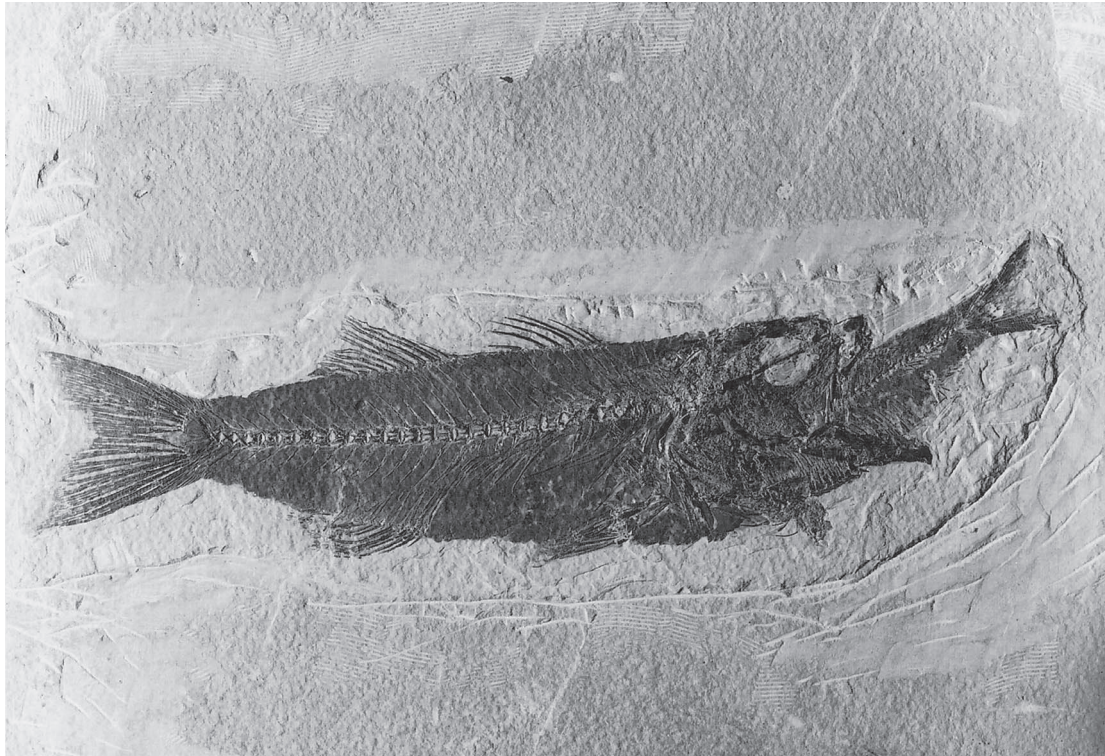


4

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

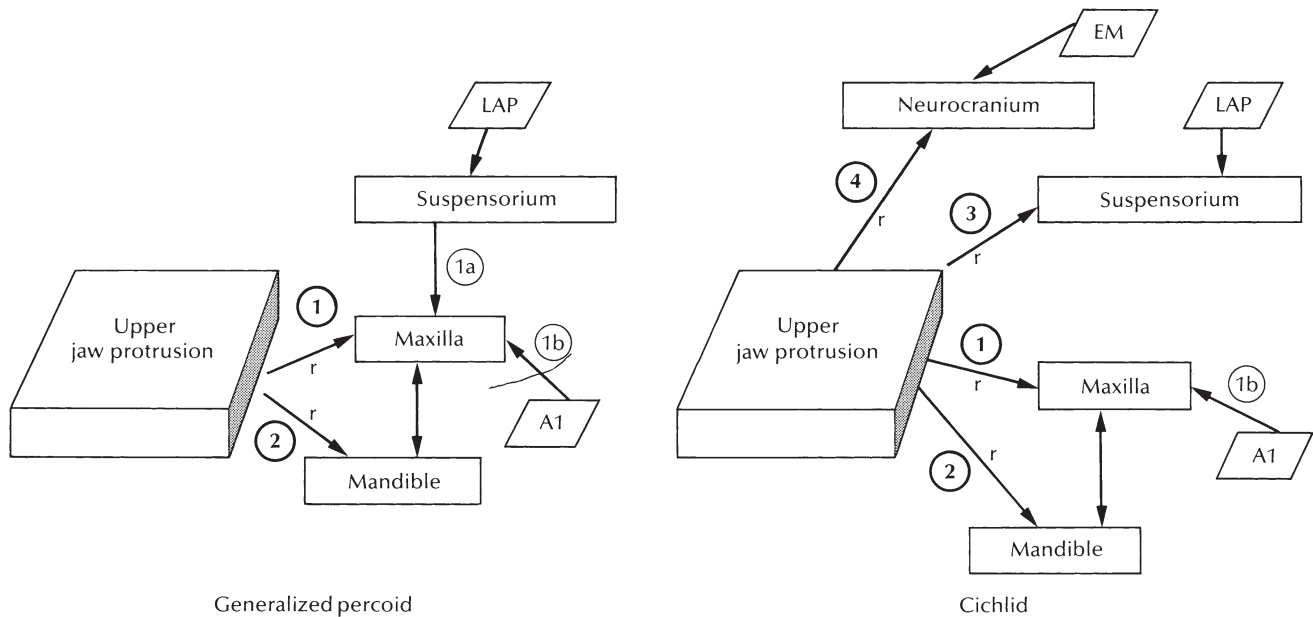


Fig. 1 Mechanical pathways which affect upper jaw protrusion in cichlid fish as compared with the generalized percoid. The research identified the morphological elements that are involved in the protrusion and illustrated the mechanical pathways controlling jaw movement, and the forces involved in this 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

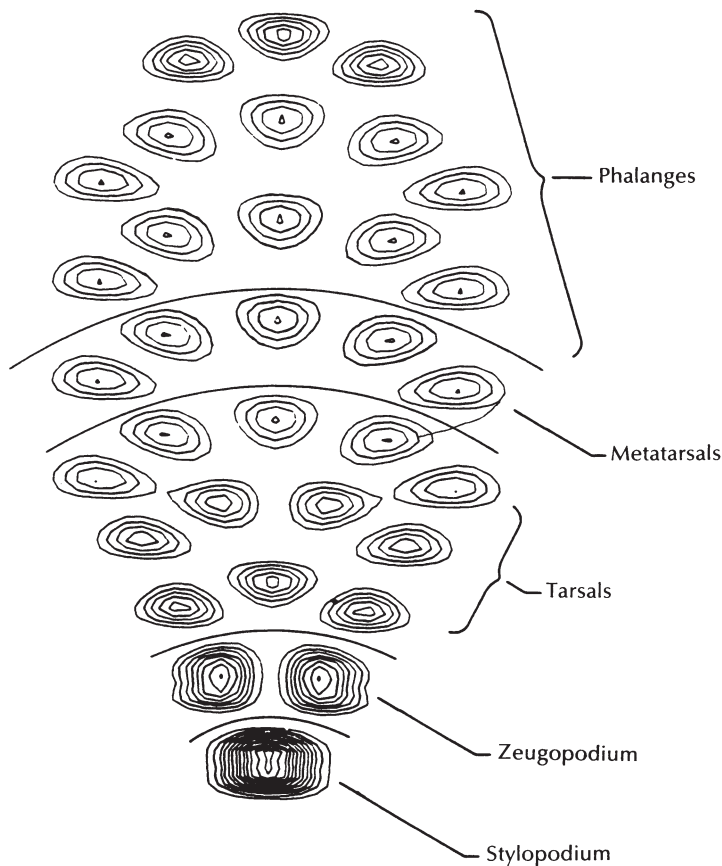


Fig. 2 The contour plots represent the solutions to field equations generated by a model of pattern formation for a hind limb with five digits. They demonstrate the possibility of generating specific descriptions of activity in limb buds which will describe patterns of organization and constraints on 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 fabricational 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 fabricational 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

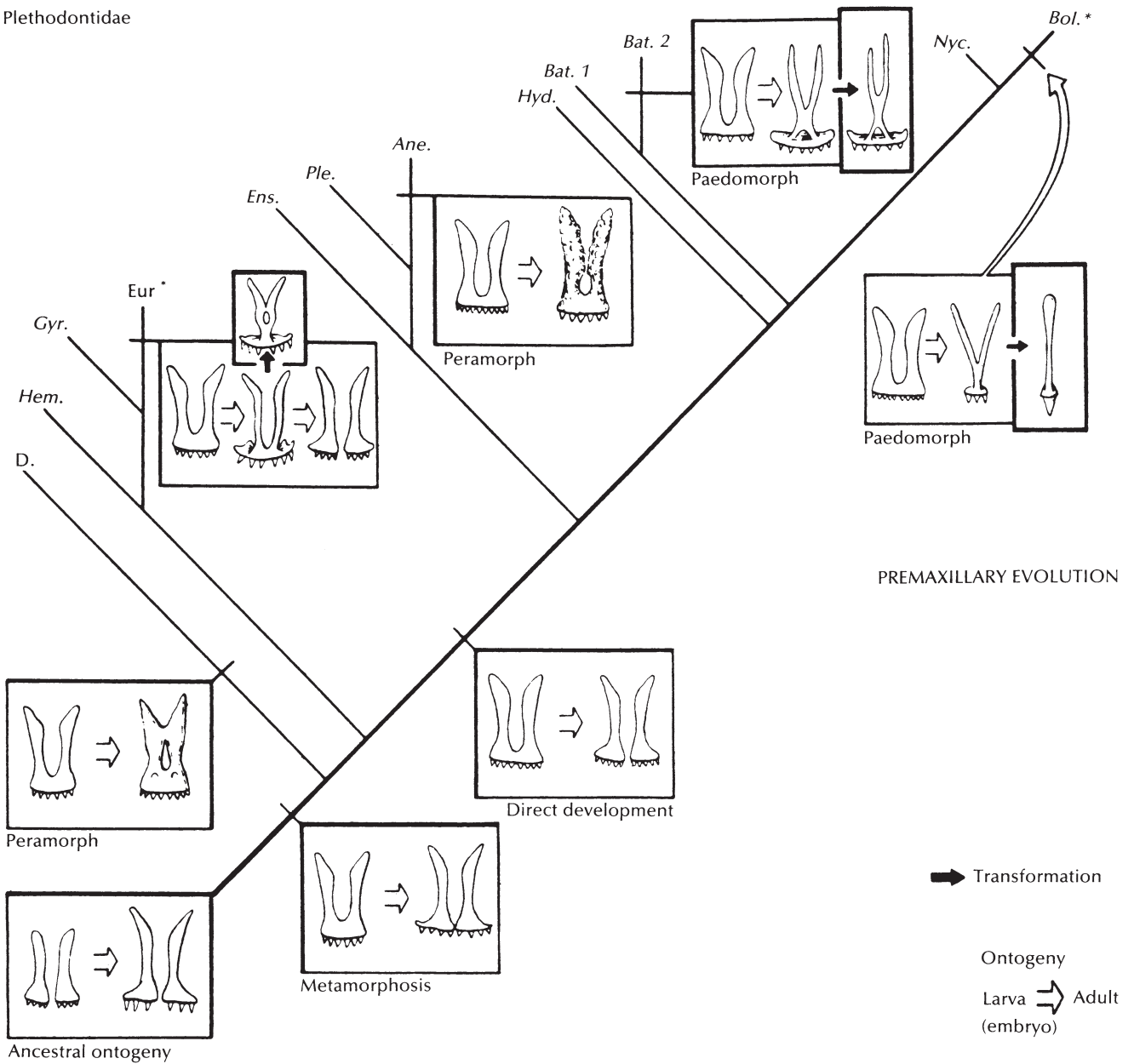


Fig. 3 The use of a phylogenetic hypothesis as the framework onto which the recurring forms of the pre-maxilla of plethodontid salamanders could be mapped illustrates the use of several lines of morphological evidence to elucidate an evolutionary question. The ancestral ontogeny is indicated at the base, 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.

References

- Alberch, P., Gould, S.J., Oster, G. & Wake, D.B. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* **5**, 296–317.
- Fisher, D.C. 1985. Evolutionary morphology: beyond the analogous, anecdotal, and the *ad hoc*. *Paleobiology* **11**, 120–138.
- Goodwin, B.C. 1984. Changing from an evolutionary to a generative paradigm in biology. In: J.W. Pollard (ed.) *Evolutionary theory: paths to the future*, pp. 99–120. John Wiley & Sons, Chichester.
- Gould, S.J. & Lewontin, R.C. 1979. The Spandrels of San Marcos and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London* **B205**, 581–590.
- Hickman, C.S. 1980. Gastropod radulae and the assessment of form in evolutionary paleontology. *Paleobiology* **6**, 276–296.
- Hickman, C.S. 1988. Analysis of form and function in fossils. *American Zoologist* **28**, 775–793.
- Hildebrand, M., Bramble, D.M., Liem, K.F. & Wake, D.B. (eds) 1985. *Functional vertebrate morphology*. Belknap Press, Cambridge, Ma. & London.
- Kingsolver, J.G. & Koehl, M.A.R. 1985. Aerodynamics, thermoregulation, and the evolution of insect wings: differential scaling and evolutionary change. *Evolution* **39**, 488–504.
- Kontrovitz, M. & Meyers, J.H. 1988. Ostracode eyes as paleoenvironmental indicators: physical limits of vision in some podocopids. *Geology* **16**, 293–296.
- Lauder, G.V. 1981. Form and function: structural analysis in evolutionary morphology. *Paleobiology* **7**, 430–442.
- Lewontin, R.C. 1987. The shape of optimality. In: J. Dupre (ed.) *The latest on the best; essays on evolution and optimality*. MIT Press, Cambridge, Ma.
- Lowell, R.B. 1987. Safety factor analysis of tropical versus temperate limpet shells: multiple selection pressure on a single structure. *Evolution* **41**, 638–659.
- Raup, D.M. 1966. Geometric analysis of shell coiling: general problems. *Journal of Paleontology* **40**, 1178–1191.
- Rudwick, M.J. 1964. The inference of structure from function in fossils. *British Journal for the Philosophy of Science* **15**, 27–40.
- Seigel, A.F. & Benson, R.H. 1982. A robust comparison of biological shapes. *Biometrics* **38**, 341–350.
- Seilacher, A. 1973. Fabricational noise in adaptive morphology. *Systematic Zoology* **22**, 451–465.
- Signor, P.W. 1982. A critical re-evaluation of the paradigm method of functional inference. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **164**, 59–63.
- Stanley, S.M. 1975. Adaptive themes in the evolution of the Bivalvia. *Annual Review of Earth and Planetary Sciences* **3**, 361–387.
- Wake, D.B. & Larson, A. 1987. Multidimensional analysis of an evolving lineage. *Science* **238**, 42–48.

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 pre-fabricated 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

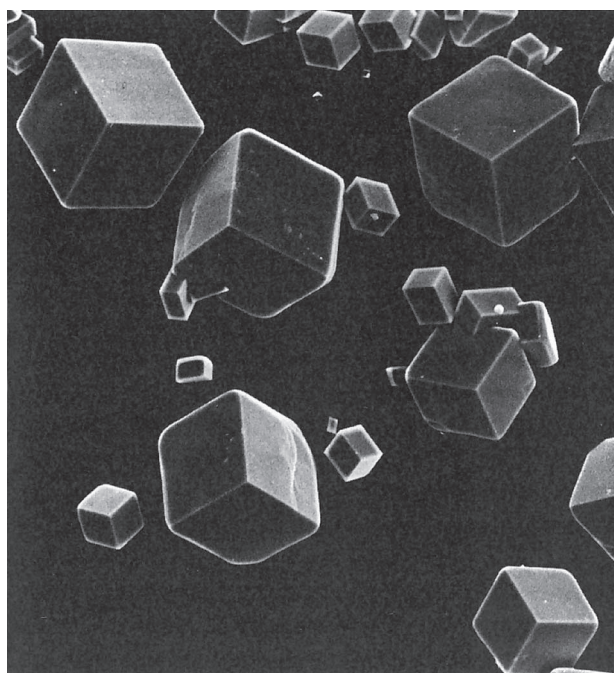


Fig. 1 Synthetic crystals of calcite (greatly magnified).

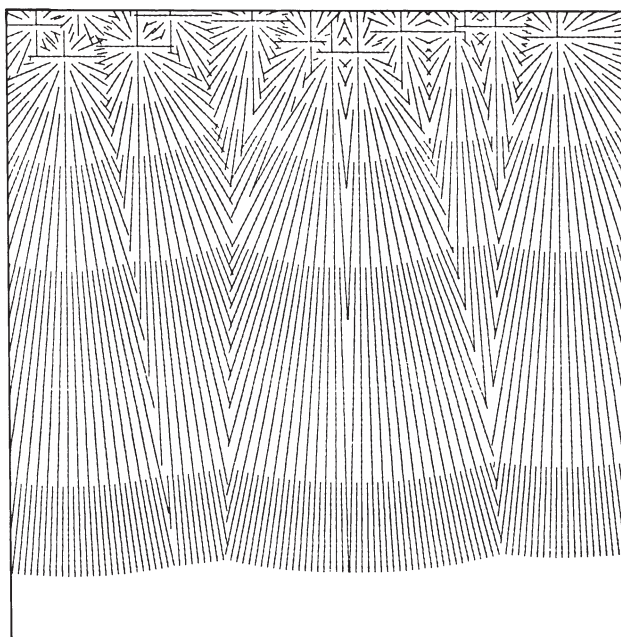


Fig. 2 Two-dimensional computer simulation of the spherulitic growth of aragonite fibres. The program allows equally spaced radial lines to grow from randomly distributed 'nucleation sites' until they intersect. (Program and simulation by F.A. Shaw.)

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 (epitheca, 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

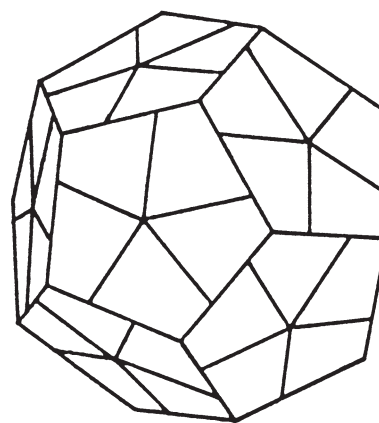


Fig. 3 The calcite coccosphere of the alga *Braarudosphaera bigelowi* is a regular dodecahedron composed of 12 pentaliths, each in turn made from five calcite crystals.

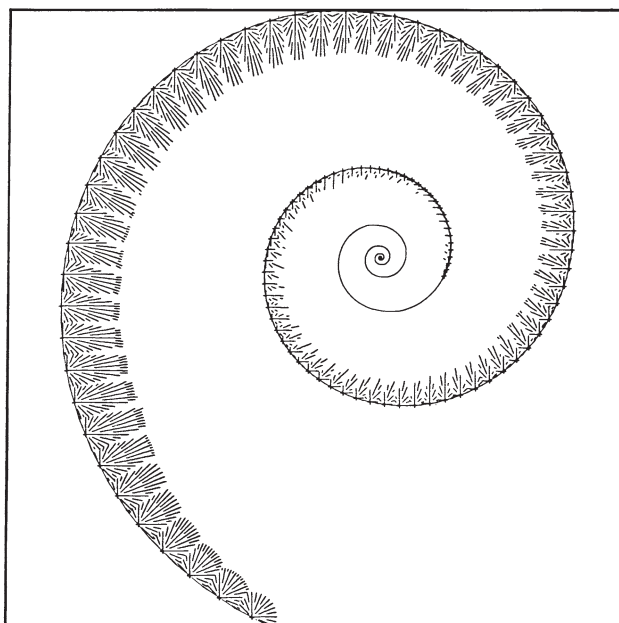


Fig. 4 Computer-drawn model of the growth of the outer layer of the *Nautilus* shell. Aragonite fibres represented by straight lines grow in from the periostracum (curved line) to form spherulites. (Program and simulation by F.A. Shaw.)

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.

References

- Bengtson, S. 1985. Taxonomy of disarticulated fossils. *Journal of Paleontology* **59**, 1350–1358.
- Jones, D.S. 1983. Sclerochronology: reading the record of the molluscan shell. *American Scientist* **71**, 384–391.
- Lowenstam, H.A. 1981. Minerals formed by organisms. *Science* **211**, 1126–1131.
- Mann, S. 1988. Molecular recognition in biomineralization. *Nature* **332**, 119–124.
- Seilacher, A. 1979. Constructional morphology of sand dollars. *Paleobiology* **5**, 191–221.
- Vermeij, G.J. 1970. Adaptive versatility and skeleton construction. *American Naturalist* **104**, 253–260.

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

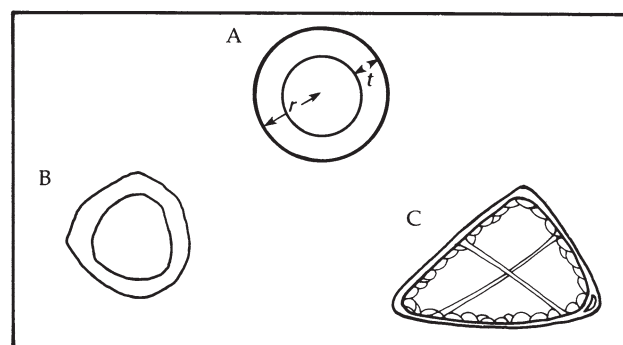


Fig. 1 A, Cross-section of a tube showing radius (r) and thickness (t); $r:t = 2.4$. B, Thick-walled section near base of Irish Elk antler; $r:t = 3$. C, Section of first phalanx of pterosaur, showing devices for combining strength and lightness: thin walls, triangular section with thickened corners (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).

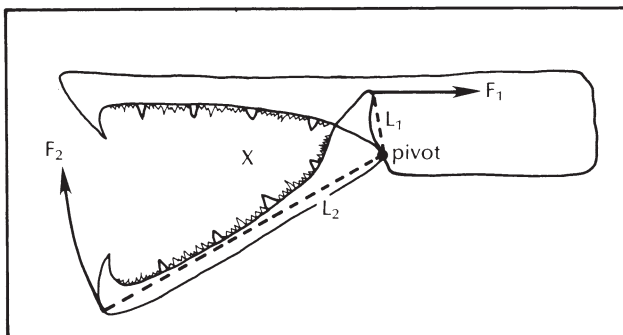


Fig. 2 Mechanics of cheliceral claw of a pterygotid eurypterid; VR ($L_1:L_2$) = 0.2 for tip of movable finger, therefore MA ($F_1:F_2$) is also low, and adapted for fast capture of prey. Prey inserted into claw at X could be sliced with high MA.

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.