generally oblique to the shell surface and tends to be conical, but is rather irregular in size and shape. Cephalopod boreholes are not yet known from the fossil record.

Fossil record of predation

Direct records of ancient predation are relatively rare in the fossil record; as Bishop (1975) noted, the evidence of predation is normally destroyed (literally eaten) in the process of its formation. However, several lines of evidence provide some insight into the evolutionary history of predation. The body fossil record of potential predators provides information on the general ranges of different carnivorous organisms. The predatory behaviour of fossil organisms may be inferred indirectly from morphological comparisons with living analogues known to have carnivorous habits, e.g. cephalopods and naticid gastropods. The fossil record commonly provides direct indications of a predaceous mode of life because the organs used in manipulation, biting, and ingestion of prey are typically heavily skeletonized and thus preservable. Such tools include the crushing claws of crustaceans, modified chelicerae of eurypterids, and a wide array of pavement and biting teeth in vertebrate groups.

Cephalopods with probable chitinous beaks are abundant from the Late Cambrian or Early Ordovician onward, but the direct fossil record of

calcified beaks (rhyncholites) does not begin until the Late Palaeozoic. Durophagous arthropods include mainly phyllocarids and eurypterids in the Palaeozoic; these had appeared by the Late Ordovician but attained maximum diversity in about the Middle Devonian. The decapod crustaceans in the Triassic evolved more efficient mechanisms of shell crushing by claws or maxillipeds. In the Jurassic, new groups of shell-crushing crustaceans evolved, including the stomatopods and brachyuran crabs.

A major increase in durophagous predators involved the abrupt appearance of varied jawed fishes in the Devonian Period, including the placoderms, ptyctodonts, hybodonts, and others (Fig. 2). Certain sharks, such as *Helodus*, with shell-crushing pavement teeth, have been implicated by Alexander (1981) as producers of distinct crush marks in Carboniferous brachiopods.

The large marine predators of the Mesozoic were dominated by reptiles within the subclass Diapsida: the placodonts (Placodontia), nothosaurs and plesiosaurs (Sauropterygia), ichthyosaurs (Ichthyosauria), mosasaurs (Squamata; family Mosasauridae), and marine crocodiles (Crocodylia; family Metriorhynchidae, Teleosauridae). The evolution of large marine predator communities in the Mesozoic can be divided into four main periods of stability and slow diversification, separated by periods of reorganization or extinction (Massare 1987, 1988).

Sharks and large fish continued to diversify through the Late Cretaceous, and were the important marine predators in the Early Tertiary. Sharks probably reached their peak with the giants of the Miocene. Whales appeared in the Eocene, but early forms, the zuglodons, were heterodont, long-bodied ambush predators more similar in body form to the Cretaceous mosasaurs than to modern whales. Seals, sea-lions, and modern whales appeared in the Late Oligocene and Miocene. Thus by the later epochs of the Tertiary, the marine predator communities had begun to take on a modern aspect.

Actual cases of predators *in situ* on prey, or of prey within stomach contents, provide compelling evidence for carnivory but are too rare to be of more than anecdotal interest. Notable examples include fossil asteroids (starfish) *in situ* on probable bivalve prey from the Devonian of New York and specimens of fish from various units, particularly the Cenozoic Green River Formation, with partially swallowed smaller fishes inside them (see p. 305). Certain late Palaeozoic sharks similarly display stomach contents, including fragments of brachiopods and crinoids.

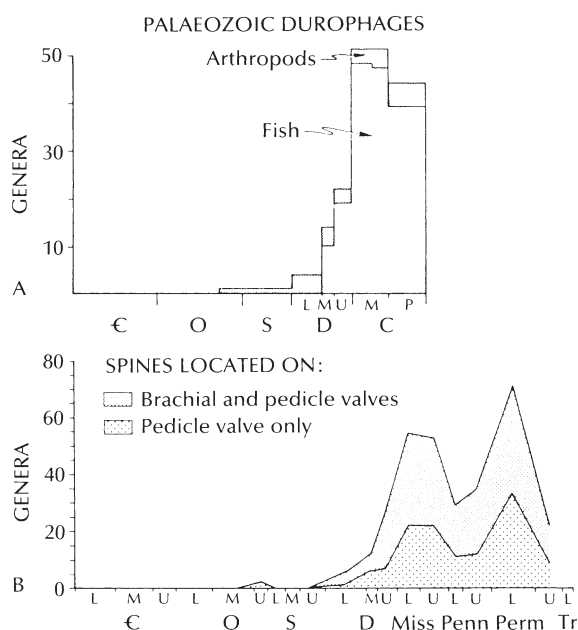


Fig. 2 Predation in the Late Palaeozoic. A, Genera of Palaeozoic durophagous predators; a few durophagous arthropod genera appear as early as the Late Ordovician, but the major radiation begins in the Middle Devonian; fish comprise the vast majority of the radiation, but there is an initial increase in arthropod durophages as well. B, Brachiopod genera with spines on the pedicle or both valves; note that the trend in numbers of genera with spines on both valves generally parallels the trend in number of genera with spines on the pedicle valve. (From Signor & Brett.)

A second source of data on ancient predation comes from the trace fossil record. Traces of successful or attempted predatory attacks include the distinctive marks made by biting and gnawing of predators on hard shells as well as drill holes of predatory molluscs (Fig. 1). Bite marks provide strong indications of predatory attack, although they usually cannot be linked to specific predators. Exceptions include several instances of circular punctures in Carboniferous ammonoids; the size and spacing of the holes implicates the associated cladodontid shark *Symmorium* as the predator. Classic examples of bite marks are known from Cretaceous ammonoids, where the holes match the size and spacing of the teeth of associated mosasaurs (Fig. 1A).

Sublethal, healed fractures and punctures are common in certain types of Palaeozoic brachiopods and bivalves (Fig. 1C, D). Alexander (1981, 1986) recognized lethal and sublethal (healed) shell damage in assemblages of Ordovician to Pennsylvanian brachiopods, and observed an increased proportion

of lethal fractures in the later Palaeozoic. Together with the decline in frequency of repaired damage, this evidence suggests an increased intensity and effectiveness of predatory attack. Vermeij (1977) similarly documented trends in healed breakage amongst post-Palaeozoic molluscs, primarily gastropods. Distinctive scalloped fractures in the outer lips of the gastropod shells can be identified as having been made by peeling crustaceans (Fig. 1E). The oldest instances of this lip-peeling type of fracture are known from the Middle Ordovician, but case studies from the Ordovician and Silurian suggest that lip-peeling was exceedingly rare. In contrast, about 10–20% of individuals in some Devonian gastropod assemblages have suffered peeling, indicating levels of predation comparable to those of the Late Palaeozoic (Schindel *et al.* 1982) and Mesozoic (Vermeij 1977, 1987). Shell repair cannot be interpreted unambiguously because it monitors not only predatory attack, but also the ability of shells to resist attack.

In contrast, the boreholes of carnivores testify to lethal attacks. However, it is critical to distinguish between non-predatory, domicinal borings and those produced by predators or parasites on live organisms. Carriker & Yochelson (1968) noted several diagnostic characteristics of the latter, including penetration through a single valve, few holes per shell, holes drilled perpendicular to shell surfaces, and evidence for prey and site selectivity.

The earliest evidence for drilling predation is derived from the Early Cambrian problematical, discoidal fossil *Mobergella* which displays minute drill holes in selective positions indicating probable predatory attack. Small cylindrical borings are also known through much of the Early Palaeozoic, although the affinities of these and the habits of their producers are not well understood. Many may have been produced by semiselective parasites living within the sediment. However, the first boreholes likely to have been made by gastropods occur in Devonian rocks. Circular–parabolic holes, closely resembling those produced by naticid gastropods, from the Middle Devonian of New York State, display a considerable degree of host and site selection (Fig. 1F), as well as the presence of a raised boss in the centre of incomplete holes, which is often considered diagnostic of the naticid gastropod mode of boring. Similar holes on related prey species are known from the Carboniferous. However, it appears that this early group of predaceous snails, probably a clade of archaeogastropods, became extinct at the end of the Palaeozoic. The drilling

habit re-evolved during Middle–Late Triassic times, probably by a group of Mesogastropoda that became extinct before the end of the Triassic. Gastropod boreholes of both muricid and naticid affinity appear in the late Early Cretaceous (Albian). Throughout later Cretaceous and Cenozoic times gastropod drilling became an extremely potent mode of predation in marine communities. Relatively high percentages of molluscs in some faunas display predatory attacks by gastropods. These snails show a great deal of stereotypy in their mode of attack and position of boring on the shells of prey (Reyment 1971).

Coprolites (Section 4.12) provide another trace of predation and their fossil record has been systematically documented by Häntzschel *et al.* (1968). However, coprolites are very scattered and only a few specimens have been attributed directly to particular host species; notable examples occur amongst Jurassic ichthyosaurs, whose coprolites commonly contain fragments of molluscan shells.

The third source of evidence for predation is a very indirect one, derived from apparent antipredation adaptations in probable prey species. Signor & Brett (1984) noted a coincidence between the rapid diversification of durophagous predator groups and various trends in the skeletal morphology of potential prey, starting in the Late Silurian to Devonian periods (Fig. 2). Aspects of skeletal morphology that were adaptive for resistance to predatory attack appeared rather abruptly in the Siluro-Devonian and increased toward the end of the Palaeozoic. Trends include the loss of umbilici in gastropods, and increased shell thickness and spinosity amongst brachiopods, gastropods, cephalopods, and crinoids (Fig. 2B).

Vermeij (1977) documented a great acceleration in the intensity of predation beginning in later Triassic and Jurassic times, which he termed the Mesozoic marine revolution. He noted the abrupt rise of durophagous groups such as crabs, stomatopods, and various shell crushing vertebrates, and documented several apparent antipredatory trends in molluscan groups. These include a tendency toward the evolution of thicker shells with narrow, toothed apertures, and the development of ribs and spines in several groups. Probable coevolution of predators and their prey may have promoted an increased diversity of defensive adaptations on the part of potential prey organisms. It would appear that the intensity of predation in marine systems has increased rather steadily at least from Late Cretaceous times to the present day, and may be responsible in

part for the relatively higher species richnesses of many modern marine communities, as well as for many peculiar morphological adaptations of molluscan prey groups.

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4.13.2 Terrestrial

J. A. MASSARE & C. E. BRETT

Arthropods

The first partially terrestrial animals, myriapods of Early Silurian (Llandoveryan) age, apparently were predaceous and fed upon small aquatic animals (Niklas 1986). Later Palaeozoic terrestrial arthropods (collembolans, insects, mites) were primarily herbivorous; however, in the Carboniferous certain large insects of the Order Protodonata, as well as spiders, specialized as predators on other insects. During the Mesozoic and Cenozoic a number of terrestrial arthropod groups (e.g. spiders, many beetles) became specialized as predators.

Tetrapods

The first terrestrial vertebrates, early labyrinthodont tetrapods, were probably entirely predaceous, feeding on fish and other aquatic animals, as well as smaller amphibians. These predators, beginning with the ichthyostegids in the Late Devonian, possessed sharp, spike-like, and undifferentiated teeth for impaling prey. Maximum usable prey size was limited by the size of the mouth gape. Later, the evolution of shearing-type teeth in the pelecosaurs permitted active slicing, and thus consumption of larger bodied prey animals. Herbivorous land vertebrates do not appear in the fossil record until the Late Carboniferous and carnivores continued to outnumber herbivores until at least the Middle Triassic. The shift toward increased numbers of herbivores is associated with the origin of therapsids in the Middle Permian. This transition may have been related, in turn, to the desiccation of coal swamps and concomitant loss of the palaeodictyopteran insect fauna (Niklas 1986).

Bakker (1977, 1986) subdivided terrestrial tetrapod communities into four great groupings or *megadynasties*, based on dominant herbivore and carnivore types; he stressed increasingly complex predator-prey interactions and, to a large extent, decreasing predator:prey ratios through time. Bakker used ratios of estimated biomass of predators to that of potential prey species, in particular, based on well preserved local fossil assemblages, to make inferences regarding metabolism and lifestyle of carnivorous tetrapods.

Megadynasty I. Early terrestrial ecosystems of Megadynasty I (Carboniferous–Early Permian) were dominated by primitive reptiles and amphibians. The top predator was the synapsid reptile *Dimetrodon*, which was almost certainly ectothermic (cold-blooded), as evidenced by bone microstructure. Predator:prey ratios in these terrestrial ecosystems were characteristically high: large biomasses of predators were supported by small populations of moderate sized herbivores.

Megadynasty II. Megadynasty II (Early Permian–Middle Triassic) is referred to as the time of protomammals, indicating dominance by the mammal-like therapsid reptiles (Fig. 1A). A variety of osteological and morphological evidence indicates that therapsids were endothermic (warm-blooded) (see Bakker 1977; Benton 1979). Therapsids include diverse carnivorous, insectivorous, and herbivorous species. In populations from the Karoo beds of South Africa, predator:prey ratios average about seven per cent, only slightly higher than modern mammalian systems. The age of protomammals involved three waves of diversification (dynasties) and lasted approximately 15–20 Ma before giving way to Megadynasty III in Late Triassic times.

The Middle Permian (Kazanian) witnessed an explosive adaptive radiation of predatory therapsids, the largest of which were bear-sized, dome-headed anteosaurs. These predators were substantially more diverse than those of the Early Permian, including five families, as opposed to the single Sphenacodontidae which had previously occupied the role of large predator. The Kazanian therapsid fauna was decimated by a mass extinction and replaced in Late Permian (Tartarian) time by newly evolved groups of therapsids dominated by predatory, sabre-toothed dicynodonts; low predator:prey ratios (5–12%) prevailed. In turn, the Tartarian fauna underwent a mass extinction at the end of the Permian and elimination of all top predators enabled two new groups to expand into that role during Early Triassic (Scythian) time: the dog-like cynodont therapsids and, more significantly, archosaurs belonging to the Erythrosuchidae (Fig. 1B). The latter are forerunners of the thecodonts, including the crocodile-like phytosaurs and proterochampsids, which occupied roles of both top- and medium-to-small sized predators during the Middle–Late Triassic. Coevolution of prey defences is indicated by the appearance of heavily armoured aetosaurs.

Bakker (1986) argued that the evolutionary re-

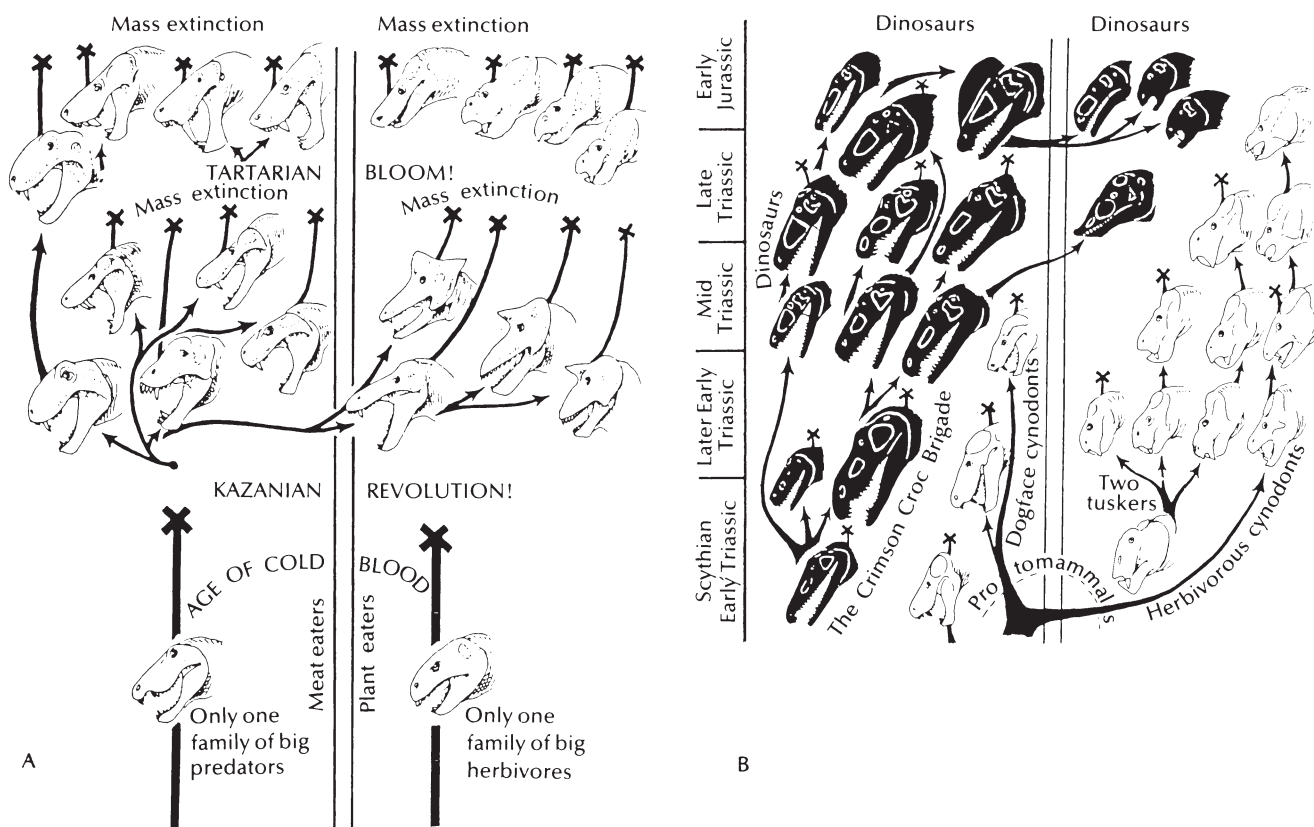


Fig. 1 Early adaptive radiations of terrestrial predators and their prey. Each head on the diagrams represents a single reptile family. A, Early Permian predator–prey systems (base of chart) were dominated by slowly evolving ectothermic predators belonging to a single family. Appearance of probable endothermic therapsid ‘protomammals’ triggered an adaptive radiation in the Middle Permian (Kazanian revolution). Within a few million years five families of predators and four of herbivores had appeared. Most of these lineages were terminated by a mass extinction event. Surviving therapsids gave rise to a second adaptive radiation in protomammals in the Late Permian (‘Tartarian bloom’). B, During the Triassic, archosaur families replaced the mammal-like reptiles in predator guilds (left side of chart). Early archosaurian predators included mainly the erythrosuchians (‘crimson crocodiles’). Later, in the Late Triassic–Early Jurassic, dinosaurs displaced the erythrosuchid predators and also invaded herbivore guilds to displace the mammal-like reptiles. (From Bakker 1986.)

placement of therapsid predators by thecodonts is consistent with osteological evidence for endothermy in these archosaurs. Conversely, Benton (1979) contended that the increasingly arid climates of the Triassic favoured archosaurs because they were ectothermic; he noted that ectotherms need to eat less and can conserve water better than endotherms.

Megadynasty III. Megadynasty III (Late Triassic–Cretaceous) was the age of dinosaurs. Bakker documented low predator:prey ratios within dinosaur dominated communities, suggesting high metabolic rates among theropod dinosaurs, resembling those seen in modern predaceous mammals. This appears to corroborate other osteological and

physiological evidence which indicates that dinosaurs were warm-blooded and active social creatures (but see Benton 1979).

Bakker (1986) documented a Mesozoic ‘arms race’ between dinosaurian predators and prey. Early predators included the Late Triassic coelurosaurs: slender, agile, and bipedal predators with teeth specialized for forming long slashing wounds. Later predatory carnosaurs displayed an enormous increase in size from two-ton *Allosaurus* to five-ton *Tyrannosaurus*. Early theropods (e.g. *Ceratosaurus*) had a flexible lower jaw enabling them to gulp large chunks of flesh. Later, jaw flexibility was sacrificed in favour of a firm, strong bite. Even the large *Tyrannosaurus* had extremely well developed hind limbs and feet capable of sustained, relatively

high running speeds. Other lineages of saurischian dinosaurs evolved different mechanisms for killing prey. A spectacular example is the Cretaceous species *Deinonychus* which possessed huge, curved, sabre-like claws for impaling and slashing prey. *Baryonyx*, from the Lower Cretaceous of the U.K. possessed extremely large claws on the front limbs, which it apparently used to hook prey much in the way that grizzly bears utilize their claws to catch salmon.

In turn, Mesozoic herbivorous dinosaurs responded to the increasingly efficient and large predators by evolving a variety of defences. The sauropods took refuge in their large size. Bakker (1986) argued that they were also capable of some evasive action and perhaps could ward off attacks by swinging their large tails and battering their predators. Evidence from trackways suggests herding behaviour in brontosaurs which presumably was a defensive social strategy in response to predation pressure on the young. Juvenile dinosaurs were maintained near the centres of migrating herds to be protected by adults, much in the fashion of herds of large ungulate mammals today. Other dinosaurs, particularly Ornithischia, evolved more spectacular defense strategies. Stegosaurus not only had large bony plates on the vertebral column, but also possessed a tail armed with sharp spikes which was clearly a formidable defensive weapon. Ankylosaurs evolved extremely rigid armour plating over much of the body, and in some cases (e.g. *Ankylosaurus*) possessed a huge bone-crushing club at the end of the tail. Perhaps the most spectacular of the defensive weaponry was that of the ceratopsian dinosaurs (e.g. *Triceratops*). The massive heads of these Cretaceous dinosaurs were armoured with a heavy shield and adorned with one to five sharp horns, which could impale enemies.

Dinosaurian predators of the Mesozoic were joined by a variety of other predatory vertebrates. From Triassic times onward, crocodiles were important predators in freshwater bodies. The early birds, from the Jurassic *Archaeopteryx* to the end of the Cretaceous, were entirely carnivorous and apparently evolved directly from small predatory coelurosaurids dinosaurs. In addition, pterosaurs occupied many predatory niches presently occupied by numerous birds.

Megadynasty IV. Although mammals, including insectivorous species, originated in the Triassic approximately contemporaneously with dinosaurs, and their diversity exceeded that of archosaurs by

the Late Cretaceous, mammalian predators remained small with no large predatory species until the Early Palaeogene. The rise of the larger mammals of Megadynasty IV is a spectacular case of ecological replacement following on from the extinction of the dinosaurs.

The earliest eutherian mammalian predators of the Tertiary, the arctocyonids, had five spreading clawed digits, short highly flexed limbs, and thick muscular tails. They were probably capable of climbing, digging, holding prey, and running over uneven or vegetated terrain. Generalized in locomotor and feeding adaptations, these forms gave rise to both the early carnivores and herbivores. The middle and late Palaeocene mesonychids improved upon the primitive form with stiffer, more elongate limbs as adaptations for a more cursorial mode of life. The second wave of mammalian predators, the Creodonta, evolved advanced dental adaptations for meat eating — carnassial teeth. Hyaenodonts were the main cursorial predators and the stocky, more heavily built oxyaenids were the ambush predators. True carnivores (Order Carnivora), the third wave of mammalian predator diversification, appeared in the Late Eocene, and coexisted for a while with the creodonts (Bakker *in* Fatuyma & Slatkin 1983). The earliest true carnivores were small weasel-sized viverids and myacids. The predator communities of the White River Badlands U.S.A. provide a glimpse of a Middle Tertiary community. Such Oligocene communities were a mixture of archaic and modern carnivores. The predators were predominantly small-sized (less than 60 kg). Locomotor adaptations suggest that there was an emphasis on climbing ability or short-distance ambush predation, but there were cursorial predators as well. The fauna lacked bone-crushing carnivores comparable to modern hyaenas (Stanley *et al.* *in* Fatuyma & Slatkin 1983).

In the Late Oligocene and Early Miocene, predator communities began to take on a more modern aspect. Dogs, some bear-dogs (amphicyonids), and, later in the Miocene, the hyaenas independently evolved the long-limbed, fleet-footed adaptations of running predators. From the Oligocene onward members of the cat family filled most of the ambush predator niches. The sabre-tooth cat lineage included heavily built forms that specialized in preying on large, relatively slow-moving ungulates. Their demise was probably related to the extinction of most of their large, herbivore prey species at the end of the Pleistocene. The second lineage of cat evolution, which survives today, included generally

smaller species that were built for greater agility. They specialized in faster, smaller prey. Thus the evolution of predators in the Northern Hemisphere was a series of radiations, each beginning with fairly unspecialized forms, often as primitive or more so than the pre-existing predator groups. Successive radiations evolved better cursorial and dental adaptations, climaxing in the predator faunas of the Late Pleistocene.

The predator faunas of the island continents in the Tertiary were quite different. Giant birds occupied the cursorial predator niches in South America until the Pliocene, when the Central American land bridge allowed North American predators to invade South America. The South American ambush predators were cat-like marsupials that show striking parallels with the true cats of the northern hemisphere. In Australia, a variety of wolf-like marsupials filled the terrestrial cursorial predator niches.

Study of Cenozoic and Recent mammalian predator guilds indicates that predator diversity is tightly correlated with prey richness (Van Valkenburgh 1988). Furthermore, the basic array of predator feeding types has remained relatively constant for at least 32 million years, despite great taxonomic turnover. Van Valkenburgh concluded that competition has played a key role in the maintenance of this diversity.

Although mammals clearly dominated the large predator guilds during Cenozoic time, other vertebrates have become highly successful in the roles

of smaller to medium sized predators. Lissamphibia (e.g. frogs, toads) have become specialized at insect capture. The rise of these amphibians, together with small rodents, has also triggered a major adaptive radiation of snakes, specializing in whole-prey ingestion as a result of highly flexible jaw articulations. The rise of passerine birds tracks the adaptive explosion of their insect prey; a number of raptorial predatory birds also appeared in the Cenozoic.

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4.14 Parasitism

S. CONWAY MORRIS

Introduction

Parasitism is a symbiotic association whereby an individual derives nutritional benefit at the detrimental expense of another, by means of a long-term association. Usually such individuals concerned are separate species, but intraspecific parasitism, such as that typified by the stunted male fused to the female ceratioid angler fish of the deep sea, is not unknown. Clearly, this definition of parasitism may grade into other types of symbiosis (e.g. commensalism), as well as the protracted predatory

activity that is typical of many bloodsuckers (e.g. ticks, lampreys). In addition, the concept of parasitism may be expanded to include species with a parasitic stage at some point in their life cycle, usually juvenile. These so-called parasitoids characterize many phytophagous insects, and indeed if parasites and parasitoids are taken together they probably outnumber free-living species on the planet today.

However, despite the abundance of parasitic species in all habitats, and the fact that there are representatives in the majority of metazoan phyla

(conspicuous exceptions include the echinoderms, brachiopods, and other lophophorates), their fossil record is lamentable. This is because of the soft-bodied nature of most parasites and their normal location in soft tissues with a minimal preservation potential (e.g. gut, muscle), combined with a general absence of effect on hard skeletal tissues. Furthermore, even when a pathological disturbance of hard parts can be assigned with confidence to parasitic inflammation, it is often impossible to identify the group responsible. However, although the evidence for fossil parasites is both slender and widely scattered (Conway Morris 1981; Hengsbach 1990), in principle such a record could throw new light on host–parasite relationships. Major questions include: How did such associations arise? Was it by deterioration from a more benign symbiosis or does the parasitic condition arise abruptly from a free-living form? To what extent do parasites coevolve with their hosts, or are their rates of evolution and cladogenesis more or less unrelated to that of the host? How do parasites weather host extinction, especially in cases of strict host-specificity?

The fossil record of parasites

Several phyla are particularly important as parasites, but nearly all lack preservable hard parts and their body fossil record is scanty. Of the platyhelminthes, even the fossil record of the largely free-living turbellarians is highly questionable, while no fossils are known of the parasitic cestodes, trematodes, and monogeneans. Similarly, the sparse nemertean fossil record contains no obviously parasitic species. However, amongst the nematodes, a scattered record of free-living species (mostly from Cenozoic ambers) is augmented by a few parasitic forms. These include examples from Eocene lignites in East Germany, where beetles have been parasitized by nematodes (Fig. 1A). In the Baltic ambers other nematodes occur in close association with a dipteran (Fig. 1B), and an investigation of New World ambers may well reveal other parasitic associations that will supplement existing reports of free-living examples. Parasitic nematodes have also been reported from mammals entombed in the Siberian permafrost, but the most esoteric location is within a kidney stone of a cave bear from the Pleistocene of Germany. Saprobiotic nematodes described in association with a Carboniferous scorpion could be of relevance if such a life habit was a precursor to true parasitism. However, some nematologists refute the identification of these fossils as nematodes, and if this is

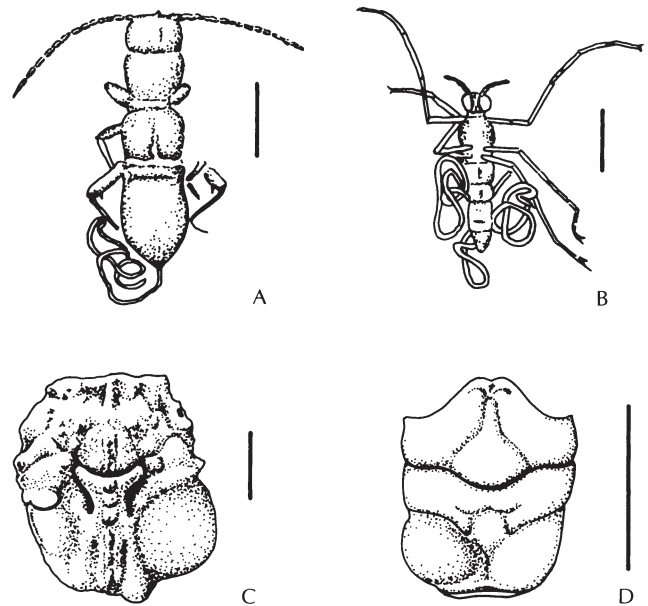


Fig. 1 A, The nematode *Heydenius antiquus* protruding from a cerambycid beetle *Hesthesis immortalia* Oligocene lignite, East Germany. (After Heyden 1862.) B, Three nematodes (*Heydenius matutinus*) associated with a dipteran; Baltic amber, Oligocene. (After Menge 1866.) C, *Notopocorystes stokesi* with swelling (lower right) on branchial region of cephalothorax, attributed to a bopyrid isopod; Albian, southern England. (After Förster 1969.) D, *Pithonoton marginatum* with swelling (lower left) on branchial region of cephalothorax, attributed to a bopyrid isopod; Upper Oxfordian, Poland. (After Radwanski 1972.) Scale bars equivalent to 1 mm (A, B), 10 mm (C), and 5 mm (D).

accepted their taxonomic placement becomes debatable. The nematomorphs, which are probably related to the nematodes, are free-living as adults, but a parasitic larva has been identified in association with fish remains in Eocene lignites from East Germany.

No fossil acanthocephalans are known. However, on the basis of a proposed relationship with the free-living priapulid worms, putative ancestral types were identified amongst the prolific priapulid fauna in the Middle Cambrian Burgess Shale (Conway Morris & Crompton 1982). More recently, however, an alternative relationship — between acanthocephalans and rotifers — has been advanced. The arguments rely largely on ultrastructural comparisons and some proposed organ homologies, but the fossil record is unlikely to assist in this matter as fossil rotifers are not known.

If the record of parasitic fossil worms is slender, that of parasitic arthropods is only marginally more satisfactory. Parasitic insects are best known from the Cenozoic, with ambers yielding some of the

finest examples. Mesozoic examples are more limited, but include Cretaceous fleas, whose presence has been used to infer the nature of the original hosts. Arthropod–plant relationships have been traced back to the early stages of terrestrial invasion in the Devonian, but accepted examples of parasitic activity in the form of plant galls do not appear until substantially later. Although the earliest putative examples are Permian, the bulk of the record is from the Cainozoic.

In the marine realm a moderately secure record is available from the Jurassic onwards. The most striking examples are siphonostome copepods that were recovered from gill chambers of Lower Cretaceous fish; their exceptional preservation is a result of diagenetic phosphatization. The activity of parasitic copepods has been inferred also from galls on echinoderms that range in age from Jurassic to Miocene. Evidence for the activities of other parasitic arthropods in marine communities is entirely dependent on what are effectively trace fossils. The most impressive roster of examples comes from the swellings in the branchial regions of decapods (Fig. 1C, D); these are attributed to the activity of parasitic isopods (Epicaridea). Although it has been traditional to ascribe these manifestations to members of Bopyridae, the absence of the actual isopods in the branchial chambers make such assignments somewhat tentative. The first examples of infestation are recorded from the Upper Jurassic but, despite a rise in the number of species parasitized towards the end of the Jurassic, thereafter such examples appear to be rare in the fossil record. Whether decapods were able to evolve resistance to infestation over geological time is not known. Finally, amongst the isopods, a possibly parasitic species has been described from the Cretaceous of Texas.

Although most cirripedes (barnacles) are free-living, the parasitic ascothoracicans are represented by characteristic borings and cysts in Cretaceous echinoids and octocorals. However, the cancer-like rhizocephalan cirripedes, the adult of which forms a ramifying mass in the host tissue, appear to have been unrecognized in the fossil record.

Excluding leeches, which have a questionable fossil record from the Silurian and Jurassic, the record of parasitic annelids is effectively confined to the myzostomids. In Recent faunas these unusual organisms infest echinoderms, especially crinoids, and may provoke cyst-like swellings. It is, therefore, not surprising that many of the galls and other swellings in fossil echinoderms have been attri-

buted to myzostomids, but the great majority of such identifications are suspect. Reasonably secure examples, however, are known from the Middle Palaeozoic onwards, but the number of convincing examples is low (Arendt 1985).

Another popular culprit for other excavations in echinoderms (especially those that are cup-shaped) are parasitic gastropods. Analogues in the Recent suggest that some (especially from Cretaceous echinoids; Kier 1981) are probably correctly assigned. However, considerable doubt surrounds many others from Palaeozoic and Mesozoic echinoderms, especially as the coelomic cavity usually appears to have remained untapped by the putative gastropod. These galls, excavations, and other disturbances are widespread in fossil echinoderms (Fig. 2A, C, D, F), being well preserved because of the ability of stereom tissue to mould itself to local disturbances. However, the nature of the irritant is usually problematical, and in many cases it is questionable whether they can be usefully classified as parasitic interactions. This is because in many instances sections of the disturbed area give no clues as to the nature of the possible organism that provoked the reaction. A notable exception is provided by the funnel-shaped phosphatic structures referred to *Phosphannulus* (Fig. 2E). These have been found within perforated swellings on crinoid stems, ranging from Ordovician to Permian. Although the affinities of this organism are speculative, it appears that having settled on the surface of the crinoid stem it enveloped itself within the stereom, maintaining a connection with the exterior and also establishing a link to the central canal, from which it may have derived nourishment. What appear to have been free-living examples of *Phosphannulus*, however, are also known, including the earliest examples from the Upper Cambrian. It seems possible, therefore, that the genus was a facultative parasite, although particular species may have been wedded to a particular mode of life.

The catalogue of other possible parasitic interactions is lengthy, but relatively inconclusive. Some pathologically deformed fossils, including ammonites (Morton 1983), may reflect parasitic infestation. More specifically, the formation of a pearl in modern bivalves is frequently provoked by the settling of a parasitic larva, often that of a trematode, and its subsequent encapsulation by the irritated mantle tissue. The fossil record of pearls is slender, but in bivalves extends back to examples in the Silurian of Bohemia (Kriz 1979). Whether these examples (and possibly similar structures noted in Devonian

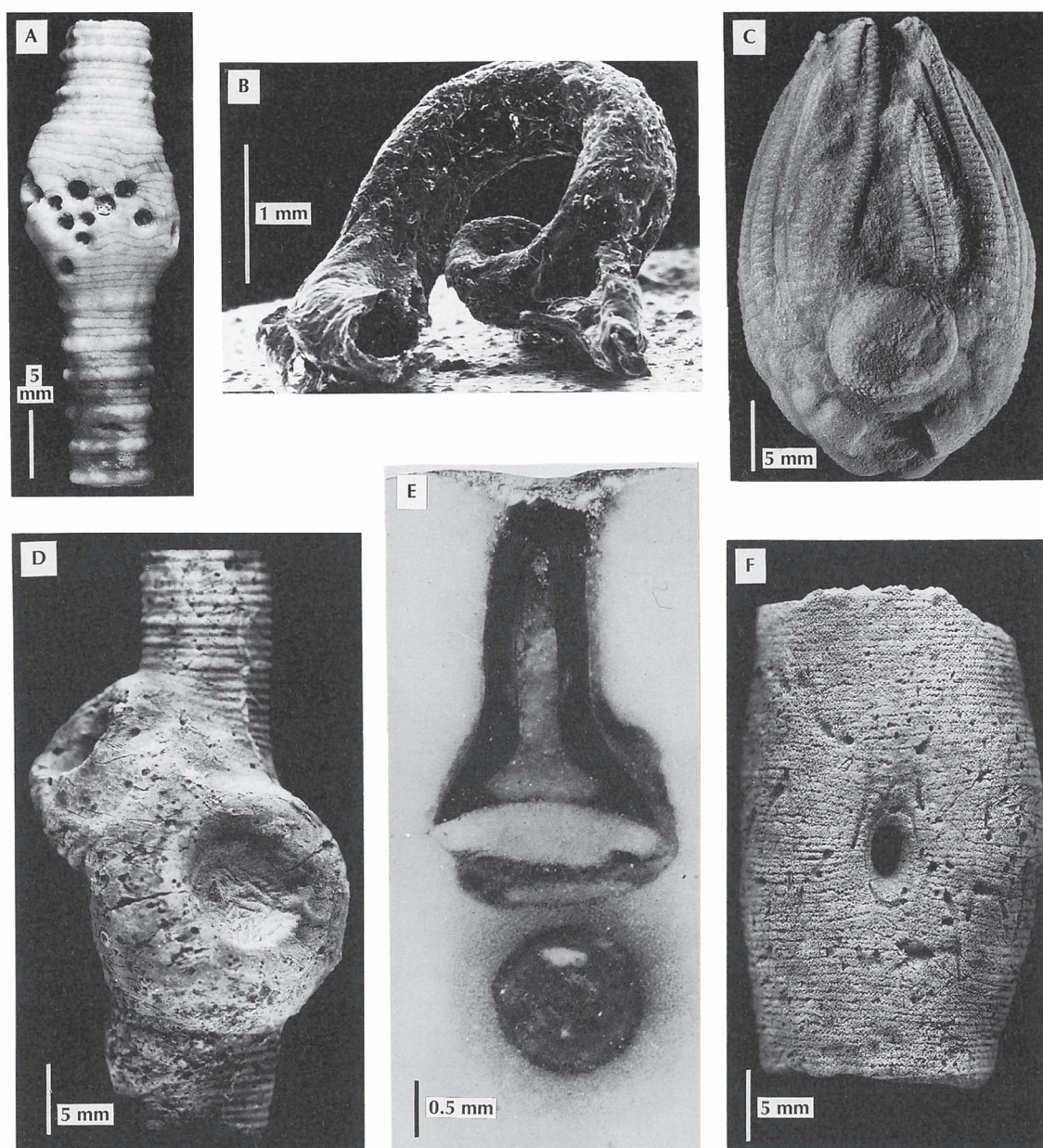


Fig. 2 A, Swelling and associated pits on crinoid stem; Silurian, Gotland. (After Franzen 1974.) B, 'Tubotheca' from the graptolite *Dictyonema*; Ordovician, Sweden. (Photograph courtesy of P.R. Crowther.) C, Gall-like swelling with two pits on calyx of the crinoid *Eucalyptocrinites caelatus*; Silurian, Ontario. (From Brett 1978.) D, Gall-like swellings on a crinoid stem; Devonian, Morocco. (From Franzen 1974.) E, Transverse section of *Phosphannulus* in a crinoid stem (note axial canal at base of figure); Permian, Kansas. (From Welch 1976.) F, Inflated crinoid with central hole; locality uncertain. (From Franzen 1974.)

goniatites and Silurian tentaculites) can be attributed to platyhelminth infestation is speculative, especially as it appears that a variety of foreign bodies could provoke pearl formation. Phosphatic calculi that occur in some residues with conodonts have been tentatively ascribed as a response to parasitic attack, while similar structures have been recorded also in association with Silurian bryozoans (Oakley 1966).

Another category of disturbance that has been moderately well documented is a variety of galls and other tumour-like swellings in trilobites ranging in age from Middle Cambrian to apparently the Devonian. The parasite is believed to have been housed beneath the exoskeleton and survived the moulting intervals of the host. However, its original nature is entirely speculative, and the lack of specific siting suggests that it may not have targeted a

particular organ. Other blister-like structures have been described from Silurian brachiopods (so-called Ziegler's blisters) and also graptolites, although whether the former are of parasitic origin is not certain. A more dramatic example of infestation in sessile members (dendroids and tuboids) of the latter group, however, is recorded by vermiform tubules (Fig. 2B) that extend from the colony. These 'tubothecae' consist of immensely thickened cortex, and evidently represent an attempt by the zooids of the colony to encapsulate the parasite by secretory organs that in normal circumstances were employed in constructing the periderm. That these attempts were unsuccessful is evident from the open distal aperture of the tubotheca. Although the cortical coating appears to have mimicked the vermiform nature of the parasite, its affinities are unknown and so far as is known the related pterobranchs of the Recent do not host similar parasites. Examples of vermiform traces within rugose corals have been ascribed to parasites that gained access to the gastric cavity in order to gain food (Oliver 1983).

Although numerous Recent protozoans are known as parasites, the lack of hard parts and minute size means that the fossil record is effectively non-existent. Possible examples of parasitic foraminifera are known from the Cretaceous, but this inference remains speculative. In addition, possible ectoparasitism by ciliates or amoebae on Ordovician chitinozoans was documented by Grahn (1981).

It can be seen, therefore, that although parasitic activity can be traced to the Cambrian, the record is invariably slender and presents more a series of isolated vignettes than a complete story. Documentation is further hindered by the difficulty in deciding whether some fossil symbioses are genuinely parasitic. In particular, a number of epizoans, including those located within the mantle cavity of brachiopods and bivalves, probably verged on being parasites. It is noticeable, moreover, that unequivocal assignment of parasites to known groups is very seldom possible before the Jurassic, and it is no coincidence that the rise of modern faunas from this time strengthens uniformitarian assumptions.

Future research

While the fossil record provides at present only the outline of the history of parasitism, there is hope that future investigations will extend present knowledge. The growing roster of exceptionally preserved biotas may lead to new discoveries, especially as nearly all parasites are either soft-bodied or have

only delicate skeletons. In some such Lagerstätten the quality of preservation of soft tissue, including muscles, suggests that encapsulated parasites may be identified. Another possibly fruitful source of investigation are coprolites, not least because many parasites release prodigious quantities of eggs whose tough walls would raise fossilization potential.

Other symbiotic associations in the fossil record may provide useful analogies to the origins and evolution of parasitism. At present, e.g., it is not clear whether parasitism arises from a shift of a more benign association, or represents a more abrupt invasion. It is, however, apparent that in some examples commensalism can persist for millions of years without the balance deteriorating to the detriment of one partner. One of the best known of such associations, that between Palaeozoic crinoids and their coprophagous gastropods (platyceratids), persisted for c. 200 million years without a shift towards a parasitic mode of life. There is also evidence that in some commensal associations the rate of morphological evolution in the host exceeds that of its partner.

If the fossil record of a parasitic association could be traced in sufficient detail, it might be possible to determine whether the parasite weathered host extinction. Particular interest revolves around monospecific associations, as the adaptive advantages of having a restricted host repertoire are not always apparent. It may be that an escape avenue is opened by paedomorphic mutants restricting their life style to the secondary host, until a new primary host can be found after the extinction event. Such evolutionary 'bottle-necks' may well be of particular importance in driving parasite evolution.

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4.15 Palaeopathology

L. B. HALSTEAD

Introduction

Palaeopathology is the study of ancient disease and, by its very nature, must be restricted to lesions that affect fossilizable materials. The healing of shells damaged during life is commonly observed, but only among vertebrates, with their internal skeletons, have any systematic attempts been made to study trauma and disease.

Palaeontologists have often failed to recognize the effects of disease, and hence misinterpreted material. This is exemplified by the description of the first complete skeleton of Neanderthal man. For most of the twentieth century, reconstructions of Neanderthal man have portrayed a shambling, almost ape-like posture with a bull-neck and head thrust forward — the stereotype of our brutish caveman ancestor. Apart from the incisors this individual had lost all his teeth and must have been about 60 years old. The neck vertebrae were severely distorted by osteoarthritis, as indeed was most of the vertebral column. The posture and gait attributed to this skeleton may have been accurate, but they were of a diseased old man and were not attributable to the rest of his race.

The problems of interpreting fossils may be compounded when medical scientists identify features resulting from the processes of fossilization as pathological conditions. For example, it was claimed that a small coelurosaur dinosaur *Compsognathus* died from tetanus because the posture in death

mirrored that of a tetanic spasm. In fact, a drawing back of the head and raising of the tail in articulated skeletons is a normal consequence of flesh rotting away and shrinkage of fibrous connective tissue of ligaments, so the posture is entirely a post-mortem effect.

Some lesions are quite unambiguous, such as the wound in the skull of an Oligocene false sabre-tooth cat *Nimravus* which was stabbed in the head by a sabre-tooth *Eusmilus*. Although there was severe damage to the frontal sinuses, the wound healed. Nothing could have inflicted such a wound apart from the canine of a sabre tooth. In some instances, simply the pattern of tooth marks enables the nature of the predator to be identified; it may even be possible to reconstruct an attack in fine detail, as in the case of one ammonite bitten 16 times by a (presumably inexperienced) mosasaur.

Fracture healing

The vertebrate skeleton (especially the limb bones) may fracture when subjected to sudden trauma. However, bone has the ability to regenerate dead and broken parts, and healed fractures are not uncommon among fossil vertebrates. Generally, limb bone fractures occur in young animals, although they carry evidence of such events throughout their lives. Fracturing of limbs in adult animals usually leads to death and, as there is no sign of healing, it is not possible to determine whether the break

occurred during the animal's life or is a post-mortem effect.

The normal processes of fracture healing can produce bony structures that are easy to misinterpret. The first stage in fracture healing is the formation of a blood clot or *haematoma* callus, together with the necrosis or death of bone adjacent to the fracture. The haematoma is replaced by fibrocartilage but, on occasion, may become ossified. The original femur of Java Man, *Pithecanthropus erectus* (now known as *Homo erectus*), has an extensive, irregular bony excrescence on the upper part of the shaft; this has been interpreted as a bone cancer but probably represents the ossification of a haematoma.

The next stage in healing is the growth of a bony callus that completely surrounds and encloses the region of the fracture. Bony trabeculae replace the fibrocartilage callus, new bone is produced to reconstruct the limb bone and the necrotic bone is resorbed. Occasionally the bony callus is not resorbed, as occurred in a specimen of the sauropod dinosaur *Apatosaurus* where two tail vertebrae are united by a bony callus. This too has been interpreted as a bone cancer. There is a tendency for any evidence of the proliferation of bone to be attributed to cancer, whereas unequivocal bone cancer is virtually unknown in the fossil record.

Skeletal degeneration

Two major degenerative diseases affect the vertebrate skeleton: *osteoporosis* and *osteoarthritis*. In osteoporosis, the compact cortical bone is thinned and the trabeculae of the cancellous bone are similarly reduced. The outward shape of the bone is unchanged, but up to 75% of bone mass may be lost. No study of osteoporosis in the fossil record has been undertaken. Osteoporosis has been claimed among such marine reptiles as ichthyosaurs and plesiosaurs, but these are characterized by their light spongy bone — a feature of all aquatic tetrapods that is unrelated to this degenerative disease.

Osteoarthritis is a disease of the joints associated with ageing; it seems to begin with an alteration of the nature of the synovial lubricating fluid occasioned by disruption of the blood supply. The presence of blood in the fluid results in the lubricant ceasing to function adequately, so that the articular cartilage is plucked off. Eventually bone grinds directly onto bone, producing a highly burnished surface that looks like ivory and is termed *eburnation*. Abrasion of the bone induces a reactive proliferation around the margins of the joints. This

'lipping' or *osteophytosis* can generally be taken as evidence of advanced osteoarthritis. On occasions, this reactive proliferation may result in the fusing or *ankylosis* of adjacent bones. The fusion of dinosaur vertebrae in the mid dorsal region has been attributed to osteoarthritis but, as it only ever affects the two mid dorsal vertebrae, this particular fusion cannot be pathological.

A case of initially unrecognized osteoarthritis was present in a Jurassic shortnecked plesiosaur, *Liopleurodon macromerus*, where progressive increase in lipping of the vertebral centra of the neck was carefully documented in the description of the skeleton; in fact, this was a typical example of osteophytosis (Tarlo 1959).

Common examples of osteoarthritis were found among fossil cave bears. During their hibernation, the greatest mortality occurred among (1) young bears who had been unable to accumulate enough fat to see them through the winter; and (2) slow, old bears, who similarly had been unable to obtain sufficient food. The old bears were generally suffering from osteoarthritis, as evidenced by the osteophytosis of their vertebrae (Fig. 1).

Infections of the skeleton

Evidence for bacterial infections comes from their indirect effect on the skeleton. When infection in-



Fig. 1 Arthritic vertebra from Pleistocene cave bear. (From Halstead & Middleton 1972.)

vades the skin so that it reaches the surface of the bone, the periosteum is infected (a condition termed *periostitis*) and this in turn affects the underlying bone. The surface becomes necrotic and develops a characteristic pitted texture. If the infection invades the cavity of the bone, the condition is termed *osteomyelitis*. Bacteria proliferate and pus accumulates within the cavity. Sinuses develop to drain away the pus and large areas of bone become necrotic. The necrotic bone is replaced by bony outgrowths developed from the surviving healthy bone. This mixture of necrotic and proliferating tissue gives the bone a characteristically roughened surface (Fig. 2).

Where bacteria gain entry into deep tissues, they may become 'walled up' to form an abscess. If this occurs adjacent to hard tissue (such as alongside the root of a tooth) a cavity is eroded to accommodate the developing abscess. This can be seen in the teeth of large mammals, such as elephants (Fig. 3; Bricknell 1987).

A more direct involvement in the destruction of skeletal tissues by bacterial infection is seen in *periodontal disease*. At the edge of the gums, between the teeth, particles of comminuted food may become trapped. The bacteria create their own micro-environment with a low pH, causing the tooth to be dissolved away at the gingival margin. This leaves a characteristic horizontal groove (Bricknell 1987), encouraging further infection, and facilitating the trapping of further food particles. Infection gradually travels down the periodontal membrane, the zone of collagenous fibres which embed the tooth in its alveolus or socket. Dental abscesses in particular develop at the apex of the roots of the teeth, where the travelling infection comes to rest. It is here that the cavitation of the roots and surrounding bone begins to develop.

Patterns of disease

The study of skeletal diseases has concentrated on fossil man and, more recently, on animal remains from archaeological sites (Baker & Brothwell 1980). The palaeontological literature has passing records scattered among the descriptions of fossils. Recently, in a preliminary study of diseases in Quaternary elephants, Bricknell (1987) documented the prevalence of certain diseases through time (Fig. 4). The incidence of periodontal disease in particular showed a striking correlation with climatic changes. This may not have been a direct effect, and was more likely related to the greater diversity of plant

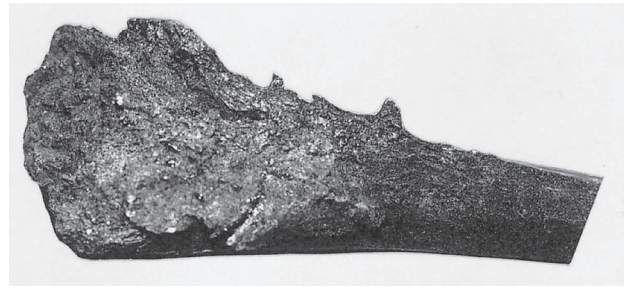


Fig. 2 Osteomyelitis of rib from woolly mammoth. (From Bricknell 1987.)

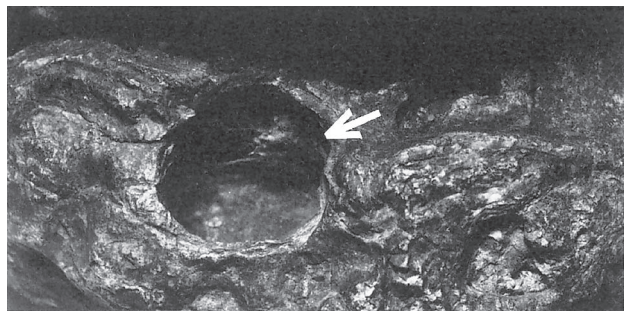


Fig. 3 Cavity in root of tooth from straight-tusked elephant. (From Bricknell 1987.)

life and an increase in fruiting plants which provide a suitable substrate for the bacteria that cause periodontal disease. The distribution of other types of disease, such as other bacterial infections, follows a comparable pattern, but the Wolstonian cold period seems to have an unusually high incidence. Curiously, fractures of limb bones seem to be confined to the interglacials, with the exception of the last (Devensian) glaciation. The distribution of osteoarthritis also seems to follow a climatic pattern, with an increased incidence in the warmer interglacials.

There has always been an underlying assumption that, with the possible exception of diseases associated with ageing (such as osteoarthritis), prehistoric life was especially healthy. The results of Bricknell's survey suggest that patterns of disease match climatic regimes. The spread of disease is often tacitly attributed to the activities of man, but this study of Quaternary mammals demonstrates the success of pathogenic bacteria in the more humid, warmer climatic regimes, without any encouragement from the activities of human beings.

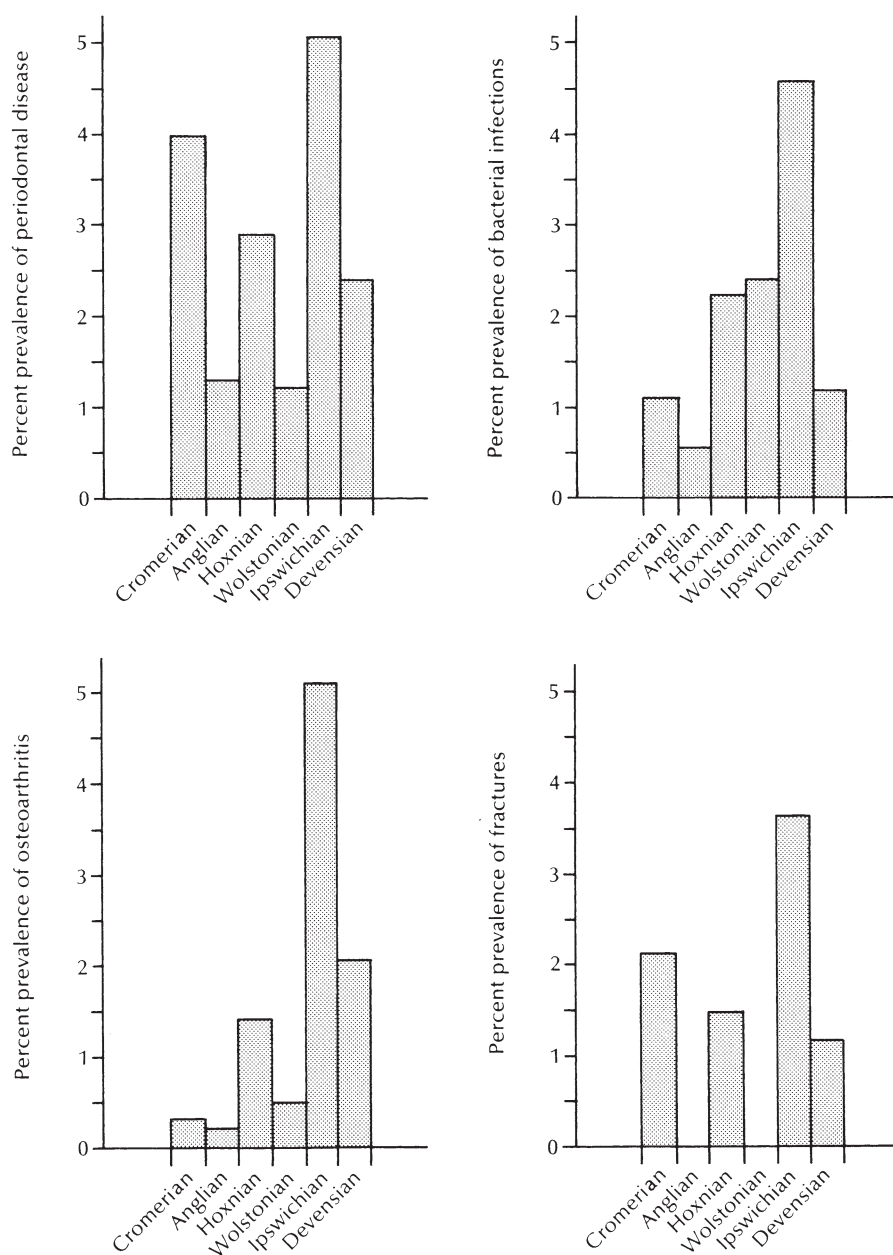


Fig. 4 Distribution through time of disease and trauma in Quaternary elephants. (From Bricknell 1987.)

Pseudopathology

The study of palaeopathology requires a detailed knowledge of both pathology and the processes of fossilization. One of the major problems is in identifying specific pathologies and distinguishing them from pseudopathologies. The action of boring bivalves can simulate dental abscesses; burial in an acidic environment can result in the surface erosion of bone, which can mimic periostitis or even osteomyelitis. Even the excavation of fossil bones can produce pseudopathologies: depressed fracturing

of skull bones may result simply from pressure on the overlying sediments, while digging implements can produce pseudohunting injuries. Erosion of the bone surface can often be produced by rootlets. Saprophytic fungi attack bone, and they are known from the time of the first bone preserved in the fossil record. In general, however, a close examination of the details of surface structure and also in cross-section (as a thin section under the light microscope) will determine the authenticity or otherwise of the supposed pathologies.

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4.16 Trophic Structure

J. A. CRAME

One of the most exciting breakthroughs in community palaeoecology in recent years was the discovery that fossil assemblages can be classified according to the feeding characteristics of their constituent species. This resulted in an entirely new way of comparing and contrasting palaeocommunities.

The trophic structure of a community can be defined as the cumulative feeding habits of its component species. These feeding habits are in turn based on two fundamentally different food chains: a grazing one centred on green plants and a detritus one centred on dead organic matter. Both these chains are terminated by predators. It is important to emphasize at the outset the distinction between feeding habit and trophic level. Whereas the former relates to what an organism eats, the latter refers to its position in the steps of energy transfer (Scott 1976). Each species occupies a specific position (or positions) in a food web (Fig. 1).

Marine biologists had, of course, been classifying feeding mechanisms for many years. However, their schemes were based largely on features such as food particle size, and little attention was paid to precisely what was eaten or where. These were just the sorts of details that were of interest to the community palaeoecologist, and, when added to existing schemes, produced a number of basic feeding groups (or trophic categories). Several simplified classification schemes for benthic marine invertebrates are now in existence (Table 1) (Walker & Bambach 1974).

When fossil communities were analysed using these new schemes, it became apparent that the vast majority of species fell into just three basic categories: suspension feeders, detritus feeders, and predators (Table 2). In fact, so striking was this regular tripartite division that it was suggested that these categories could form the end members of a triangular (or ternary) diagram and be the basis of a rapid system for classifying palaeocommunities

Table 1 A simplified classification of marine invertebrate trophic groups. (Adapted from data given by Walker & Bambach 1974.)

Group	Feeding habits
1 Suspension feeders	Higher level (epifaunal or infaunal)
2 Suspension feeders	Lower level (epifaunal or infaunal)
3 Deposit feeders	Sediment–water interface (epifaunal)
4 Deposit feeders	Shallow, in-sediment (infaunal)
5 Deposit feeders	Deep, in-sediment (infaunal)
6 Browsers	(Epifaunal)
7 Predators	(Passive or active; epifaunal or infaunal)
8 Scavengers	(Epifaunal or infaunal)
9 Parasites	

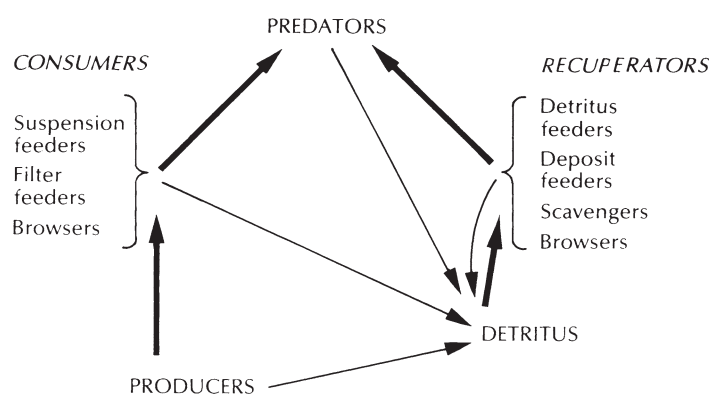


Fig. 1 The relationship between feeding habit and trophic level. Within each of the basic food chains (a consumer one based on green plants and a recuperator one based on dead organic matter), species of various feeding habits can be arranged into trophic levels at each stage of energy transfer. Heavy arrows = energy-flow pathways; light arrows = donors of organic detritus. (From Scott 1976.)

Table 2 The principal marine invertebrate trophic groups (Data from Walker & Bambach 1974, and Scott 1976.)

Group	Food and feeding method	Examples
1 Suspension feeders	Food – small particles such as phytoplankton and zooplankton; dissolved and colloidal organic molecules; resuspended organic detritus. Feed by – flagellae, ciliated lophophores, ctenidia and tentacles.	Sponges, anthozoans, hydrozoans, stromatoporoids, bryozoans, brachiopods, many bivalves, some gastropods, some annelids and crustaceans, pelmatozoans and graptoloids.
2 Deposit feeders*	Swallow or scrape particulate organic detritus, living and dead smaller members of benthic flora and fauna, and organic-rich grains.	Some crustaceans, echinoids, ophiuroids, bivalves, gastropods and annelids; scaphopods, holothurians.
3 Predators	Either active search and seizure (involving swallowing whole, biting and chewing or external digestion) or passive (waiting for prey to pass) techniques.	Larger anthozoans, cephalopods, many gastropods, some annelids and crustaceans, asteroids, some echinoids and ophiuroids.

* In palaeontological studies, deposit feeders are usually included in the more general category of ‘detritus feeders’. This also includes scavengers, which eat larger particles and dead organisms upon and within the sediment (e.g. some gastropods), and most browsers (or herbivores). The latter are first level consumers that scrape, rasp, or chew live algae and other plants (e.g. *Amphineura* and some gastropods).

(Fig. 2; Scott 1976, 1978). In practice, it was found that precise habitat requirements needed to be recorded too, and so a second ‘substrate-niche’ triangle is usually depicted alongside the ‘feeding-habit’ one (Fig. 2). Substrate-niche names are usually appended as prefixes to the feeding-habit ones, giving a community a title such as ‘vagrant-epifaunal, detritus-suspension feeding’.

One of the obvious applications of this method of describing trophic structure is in differentiating contemporaneous communities within particular environmental settings. For example, both Cretaceous and Cenozoic communities occurring along onshore–offshore gradients plot in distinctive fields within the ternary diagrams (Fig. 3; Scott 1978). Although the database is still comparatively small, it is also possible to trace the trophic groups associated with certain habitats through time.

For example, in lower shoreface and nearshore communities between the Early Palaeozoic and the Cretaceous, there was a marked shift from epifaunally- to infaunally-dominated detritus-suspension feeding types (Scott 1976).

There are, of course, other ways of depicting the trophic structure of palaeocommunities. In his very detailed analysis of macrobenthic assemblages from the Korytnica Clays (Middle Miocene, central Poland), Hoffman (1977) used a series of tables to illustrate ‘trophic–substrate–mobility niches’. These are simple two-dimensional diagrams which plot food location (infauna and epifauna, subdivided into mobile and sessile) against feeding category (suspension and deposit feeders, predators etc., subdivided into various positions in the water column and sediment). Each of these diagrams is supported by a histogram showing the distribution

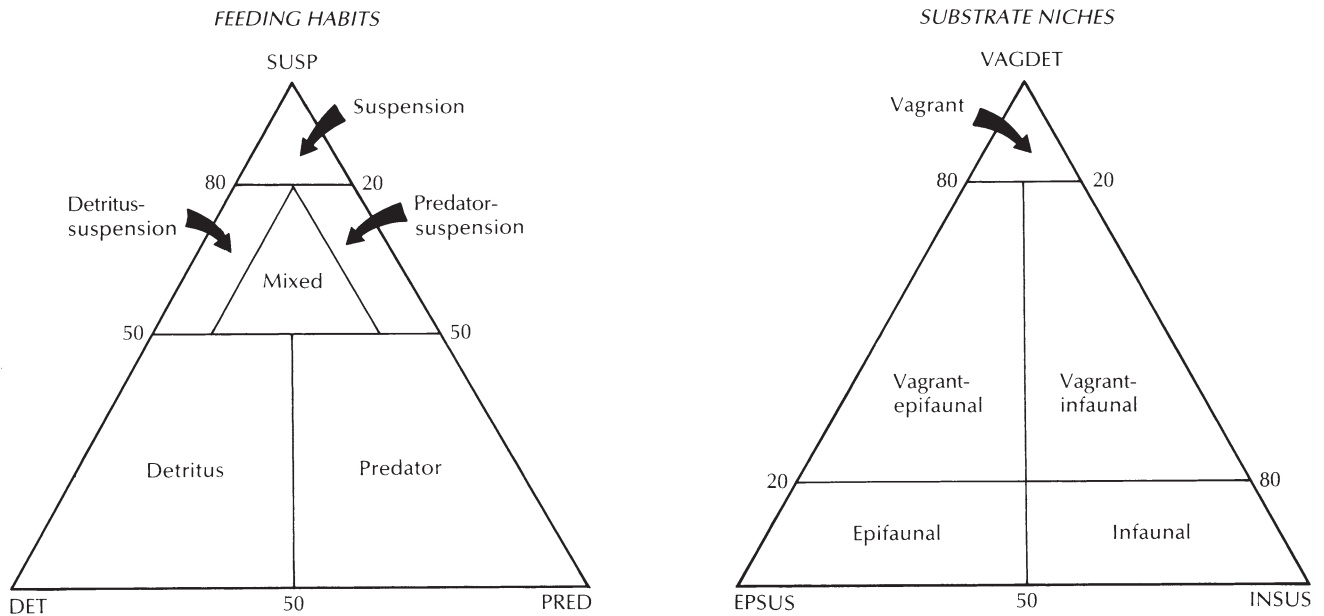


Fig. 2 Descriptive trophic structure. SUSP = suspension feeders, DET = detritus feeders, PRED = predators, VAGDET = vagrant detritus feeders, EPSUS = epifaunal suspension feeders, INSUS = infaunal suspension feeders. Within the feeding habit triangle, a suspension-feeding community consists of more than 80% suspension-feeding species. A detritus-suspension community would be one composed of 50–80% suspension feeders, 10–50% detritus feeders, and less than 10% predators. Within the substrate niche triangle, an infaunal community comprises less than 20% vagrant organisms and no more than 50% epifauna. A vagrant-infaunal community comprises 20–80% vagrant animals and more infauna than epifauna. (From Scott 1976.)

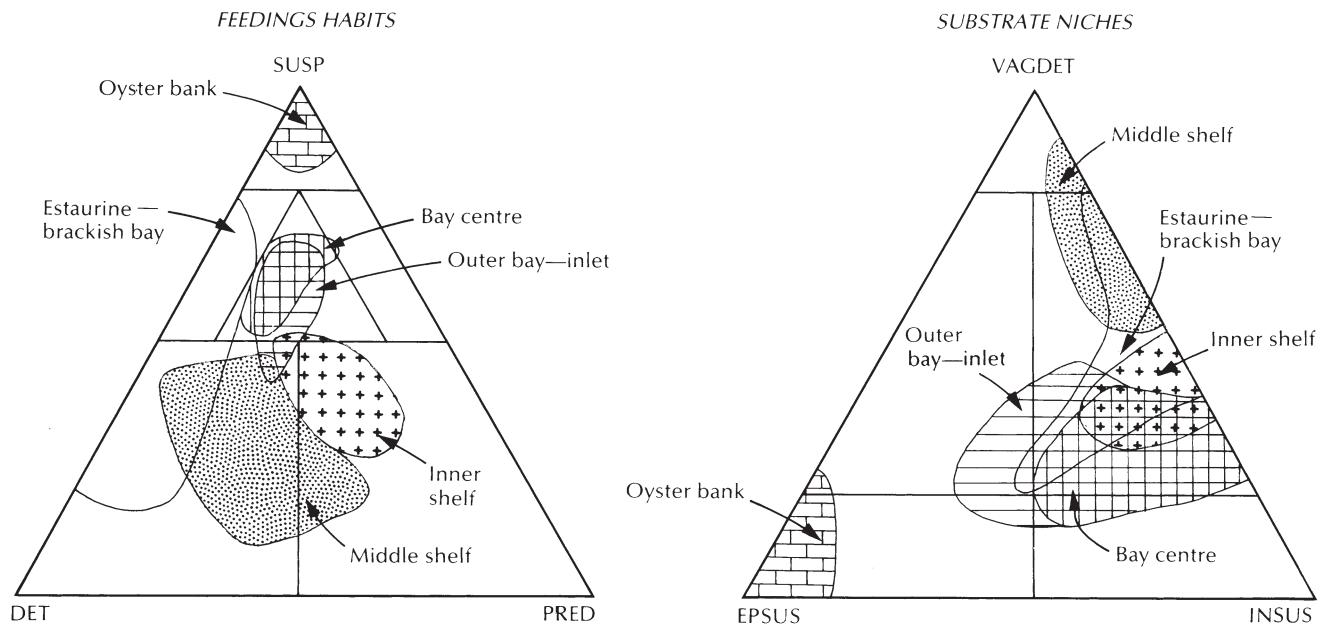


Fig. 3 Trophic structure of some Cenozoic shallow-marine environments. Note that the only significant overlap occurs between Bay centre and Outer bay—inlet communities. Abbreviations as for Fig. 2. (From Scott 1978.)

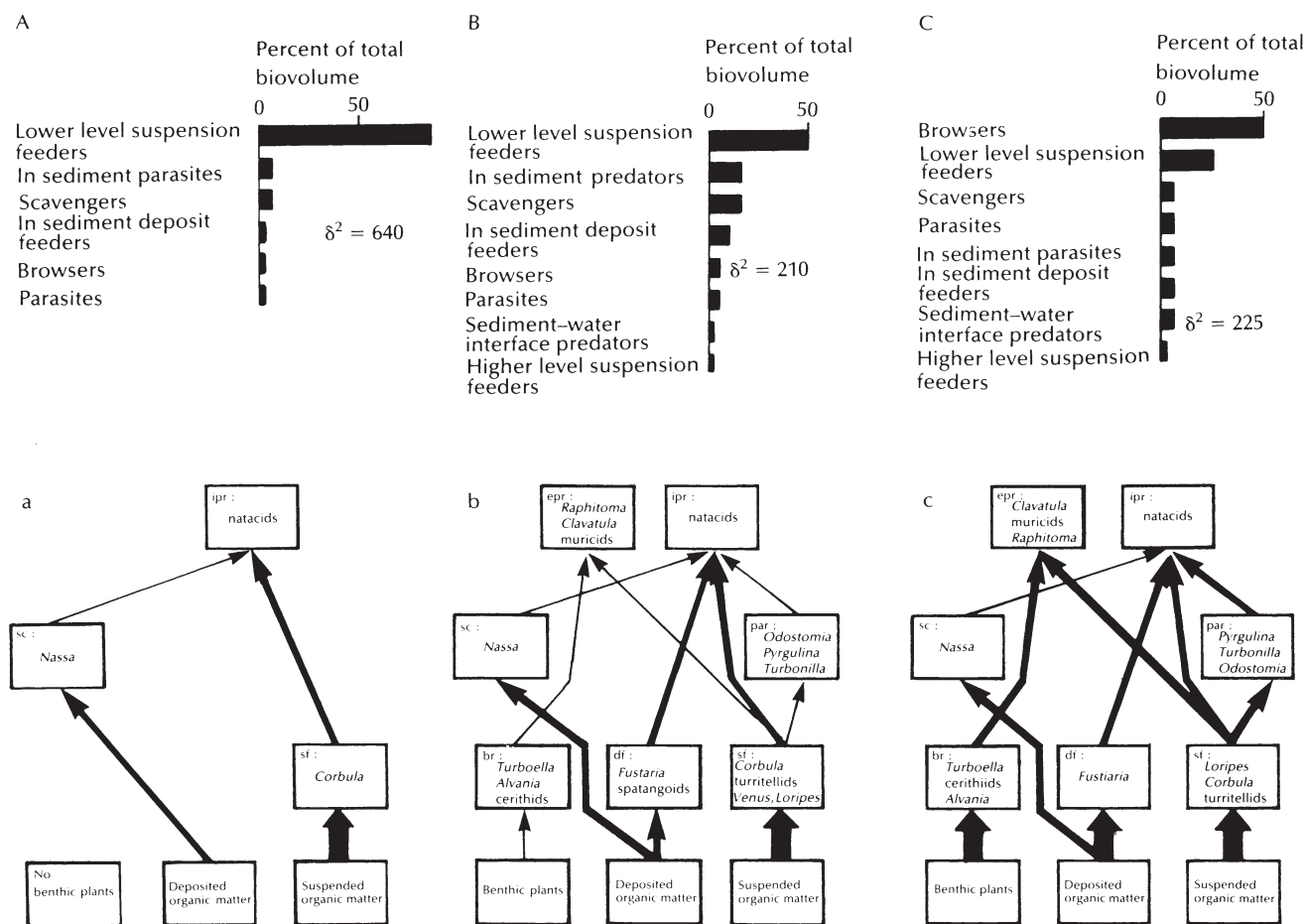


Fig. 4 Trophic structure of three communities from the Middle Miocene Korytnica Clays, central Poland. Their frequent association is thought to reflect an ecological succession in a small shallow basin from a pioneer stage on barren muddy bottoms (*Corbula* community), through an intermediate stage (*Corbula*–scaphopod community), to a mature (climax) stage marked by the development of extensive seagrass stands (*Turboella*–*Loripes* community). An index of trophic uniformity within each community is derived from the dispersion of total biovolume amongst the various trophic groups (upper histograms). The index (or Nesis) value (δ^2) is the total biovolume of the assemblage divided by the number of trophic groups (see Hoffman 1977, p. 244). The high value in the *Corbula* community (A) is due to the dominance by a single species (the shallow-burrowing, suspension-feeding bivalve *Corbula gibba*). Much lower values in the *Corbula*–scaphopod (B) and *Turboella*–*Loripes* communities (C) can be linked to the wider dispersion of biovolume amongst the various trophic troupes.

The trophic web reconstruction for the *Corbula* community (a) is a very simple one based largely on a short suspension-feeder food chain. However, in the succeeding *Corbula*–scaphopod community (b) the web is appreciably more complex, and comprises two distinct subwebs (the suspension-feeding and deposit-feeding ones). Finally, in the climax *Turboella*–*Loripes* community (c) there are at least three equally important subwebs. Note that separate subwebs can be terminated by the same predator (top row of boxes). epr = epifaunal predators, ipr = infaunal predators, sc = scavengers, par = parasites, br = browsers, df = deposit feeders, sf = suspension feeders. (From Hoffman 1977, 1979.)

of biovolumes (representing biomass) amongst the various trophic categories (Fig. 4). In fact, the preservation of these assemblages was so good that trophic webs could be constructed for each community. Although this entailed estimating unpreserved components of the ecosystem, and involved a considerable amount of simplification, the resulting models proved to be valuable aids in the study of community structure and function (Fig. 4).

One potentially serious drawback to the techniques outlined so far is the fidelity of the fossil record (Section 3.12). Estimates of the proportion of a biocoenosis unlikely to be preserved (i.e. the soft-bodied component) range from 50 to 75%. Deposit-feeding groups of annelids and arthropods are particularly likely to be missing from a fossil assemblage. There may, however, be ways of partially offsetting this problem. Firstly, there may be direct

evidence of deposit feeders in the form of either faecal pellets or bioturbation. It may also be possible to calculate the proportion of individuals at various trophic levels in an assemblage and compare these ratios with those in a modern community. Using estimates of the efficiency of energy transfer between trophic levels of 10–20%, it may be clear, for example, that the ratio of carnivores to primary consumers is too high. In that case, soft-bodied organisms must have been an important component of the ecosystem (Stanton *et al.* 1981).

A trophic web based solely on numerical abundances arguably gives a poor picture of the original community. Ideally, trophic analyses should be based on estimates of energy flow from one level to another and this would appear to be beyond the scope of the palaeontologist. Nevertheless, in a pioneering study of molluscan assemblages from the Middle Eocene Stone City Formation of south-east Texas, Stanton *et al.* (1981) suggested several ways in which abundance data could be refined to make them more representative of the passage of energy through a community. Such techniques, which are particularly amenable to certain predatory gastropod taxa, include the production of survivorship curves (Fig. 5). From these it is apparent that *Polinices aratus*, the numerically dominant predator, was subject to very high juvenile mortality. In at least five other predatory taxa (such as the fascioliid *Latirus moorei*; Fig. 5), it was found that a much greater proportion of their populations attained adulthood; these were thus inferred to have been more important components of the Stone City Formation foodweb (Stanton *et al.* 1981, Table 2).

Another useful measure of a species' significance in a trophic web may be its total biomass, for in predators this should be related to the biomass of prey consumed. The number of prey required to support a predator population is proportional to the amount of energy input necessary to produce and maintain the predator population (Stanton *et al.* 1981; see their Table 2 where biovolumes are used to calculate the biomass formed by secondary production). In the Stone City Formation, biomass values again showed that predatory gastropods, such as *Latirus moorei*, two species of turrids, and *Retusa kellogii* (opisthobranch), were much more prominent than *Polinices aratus* (the naticid). The influence of the turrids is particularly important as they fed on non-preserved prey (primarily polychaetes). If further turrids have similar size-frequency distributions, it has been estimated that the proportion of soft-bodied prey in the food web

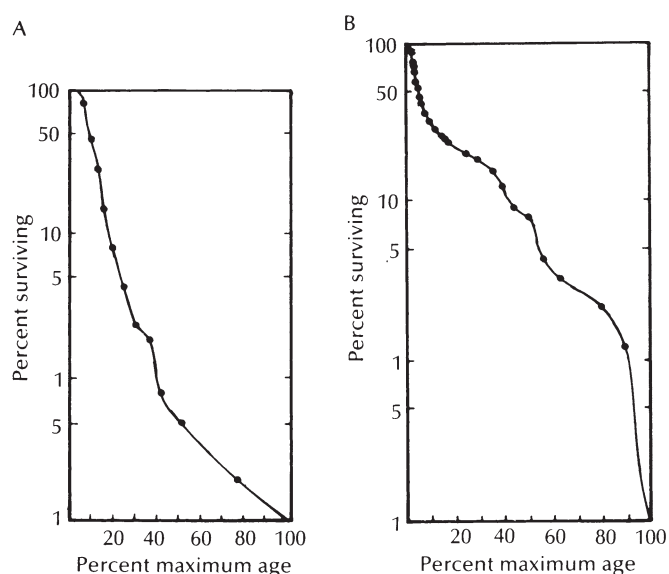


Fig. 5 Survivorship curves. A, for *Polinices aratus* (naticid). B, for *Latirus moorei* (fascioliid). Note that size values were converted to age values using the logarithmic relationship that exists between the two. (From Stanton *et al.* 1981.)

may have been as high as 50%.

A more serious problem faced by the community palaeoecologist is that many benthic organisms defy simple trophic classification. Take, for example, those types that can readily interchange between deposit- and suspension-feeding strategies. These include representatives of several polychaete families, a number of ophiuroids and irregular echinoids, and a significant proportion of the bivalve superfamily Tellinacea (species of *Scrobicularia*, *Macoma*, *Tellina*, etc.). By switching between these two feeding modes, organisms may well be able to overcome periods of food shortage. This in turn would permit colonization of unpredictable habitats, such as estuaries or shallow temperate seas.

Some recent discoveries from the deep seas have had a profound effect on our understanding of trophic structure. Not the least of these is the startling revelation that many abyssal bivalves (perhaps 25–30% of the total fauna) are predators! Using a raptorial inhalant siphon, representatives of at least four families within the subclass Anomalodesmata (Parilimyidae, Verticordiidae, Poromyidae and Cuspidariidae) actively seek out and capture prey (Fig. 6) (Morton 1987). The giant tube-worm and bivalve communities recently discovered around certain sea floor volcanic vents (such as in the Galapagos rift) also display some very unusual feeding traits. Forms such as the pogonophoran *Riftia pachyptila*, the vesicomyid bivalve *Calytogen*

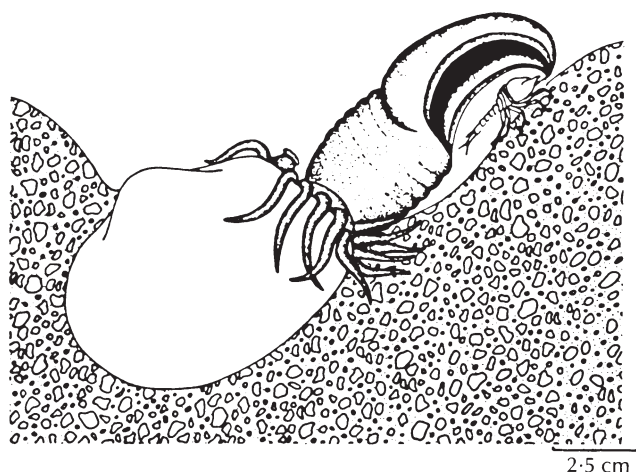


Fig. 6 In predatory bivalves active prey capture is achieved using an inhalant siphon which can be rapidly extended (through hydraulic pressure changes within the mantle cavity). The siphon is retrieved (with the prey enclosed) by the action of pallial retractor muscles. Here the poromyid *Poromya granulata* uses a large hood at the end of the siphon to ensnare a tiny crustacean, the principal diet item of predatory bivalves. (From Morton 1987.)

magnifica (giant white clam), and the mytilid *Bathymodiolus thermophilus* are now known to be gutless. They obtain nutrients by means of endosymbiotic sulphide-oxidizing bacteria contained in the gill regions. These act to detoxify the sulphide-rich volcanic waters, producing a series of carbohydrates and amino acids that can then be utilized by the organisms as a food source. Similar gutless bivalves, together with forms possessing hypertrophied alimentary systems, have recently been shown to characterize other environments with extraordinary energy sources (such as the anoxic muds associated with marine grass beds and the effluent from fish farms and pulp mills). Among these are shallow-water solemyid, lucinid, and thyasirid bivalves, all of which possess rich supplies of sulphide-oxidizing bacteria (Fig. 7; Reid & Brand 1986). No longer can bivalves such as these be simply classified into either deposit- or suspension-feeding categories.

Finally, a note of caution should be expressed about interpreting the role of predators within palaeocommunities; in many instances it is virtually impossible to pinpoint their exact prey. Some Recent species of whelks, for example, feed on representatives of up to eight separate phyla, and the Nassariidae (also frequently interpreted as carion feeders) include at least one deposit-feeder (*Ilyanassa obsoleta*). Similarly, the Cymatiidae contains an algal-grazer (*Apollon natator*) and several

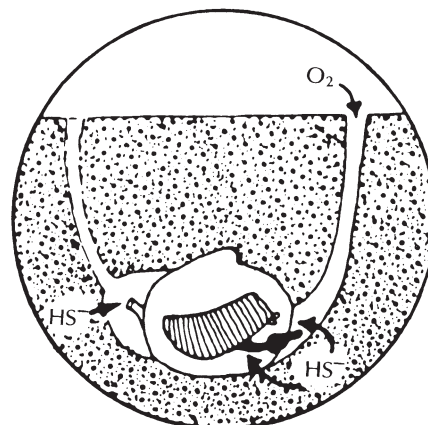


Fig. 7 Sulphide-oxidizing symbiosis in the Lucinacea. In addition to suspension-feeding, many species within this bivalve superfamily obtain nutrients from endosymbiotic bacteria. In common with other groups demonstrating this phenomenon, lucinaceans live in deep burrows; it is thought that these (or complementary tube-like structures) are essential for the accumulation of both dissolved oxygen (from surface waters) and hydrogen sulphide (from the enclosing anoxic muds). Besides having a hypotrophied gut, lucinaceans typically display prominent ctenidia (vertical shading) which are packed full of bacteriocytes. The postero-dorsal margins of the gills are typically fused with the muscular mantle edge and it is thought that this arrangement may facilitate the pumping of sulphide-rich waters over the bacteriocytes (especially via the exhalant siphon). Anterior foot in black. (From Reid & Brand 1986.)

members of the Cancellariidae are probably parasitic (Taylor 1981).

Clearly, the maintenance of trophic structural analysis as a viable technique in palaeoecology is going to involve the very close collaboration of palaeontologists and biologists.

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4.17 Evolution of Communities

A. J. BOUCOT

It has long been known that fossils do not occur in a random manner. Particular mixtures of taxa, with particular relative abundances, characterize every time interval and environment. These ‘mixtures’ may be termed *communities*, employing biological parlance, although some prefer the term *association* or *assemblage*. Some palaeontologists refuse to use the term *community*, preferring *assemblage*, because of the absence of soft-bodied organisms. But it is obvious that virtually all descriptions of both modern and fossil communities deal with only a small part of the total biota present, i.e. the term *community* commonly approximates to the definition of a *guild*. Thus, we have rodent communities, coral communities, brachiopod communities, trilobite communities, planktic foraminiferal communities, benthic foraminiferal communities, lichen communities, larger carnivore communities, tree communities, etc.

Palaeontologists and biostratigraphers of the nineteenth century did not pay much attention to what are now termed fossil communities. This probably reflects their overwhelming concern with dating and correlation of beds in which emphasis was placed on the taxa common to different collections. The study of communities emphasizes instead the taxonomic differences between collections. Only in the latter part of this century has extensive interest developed in communities, particularly because of their potential for providing a better understanding of past environments.

A community may be defined as *a recurring association of taxa, in which relative taxonomic abundances remain more or less fixed*. For example, brackish water

oysters remained dominant in their community from the later Mesozoic to the present, just as the brachiopod *Pentamerus* remained dominant in its community from the later Early Silurian to the earlier Late Silurian, and the shells in a lower dominance, later Cenozoic *Pecten* community retained similar relative abundance through time.

The term *biofacies* is used in various ways (Section 4.18): some workers employ it when referring to what are essentially biogeographical units, such as a ‘Gondwanic biofacies’; others employ it for very broad environmental units within a biogeographical unit, such as ‘deep-water biofacies’ or ‘black shale biofacies’; still others use it for individual community types, such as ‘pentamerid biofacies’, ‘stringocephalid biofacies’, or ‘brackish water oyster biofacies’.

Community evolution deals with the Darwinian species-level evolution shown by the genera present in specific community types. These narrowly defined ‘community types’ may be referred to as *community groups* (Boucot 1978, 1981, 1983, 1986, 1987; Fig. 1); the term was devised to describe a community type undergoing species-level evolution among its constituent genera in evolutionary time — particularly the less abundant, commonly more endemic, and more stenotopic genera. Those who study modern communities commonly name them after the dominant, abundant taxa — those which evolve very little — whereas the changes in communities chiefly affect the uncommon genera and their rapidly evolving species. It makes sense, therefore, to name community groups after the abundant, slowly evolving genera, and the com-

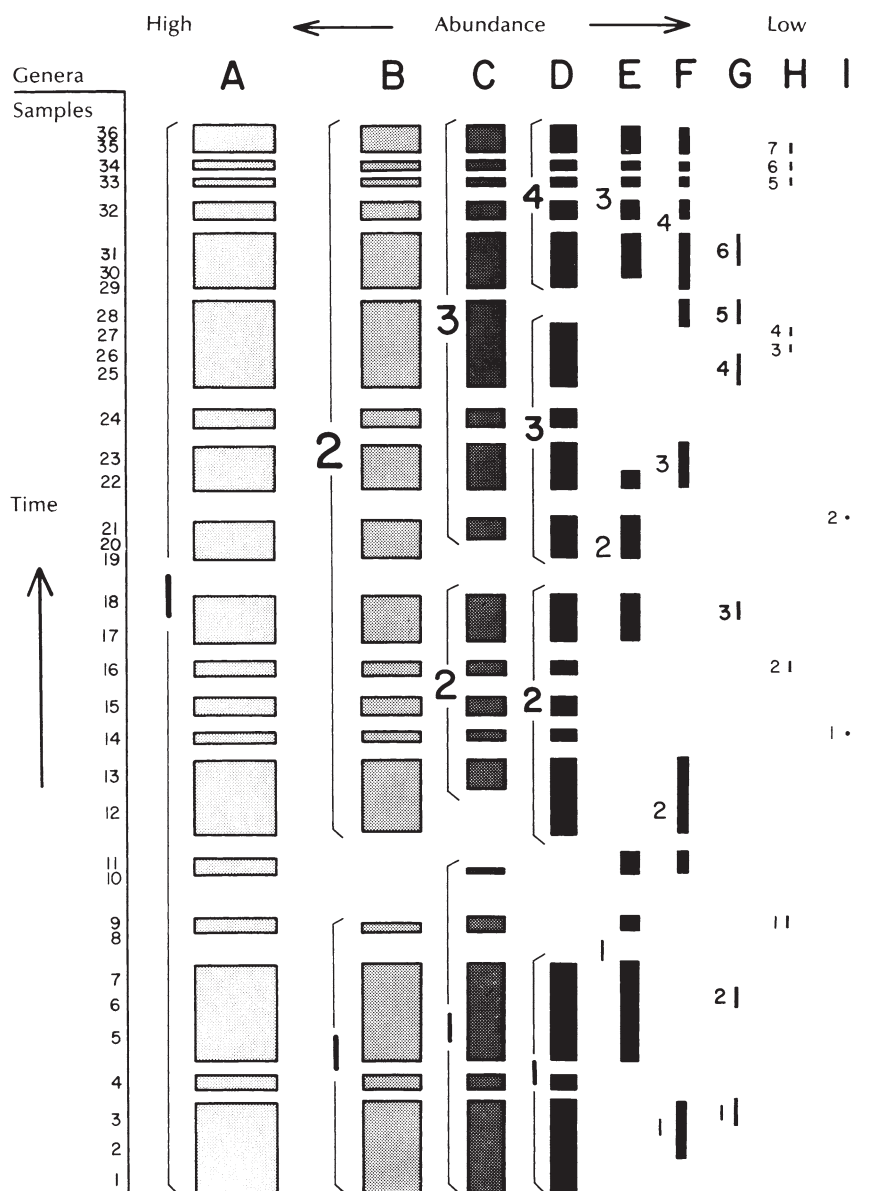


Fig. 1 Diagrammatic representation of the fossil record of a *community group* through an interval of time measured in a few fives or tens of millions of years. The genera (lettered) and their described species (numbered) are assigned line widths based on their relative abundance as individual specimens. Note that species of the rarer genera tend to be both more rapidly evolving, and also have a much poorer fossil record correlating with their numerical abundance (i.e. are rarer) as individual specimens. The ancestor–descendant relations are presumably phyletic in nature. Sampling gaps indicated on the figure may be due to non-deposition, erosion, collecting failure (commonly caused by covered intervals), or presence of another community group because of local or regional environmental shifts. (From Boucot 1983.)

munities after the less common, rapidly evolving genera and their time-sequences of species.

An excellent example of community evolution was provided by Ziegler (1966), whose late Lower Silurian time sequence of species of the brachiopod *Eocoelia* has been well tested in eastern North America, the U.K., and Scandinavia (Boucot 1975) for nearshore, subtidal marine, level-bottom, moderate turbulence, possibly turbid conditions. The

Eocoelia community, as now construed, commonly comprises more than 90% *Eocoelia* shells, chiefly disarticulated in a muddy matrix, and with a high population density (so-called 'pearly beds'). [*Community succession*, defined as the presence of one taxon making it possible for the same area to be subsequently colonized by a second taxon, is *not* community evolution.]

Community evolution also deals with the initial,

quantum evolution of distinctly different, narrowly defined biofacies types from either newly evolved higher taxa or new mixtures of previously existing taxa. This phase of community evolution sees the first appearance of new community groups, and is followed by subsequent species-level changes within the initial genera, particularly, the less abundant ones.

The community groups present within any *one* major subdivision (level-bottom environment, reef complex of communities, sponge forest, pelmatozoan thicket, etc., as well as comparable non-marine units) have concurrent times of appearance and disappearance from the base of the Cambrian to the present. These concurrent times within the level-bottom environments mark the boundaries of *ecological–evolutionary units* (see below).

The level-bottom community groups of the marine environment tend to be not only dominant in terms of area occupied and overall numbers of specimens per time interval, but also in stratigraphical duration. The fossil record consists of a fixed number of time intervals, each one of which contains a relatively homogeneous biota. Boucot (1983, 1987) termed these units *ecologic–evolutionary units*. There are 12 such major units from the Cambrian to the present (Fig. 2).

Within marine benthic environments the level-bottom community groups have the full time range of the appropriate ecological–evolutionary units, but the non-level-bottom community groups (reef complex communities, pelmatozoan thicket communities, sponge forest communities, bryozoan thicket communities, etc.) commonly appear in time significantly later than the level-bottom groups. They do, however, commonly share the same extinction time.

The reasons for relative fixity of community groups are poorly understood. They may involve a significant measure of both coevolution at one trophic level or another, and of stabilizing selection in so far as the taxa present are concerned. Biologists have not yet uncovered any very effective means of measuring levels of coevolution in modern communities, although they suspect that there are major differences in levels of coevolution (viz. the coral reef community complex vs. level-bottom communities, and tropical rainforests vs. grasslands).

The boundaries of ecological–evolutionary units commonly mark major extinctions followed by adaptive radiations (Boucot 1983, 1987). Ecological–evolutionary subunit boundaries, such as those between the Silurian–Devonian and Mississippian–

Ecological–Evolutionary Units	Time Intervals	Major* Extinctions	Major* Adaptive Radiations	Major* Community Reorganizations	Major* Dispersal Event
	Ediacarian	E1	A1	C1	
I	LЄ	E1	A1	C1	
II	M–UЄ	E5	A3	C3	
III	LO	E5	A3	C3	
IV	M–UO	E2	A2	C2	
V	$\frac{2}{3}$ LS			C3	
VI	$\frac{1}{3}$ LS– $\frac{1}{2}$ UD	E2		C4	D1
VII	$\frac{1}{2}$ UD			C4	
VIII	C + P	E1	A2	C2	
IX	L Tr			C4	
X	M–UTr	E3	A2	C2	
XI	J + K	E4	A2	C2	
XII	Cenozoic			C4	

Fig. 2 Phanerozoic ecological–evolutionary units. E = major extinctions (numerals indicate rank, 1 highest), A = major adaptive radiations (numerals indicate rank, 1 highest), C = major community reorganizations (1 highest), D = major dispersal event. (From Boucot 1987.)

Pennsylvanian, are similarly marked by minor extinctions followed by minor adaptive radiations.

One consequence of community evolution at the species level is that the number of species (and genera) does not change significantly *within* a specific community group in any specific ecological–evolutionary unit, i.e. diversity is not in a continual state of flux.

There have been many suggestions made about the factor(s) involved in extinctions (Section 2.12), but few about those controlling adaptive radiations. Major, time-concurrent, adaptive radiations within the same portion of the ecosystem affect varied, taxonomically unrelated organisms and many different community groups. The level of randomness involved is unknown, as is whether the presence of potentially empty niches is most important (most adaptive radiations tend to follow major extinctions). However, the absence of the reef complex of communities during many ecological–evolutionary units (Middle–Upper Cambrian,

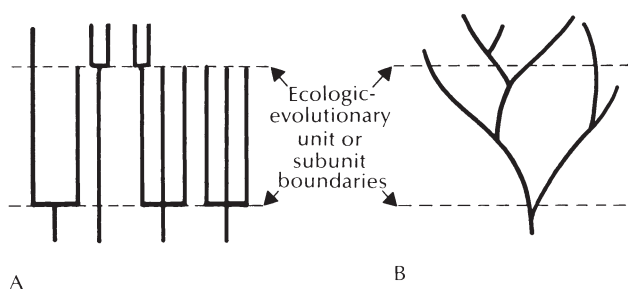


Fig. 3 A, Cladogenetic pattern characteristic of the organisms belonging to individual ecological–evolutionary units. Note that cladogenesis is restricted to that brief moment in time when new community groups first appear. Cladogenesis here refers to *metacladogenesis*, i.e. quantum evolution mediated phenomena. Biogeographically mediated *diaccladogenesis* can, of course, occur anywhere within an ecological–evolutionary unit. *Metacladogenesis* refers to major cladogenetic events resulting in new families and higher taxa (Boucot 1978), whereas *diaccladogenesis* refers to minor cladogenetic events giving rise merely to new genera and species, such as the post-Miocene species occurring on either side of the Isthmus of Panama. B, Cladogenetic pattern of the standard, hypothetical, random through time type, which ignores the constraints imposed by what we know about community evolution. Note that this view permits cladogenesis to occur at any time within an ecological–evolutionary unit, and is also consistent with important changes in species-level diversity within any ecological–evolutionary unit as contrasted with the conclusion outlined in A. Such random, within-unit changes in diversity do not occur. It is only by ‘superimposing’ family trees derived from ecologically unrelated, major parts of the global ecosystem (such as level-bottom, reef complex of communities, pelmatozoan thickets, etc.) that one can simulate the unnatural random cladogenetic pattern. (From Boucot 1986.)

Lower Ordovician, Famennian half of Upper Devonian, Mississippian, Lower Triassic) suggests that the empty niche possibility is incapable of explaining all the facts.

Another consequence of community evolution is that the commonly presented, hypothetical, random type of family tree (Fig. 3B) does not agree with the

more espaliered tree (Fig. 3A) indicated by species-level evolution within community groups. This is a consequence of the fact that the community types (community groups) within each ecological–evolutionary unit remain relatively constant in their generic content. The evolutionary changes consist of phyletic-anagenetic changes within each genus (particularly the more stenotopic, more endemic genera, that also tend to be far less common as individual specimens). There is not a constantly changing overall species- or genus-level diversity within either individual community groups or within major portions of the ecosystem, such as the level-bottom, during any one ecological–evolutionary unit. An apparently ever changing overall diversity may, however, be observed statistically if disparate portions of the ecosystem are grouped together uncritically, (such as the level-bottom, reef complex of communities, sponge forests, bryozoan thickets, pelmatozoan thickets) which commonly have different origination times within any particular ecological–evolutionary unit.

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4.18 Biofacies

P. J. BRENCHLEY

Definition

The term *biofacies* refers to 'the total biological characteristics of a body of rock' (Moore 1949) but has been used in two rather different ways: in a stratigraphic sense to refer to 'a body of rock which is characterized by its fossil content which distinguishes it from adjacent bodies of rock', and in an ecological sense to refer to 'a biota or association of fossils which characterize a region or body of rock'.

Biofacies in stratigraphy

When the term 'biofacies' is used in a stratigraphic sense, the emphasis is on a geographically or vertically restricted body of rock which is distinct because of its fossil content (Fig. 1). The stratigraphic value of biofacies is illustrated by the widespread use of fossil names to characterize particular rock units, e.g. *Pentamerus* Beds, 'Posidonia' Shales (Posidonienschiefer), and *Wilsonia* Shales. These three examples can be used to illustrate the role of biofacies and show how biofacies differ from biozones.

The *Pentamerus* Beds are a varied sequence of mudstones with interbedded calcareous sandstones containing abundant *Pentamerus oblongus* developed in the Lower Silurian of the Welsh borderland. *Pentamerus* is part of an ecologically controlled community and occurred diachronously across the shelf during the Lower Silurian transgression. Thus the *Pentamerus* biofacies occurs locally wherever the depth, substrate, and other combination of ecological factors were suitable. Its presence is environ-

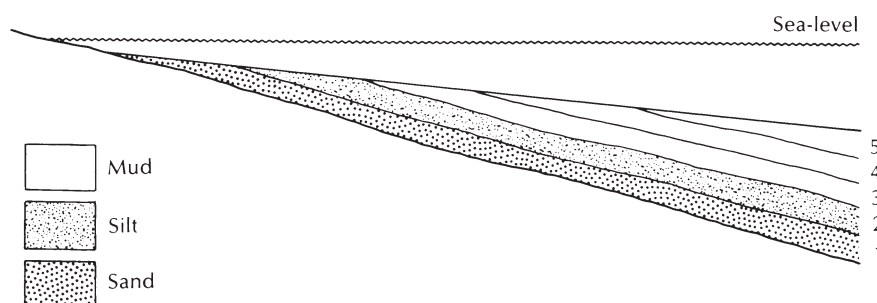
mentally significant, but it has no value in correlation.

The 'Posidonia' Shales (Section 3.11.6) are bituminous, laminated shales of Toarcian (Jurassic) age, widely developed throughout Germany. They are characterized by the exceptional preservation of a variety of fossils, but particularly by an abundance of the bivalve 'Posidonia' (= *Bositria*). The onset of deposition of bituminous shales was apparently nearly synchronous over a wide areas and was related to the Toarcian transgression. However, deposition of the shales persisted longer in basin areas than on more positive regions, so the upper boundary is diachronous. The Toarcian sequence can be effectively zoned and correlated using the common ammonites, while the 'Posidonia' Shales represent a distinctive unit in that succession reflecting particular environmental conditions which determined a characteristic biota.

The *Wilsonia* Shales (cf. *Sphaerirhynchia* (*Wilsonia*) *wilsoni*) are a subdivision of a generally monotonous sequence of black shales and thin laminated siltstones found at the shelf to basin transition in the Ludlow (Silurian) of the Welsh borderland. The slight vertical changes in the rather sparse fauna are more obvious in the field than any changes in lithology, and it has been found useful to recognize a sequence of *Cyrtoceras* Mudstones, *Wilsonia* Shales, and *Orthonota* Mudstones. The *Wilsonia* Shales pass shelfwards into mudstones with a deep-shelf fauna and basinwards into shales containing mainly graptolites. Here we have an example of a mappable field unit comparable to a formation, but more effectively recognized on the basis of its fauna.

The use of fossil names to characterize formal

Fig. 1 Distribution of five biofacies developed during a transgression. Note that biofacies 1 and 2 coincide with lithofacies, but that biofacies 3, 4, and 5 are developed within a single mud lithofacies.



lithostratigraphic units is now deemed invalid and most of the 'biofacies' have either been redefined as formations based on their total lithological and biological characteristics, or have become obsolete. Particularly distinctive biofacies will, however, probably persist in the literature as informal units.

Ecological use of biofacies

The term 'biofacies' in an ecological and environmental sense is usually used to express the lateral or vertical variation in biota in relation to differences in environment. For example, trilobite biofacies in the Cambrian of the western U.S.A. have been described in terms of their environmental position, i.e. inner shelf, outer shelf and slope. Biofacies have also been applied in an even more general sense to express broad lateral changes in biota according to environment. Thus, House (1975) described the marine Devonian of Europe in terms of *biofacies regimes* which represent the characteristic Devonian faunas of the *near shore*, *shelf*, and *basinal* regions. In a more detailed biofacies analysis of Ordovician rocks in the Upper Mississippi Valley, U.S.A., factor analysis was used to define seven faunas distributed over 65 000 km² of outcrop within a single member (the Mifflin Member of the Platteville Formation). Each of these bivalve/brachiopod faunas differed and their geographical occurrence could be mapped to show biofacies distributions in an extensive, shallow epeiric sea (Bretsky *et al.* 1977).

One of the valuable facets of the term 'biofacies' is that it can be applied to faunal associations identified with very different degrees of taxonomic precision. In some environmental studies it may be important to define the associations by the assemblages of species, but in other situations a very broad characterization of the fauna, such as 'coral/brachiopod association', may be appropriate.

Terms commonly used in palaeoecology which are closely related to biofacies are: *faunal association*, *community*, *palaeocommunity*, and *benthic assemblage*. The first three of these terms attempt to express a distinct association of taxa which probably lived together. The regional distribution of faunal associations or communities on the sea floor or in a body of rock can be referred to as a 'biofacies'. For example, Bretsky (1969) described three communities, the *Sowerbyella*–*Onniella* community, the *Orthorhynchula*–*Ambonychia* community, and the *Zygospira*–*Hebertella* community, from Upper Ordovician rocks of the Central Appalachians. The communities were recognized as distinct associations of taxa, and the geographical distribution of such communities can be shown on a biofacies map (Fig. 2).

The term *benthic assemblage* has been used by Boucot (1975) to identify communities which lived in the same position relative to the shoreline. Benthic assemblages are therefore approximately depth related, although temperature, substrate, and other ecological controls may be important in deter-

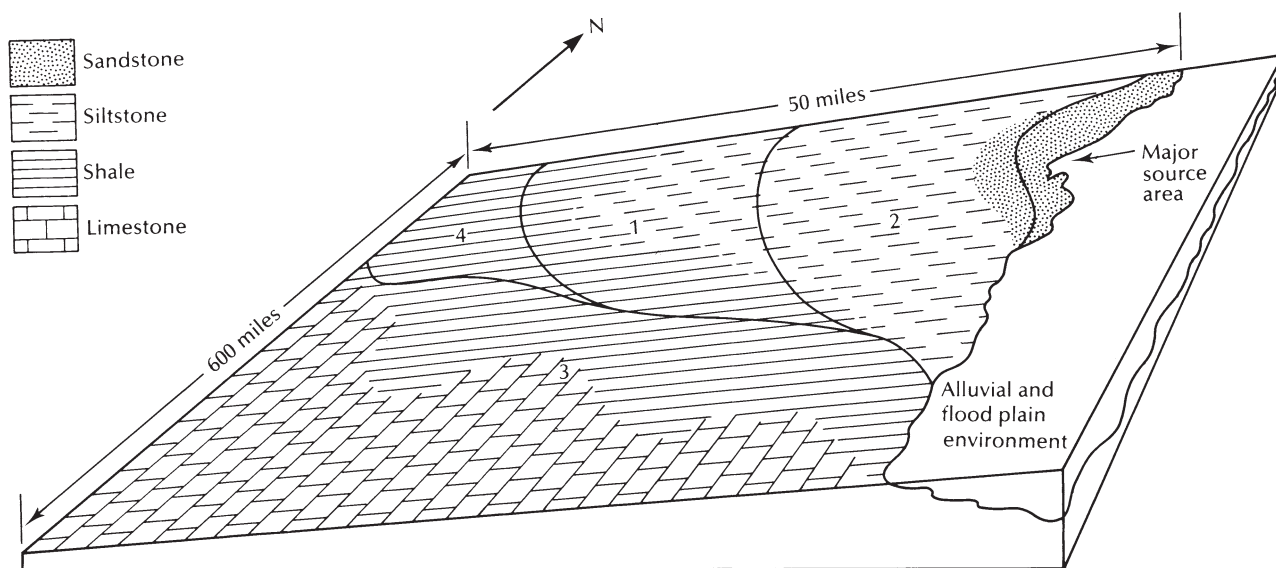


Fig. 2 Biofacies map of Upper Ordovician community distribution in the Central Appalachian region, U.S.A. 1 = *Sowerbyella*–*Onniella* community, 2 = *Orthorhynchula*–*Ambonychia* community, 3 = *Zygospira*–*Hebertella* community, 4 = offshore faunas. (After Bretsky 1969.)

mining their location. Boucot identified six benthic assemblages in his treatment of Silurian–Devonian communities. According to Boucot, nearshore and inner shelf faunas can be referred to benthic assemblages 1 and 2, mid-shelf faunas to benthic assemblages 3 and 4, and outer shelf and upper slope faunas to benthic assemblages 5 and 6 (Fig. 3). Faunas of quite different ages can be assigned to the same benthic assemblage because they have the same range of fossil groups though the taxonomic composition is different in detail. Such a similarity of faunas was recognized in nearshore carbonate communities of Ordovician and Devonian age and was characterized as *congruent communities*. They could equally well have been characterized as *ecological stable biofacies*. This usage has been applied to the persistent community found in dysaerobic sediments of Middle Devonian–Early Permian age, which has been referred to as the *dysaerobic biofacies* (Section 4.19.4).

Recent biofacies

The concept of biofacies draws strength from studies of modern benthic faunas. Petersen (1915), using grab samples in Danish waters, showed that there were areas of the sea floor characterized by particular associations of bivalve, echinoid, and polychaete worm species. The distribution of these level-bottom communities is approximately related to distance offshore and depth of water, and hence it is possible to map out approximately shore-parallel biofacies. In general, ecological zonation of faunas on level-bottom shelves is relatively simple because: (1) there is an absence of dense flora, and hence the communities are principally influenced by physico-chemical aspects of the environment and biotic interactions amongst members of the community; (2) level-bottoms lack micro-landscape and are environmentally relatively homogeneous, so the faunal associations occupy a single habitat rather

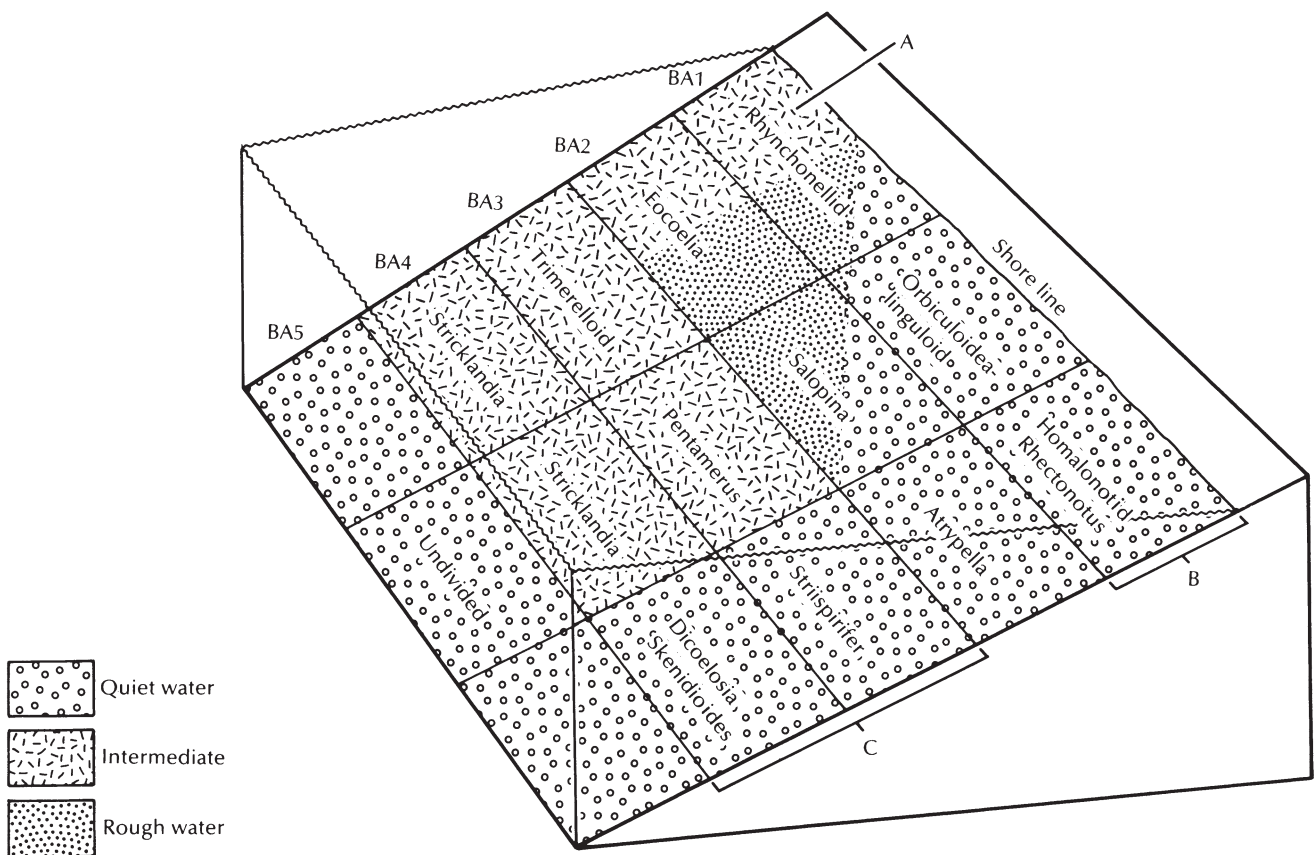


Fig. 3 Relationship between Silurian epifaunal benthic assemblages and communities. Three possible applications of the term 'biofacies' are shown. A, Term refers to rocks containing a particular community. B, Term refers to all nearshore communities. C, Term refers to rocks containing a group of communities with some taxonomic similarities. (After Boucot 1975.)

than a mosaic of micro-habitats; (3) substrate type approximately reflects the hydrodynamic conditions of the area and is often roughly correlated with several physico-chemical parameters, such as turbidity, mobility of substrate, oxygen, and organic content; (4) a large proportion of level-bottom dwelling animals are suspension feeders and the trophic structure is relatively simple (Thorson 1971).

It has been claimed by Thorson that level-bottom communities which occupy approximately the same position relative to shore (e.g. belong to the same benthic assemblage) have a similar appearance wherever they are found in the world. These belts of similar communities, with different species but sharing some genera were termed *parallel communities*.

Communities which inhabit rocky shorelines and to a lesser extent carbonate-producing regions have a much more complex and patchy distribution. Although there is a general shore-parallel distribution of communities in carbonate regions, local heterogeneity of the sea floor, particularly where reefs are present, produces a mosaic pattern of biofacies on a local scale.

Biofacies distribution

Most marine biofacies are broadly related to water depth and sediment substrate, but other physico-chemical parameters, such as availability of oxygen, salinity, or substrate mobility may modify any simple distribution pattern. Biofacies which are preserved in adjacent positions in vertical sequence are believed to have generally occupied adjacent positions on the sea floor and therefore behave in a similar manner to lithofacies, according to Walther's Law. At any one time, biofacies distribution, reflecting the community distribution of that time, will be somewhat different in different faunal provinces, particularly if they belong to different climatic belts. In general, biofacies have a greater biomass and are more diverse in tropical than arctic regions, and tropical carbonate shelves are probably partitioned into more biofacies than are clastic shelves in colder regions.

In any one faunal province, biofacies generally show distinct changes in taxonomic diversity and biomass in any onshore to offshore transect. In modern environments, biofacies generally decline in biomass towards the deeper parts of the shelf and then rapidly down the continental slope. Diversity is usually low in any one nearshore environment, but because of the large number of nearshore

environments the total diversity of the nearshore region can be high. Diversity is relatively high across the continental shelves and can remain moderately high to the base of the slope, to depths as great as 4000 m. The pattern of onshore-offshore change in different for different parts of geological history, as will be described below.

Biofacies distribution in the Phanerozoic

Cambrian biofacies. On Cambrian clastic shelves biofacies containing trilobites, inarticulate brachiopods, and molluscs are rather poorly differentiated and no clear onshore-offshore trends have been defined. The very diverse, mainly soft-bodied, Middle Cambrian, Burgess Shale fauna of British Columbia (Section 3.11.2) is evidence that Cambrian faunas were far richer than is suggested by the shelly assemblages, and that ecological zonation may have been more refined than is recorded by the commonly preserved fossils.

In carbonate shelf and slope environments of the western U.S.A. a clear differentiation has been recognized between trilobite faunas living on the platform and shelf edge (*Hungaia* fauna) and a trilobite fauna which occupied deeper-water sites (*Hedinaspis* fauna).

Ordovician and Silurian biofacies. Following the extinction of a substantial part of the Cambrian fauna, there was a major radiation in Early Ordovician times which produced a varied benthic fauna of suspension-feeding animals with skeletons. These suspension-feeding faunas became partitioned into a number of biofacies, approximately related to water depth, in the early part of the Ordovician. Progressively during the Early and Middle Ordovician there was colonization of the deeper parts of the shelves (Sepkoski & Sheehan 1983). This established a pattern where about five or six communities (biofacies) occurred in any transect across a level-bottom clastic shelf in the later Ordovician and Silurian (see Fig. 3). The communities were generally brachiopod-dominated, but bryozoa, corals, and crinoids were also important elements, and trilobites and bivalves were often associated with the fauna (McKerrow 1978).

Nearshore biofacies typically had a low species diversity and a very variable biomass which could be high when environmental conditions were favourable. The faunas were characterized by articulate brachiopods, particularly large orthids,

bivalves, and sometimes inarticulate brachiopods such as *Lingula*. Along a traverse outwards across the shelf there was a general increase in taxonomic diversity towards the shelf margin, though there could be local areas of particularly high diversity in mid-shelf regions where carbonate build-ups developed. Abundance of fossils and total biomass was generally high into mid-shelf regions, but decreased towards the outer shelf and declined very rapidly down the slopes. The exact patterns of diversity and biomass depended on the depth of the shelf–slope break and the influence of other limiting factors, such as oxygen. Typical mid-shelf biofacies in the Silurian have diverse brachiopod faunas with pentamerids, atrypids, strophomenids, and orthids, with variable numbers of associated bryozoa, tabulate and rugose corals, crinoids, and

trilobites. In biofacies of greater shelf depths, tabulate corals, bryozoa, and crinoids are rarer, trilobites are relatively more important, and the brachiopod fauna, though still diverse, is commonly composed of relatively small-shelled forms. At the shelf edge the diversity and abundance of the brachiopod fauna declines sharply, and slope faunas are usually sparse with some trilobites and molluscs (and relatively more pelagic elements) with increasing depth.

This pattern of biofacies applies to clastic shelves in temperate regions. Diversity and biomass were generally lower in colder regions where there were fewer communities and the shelf was partitioned into fewer biofacies. In contrast, carbonate facies of tropical regions had very diverse faunas and a large biomass. Carbonate environments on broad epeiric platforms were often very extensive in the Lower

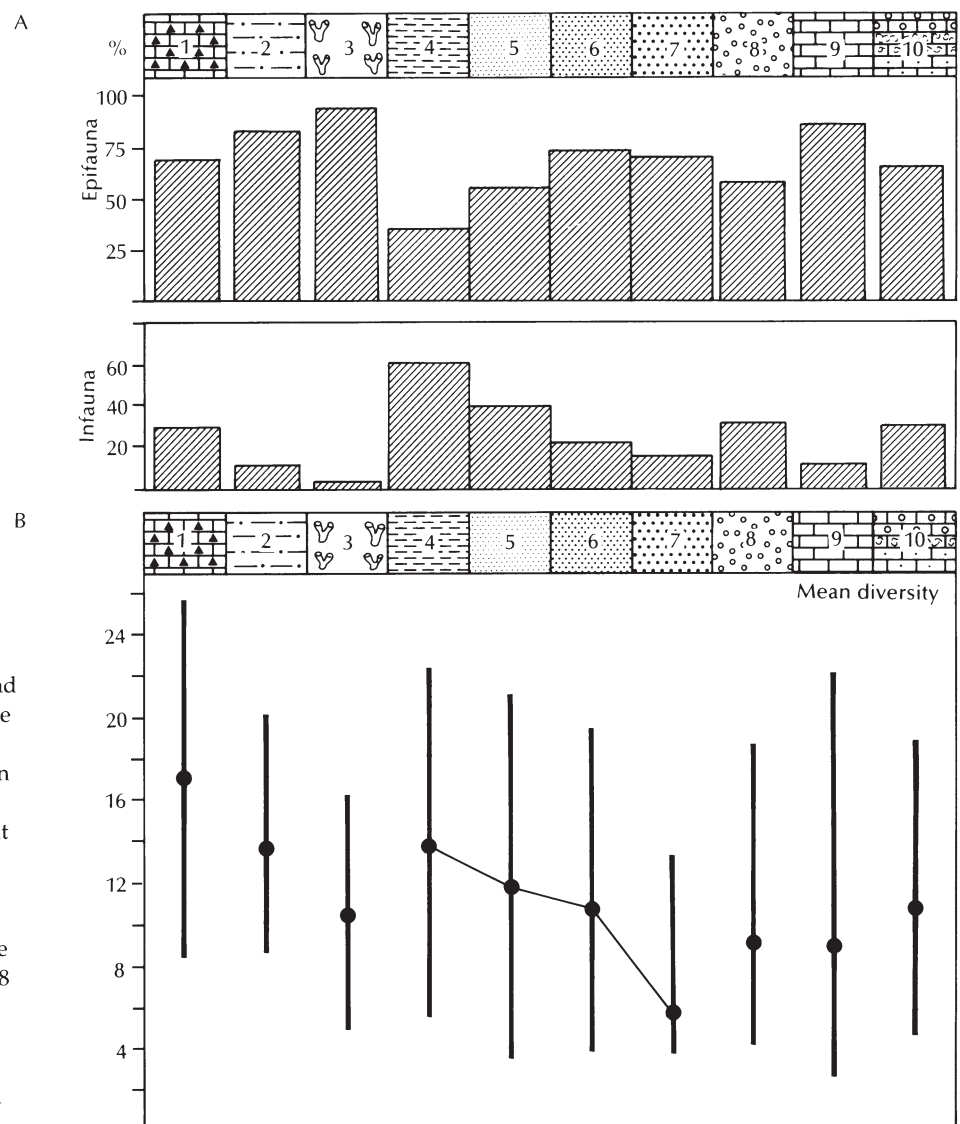


Fig. 4 A, Diagram to show the relative abundance of epifaunal and infaunal bivalves according to type of substrate in the Corallian. B, Diversity indices (using rarefaction method at 60 individual levels) of the macroinvertebrates in different substrates. 1 = condensed limestone, 2 = condensed ferruginous sediments, 3 = patch reefs, 4 = clays, 5 = silts, 6 = fine sand, 7 = medium-coarse sand, 8 = oolites, 9 = fine-grained limestone, 10 = coarse-grained limestone. Note diversity change between clays (4) and coarse sand (7). (After Fürsich 1976.)

Palaeozoic, giving rise to regionally developed biofacies. However, in areas where reefs were developed, the biofacies could be very patchy.

Upper Palaeozoic biofacies. The broad patterns of diversity and abundance established in the Lower Palaeozoic were probably continued into the Upper Palaeozoic. The largest changes in the appearance of biofacies arose from the increasing importance of terebratulid and productid brachiopods. There was a significant change in Devonian biofacies caused by the Late Frasnian extinction (Section 2.13.3) of the Pentameridea, Atrypaidea, and Orthacea and the subsequent enrichment of the rhynchonellid and productid faunas (McKerrow 1978).

Mesozoic biofacies. The end-Permian mass extinction (Section 2.13.4) destroyed the major part of the Palaeozoic benthic associations and new faunal associations established themselves in the Triassic. Mesozoic biofacies are generally dominated by bivalves with variable proportions of gastropods, brachiopods, echinoids, crinoids, and corals. The partitioning of level-bottom shelves into belts occupied by distinct benthic assemblages has not been clearly demonstrated in the Mesozoic, although there are obvious changes in faunal composition with increasing water depth. There is generally a correlation between taxonomic composition and substrate but, because some bivalves are eurytopic, this correlation is not always pronounced. A detailed study of Corallian (Jurassic) palaeoecology (Fürsich 1976) recognized 17 faunal associations occupying a range of environmental situations from nearshore to open shelf. Some of these associations showed a close correlation with substrate, others little or no such correlation. In general, deposit-feeding bivalves had a preference for fine silts or argillaceous silts, but avoided clays; epifaunal suspension feeders dominated condensed facies and patch reefs but avoided soft clay substrates; and infaunal suspension feeders were particularly common in clay substrates (Fig. 4). Mean diversities of the fauna were high in condensed facies and clays, and generally showed a marked decrease in diversity with increasing grain size (Fig. 4). This diversity–grain size relationship was interpreted to reflect an increasing environmental instability in

more energetic nearshore environments relative to the more stable offshore regions.

Tertiary to Recent. The end-Cretaceous extinction (Section 2.13.6) modified the Mesozoic biota by the loss of ammonites, belemnites, inoceramid and rudist bivalves, and several groups of gastropods. In addition, the abundance of brachiopods was reduced and many echinoid taxa disappeared.

Several groups which were often present in the Cretaceous, but in subordinate proportions, diversified in the Early Tertiary; predatory gastropods, Neogastropoda, polychaete worms, heterodont bivalves, the Veneracea, and Tellinacea all probably diversified at this time. Reef-building corals and associated algae also apparently diversified in the Eocene. Typical Tertiary biofacies are dominated by bivalves and gastropods, and from Miocene times had a taxonomic composition, at generic level, similar to biofacies found in the Recent.

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4.19 Fossils as Environmental Indicators

4.19.1 Climate from Plants

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Vegetational physiognomy

Vegetation, unlike marine organisms, is directly exposed to the atmosphere. The physiognomy (structure and composition) of environmentally equilibrated (climax) vegetation is in large part controlled by, and therefore reflects, climate (Wolfe 1979). Interpretations of climate based on vegetational physiognomy, foliar physiognomy, or wood anatomy are more reliable for pre-Neogene studies than taxon-dependent climate signals (those used in Nearest Living Relative — NLR — methods). Fundamental vegetational types can be recognized in modern vegetation and, provided water is not limiting, correlate with temperature regimes (Fig. 1). These vegetational types can be recognized with some confidence back to late Cretaceous (Cenomanian) times.

Features of leaves useful in determining palaeoclimate

Angiosperm vegetative organs exhibit considerable morphological diversity and flexibility with respect to climate. The following features are those of angiosperms except where indicated:

Leaf margins. In modern vegetation the ratio of non-entire (toothed) to entire (smooth) margined leaves correlates strongly with mean annual temperature (MAT) (Wolfe 1979; Fig. 2). Generally, in the Northern Hemisphere a change of 3% in this ratio corresponds to a change in MAT of 1°C. In the Southern hemisphere, with a higher proportion of evergreen taxa, a 4% change corresponds to 1°C. Because major tooth types had evolved by the Cenomanian, and because Cenomanian leaf margin ratios correlate with palaeolatitude, this technique seems applicable from the early Late Cretaceous to the present. A minimum of 20 leaf species are required at any one locality to make this technique reliable, and taphonomic factors have to be taken into consideration.

Leaf size. This is related strongly to temperature, humidity/water availability, and light levels. Large leaves occur in humid understories, and size decreases with decreasing temperature or precipitation. Size classes are used to characterize vegetational types and to construct leaf size indices (which are used to characterize overall leaf size parameters for a given vegetational type). In fossil assemblages leaf size suffers strong taphonomic bias.

Drip tips. Highly attenuated leaf apices occur most frequently in evergreen leaves in humid environments, and are particularly common in the understorey of multistratal rain forests. Drip tips may

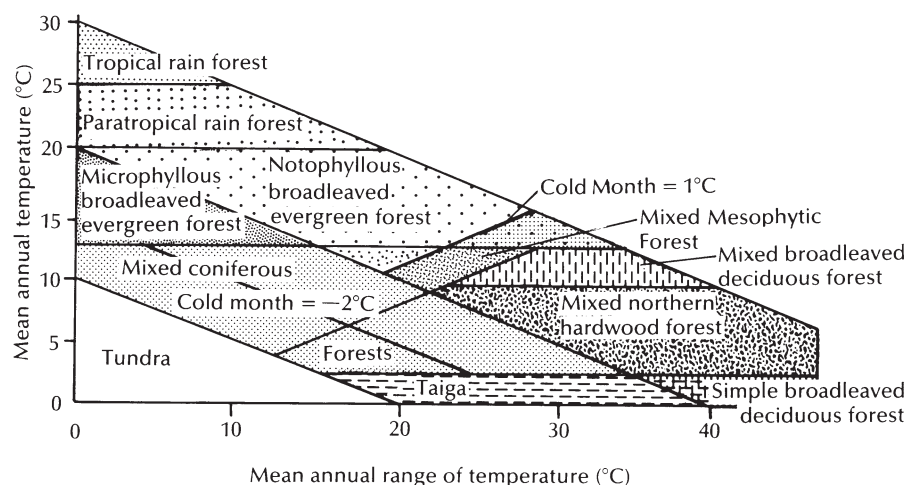


Fig. 1 Correlation of fundamental vegetational types with temperature regimes.

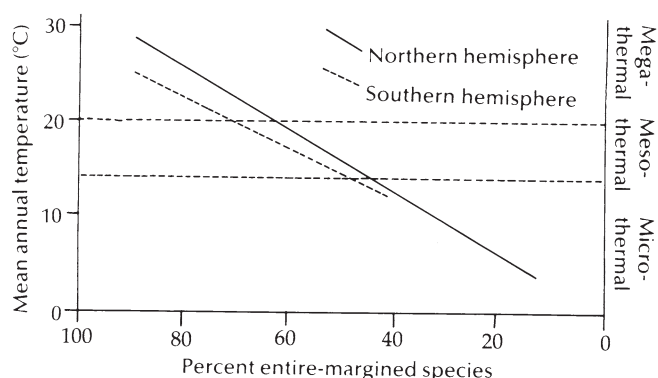


Fig. 2 Correlation of ratio of non-entire (toothed) to entire (smooth) margined leaves with mean annual temperature.

enhance drainage of surface water from the leaf and thus retard the growth of epiphytes.

Leaf texture. Leathery (*coriaceous*) leaves typically are evergreen and predominate in megathermal and mesothermal vegetation (see Fig. 2). Thin (*chartaceous*) leaves are typically deciduous and are most common in microthermal climax or successional mesothermal vegetation.

Leaf shape. Stream-side vegetation contains a high proportion of narrow (*stenophyllous*) leaves. Lobed or compound leaves (also associated with deciduousness) occur with greatest frequency in successional vegetation or understory communities, and therefore warn of bias in the climate signal. Thick cylindrical leaves in any plant group are evidence of aridity, growth in saline water, or an inefficient vascular system.

Leaf cuticles. In all terrestrial plant groups thick cuticles with numerous trichomes (hairs) are characteristic of plants adapted to desiccating conditions (drought or salinity). Sunken stomata, particularly if overarched by papillae, and low stomatal density are also indicative of water stress. Conversely, thin, smooth cuticles suggest water-rich conditions.

Wood anatomy

Manoxylic (parenchymatous) wood (e.g. modern relict cycads) is frost-sensitive, while *pycnoxylic* (mostly composed of secondary xylem) wood (conifers and angiosperms) is usually frost-resistant.

Tree rings. In situations where climatic conditions

vary frequently, pycnoxylic wood produces rings as a consequence of variations in growth rate. Rings may be produced on an annual basis where temperature, light, or water availability fluctuates on a yearly cycle, or less regularly in environments with more erratic variations in growth conditions (e.g. sporadic droughts).

Annual rings consist of early (spring) wood with large cell lumina and thin cell walls that grade into late (summer) wood, in which the lumina are smaller and the walls thicker. Wide rings generally reflect benign conditions, but ring width is also a function of position within the tree (position within the trunk, or trunk versus branch) (Creber & Chaloner 1985). High early wood–late wood ratios indicate a high rate of spring and summer growth followed by rapid onset of dormancy. At high latitudes this may be controlled by light rather than temperature.

Inter-annual variations in ring width are described using a statistic known as *mean sensitivity*:

$$ms = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(X_{t+1} - X_t)}{X_{t+1} + X_t} \right|,$$

where X_t is a ring width, X_{t+1} is the width of the adjacent younger ring, and n is the number of rings so measured in a sequence. Woods with a mean sensitivity of < 0.3 are termed *complacent* and indicate uniform growing conditions from year to year. *Sensitive* woods ($ms > 0.3$) are typical of trees growing at the edge of their range and/or in variable environments.

Intra-annual variation is marked by *false rings*. Unlike true rings these often do not form complete circles as seen in cross-section, and may be gradational to normal (usually early) wood on both concave and convex sides. False rings reflect temporary trauma within the growing season caused by waterlogging of roots, low temperatures, or severe insect attack, for example. *Frost rings* are characterized by cell wall disruption due to freezing of cell contents. Pycnoxylic wood is known from the Late Devonian to the present.

In angiosperm woods average vessel diameter divided by the frequency of vessels per mm^2 in cross-section estimates the susceptibility of a tree to air embolism (formation of air bubbles and damage to conductive elements) caused by transpirational stress or freezing. As with leaves, the reliability of the climate signal in wood increases with sample size and taphonomic understanding.

NLR methods

Plant reproductive organs have little inherent climatic signal but climate may be deduced from extrapolation of the tolerances of their NLRs. Following Axelrod & Bailey (1969), four steps are required in NLR analysis:

- 1 NLR of all taxa in an assemblage should be identified to modern genus level.
- 2 NLR determinations should also be attempted at species level (because generic tolerances are too broad).
- 3 The average MAT and average mean annual range of temperature (MAR) are estimated based on habit 'preferences' of modern NLRs.
- 4 The effective temperature (average temperature at the beginning and end of a period free from frost or chill) and equability of the palaeoclimate are calculated using the average MAT and MAR.

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4.19.2 Temperature from Oxygen Isotope Ratios

T. F. ANDERSON

Introduction

Oxygen isotope ratios ($^{18}\text{O} : ^{16}\text{O}$) of well preserved marine calcareous fossils are indicative of the temperature of ancient ocean waters. This approach is based on the fact that the difference in $^{18}\text{O} : ^{16}\text{O}$

ratios between calcium carbonate and the water from which it precipitates is a function of temperature. Oxygen isotope ratios are expressed in the δ notation:

$$\delta^{18}\text{O} = \left[\frac{(^{18}\text{O} : ^{16}\text{O})_{\text{sample}} - (^{18}\text{O} : ^{16}\text{O})_{\text{standard}}}{(^{18}\text{O} : ^{16}\text{O})_{\text{standard}}} \right] \times 10^3. \quad (1)$$

Units are per mil or parts per thousand. The standard material for carbonates is PDB, a late Cretaceous belemnite from the Pee Dee Formation of South Carolina; for water, the standard is SMOW, i.e. standard mean ocean water (see Anderson & Arthur 1983). Oxygen isotope palaeotemperatures for calcite can be calculated from:

$$T^{\circ}\text{C} = 16.0 - 4.14\Delta + 0.13\Delta^2, \quad (2)$$

where $\Delta = \delta^{18}\text{O}_{\text{calcite (vs. PDB)}} - \delta^{18}\text{O}_{\text{water (vs. SMOW)}}$ (Anderson & Arthur 1983). Thus, $\delta^{18}\text{O}$ of calcite increases as temperature decreases. Palaeotemperature estimates can be made with an uncertainty of $\pm 0.5^{\circ}\text{C}$, because $\delta^{18}\text{O}$ values are measured to a precision of 0.1 per mil.

Factors other than analytical precision control the uncertainty in isotopic palaeotemperatures:

1 The manner in which isotopic fractionation between biogenic calcium carbonate and water varies with temperature must be known. Equation (2) applies to inorganic precipitation of pure calcite at isotopic equilibrium and to a number of low-magnesium calcite fossil groups including bivalves, belemnites, brachiopods, and planktic foraminifera. Slightly different equations apply to preserved aragonite and high-magnesium calcite shells (Anderson & Arthur 1983). In addition, physiological effects during shell secretion in some organisms result in departures from equilibrium fractionation; notable examples are corals and echinoids.

2 It is necessary to estimate the $\delta^{18}\text{O}$ of the water in which the shell grew. In the hydrologic cycle, evaporation preferentially removes H_2^{16}O from water, while precipitation and runoff returns H_2^{16}O . Local variation in the hydrologic balance of ocean waters of normal salinity can produce small variations in $\delta^{18}\text{O}$. (The range for modern seawater is 2.5 per mil.) This effect is normally ignored in estimating isotopic palaeotemperatures because hydrologic data on ancient ocean water is lacking. Also, because H_2^{16}O is preferentially stored in polar icecaps and continental ice sheets, oceans are enriched in ^{18}O during glacial epochs relative to nonglacial epochs. For example, the growth and decay of continental ice

sheets during the Late Quaternary produced excursions of at least 1 per mil between glacial and interglacial oceans. The effect of Palaeozoic glaciations on the $\delta^{18}\text{O}$ of contemporaneous seawater was probably similar.

3 Reliable isotopic palaeotemperatures can be obtained only from those fossils that have been preserved from diagenetic alteration. Cemented or partially recrystallized fossils will generally give erroneous palaeotemperatures, because secondary carbonates reflect the temperature and isotopic composition of diagenetic solutions.

Isotopic palaeotemperatures from the Cenozoic and Late Cretaceous

The most continuous record of marine temperature variations for the past 100 million years has been constructed from isotopic analyses of well preserved foraminifera in deep-sea sediments. Diagenetic alteration of foraminiferal tests is minor and relatively easy to determine microscopically. In addition, the effects of continents on the temperature and $\delta^{18}\text{O}$ of ocean water in the pelagic realm is minimal.

The Quaternary oxygen isotope record of foraminifera shows oscillations with periods of about 10^5 years between $\delta^{18}\text{O}$ maxima during glacials and $\delta^{18}\text{O}$ minima during interglacials (see Savin 1977, fig. 8; Anderson & Arthur 1983). Although the direction of these isotope shifts is qualitatively compatible with temperature changes, it is now generally accepted that the amplitude of Quaternary $\delta^{18}\text{O}$ oscillation reflects changes in continental ice volumes more than changes in seawater temperatures.

Marine temperatures for the Tertiary and Late Cretaceous have been estimated from isotopic data on Deep Sea Drilling Project cores. Composite oxygen isotope records for planktic and benthic foraminifera from subtropical sites in the North Pacific illustrate the major features of palaeoclimatic changes over the past 130 million years (Fig. 1). The planktic record reflects temperature and $\delta^{18}\text{O}$ variations in low-latitude surface waters; the benthic record reflects conditions at the high-latitude source regions of deep-water masses. The data suggest general cooling in the Pacific over the past 100 million years. Temperatures of subtropical surface waters were evidently warmer in the Albian/Cenomanian and the Eocene than in intervening times. Temperature trends in deep waters are correlated with those of surface waters from the Middle Cretaceous through the Early Tertiary. However, bottom waters during this interval (especially during the Cretaceous) were considerably warmer than at present. In other words, the latitudinal contrast in ocean temperatures had increased during the Tertiary, resulting principally from apparent cooling at high latitudes. Abrupt positive shifts in the Tertiary benthic $\delta^{18}\text{O}$ trend probably reflect the initiation (Eocene–Oligocene) and rapid expansion (Middle Miocene) of the Antarctic icecap, as well as a decrease in high latitude surface temperatures.

Palaeotemperature trends from shallow-marine bivalves from northwest Europe (Fig. 2) are similar to those for Pacific low-latitude surface waters (Fig. 1), suggesting that global palaeoclimatic changes were not obscured by the influence of continents on the temperature and $\delta^{18}\text{O}$ of nearshore seawater. In contrast to the deep-sea record, the isotopic data from bivalves suggest that the shallow

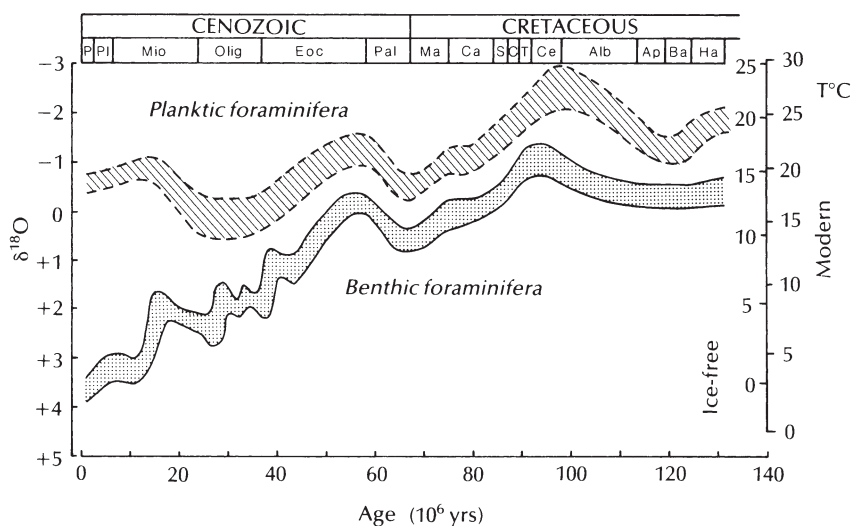


Fig. 1 Oxygen isotope record of foraminifera from the central North Pacific for the past 130 million years. $\delta^{18}\text{O}$ scale is shown on the left vertical axis; the corresponding temperature scales for modern and ice-free oceans ($\delta^{18}\text{O} = 0$ and -1 per mil respectively) are shown on the right vertical axis. (Reproduced, with permission, from the *Annual Review of Earth and Planetary Sciences*, Vol. 5 © 1977 by Annual Reviews Inc.)

Fig. 2 Oxygen isotope record of shallow-marine bivalves from northwest Europe for the past 100 million years. $\delta^{18}\text{O}$ and temperature scales are the same as Fig. 1. (Data from Buchardt 1977 and Burdett, J. & Arthur, M. pers. comm. 1987.)

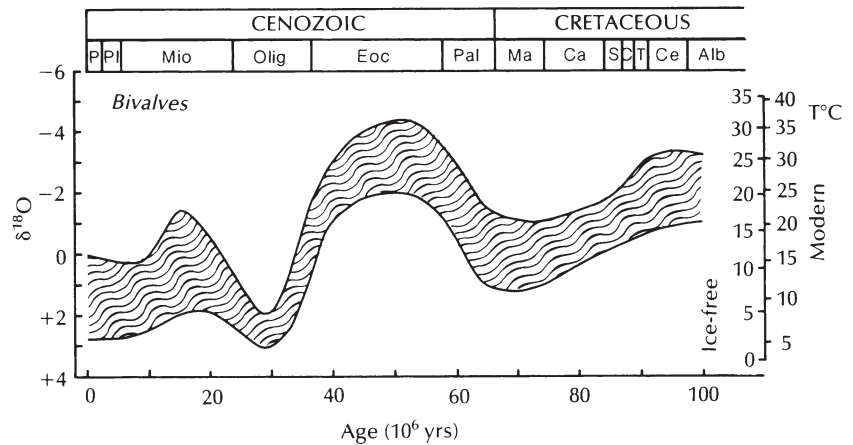
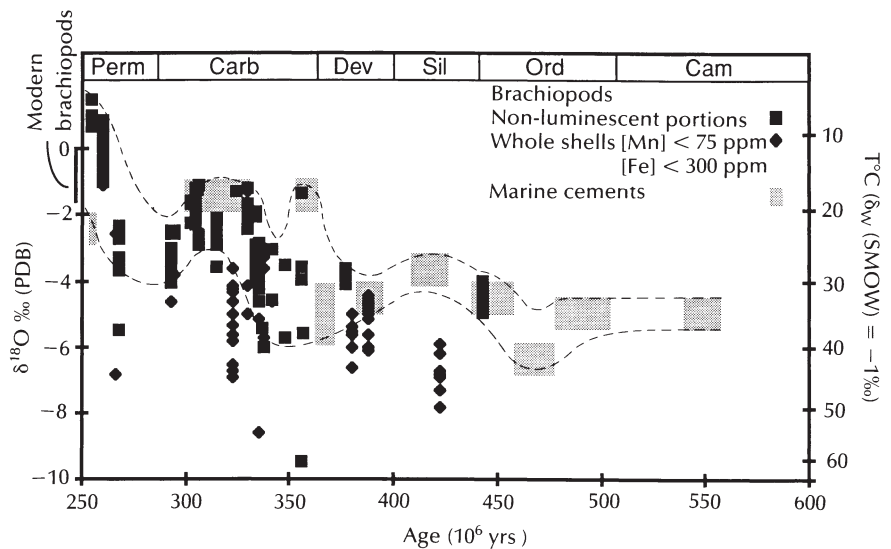


Fig. 3 Oxygen isotope record for Palaeozoic brachiopods and marine cements. The temperature scale (right vertical axis) is for ice-free oceans. (After Popp *et al.* 1986, by permission of the Geological Society of America, and Veizer *et al.* 1986.)



oceans of northwest Europe were significantly warmer during the Eocene than during the Middle Cretaceous.

Isotopic palaeotemperatures from the Palaeozoic

Isotopic palaeotemperature determinations on Palaeozoic fauna are limited necessarily to shallow-marine taxa. The most serious problem with Palaeozoic fossils is the preservation of the original isotopic signal through early diagenesis and long-term burial. Several recent studies have suggested that trace element compositions and microscopic textural characteristics can be used to identify isotopic preservation in fossil brachiopods (Popp *et al.* 1986; Veizer *et al.* 1986). Specifically, portions of

brachiopods which are not cathode luminescent and whole brachiopod shells with low Mn and Fe contents have probably suffered only minimum diagenetic alteration. Data on well-preserved brachiopods from a range of locations, supplemented with estimates for primary marine cements, indicate that $\delta^{18}\text{O}$ values increased irregularly during the Palaeozoic, with a major positive shift from the Devonian to the Carboniferous (Fig. 3). The extent to which this and similar $\delta^{18}\text{O}$ age trends for cherts and sedimentary phosphates represent decreasing temperatures or increasing $\delta^{18}\text{O}$ of ocean water is a major controversy in stable isotope geochemistry. The resolution of this controversy will have a profound impact on our interpretation of surface temperature variations and hydrosphere–lithosphere interactions through time (Anderson & Arthur 1983; Veizer *et al.* 1986).

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4.19.3 Salinity from Faunal Analysis and Geochemistry

J. D. HUDSON

Introduction

Salinity is one of the main controls on the distribution of the aquatic biota, and the estimation of palaeosalinities has concerned many palaeoecologists. Most work has involved benthic invertebrates with calcium carbonate hard parts, although palynology has important applications. Fossil occurrences of particular taxa or assemblages may be compared to modern distributions. Alternatively, fossils can be analysed geochemically, as convenient samplers of the waters they inhabited. Sedimentological evidence also should be sought.

The usual result of such studies is an empirical estimate of the palaeosalinity, or range of salinities, experienced by the organisms, and is generally expressed in parts per thousand or in the 'Venice System' (Fig. 1). The recognition of fully-marine faunas is generally not controversial; nor, in Mesozoic and Cenozoic rocks, is that of freshwater lake faunas. Most palaeoenvironmental interest thus centres on the brackish water and hypersaline faunas of estuaries and other coastal environments, and of saline lakes.

Most brackish systems are labile, and the range and rate of salinity change may have as great an

effect as mean salinity. Water bodies whose salinity varies are commonly also variable in temperature, depth, food supply, etc., and are often underlain by soft, organic-rich substrates. Therefore effects on biotic distribution caused directly by salinity are hard to disentangle from those which are due to other controlling factors.

Besides palaeoenvironmental interpretation, more fundamental questions concern: the mechanism(s) by which salinity control operates; whether there is a special brackish water fauna as opposed to merely a reduced-marine one; the evolutionary origin of brackish water faunas; and the relationship of brackish water faunas to the invasion of freshwaters or land by various groups of organisms. On the long time-scale, there is also the possibility that the composition of seawater itself may have changed. Palaeontology supplies essential historical data bearing on these biological and geochemical questions.

Faunal analysis

The normal palaeoecological precautions about working with *in situ* assemblages obviously apply; in particular, because salinity in estuaries and lagoons can vary so rapidly, the importance of finely-controlled collecting cannot be overstressed. Even so, some time-averaging of fine-scale variation inevitably occurs.

Many higher taxa of plants and animals today are effectively marine-stenohaline and their occurrence, especially in combination, can be used to infer fully marine salinity: *viz.* corals, cephalopods, echinoderms, bryozoans, articulate brachiopods, planktic and larger benthic foraminifera, and many calcareous red and green algae. Most of these, however, include some partially euryhaline forms extending into polyhaline waters. Only a small number of higher taxa thus account for most of the modern brackish and freshwater shelled fauna, i.e. bivalves, gastropods, ostracodes, smaller benthic foraminifera, and charophyte algae. Non-calcified arthropods are important but seldom preserved except as trace fossils (conchostracans being an exception). Many 'fish' are and have been euryhaline, although often also migratory and subject to vagaries of preservation. Even among these groups, few lower taxa have given rise to genera or species tolerant of mesohaline or more dilute waters. Most freshwater taxa are strictly stenohaline.

It follows from these considerations that brackish and freshwater faunas are of low taxonomic diver-

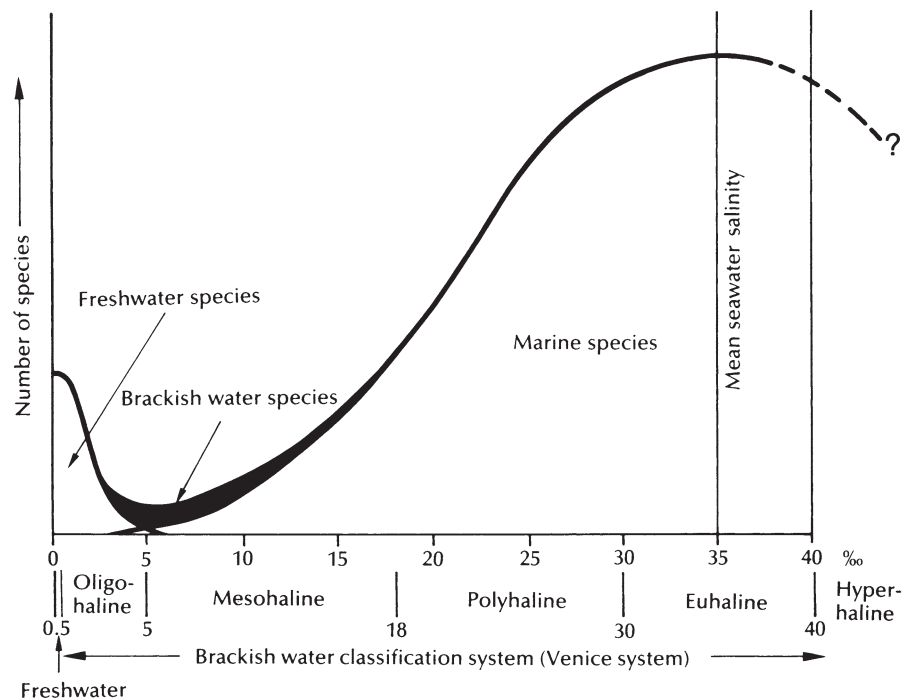


Fig. 1 Modified Remane diagram showing the relationship of species diversity–salinity. The vertical axis indicates that marine species are more numerous than freshwater ones. No precise quantitative significance is intended.

sity and comprise distinctive taxa. Few taxa are specifically adapted to brackish water and most of these are not normally capable of fossilization. They occur along with the more euryhaline members of the marine fauna and in mesohaline waters the latter generally dominate. A few freshwater forms penetrate oligohaline waters. Thus the diversity minimum is generally identified at 5–9‰ salinity, as first recognized by Remane in the Baltic Sea (Fig. 1). The reasons for this minimum have been much debated. It now appears that it does not correspond to a particularly sharp change in ionic ratios in most estuarine or lagoonal settings. A change from (Na^+ , Cl^-) to (Ca^{2+} , HCO_3^-) dominated chemistry does, however, occur in more dilute waters in some areas and creates a sharp distinction between marine-derived brackish and non-marine ostracode faunas (Forester & Brouwers 1985). In inland lakes, ionic ratios, more than total salinity, control ostracode distributions (Forester & Brouwers 1983).

Brackish waters are often very productive because nutrients introduced from the land and estuarine circulation, with inflow of enriched subsurface seawater, can turn estuaries into nutrient traps. This combination of high fertility with physiological stress gives brackish water faunas their well known character of containing few species but many individuals. The species tend to be morphologically 'generalized' and the individuals small. This is both because the species are opportunists, *r*-selected for

rapid exploitation of unstable resources and therefore commonly of small adult size, and because populations may contain many juveniles.

The faunas of hypersaline lagoons have some similarities to those of brackish lagoons, and the same major groups are involved. However, the lower taxa are generally different (e.g. miliolid rather than rostraliid foraminifera), and so are the sedimentary facies associations. Saline continental lakes may have different chemistry from seawater and have special faunas. Large inland seas of marine origin, such as the Caspian Sea, are also special cases.

Geochemistry

The trace element content of carbonate and phosphate shells must be related to that of the water their bearers inhabited, but there are many chemical, physiological, and diagenetic complications in applying this relationship in fossils. Relationships between the strontium:calcium ratio, for example, and salinity have been established for particular marine taxa and regions, but cannot as yet be generalized. In simple lacustrine settings the strontium:calcium ratio of ostracode shells correlates with salinity (Chivas *et al.* 1985). The distribution of the stable isotopes of carbon and oxygen, while also not free of complications, has been of more general utility (Dodd & Stanton 1981). The $^{18}\text{O}:^{16}\text{O}$ ratio in seawater has been rather constant ($\delta^{18}\text{O}_{\text{SMOW}} =$

–1 to 0‰; Section 4.19.2), at least since the Late Palaeozoic. Meteoric water is variably ^{18}O depleted ($\delta^{18}\text{O} = -3\text{‰}$ in the humid sub-tropics, -50‰ in polar ice). Dissolved bicarbonate in seawater is relatively ^{13}C rich ($\delta^{13}\text{C}_{\text{PDB}} = 0$ to 3‰); river and lake bicarbonate generally contains carbon derived from the oxidation of plant material, and is thus variably ^{12}C enriched ($\delta^{13}\text{C} = -5$ to -12‰). In a simple river estuary, therefore, salinity, $\delta^{18}\text{O}$, and $\delta^{13}\text{C}$ are all linearly correlated, and the isotopic variations are reflected in the shells of molluscs living along the estuary (Mook 1971). (Temperature also affects $\delta^{18}\text{O}$, as discussed in Section 4.19.2, but seawater–freshwater mixing in a small area generally outweighs the temperature effect.)

These principles can be applied to well-preserved fossils. The best criterion of isotopic preservation is the retention of original aragonite in molluscs. Complications include the fact that $\delta^{18}\text{O}$ can be increased by evaporation of freshwater as well as by mixing, so that low-salinity water can attain positive $\delta^{18}\text{O}$ values, as in the Florida Everglades (Lloyd 1964). Humid-region lakes generally have negative $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values in fossils; arid-zone lakes can be variable in both ratios. Especially in the Palaeozoic, time-related changes have occurred in the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of even fully-marine carbonates, making salinity-related changes harder to detect.

Conclusions

By using a combination of facies analysis, diversity studies, and taxonomic uniformitarianism, brackish water faunas of marginal-marine environments can be recognized with some assurance. In Cenozoic and even Mesozoic rocks faunal assemblages can be assigned to specific salinity ranges (e.g. Fürsich & Werner, 1986). Where fossils are well preserved, isotopic analyses provide further quantification. In Palaeozoic rocks, taxonomic uniformitarianism is at best doubtful, and variations in the isotopic composition of ocean water may have occurred. We have the prospect of studying the origin and evolution of the brackish and freshwater fauna that we know today, which goes back at least to the Mesozoic. It is uncertain whether Palaeozoic brackish water taxa (e.g. in the Carboniferous Coal Measures) are the direct ancestors of the modern taxa. We may eventually elucidate the fundamental controls on the nature and history of these successive faunas (Gray 1988).

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4.19.4 Oxygen Levels from Biofacies and Trace Fossils

D. J. BOTTJER & C. E. SAVRDA

Introduction

Marine strata deposited in environments characterized by low levels of bottom-water oxygenation are common in the Phanerozoic stratigraphic record. These strata are important as petroleum source beds and as the common host rock for many fossil-Lagerstätten, such as the Cambrian Burgess Shale (Section 3.11.2) and the Jurassic Posidonienschiefer (Section 3.11.6). Such strata also act as important indicators of both long- and short-term fluctuations in levels of oxygenation and, hence, circulation rate in the Earth's oceans. These factors have produced a need for continued refinement of biofacies models that permit the reconstruction of palaeo-oxygenation of ancient basin bottom-waters.

Early attempts to provide a framework for reconstruction of palaeo-oxygen levels employed a uniformitarian approach, through analysis of faunas and sediment fabric across oxygen gradients in Recent marine basins (Byers 1977). These studies divided such environments into aerobic (more than 1.0 ml/L O₂), dysaerobic (0.1–1.0 ml/L O₂) and anaerobic (less than 0.1 ml/L O₂) zones (Fig. 1A). In turn, these marine zones have been used to define oxygen-related biofacies in ancient strata (Byers 1977). Aerobic biofacies have been recognized on the basis of a thoroughly bioturbated sedimentary fabric and diverse assemblages of relatively large, heavily calcified body fossils. Dysaerobic biofacies, also characterized by bioturbated sediments, have been defined on the basis of the occurrence of low diversity assemblages of small, less heavily calcified body fossils or the absence of body fossils altogether. Anaerobic biofacies have been delineated on the basis of the preservation of primary varve-like lamination and the absence of *in situ* macrobenthic body fossils. Anaerobic strata may, however, contain well preserved remains of nekctic or epiplanktic invertebrates and vertebrates.

This oxygen-related biofacies model has been significantly refined and expanded through additional studies of both modern environments and the stratigraphic record (Savrda & Bottjer 1986, 1987). Major refinements include: (1) the addition of two other potentially useful biofacies, the anoxic and exaerobic biofacies; and (2) the development of a sensitive trace fossil model for reconstructing palaeo-oxygen levels *within* the broad dysaerobic realm.

Development of the biofacies model

As originally defined, anaerobic environments may contain extremely low concentrations of dissolved oxygen. Despite the exclusion of bioturbating macrobenthic organisms, these environments may host preservable benthic microfauna, such as foraminifera and other soft-bodied components, that may result in microbioturbation (a subtle incomplete disruption of primary lamination). In contrast, anoxic biofacies represent environments totally devoid of oxygen. Anoxic biofacies, although they may be characterized by similar allochthonous faunal elements, may be distinguished from anaerobic biofacies by the absence of *in situ* benthic microfossils and microbioturbation (Fig. 1A).

Early oxygen-related biofacies models postulated a decrease in organism size and degree of calcifi-

cation, as well as a drastic reduction in the relative percentage of fauna possessing calcified skeletons, as oxygen levels decrease toward the dysaerobic–anaerobic boundary (Fig. 1A). Application of these earlier models led to the interpretation that all macroinvertebrate fossils found in laminated strata were planktic, nekctic, or epiplanktic. However, more recent studies (e.g. Savrda & Bottjer 1987) of modern marine environments have demonstrated that large, well calcified macrobenthic invertebrates may occur in the lower ranges of the dysaerobic zone. In addition, subsequent studies of ancient strata suggest that some shelled epibenthic organisms may have lived on the sea floor in environments where substrates were sufficiently oxygen-deficient to exclude more active, bioturbating infauna (e.g. Savrda & Bottjer 1987). In portions of the Monterey Formation (Miocene, California) the bivalve *Anadara montereyana* occurs *in situ* almost exclusively in strata deposited at the dysaerobic–anaerobic boundary. Based on this occurrence, Savrda & Bottjer (1987) proposed a new oxygen-related biofacies, the *exaerobic zone*. They further postulated that these bivalves may have favoured such oxygen-deficient environments because of a symbiotic association with sulphur-oxidizing bacteria, although other (as yet undiscovered) processes may also be responsible for producing this phenomenon. By considering variations in basin configuration and palaeoceanographic conditions, deposition under exaerobic conditions may also explain the occurrence of other epibenthic faunal elements (principally bivalve molluscs and brachiopods) in laminated, unbioturbated strata that are transitional between laminated strata which lack *in situ* body fossils, and bioturbated dysaerobic strata, in a wide variety of Phanerozoic marine sequences.

The use of trace fossils

In the biofacies model, general sedimentary fabric plays a crucial role in determining the boundary between the anaerobic (or exaerobic) and dysaerobic zones. Recent studies have shown that discrete trace fossils can be incorporated into a model for determining palaeo-oxygen levels within the dysaerobic biofacies (e.g. Savrda & Bottjer 1986). The trace fossil model involves the synthesis of ichnological criteria that are based on trends in diversity, burrow diameter, and vertical extent of biogenic structures, all of which decrease with reduced oxygen availability in bottom-waters (Fig. 1A). These trends are analysed along with cross-cutting relationships of

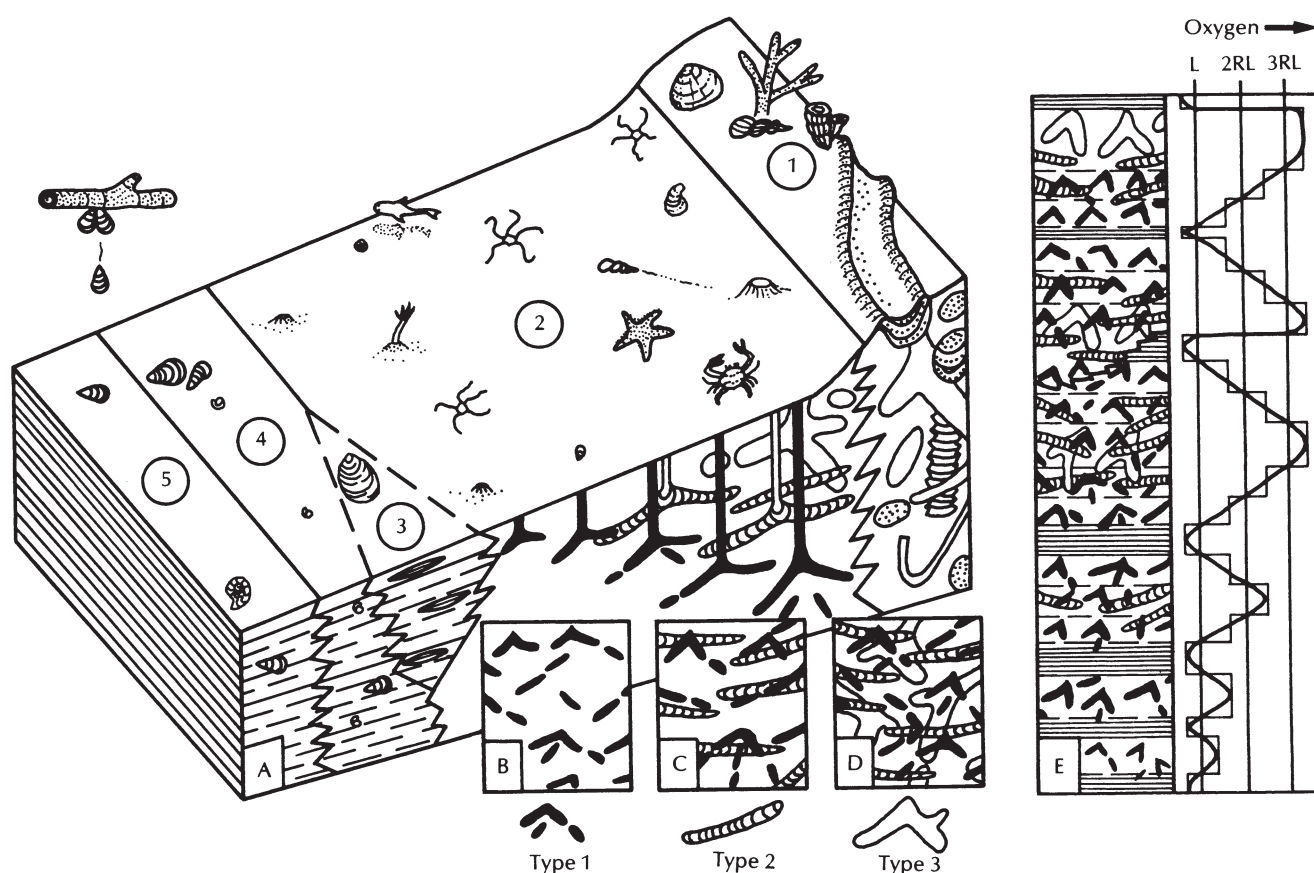


Fig. 1 A, Schematic representation of five oxygen-related biofacies described in the text. In order of decreasing levels of oxygenation, these are: (1) *aerobic*; (2) *dysaerobic*; (3) *exaerobic*; (4) *anaerobic*; and (5) *anoxic* biofacies. Presence and extent of the exaerobic zone depends on basin configuration and palaeoceanographic conditions (see Savrda & Bottjer 1987). Note reduction of diversity, burrow diameter, and vertical extent of biogenic structures with decreasing oxygenation within the dysaerobic zone. B–D, Schematic illustration of trace fossil assemblages and cross-cutting relationships expected in strata deposited at various points along the dysaerobic oxygenation gradient. E, Schematic illustration of the construction of palaeo-oxygenation curves for strata deposited in dysaerobic environments employing the trace fossil tiering model detailed by Savrda & Bottjer (1986), with permission from Macmillan Magazines Ltd.

trace fossils, which allows the recognition of tiering relationships (Section 1.7.1). The model permits the delineation of oxygen-related ichnocoenosis (ORI) units, or units of strata that were deposited under similar levels of bottom-water oxygenation (Fig. 1B–D). When applied in detailed vertical sequence analyses, the trace fossil approach can be used to construct interpreted oxygenation curves that reflect rates and magnitudes of temporal change in redox conditions (Fig. 1E) (see Savrda & Bottjer 1986, 1987, for examples from the Cretaceous Niobrara Formation of Colorado and the Miocene Monterey Formation of California). Considering the preponderance of the dysaerobic biofacies in the stratigraphic record, trace fossils are thus, at our current level of understanding, the best evidence available for evaluating ancient oxygen-deficient environ-

ments. However, continued work on geochemistry and macroinvertebrate body fossils is needed to reveal additional insights into relationships between biota and oxygen levels in marine environments through the Phanerozoic.

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4.19.5 Depth from Trace and Body Fossils

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Depth as such is unlikely to have limited a fossil organism's distribution during life. However, because many critical limiting factors are in some way related to depth, their combined effect may restrict the occurrence of particular organisms to a certain bathymetric range. Ecologically, the important parameters are food supply, light penetration, substrate mobility, rate of sedimentation, temperature, salinity, and dissolved oxygen. Geologically, the useful parameter is depth. Indications of depth may be obtained from the overall characteristics of a fossil assemblage and its mode of preservation; from a detailed study of particular taxa, especially if they are still extant; by considering the balance of benthic and pelagic groups; or by the identification of ichnofacies.

Inner versus outer shelf depths may often be inferred from the dominant fossil groups in an

assemblage. Molluscan-dominated inner shelf assemblages, often with *Lingula*, may be contrasted with bryozoan/brachiopod-dominated outer shelf assemblages, often with ahermatypic corals or crinoids. Only one fossil group, however, definitively indicates shallow water — the benthic algae. Since they are dependent upon sunlight, they define the photic zone. The depth limit of the photic zone depends principally upon latitude and water turbidity. Today in the clear waters of the tropics it lies at 250 m, rising to 185 m on seamounts at 47°N, and to 90 m on oceanic plateaux at 59°N. Shelf areas like the North Sea have photic limits of 22–45 m, though this shallows to less than 1 m in estuaries.

Calcareous green algae assimilate most strongly in the red part of the spectrum and are therefore restricted to shallower water than the red algae, which are adapted to blue-green wavelengths. Rhodoliths are thus found on the shelf edge in the tropics, whereas dasyclads always indicate water only a few metres deep. Algae are noticeably absent from some carbonate facies, as for example from the basinal pioneering stages of stromatoporoid mounds in the Belgian Devonian; from Carboniferous mud mounds of the Waulsortian type (Lees *et al.* 1985); and from the Danian coral banks of southern Sweden, which grew in depths of 50–100 m.

Endolithic algal borings also show bathymetric zonation. Different types characterize particular depths, and these are well preserved in shelly shelf assemblages from the Silurian of New York State and the Miocene of North Carolina, for example

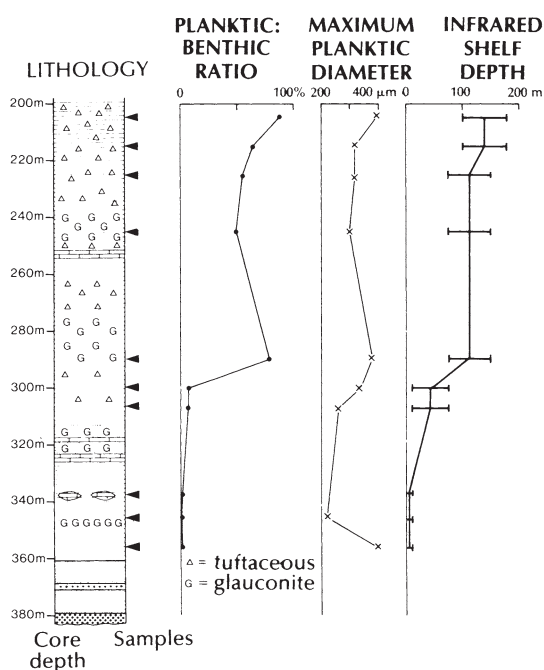


Fig. 1 Planktic:benthic foraminifera ratios and maximum planktic diameter used to indicate increasing depth during the Late Palaeocene–Middle Eocene. Sample from Deep Sea Drilling Project, Site 404, Rockall Plateau, northeast Atlantic. (Data from Murray 1979.)

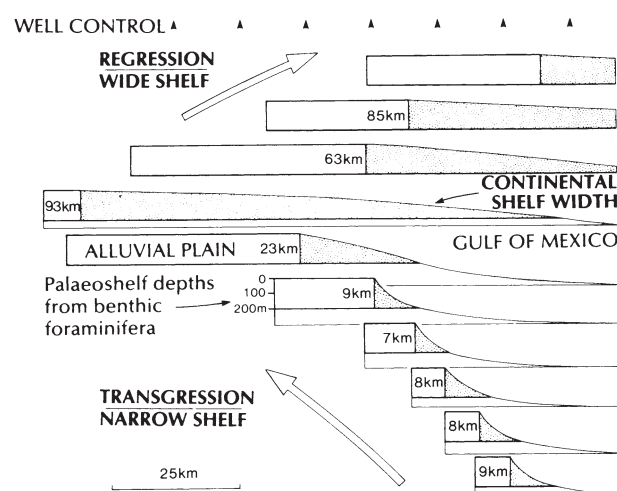


Fig. 2 Diversity of benthic foraminifera plotted at 100 m intervals through the Oligocene Anahuac Formation, subsurface Texas; reveals change in shelf gradient. (Data from Walton *in* Imbrie & Newell 1964.)

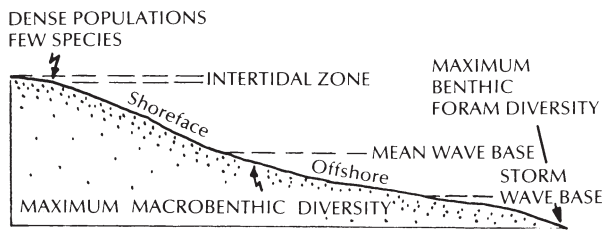


Fig. 3 Typical position of belts of maximum faunal diversity on modern depositional shelves in relation to critical physical parameters. (Data from Dörjes *in* Frey 1975 and Walton *in* Imbrie & Newell 1964.)

(Golubić *et al.* *in* Frey 1975). Shell-boring algae may be fed upon by gastropods which leave diagnostic grazing patterns. These occur on ammonites from certain Cretaceous shales, indicating a depth of no more than 30 m for their deposition.

Pelagic organisms, such as coccoliths, diatoms, radiolarians, pteropods, and graptolites, are rare in shallow water but are often abundant in outer shelf or bathyal settings. Planktic:benthic ratios provide a sensitive measure of outer shelf depths, in conjunction with maximum foraminiferal test size (Fig. 1).

Extrapolation of known present-day ranges for particular taxa is perhaps the commonest empirical method of interpreting palaeodepth. Outstanding syntheses using benthic foraminifera (Natland *in* Ladd 1957) and molluscs (Woodring *in* Ladd 1957) have plotted the fluctuating Tertiary water depths in the highly active Los Angeles and Ventura strike-slip basins. Latitude and faunal province must first be taken into account because organisms are temperature- rather than depth-dependent and classically exhibit 'tropical submergence'. The method has obvious pitfalls if the living taxon has been poorly sampled or is less common than in the fossil record, as with many ahermatypic corals (Wells *in* Hallam 1967).

Mapping belts of maximum faunal diversity may give useful depth indications. With microfauna this occurs just inside the shelf edge, a fact which has enabled changes in shelf gradient through the Oligocene of the Gulf of Mexico coast to be plotted (Fig. 2). With modern macrofauna it occurs just below mean wave base, at surprisingly shallow depths, even in macrotidal shelf seas (16 m for the southern North Sea: Dörjes *in* Frey 1975). This seems at variance with the situation in Silurian brachiopod-dominated fossil assemblages, where greatest

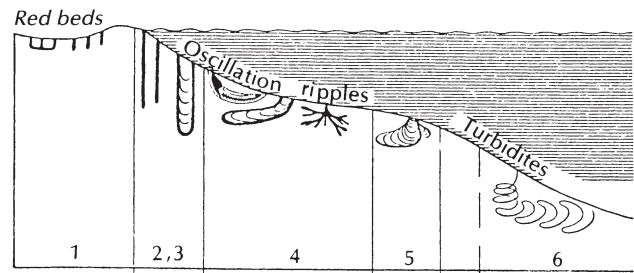


Fig. 4 The six universal depth-related ichnofacies of Seilacher *in* Hallam (1967), known from the Cambrian to the Recent: (1) *Scoyenia*; (2) *Skolithos*; (3) *Glossifungites*; (4) *Cruziana*; (5) *Zoophycos*; and (6) *Nereites*.

diversity (admittedly of preserved species only) apparently occurs nearer the shelf edge.

Studying the taphonomy of a fossil assemblage may resolve such matters, since taphonomy is strongly depth-sensitive (see Section 3.5). Distinct boundaries between animal communities occur at mean wave base and storm wave base (Dörjes *in* Frey 1975; Fig. 3). Inshore of mean wave base the preservation of skeletal remains and trace fossils is controlled by hydrographic energy. Offshore, fossils are largely *in situ* and preservation is controlled by benthic productivity, except where interrupted by storm events.

The problem of possible reworking is avoided by using trace fossils as depth indicators. Because of their long time range, depth comparisons can be made between strata of radically different age using Seilacher's universal ichnofacies concept (Fig. 4). This has also proved of great value in broad-scale basin analysis, enabling Palaeozoic subsidence patterns in the Oslo and Central Appalachian basins to be compared (Seilacher *in* Hallam 1967). The six ichnofacies do not always occur in the expected bathymetric zone (see discussion in Frey & Pemberton 1984). *Zoophycos*, for example, occurs in shallower water in the Carboniferous than in the Mesozoic; and *Skolithos* has been recorded from proximal submarine fan facies. These anomalies occur because depth itself is not the limiting factor. Instead a combination of ecologically more significant parameters, in this instance levels of dissolved oxygen and substrate mobility, which do not always decrease with depth, determine distribution.

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