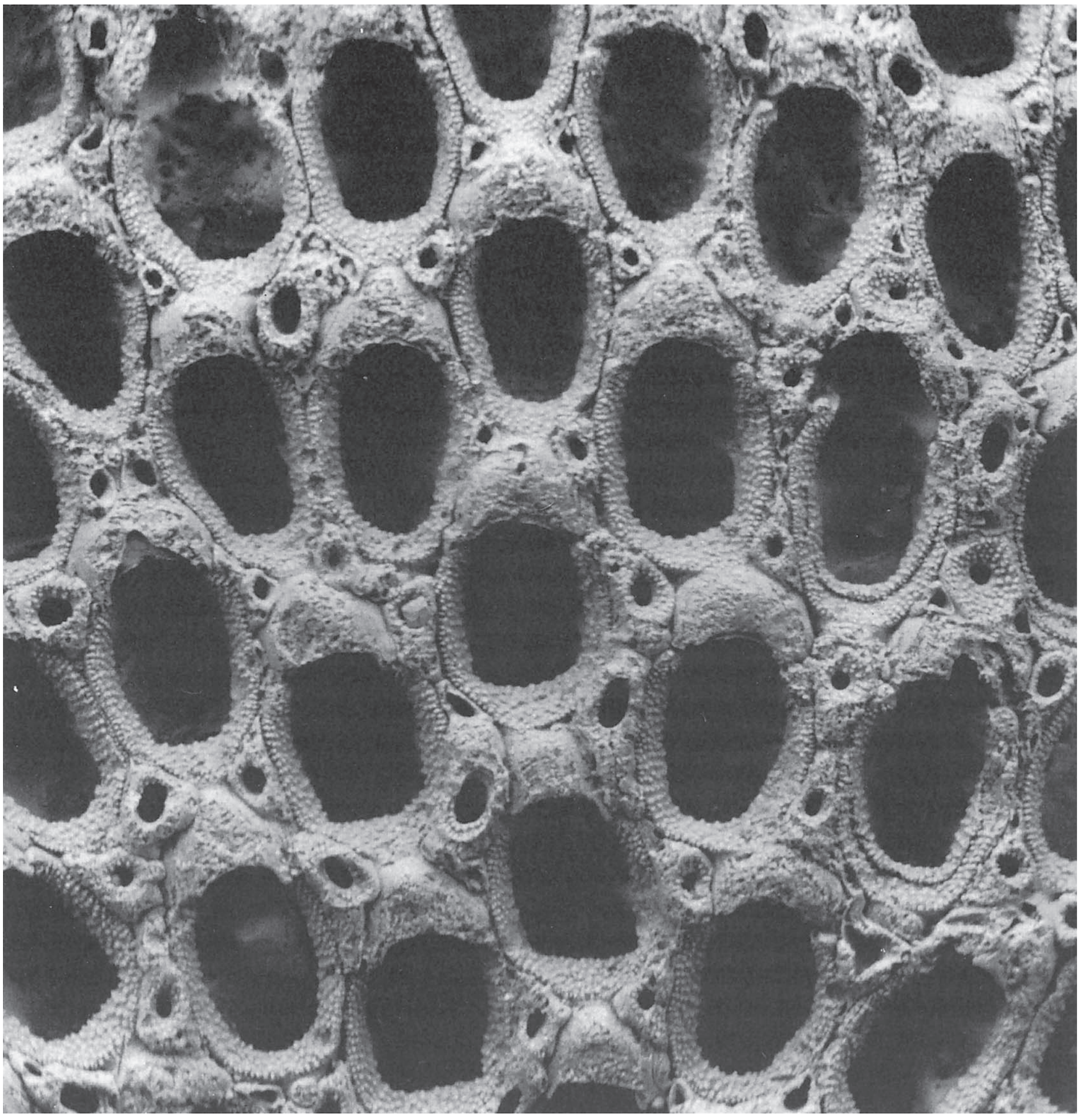
# 6
# INFRASTRUCTURE OF PALAEOBIOLOGY



Scanning electron micrograph of an uncoated cheilostome bryozoan *Akatopora circumsaepta* (Uttley), imaged using back-scattered electrons, from the Pleistocene of Wanganui, New Zealand, $\times$ 100.

# 6.1 Computer Applications in Palaeontology

J. A. KITCHELL

## Introduction

Computer techniques enable palaeontological questions to be addressed on a scale unheard of in earlier times. The capacity of the computer to organize and manipulate immense amounts of information is well known. Consequently, this article is *not* about computer applications that merely change the magnitude of analyses but is instead a response to the question 'What *qualitative* changes have resulted from this quantitative leap in computing speed, efficiency, and capability?' The focus will be on 'the new eyes' provided by the computer, emphasizing the ways in which computing techniques enhance our ability to 'see' both problems and data.

## The computer as experimental tool

True experiments are not possible within the historical sciences, because history cannot be repeated in novel contexts. Computer modelling serves instead as the experimental tool. Experimentation is made possible by the fact that simulation models, unlike analytical models, have no exact solution. Evolutionary theory and simulation modelling are in this respect analogous. Each simulation run may represent a different evolutionary trial in which differences and novel contexts are introduced by stochastic variables or changing parameter values of deterministic variables. By explicit and systematic manipulations, the palaeontologist is given the power to complete '*If* . . . *then* . . .' statements about evolutionary process and the resultant pattern.

Despite the fact that 'scientists are incessantly saying to each other "Let's play around with that" — and modelling is the quintessential way of playing with the way things might work and might be' (Judson 1980), palaeontologists historically have not developed mathematical models. Yet it is well understood that theories, whether explicitly or implicitly, *are* mathematical, even though the impetus of theory formulation is outside mathematics and distinctly empirical. As a result, theories that are made into models use the explicit language of mathematics.

The purpose of mathematical modelling is to capture in specific and explicit terms the essential bits and connections of the theory. The purpose of simulation modelling is to take this process a step further: simulation is an exploratory technique. Simulation modelling explores the consequences of a given set of assumptions. The outcome is created as a logical consequence of the theorized process, to discover the way things would be, if the theory of process were operative. Using the capability of the computer the technique is used to determine whether, given a certain formulation of a process or system, this formulation (i.e. this set of assumptions) *can* produce behaviour similar to that known empirically. Such an approach is necessary to augment and even to develop our limited intuition in dealing with complexity (e.g. solving simultaneous situations) and nonlinearity. Modelling becomes indispensable when it expands the limits of our understanding beyond both intuition and the exploration of what did happen to what *could* happen.

Another important aspect of the computer has been referred to as 'its power to feed a new mathematics *of the eye*' (Gleick 1987). What this means is that images (easily readable graphic output) have increasingly replaced more abstract formulations. Such graphics are also necessitated by the fact that there is no unique solution to many theories (models). The dynamics and range of solutions can now be shown in the form of a 'portfolio' (Fig. 1). Most of the work in palaeontology using simulation modelling has relied on this appeal of graphic imagery. Examples include the behaviours of random processes, the transformation of morphologies, and the features of time series.

In palaeontology, simulation modelling has been used largely in the following cases: (1) to model aspects of randomness, as a branching process, a diffusion process, or a random walk; (2) to model growth and form and the (descriptive) transformation of related morphologies; and (3) to model the behaviour of classical functions (e.g. the exponential and logistic). In each of these cases (except the

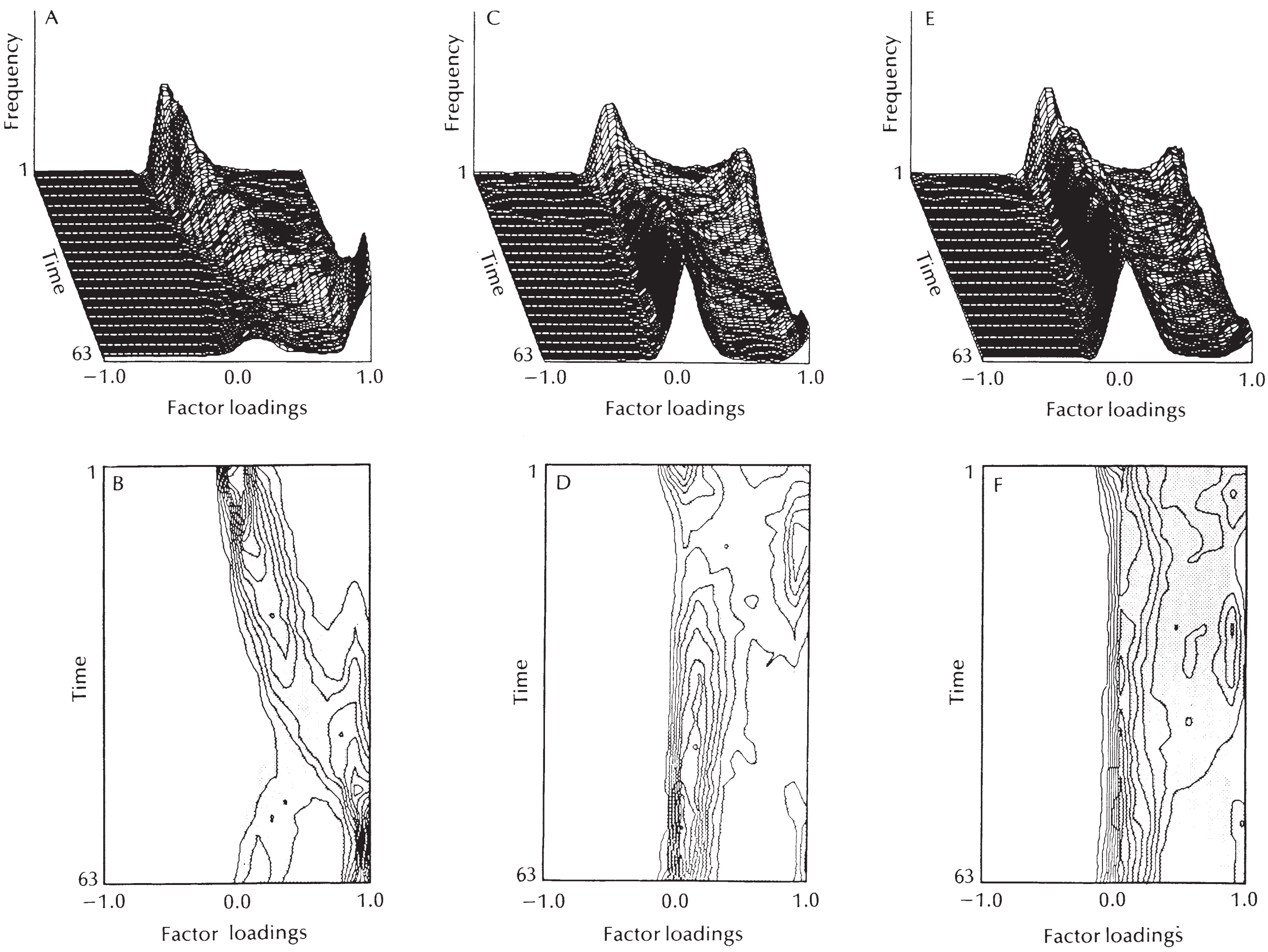



**Fig. 1** The approach that yielded these results combines simulation modelling with a statistical analysis dependent on computer solution. The research question requires that the expected distributions of temporal covariation among clades generated by a random process be known. Because there is no analytical solution to the problem, a random branching process was used to generate 45 000 simulated monophyletic clades, where the differences between each clade's history are due to the random elements of the branching algorithm. Each evolutionary 'trial' of 90 such clades, allowed to evolve for 63 time steps (where 90 and 63 were chosen to match the empirical data of number of taxa and stratigraphic stages, respectively), was then subjected to Q-mode factor analysis (to match the method of analysis of the empirical data). The frequency distribution of these 500 factor analyses are shown in A, C, and E which represent Factors I, II, and III, respectively. The stippled areas of B, D, and F represent the corresponding patterns not significantly different from expectations of a random branching process. (After Kitchell and MacLeod 1988.)

coupled logistic) the exploration of behaviour involves only kinetics. Kinetics are more inherently intuitive than dynamics, which incorporates feedback.

A more ambitious undertaking of theory development and simulation exploration involving feedback, nonlinearity, and complexity, is the work of DeAngelis *et al.* (1985) on potential coevolutionary dynamics, a series of studies motivated by (but not confined to) palaeontological questions. What this work has gained is a new intuition to replace the old expectation of linear escalation. In addition, it has shown the salient features of nonlinear dynamics (Fig. 2): how the behaviour of the individual parts are qualitatively different from the behaviour of the whole; and the influence of evolutionary change on itself, where 'playing the game changes the rules'.

## Computer-intensive statistical inference

Science is argument focused on the differential credibility of competing hypotheses. Palaeontology, a historical science, must make argument of process (where the interest generally lies) from evidence of pattern (where the information generally lies). Fortunately, hypotheses of process contain predictions of pattern, and so there can be effective argument provided by historical pattern. Statistics similarly deals with an end product (namely, some observed set of data) and makes arguments, among others, regarding what factors are, and to what extent, causally responsible.

The power of computing is currently changing the field of statistics. In general, the computer has allowed even classical statistical methods to be applied to what would once have been unmanageably large data sets. Palaeontology has benefited from this increased capability; the compilation and analyses of large databases have changed the tenor of arguments, for example, on patterns of diversification (Section 2.7), extinction (Section 2.12.3), rates of phenotypic evolution, and taxonomic turnover (Section 2.11). Palaeontology, however, has been hampered by the limits of classical statistics: the need to make *a priori* assumptions about the form of the probability distributions that are sampled by the data, and the restriction to measures whose theoretical properties are simple enough to have analytical proofs. These limits have been transcended recently by computer recursion techniques that replace analytical solutions with enormous numbers ($10^5-10^9$) of computations.

*Bootstrapping* represents such a computer-intensive method, described as the 'substitution of raw computing power for theoretical analysis' (Efron & Gong 1983). Using the traditional approach, one would hypothesize a process (or model) and deduce (or simulate) its behaviour, to compare these outcomes with empirical data. The bootstrapping approach is logically different. Bootstrapping derives its power from the assumption that the empirical sample provides an informative 'glimpse' of the real or underlying process. This empirical sample is resampled with replacement a large number of times, with the statistic(s) of interest calculated for each bootstrapped sample, in order to construct the bootstrapped probability distribution, against which the empirical sample is compared. The bootstrap is especially useful in cases where the probability distribution is unknown, or if the data violate certain (particularly parametric) distributional assumptions. A large number of palaeontological cases fall into these categories.

The bootstrap method has been applied in palaeontology to problems that include estimating confidence limits around phylogenies, assessing patterns of extinction probability and the shape of clade diversity histories, and the significance of differences in rates of evolution. A problematic feature of much palaeontological data for such methods is that the data are often ordered by (geological) time. The original bootstrap method was designed for data that are identical and independently distributed; time series do not satisfy this criterion. A method applicable to palaeontological (time series) data sampled at intervals that may or may not be constant is now available. In particular, the method recognizes the necessity of coupling the magnitude of evolutionary change with the magnitude of the time interval over which that change is measured (Kitchell *et al.* 1987) (Section 2.11). The method also works with two types of time series: those in which a change in the time series is recognized on the basis of independent criteria, and those in which a segment of the time series is identified as exceptional simply on the basis of that change (*post hoc* recognition). Such computer-intensive methods of statistical inference will undoubtedly play an increasing role in fields such as palaeontology that rely little on laws, axioms, and deductions to gain understanding.

## Sensitivity of initial conditions

Palaeontologists have used computer simulation methods to generate samplers of patterns produced by a variety of random processes, because much of the evidence in palaeontology since the nineteen-seventies is pattern data. Mathematicians and statisticians had already shown that random processes are capable of producing orderly pattern. Many of the properties of random processes were known by analytical solution. However, the ability to display these randomly-produced patterns *graphically* and by simulation did most to convince palaeontologists of the fallacy of the expectation that orderly patterns required deterministic explanations. It was shown that palaeontologically significant patterns, such as some trends and the topology of branching patterns, could be produced by random models (see review by Raup 1977). The purpose of this work was both to enlarge the intuitive understanding of palaeontologists so that they would not incorrectly equate pattern with non-randomness, and to better identify non-randomly produced patterns.

The opposite side of this coin, namely that completely deterministic processes lacking randomness can nevertheless produce random patterns, required the computer for its development. Until recently

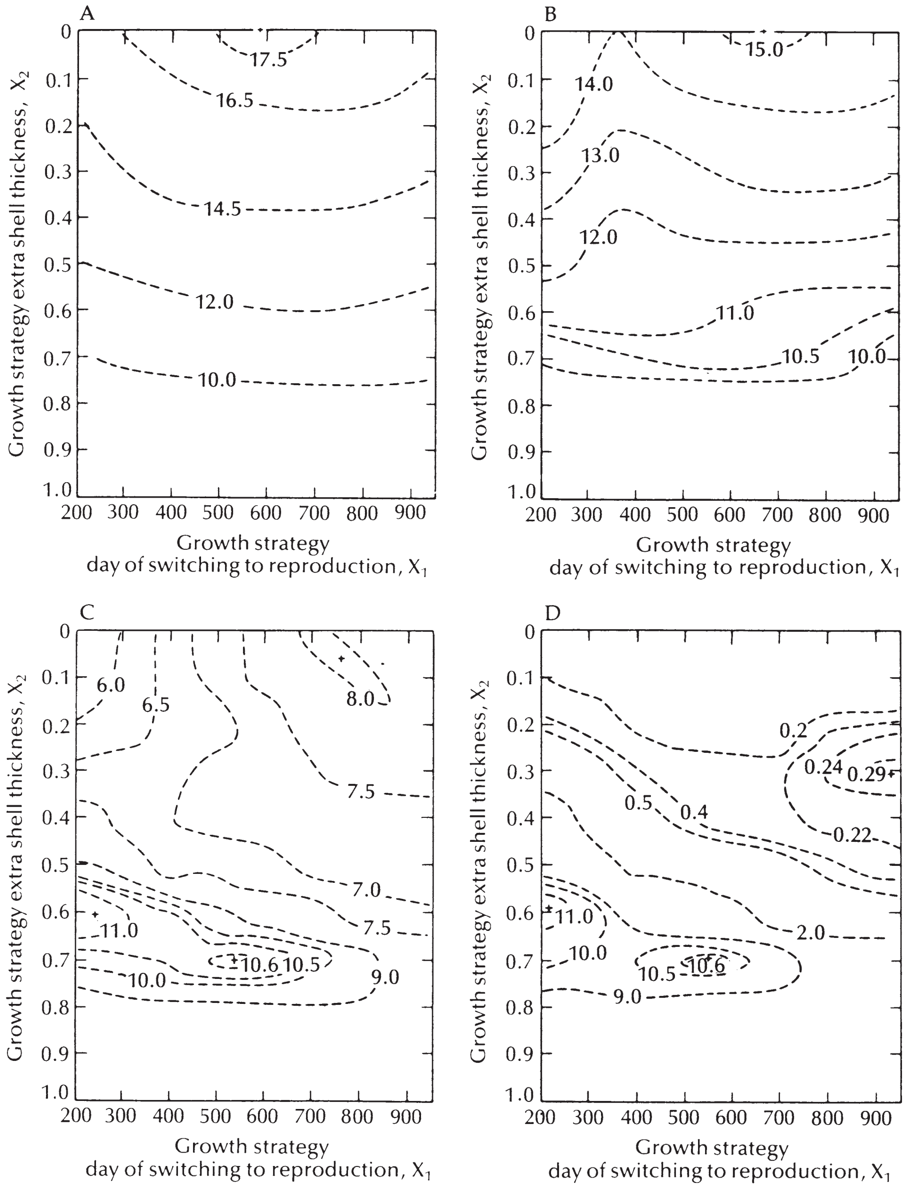



**Fig. 2** This example of computer-intensive analysis involves simulation modelling of a set of simultaneous algorithms that represent the opposing interests of a species interaction. The axes represent trade-off energetic options of a prey species (vertical axis = morphological allocation option; horizontal axis = reproductive strategy option). The contours depict the fitness consequences (in terms of total expected reproduction of the prey over its lifetime) for all possible combinations. Both the magnitude and positions of the contours change dramatically as predation intensity is increased, from zero in panel A to increasingly high values towards panel D, despite there being no change in the predatory strategy of prey selection. (From DeAngelis *et al.* 1985.)

within all the sciences, complex patterns were considered to be the consequence of complex causes. It has now been shown, however, that apparently random behaviour can derive from even simple deterministic processes. A small difference in initial conditions, for example, can lead to unexpectedly divergent behaviours. The term 'chaos' has been applied to such patterns and processes, to distinguish them from randomness. In chaos, the disorder is ordered. Such ordering is apparent in the detail of the patterns, a detail made increasingly evident by computer techniques and images.

In palaeontology, it was shown that the most simple model of diversification, and the one being applied to empirical analyses of taxonomic diversity, had chaotic behaviour. Using computer simulation runs to map the surprising array of behaviours and their abrupt and ordered thresholds, Carr & Kitchell (1980) showed that the 'coupled logistic' model of Sepkoski (1979) could produce not only logistic patterns of diversity change with time but also extremely complex and chaotic patterns of diversity change. In this latter case, the oscillations are driven internally, without external perturbation. Whereas earlier work, by warning that a high degree of order can be generated by purely random processes, had tried to dispel the palaeontologist's bias that randomness implies a random pattern, Kitchell & Carr (1985) warned against the bias that determinism implies an ordered pattern. They showed that even a completely deterministic and remarkably simple process can produce patterns of bewildering complexity. The understanding of chaotic behaviours is now being pursued in a number of cognate fields within biology, physics, and chemistry, promising to revolutionize our collective understanding of a class of complex phenomena, until recently unknown.

## Phylogenetic inference

The methodology of inferring phylogenetic (evolutionary) relationships among organisms has become both increasingly explicit and empirical (Section 5.2). Phylogenies are constructed from data on the distribution of characters (the empirical component, such as that resulting from morphometric studies), according to some criterion made operational by a computing algorithm (the explicit component). These criteria and associated algorithms used to form phylogenetic hypotheses rely either on parsimony methods, maximum likelihood methods, or compatability methods; reviews that examine the fundamental assumptions of each method were given by Felsenstein (1983).

These methods are derived from a class of problems in mathematics and statistics that focus on maximizing or minimizing some aspect of the data. In such optimality methods, the assertion is not that the historical process of evolution is optimal. Rather, optimization methods are used to choose among all tree topologies generated by an algorithm for a given set of data. Parsimony methods, for example, evaluate phylogenetic hypotheses on the basis of number of homoplasies (convergences and parallelisms); the 'best' genealogy is the one of minimum homoplasy. Because the criteria for evaluating phylogenies are unique to the method, comparing methods in terms of finding the 'true' genealogy is not possible. Instead, types of parsimony, maximum likelihood, and compatability algorithms can be compared with one another in terms of a practical goal (efficiency in computer time) and a methodological goal (minimizing tree 'length' or the required independent origins of each character).

Although small data sets may be analysed by hand (using the 'brute force' method of generating all possible cladograms; there are 15 possible for four taxa), large data sets *require* computer-assisted analyses (there are more than two million cladograms for only nine taxa, and more than $10^{20}$ cladograms for 20 taxa). Even the latter is too much for computer analysis. This raises an interesting situation; there is no exact solution to the problem of finding *the* minimum tree for even moderate-sized data sets. This problem may not be soluble: among mathematicians, there is agreement that NP- (not polynomial)-complete optimization problems (such as these) cannot be solved given current approaches and algorithms. Within palaeontology, phylogenetic approaches principally make use of morphological character data. An interesting discussion was provided by Gauthier *et al*. (1988) who showed, using both palaeontological and neontological character data, the importance of palaeontological data. Stratocladistic methodology may also prove useful as a means of integrating both character data and stratigraphic data in an analysis of phylogeny, where a total parsimony debt (summed from morphology and stratigraphy) serves as the minimization criterion.

A problem in need of redressing is that most palaeontological analyses of taxonomic data sets (e.g. patterns of diversity change, extinction, rates of evolution) have made use of data currently available. Much of these data do not reflect the methodology discussed above. As a recognized consequence, monophyletic and non-monophyletic groups are not distinguished from one another. This presents a problem of interpretation since 'monophyletic groups have a unique history that exists and is to be discovered, whereas paraphyletic groups may start off with a unique history, but their boundaries are adjusted *a posteriori* and they are in part a human invention' (Benton 1988).

## Computer-aided vision systems

The most severe restriction on palaeontology today is the lack of adequate databases to test hypotheses of interest. It is likely that major advances in the future will be made in the rapid acquisition of morphological and character-state data from automatic vision systems. Although the systems described below have not yet been widely used in palaeontology and are still in stages of development, the future of advanced computer techniques in palaeontology will undoubtedly move in these directions.

With laser disc technology, it is now possible (and currently in use in some research laboratories) to store all known species' images (e.g. holotypes) and their descriptions, and to make use of them with a dichotomously driven, interactive algorithm to resolve the identification of an unknown species. This technology permits exact comparisons on the screen. Access is also virtually instantaneous, with more than 50 000 analog images currently capable of being stored per disc and with the ability to access more than one disc at a time. The system utilizes answers provided by the user to a computer-driven key to select the most likely known species. It then automatically compares the unknown image with these selected known species, making comparative diagnostic measurements. Because of the interactive nature of the algorithm, the user maintains control of the final decision.

Programs designed for palaeontological applications that make use of artificial intelligence programming have also begun to be developed (e.g. Riedel *in press*). These programs explicitly attempt to deal with objects that are naturally variable (organisms), and may be made even more variable by preservational processes, yet are members of a single category (the species). These systems use character-state descriptions entered by the user and work within a hierarchy of character-states necessary for discrimination between possible species. As above, the final result is a 'narrow as possible' reporting of species that have these characters.

Algorithms associated with image analysis systems are also now available (and being developed) for converting data from serial sections of any fossil (whether actually sectioned or not) to three-dimensional models of that fossil, thereby allowing the user in many instances to bypass the building of physical models. The reconstructed three-dimensional form can also be viewed from all perspectives by rotation and movement simulation algorithms.

## Acquiring morphometric data by image analysis

Palaeontologists, of necessity, rely on morphological data to make evolutionary inference. A recurring problem in the sciences is that the theories of a field may occasionally far exceed the capacity of that field to acquire and analyse data necessary for evaluating those theories. Such a situation occurred in palaeontology, e.g. with the proposal of punctuated equilibrium and its associated prediction of morphological stasis. The imperative quantitative data on morphological change within and between species, and over time and geography, were not copiously available. Much of the problem stemmed from the difficulties of acquiring quantitative data on morphology in a rapid and accurate manner.

Widespread interest within numerous fields in the study of biological shape and its transformation has resulted in a series of important advances. In terms of technique, advances in computer technology have made possible increasingly powerful image analysis systems that combine image acquisition and image processing capabilities with pattern recognition analyses. Such image analysis or optical pattern recognition systems have made the acquisition of quantitative data on morphology rapid, accurate, and affordable.

The field of *morphometrics* has been redefined recently as 'the analysis of biological homology as well as geometric change' (Bookstein *et al*. 1985). Morphometrics is relevant to questions of phylogenetics, ontogenetic trajectories and their evolutionary potential for heterochrony, patterns of anagenesis and cladogenesis, ecophenotypy, and morphological integration. Such analyses are particularly informative when they combine hypotheses of phylogenetic descent with hypotheses of morphological (character) transformation.

Reviews of methodology and examples of the application of outline methods and landmark methods were given by Lohmann (1983) and Reyment (1985), respectively. The approach recommended by Bookstein *et al*. (1985) focuses more on the dynamics of change in shape. Analyses begin with a study of the major dimensions of morphological variation in time and space that characterize each species. Analytical procedures determine which parameters contribute most to intraspecific characterization and to interspecific discrimination within respective geographical and temporal contexts. A recent application of outline and landmark methods was given by Stanley & Yang (1987) who assessed the rates of morphological evolution in separate lineages of Neogene bivalves. Schweitzer *et al*. (1986) used the same basic techniques to evaluate the relative contribution of development (heterochrony) and structural regulation in two closely related species.

## Prospects

Palaeontology today is actively engaged in computer-aided research programs. The evolution of the interaction between palaeontology and computer technology is following much the same path as that of the evolution of the human brain, as we currently understand it. The computer has not simply resulted in an increase in the speed, efficiency, and size of the problems we analyse. It has introduced novelty or true innovation. It is well recognized that the biological and evolutionary sciences deal with a much greater degree of complexity in their systems of study than do the physical sciences. Computer techniques are beginning to open up the field of study of complex systems and, through vision systems, to relieve the human investigator of some of the effort in amassing empirical data.

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# 6.2 Practical Techniques

## 6.2.1 Preparation of Macrofossils

P. J. WHYBROW & W. LINDSAY

### Mechanical methods

A rock is invariably physically weakened by the presence of fossils, usually because the chemical constituents of fossils differ from those of the enclosing matrix. For at least three centuries, palaeontologists have exploited this difference by using percussion methods, normally a hammer and a chisel, to expose and to collect fossil material. Following the introduction of electricity into museums and universities in the nineteenth century, power tools were developed that 'automated' the basic manual techniques. Today, three mechanical techniques are widely used in palaeontology laboratories: *percussive*, *grinding*, and *abrasive* (Rixon 1976).

*Percussive and grinding techniques.* Percussive electric or pneumatic engraving pens (Fig. 1) are hand-held and equipped with a tungsten carbide tip. Invariably the tip supplied by the manufacturer is too coarse for most preparations and has to be substituted by tungsten carbide rod welded onto the oscillating shank of the pen. The fitting of the rod also enables a choice of either chisel or pointed tips to be fashioned. Before commencing preparation not only should the concealed morphology of the fossil be imagined (by reference to published information concerning similar fossils) but also the petrology of the matrix must be investigated (in case acid techniques can be better utilized). If

**Fig. 1** A hand-held, pneumatic engraving pen used to remove rock matrix. In the foreground is a heavy duty pneumatic chisel.

the rock cover is excessive, it can be removed by grinding. Diamond or carborundum wheels and burrs used in dentistry are ideal; for larger blocks, parallel grooves are cut using a pneumatic diamond saw and the thin rock wedges then removed by percussive methods. All preparations should be carried out at high magnifications using a binocular microscope so that the fossil–rock interface can be easily seen; a cold-light, fibre optic light source is invaluable for this (especially a system with contrasting colour filters). The position of the percussion point should ideally be at right angles to the plane of the fossil surface being exposed. The degree of force required to chip or flake away the rock and leave an unmarked specimen comes about by trial and (infrequently) error. Extreme care must be taken when microbedding planes pass through and around a fossil as flakes may contain part of it. Extensive preparation gradually weakens the structural integrity of a fossil but the percussive force used normally remains constant. Therefore, the specimen must be supported firstly by a shock absorbing cushion (such as a sandbag) and secondly by embedding in a water soluble polyethylene glycol wax of high molecular weight. For supporting delicate areas of a vertebrate skull, this wax is essential and can itself be strengthened while in its fluid state by the addition of surgical gauze (Whybrow 1982).

*Abrasive techniques.* 'Airbrasive' or 'sand-blast' machines are quick and effective aids for removing rock that is softer than the fossil. An inert gas (compressed air, nitrogen, or carbon dioxide) propels an abrasive powder, which is kept in a fluid state in a vibrating pressure vessel, through a nozzle of small diameter. Various hardnesses of powder can be used, ranging from sodium bicarbonate to the cast iron shot used in large industrial machines. Similarly, various diameters of nozzle can be selected. The abrasive action depends on particle size and the amount of gas pressure used. Exposed parts of a fossil can be protected by a coating of rubber latex from any polishing effect of the powder, and a box with a dust extraction system protects the operator from possibly hazardous particulates. A binocular microscope is essential for this work to see the degree or variability of abrasion of the rock.

## Chemical methods

Rocks and the fossils they enclose do not always respond well to mechanical techniques. The hardness of an ironstone or some limestone matrices may prohibit mechanical preparation, while the complexity or abundance of fossil remains may defy methods reliant on manual dexterity. As with mechanical methods, chemical methods aim to remove the matrix without damaging the specimen. However, in both cases, there are occasions when the information required can only be obtained by destroying the fossil and retaining the natural impression left in the rock.

Chemicals used in fossil preparation are chosen for their ability to disrupt or dissolve the rock matrix, but they must achieve this without causing the same effect on the fossil. Such differentiation is determined by the chemistry of both rock and fossil. Furthermore, the long-term conservation of the fossil in a collection, with all the hazards associated with handling, must be considered.

*Chemical disruption.* Water, sometimes in conjunction with a detergent, readily breaks down some soft shales and muds. The clay minerals swell as the strongly polar water impregnates their structure. Detergents and other surfactants assist the process by reducing surface tension at the clay–water interface. A similarly disruptive effect occurs in the presence of hydrogen peroxide ($H_2O_2$). Solutions of $H_2O_2$ are unstable and deteriorate giving off oxygen. In the presence of alkalis, rough surfaces, and metals, the process is accelerated. In rock matrices the oxygen bubbles released within the pores disrupt the sediment and weaken the matrix (see also Section 6.2.2).

*Sequestrants and chelating agents.* Polyphosphates, such as sodium hexametaphosphate $(NaPO_3)_6$, act as water softeners, sequestering the calcium, magnesium, and iron salts present. Clayey and muddy sediments are broken down in solutions of polyphosphates. In a manner similar to that of water softeners, chelating agents form stable complexes of metalic ions (such as calcium and magnesium) in rock forming minerals. Ethylene diaminetetracetic acid and its sodium salts in solution can corrode rock matrices, but it will also attack fossil material and careful control is therefore required.

*Acids.* Acids are extensively used in chemical methods of preparation (Lindsay *in* Crowther & Collins 1987). Hydrochloric acid was used in the late nineteenth century to dissolve limestone containing carbonized graptolites. Subsequently hydrofluoric, nitric, formic, acetic, and thioglycollic acids have been used in both vertebrate and invertebrate palaeontology. Hydrofluoric and nitric acids are employed for the maceration of sediment samples containing fossil pollen (Section 6.2.2) and pose particular problems of safety.

The development of vertebrate material using aqueous solutions of acetic acid was first carried out in the nineteen-forties and followed from earlier techniques devised at the British Museum (Natural History) (Rixon 1976). Acetic acid is the most commonly used acid for this work and is readily controlled and reasonably safe at low concentrations. Used in solutions of 1–10%, the reaction between the acid and calcium carbonate in the matrix occurs more readily than that between the acid and phosphates in fossilized bone (Fig. 2). The differential rate of dissolution is controlled by varying the length of immersion time and the acid concentration. The time of exposure to acid at each step of the process may vary from a few hours to several days, and the development of a specimen may take years to complete. Bone that undergoes prolonged exposure to acid will be significantly affected; for this reason the dissolution of the matrix is interrupted regularly to wash, dry, and lacquer any newly exposed bone.

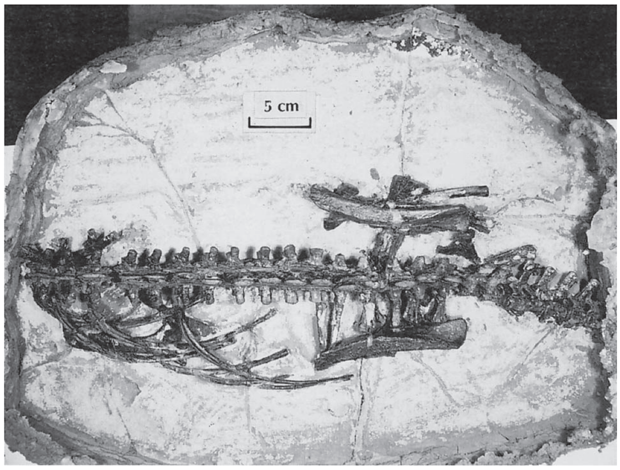


**Fig. 2** The partially exposed, post cranial skeleton of the Jurassic dinosaur *Scelidosaurus harrisoni* during preparation with acetic acid.

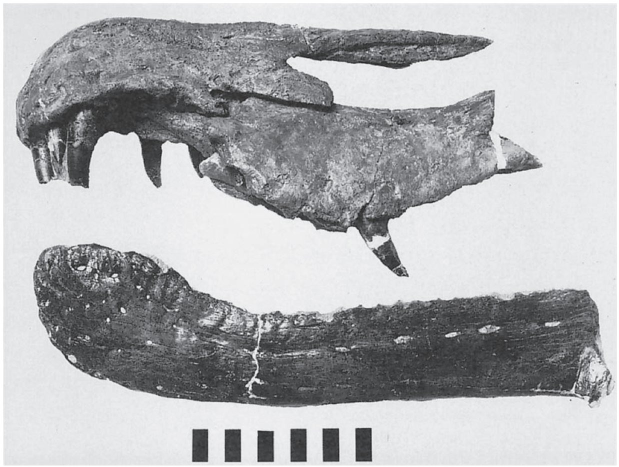

**Fig. 3** Anterior skull and jaw elements of the Lower Cretaceous dinosaur *Baryonyx walkeri* after mechanical and chemical preparation. Scale in cm.

## Consolidants and adhesives

Consolidation (hardening) of a specimen must be carried out during preparation in order to conserve it for subsequent study. A number of adhesives and consolidants are used; they should be reversible in the long term as further work on a specimen may be required. In mechanical preparation the surface of the fossil is coated with a consolidant as the rock is removed in order to prevent fractures caused by any excessive vibration (Fig. 3). Polyvinyl butyral resin, dissolved in a variety of solvents, has now replaced polyvinyl acetyl resins and serves as an adhesive when dissolved in ethyl acetate. Polymethyl-methacrylate, also dissolved in ethyl acetate, is a useful adhesive but shrinks markedly on drying and should never be used as a consolidant. Supplied as a powder monomer with a liquid polymer catalyst, polymethyl-methacrylate effectively seals wide cracks. Cynoacrylate adhesives are effective for the fast repair of small pieces of fossil, but their long-term stability is at present poorly understood and they are practically insoluble when set. Chemical methods of preparation require adhesives and consolidants that protect the fossil from chemical attack as well as supporting and strengthening it.

Polybutyl-methacrylate is used as an acid resistant consolidant and can withstand long periods of immersion in acids. Polymethyl-methacrylate as an adhesive is similarly resistant to attack by organic acids; the cynoacrylates also seem to be unaffected.

In *all* methods of preparation, which by necessity expose the fossil to risk, good records must be kept (Rixon 1976). Photographs, drawings, and written descriptions are essential and must be prepared as the specimen passes through various stages of treatment. Their value can only be appreciated when a dismembered fossil needs to be reassembled.

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## 6.2.2 Extraction of Microfossils

R. J. ALDRIDGE

Extraction techniques have been developed principally to recover microscopic fossils from rock samples, but may also be adopted for larger specimens. A variety of chemical and mechanical procedures for rock disaggregation are employed, dependent upon the composition of the rock and of the fossils sought. Residues from these processes are often large, and some concentration of the microfossil specimens may be required. Many of the chemicals used in dissolving samples and in concentrating residues are highly hazardous or toxic and the safety aspects of all techniques should be fully investigated before they are applied. Full attention must be given to hazard warnings given by the suppliers of chemicals.

### Releasing microfossils from rocks

*Calcareous rocks.* Limestones, dolomites, and calcareous clastic rocks can be broken down with dilute organic acids (e.g. acetic acid, $CH_3COOH$; formic acid, (HCOOH) to release microfossils composed of calcium phosphate (conodont elements, fish remains) or with resistant organic walls (scolecodonts, chitinozoans, palynomorphs) (Fig. 1). Some workers crush the samples into 1–3 cm chips, but this is only necessary for very impure limestones. Standard procedure is to place the sample in a polythene bucket or beaker which is then filled with warm, 10–15% acetic acid; formic acid acts more rapidly and may be used at higher concentrations, but is more corrosive and hazardous. Phosphatic material may be attacked by acetic acid in the absence of calcium acetate to buffer the solution, so powdered calcium carbonate should be added to samples with low lime content. Alternatively, samples may be buffered by using a solution comprising 7% concentrated acetic acid, 63% water, and 30% of filtered liquid remaining after digestion of previous samples.

Hydrochloric acid (HCl) dissolves phosphate, but may be used at a concentration of about 10% to recover organic-walled microfossils and siliceous (e.g. radiolarians) or silicified material. When buffered by calcium acetate, HCl can be used to extract phosphatic, siliceous, and organic specimens from a single sample, but there is always a risk of damage to the phosphate, especially when all the limestone is allowed to dissolve.

When effervescence fades or ceases, the sample is sieved; the mesh sizes of the sieves employed are dictated by the sizes of the microfossils sought. For conodont elements, an upper sieve of 1 mm mesh and a lower of 75 μm are adequate, but chitinozoans and palynomorphs require much finer bottom sieves, down to 5 μm. Undissolved rock remaining on the upper sieve is placed in new acid solution, while the sieved residue is dried and retained for concentration and picking.

There is no easy technique for recovering calcareous microfossils from calcareous rocks. Soft limestones and marls may be treated in a similar way to soft shales, but for hard limestones and chalks only crude mechanical methods are available. Normally, these involve pounding the moistened sample with a pestle in a mortar, followed by washing and concentration. An intermediate step is sometimes inserted in which the pulverized sample is washed into a container and placed in an ultrasonic cleaner for a period of two minutes to two hours. Delicate microfossils will not survive these techniques and are best studied in thin section. The procedure may be successful, though, for calcareous nannofossils such as coccoliths.

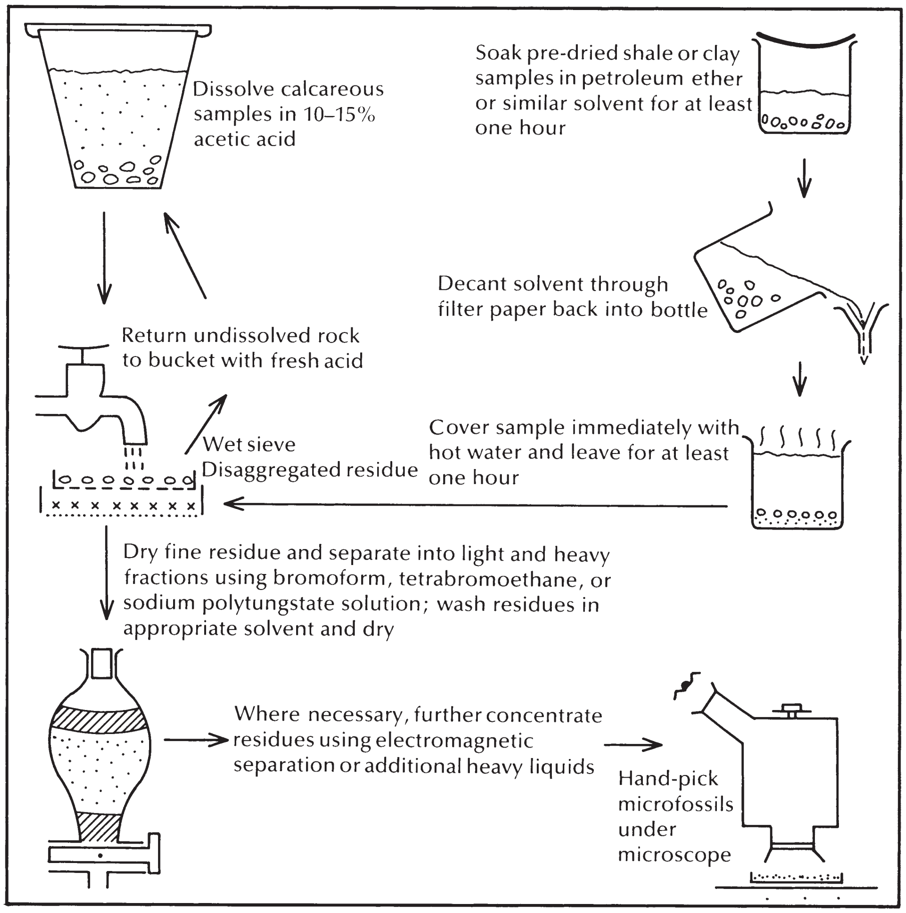


**Fig. 1** Techniques for extracting and concentrating microfossils from limestones, calcareous clastic rocks, and soft or partly indurated mudrocks.

*Argillaceous rocks.* Soft or partly indurated clays and shales may be disaggregated by a number of techniques. A relatively gentle procedure involves the use of petroleum ether, paraffin, or similar solvent on thoroughly pre-dried samples (Fig. 1). All of these solvents are highly flammable, and due regard must be given to fire risks. The rock is soaked in solvent for at least one hour; the solvent is then poured off and the rock immediately inundated with hot (not boiling) water. The clay is reduced to an uncohesive, muddy slurry, which then can be wet-sieved as appropriate. Black shales and other mudrocks that do not respond to this treatment may disaggregate on immersion in a 10–15% solution of hydrogen peroxide ($H_2O_2$) in water (see also Section 6.2.1). The reaction involves the oxidation of organic matter, which may also be accomplished by other oxidizing agents, such as sodium hypochlorite (NaClO).

Hard clays may also disintegrate when boiled in water with a dispersing agent. Those commonly used include a few grams of sodium carbonate ($Na_2CO_3$) or 20% sodium hydroxide (NaOH). Some samples respond to boiling in the detergent Quaternary 'O', with a 20% solution added to boiling water containing the sample. A combination of techniques may be applied, perhaps involving treatment with buffered acetic or formic acids for samples containing some calcium carbonate. Mechanical disaggregation may sometimes be achieved by alternate freezing and thawing of samples soaked in water, or by boiling the rock in sodium thiosulphate ($Na_2S_2O_3.5H_2O$), which will crack the shale apart as it crystallizes when allowed to dry.

*Sandstones.* For most microfossils there is no technique for extraction from sandstones or siltstones, unless the rock is poorly-cemented, when mechanical methods may be successful, or calcareous, when acids may be employed. For organic-walled microfossils, palynological techniques (below) may be tried, but palynomorphs are not normally well preserved in coarse clastic rocks.

*Cherts.* Phosphatic microfossils, such as conodont elements, can be recovered from cherts and other siliceous rocks using dilute hydrofluoric acid (HF). The sample is crushed into 1–5 cm fragments, any carbonate removed with acetic acid, and the fragments placed in 5–10% HF in an acid-resistant plastic container in a fume cupboard. After 24 hours the HF is decanted off and neutralized with calcium hydroxide; the residue is first washed with dilute HCl, then several times with water before being sieved and reprocessed as necessary. The technique works through fluoridization of the apatite of the conodont elements and is accompanied by some fracturing and distortion of specimens. *Hydrofluoric acid is extremely dangerous* and must be used in properly designed fume cupboards with the handler wearing *full protective clothing*.

## Concentration techniques

Residues from disaggregation procedures can be concentrated into light and heavy fractions by using various heavy liquids. Bromoform ($CHBr_3$, specific gravity 2.89) and tetrabromoethane ($C_2H_2Br_4$, specific gravity 2.96) are commonly used to produce a heavy concentrate containing phosphatic microfossils, but these chemicals are severely toxic. A safer alternative involves the use of water-soluble sodium polytungstate ($3Na_2WO_4.9WO_3.H_2O$), which can be made up at any required specific gravity, but is best at 2.75 or slightly higher to avoid problems of high viscosity and crystal precipitation. Light or buoyant microfossils, such as hollow foraminiferans, radiolarians, and chitinozoans, may be removed in a light concentrate by adjusting the specific gravity of the sodium polytungstate accordingly. Electromagnetic separation is useful in dealing with large residues containing iron oxides or iron-rich dolomite grains.

## Palynological techniques

Procedures for the recovery and concentration of palynological microfossils are complex, with the steps tailored to the nature of the sample being processed. A full account was given by Phipps & Playford (1984), who emphasized the dangers of HF, zinc bromide ($ZnBr_2$), and other chemicals used. *Palynological processing should only be undertaken in a purpose-built laboratory with efficient fume-cupboards, full protective clothing, and neutralization and disposal facilities available*. All equipment must be kept absolutely clean to avoid contamination.

Rock samples should be thoroughly cleaned by scrubbing and, if necessary, etching in HCl or $HNO_3$ (nitric acid) prior to crushing to 1–2 mm fragments. Any carbonate in the rock must be completely removed using warm 10% HCl, followed by thorough washing in distilled water. Silica and silicates are dissolved using HF. Cold, concentrated HF is poured onto the sample in a polypropylene beaker and stirred daily with a teflon rod until all the rock has disaggregated. The reaction may be speeded up by warming the containers in a water bath. After digestion the sample is washed with warm water and fluoride precipitates are removed by treatment with warm 40–50% HCl, followed by at least four washes in warm water. Ten per cent HCl is added to the last washing to discourage flocculation. Mineral particles may be separated from the organic residue by centrifuging in zinc bromide solution (specific gravity 2.0); if examination reveals the presence of pyrite, 10% $HNO_3$ may be added to the organic fraction for ten minutes to remove it. Unwanted, undecomposed, or partially decomposed organic material can be removed by careful oxidation (although experience is needed to avoid destruction of microfossils during this process). Concentrated $HNO_3$ is a commonly used oxidant. Fine organic debris may be removed by alkali treatment with 5% potassium hydroxide (KOH).

After processing, the remaining organic-rich residue is sieved, using appropriate mesh sizes for the palynomorphs present. Generally a 53 μm sieve is employed to retain chitinozoans and large palynomorphs, while a fine sieve of 5–7 μm is necessary for the smallest specimens. The fossils may be further concentrated prior to sieving by swirling in a large watch glass. The palynological concentrate, or a representative fraction of it, is finally strew-mounted onto slides, using glycerine jelly for temporary mounts and Canada balsam or a plastic mounting medium for permanent mounts.

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## 6.2.3 Photography

D. J. SIVETER

### Introduction

The photography of fossils involves a wide range of techniques, materials, and object sizes. Large fossils, in excess of about 15 cm in length, fall within the range of normal cameras with standard lenses; specimens up to about 2–3 mm long are best photographed using the scanning electron microscope (SEM). The middle ground between normal and SEM photography (Section 6.2.4) is generally known as *macrophotography*, and covers a magnification range on the negative from about $\times$ 0.2 to $\times$ 20 or more. Macrophotography in incident light, for which there are numerous systems available, is the type of photography used for most macroinvertebrates. The Leitz 'Aristophot' system (Whittington *in* Kummel & Raup 1965) was first used for the macrophotography of fossils in the nineteen-fifties, and has since been widely adopted (Fig. 1H). It was modified in various ways before production was discontinued in the early nineteen-eighties. In its image range the quality of photographs produced by this apparatus is excellent. The comparable Nikon 'Multiphot' system gives similar results and is still (1991) marketed. In the last decade Wild-Leitz (now Leica) have introduced a quite different system for the macrophotographic range, the photomacroscop. The most useful source on the photography of fossils is Kummel & Raup (1965); many of the techniques described therein have not been superseded.

### Preparation: cleaning and coating

Prior to photography any extraneous sediment should be removed from the surface of the fossil (Section 6.2.1). If the specimen is embedded in matrix, particular effort should be concentrated on cleaning its margins. This obviates the need for any retouching of or cutting round the fossil outline to delete non-organic material on the final print. The handling of testaceous specimens should be minimized, and they should be cleaned with an organic solvent (such as acetone) to remove any surface grease marks.

When photographing most fossils, particularly those that are of variable or light shade, better results are obtained if the specimen is first coated. A matt, uniformly dark surface is applied to the fossil which is then lightly dusted with a whitening agent for contrast. Fountain pen ink and particularly black photographic opaque have been used as darkening agents; these should ideally be applied to impart a dark grey (not black) colour. The former can be removed in large part with a mixture of ammonia and hydrogen peroxide solutions, and the latter with warm soapy water. The cleaning of darkening agents from natural mould specimens (especially in medium to coarse clastics) is very difficult or impossible, as they are fully absorbed into porous sediments; this is particularly so where Indian ink has been used. The excellent opaque produced by Phillips and Jacobs (Philadelphia) is now discontinued. Practitioners should experiment with alternatives; poster paint has, for example, been successfully used. Various inks and carbon powder (soot) have been used to darken latex and silicone rubbers.

A whitening agent sympathetically applied on the darkened surface considerably enhances the contours and surface sculpture of the fossil, as it falls more densely on those areas of greater relief, which are thus highlighted (Fig. 1). It also provides an even, glare-free reflecting surface for photography and results in prints of a similar tone — which are desirable when making plates for publication. Ammonium chloride, magnesium oxide, and antimony oxide have all been used for whitening. Ammonium chloride and antimony oxide are heated in a glass bulb and the resulting sublimate cloud directed onto the fossil (Teichert 1948; Marsh & Marsh 1975). Magnesium oxide is produced by burning magnesium ribbon and the fossil is held over the smoke. Ammonium chloride should be washed off immediately after use as it combines with water vapour in the air to form hydrochloric acid capable of etching the fossil; its deliquescence also renders it impracticable for use in areas or on days of high humidity, as the sublimate quickly becomes coarse-grained after coating. Nonetheless, many authors favour the use of ammonium chloride as control on the application of magnesium oxide is not very precise. All coating should be done in a fume cupboard, but the draught should not be so strong as to affect the flow direction of the whitening agent. After coating and prior to photography a check should be made under a binocular microscope for hairs or other artifacts. The implications for future conservation of the specimen should be considered before employing these techniques.

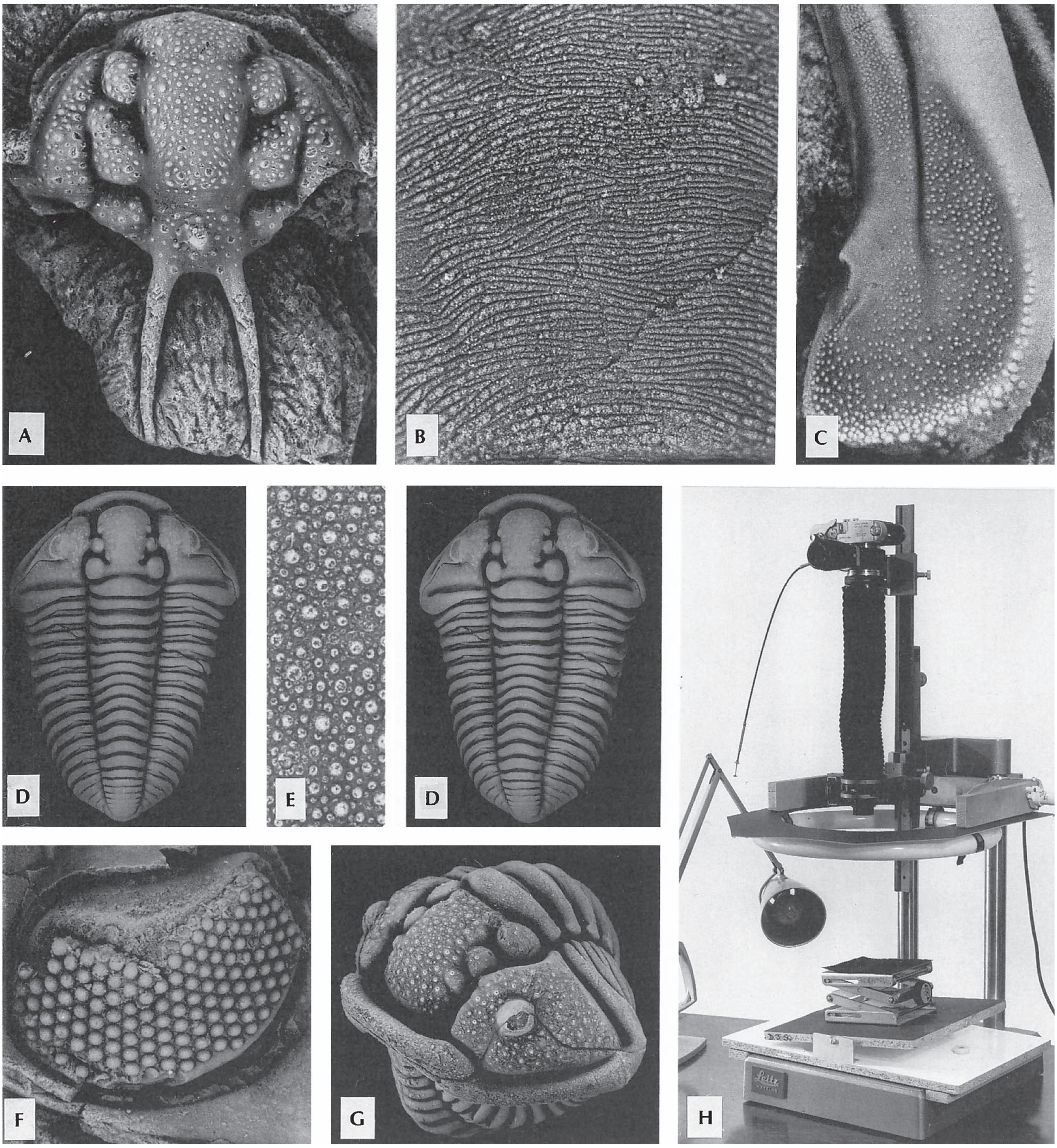


**Fig. 1** A and B taken using Nikon 'Multiphot', C–G using Leitz 'Aristophot'. A taken with the Nikon 'Makro-Nikkor' 12 cm lens, B with Nikon 'Makro-Nikkor' 6.5 cm lens, C–G with the Leitz 'Summar' 12 cm lens. A–C, E, G photographed on Kodak 'Panatomic X' film, D and F on Ilford 'Pan-F' film. All specimens are coated with ammonium chloride on top of matt black opaque. A–G, Silurian trilobites. A, Cranidium, odontopleurid, Ireland; dorsal view, × 4. B, Glabellar sculpture, proetid, Ireland; dorsal view, × 22. C, Thoracic pleural facet, calymenid, Gotland; lateral view, × 10. D, Stereo-pair, complete specimen, calymenid, West Midlands, U.K.; dorsal view, x 2. E, Glabellar sculpture, calymenid, Welsh Borderland; dorsal view, × 10. F, Eye, phacopid, Ireland; oblique view, × 7. G, Complete specimen, calymenid, Gotland; oblique view × 2.5. H, Leitz 'Aristophot' with anglepoise and ring light illumination, laboratory jack, and tilt-table for taking stereo-pairs.

## Macrophotographic equipment and methods

The photographic film should be fine grained (50 ASA or less) and have good resolving properties so that when enlarged it suffers minimal loss of definition; Ilford 'Pan-F' and Kodak 'Panatomic X' are both suitable. Fossil size on the final print depends on the negative magnification multiplied by that selected on the enlarger. Macrophotography of fossils is for most purposes adequately and economically performed with the use of 35 mm format, with final prints of up to × 30 to × 40 being satisfactorily obtained. Recourse to larger format apparatus and film (e.g. 9 × 12 cm) is preferable only where excessive enlargement is demanded, or where a wider field of view is required at a given magnification. The photographic stand should be sturdy and capable of absorbing vibrations.

The camera body is not one of the more critical pieces of equipment but the action of the shutter should be smooth if this is to be used to control exposure, and those with a reflex mirror lock-up facility that negates the vibrations from this source are most useful. Leica 'M' cameras have been used on the 'Aristophot' in combination with a separate reflex mirror unit that also incorporates a focusing magnifier and focusing screen. Nikon 'F' cameras for use with the 'Multiphot' house the reflex mirror and focusing system within the camera body. At high magnifications requiring long bellows extensions, where the slightest vibration is ruinous, it is best to control the exposure by means of the lens shutter rather than the camera shutter. When using the 'Aristophot' in the 35 mm format, the correct exposure time is best assessed empirically with the use of test films and records of film speed, lens type, aperture setting, lighting, and magnification. Through the lens metering (TTL) is available in this format with the 'Multiphot', utilizing in particular the Nikon F3 camera. However, with over-long exposures (in excess of about 1 second the readings from any type of metering system will be inadequate due to reciprocity failure, and extra time must be allowed, depending on the film type. Much macrophotography of fossils falls within the 1–15 second exposure time.

The focusing screen on the camera should be of the finely ground glass or clear glass type and focusing done at full aperture. The specimen–lens and lens–film (bellows length) distances combine to determine magnification on the negative, and at any given magnification these distances will vary according to the focal length of the lens employed. Manufacturers' handbooks normally contain graphs plotting magnification against distance for each lens. Sometimes it is desirable to produce negatives at set, whole number magnifications; this requires retention of the camera and lens in the appropriate positions and focusing by moving the specimen vertically, either by means of a heavy duty laboratory jack or a rack and pinion operated 'lift'. The specimen can be mounted by plasticine onto the jack or 'lift', the surface of which should be painted matt black to provide a contrasting background to the whitened fossil. Photographs other than those of surface sculpture should not be focused on the upper surface of the fossil but more towards the median plane of the specimen to take into account depth of field.

Lighting comprises two basic components. A directional light source, by convention shining from the northwest, is beamed at the fossil at an angle (normally low) suitable for emphasizing its relief. The shadows thus produced are partially filled in and the specimen lit overall by means of soft, diffuse, even illumination. One of the several ways of achieving the desired effect is to use an anglepoise lamp with a frosted bulb, the light strength of which is controlled by a dimmer switch, together with a fluorescent ring light (about 30 cm diameter and 60 watts) capped by a reflector (Fig. 1H). Any extraneous light should be prevented from entering the lens.

It is important to ensure that any lens used for enlarging small objects gives, in addition to sharp resolution at the plane of focus, good imaging throughout the depth of the specimen. Increased depth of field is achieved by reducing the size of the lens aperture, but beyond a certain limit (which can be empirically determined for each lens) the effect of diffraction gives progressively poorer resolution and makes it pointless to stop down further. Lenses optically corrected for the macrophotographic range, for use with the 'Aristophot' or 'Multiphot', come in several focal lengths from about 12 mm to 120 mm. Lens selection depends on the desired scale of reproduction, those with shorter focal lengths being used for greater magnifications. The original 'Aristophot' lenses, the Leitz 'Milar' and particularly the 'Summar' range, and also the later, compatible first generation 'Photar' range, give excellent results; Nikon have consistently produced four macro lenses with high resolving power for use with the 'Multiphot'. The latest, more restricted generation of 'Photar' lenses reproduce over the × 1 to × 16 range and are combined with the Leica 'R' system of cameras and bellows, featuring through-the-lens metering, for use on a copying stand. Other Leica 'R' macro lenses for use with this system enable reproduction from infinity to × 3.

The 'M400' photomacroscop of Wild-Leitz is a fully integrated unit featuring 35 mm to 9 × 12 cm format, automatic exposure control, and a 1:5 macrozoom objective, focusing being accomplished via a binocular system. With the optional use of three additional objectives and using the 35 mm format it covers the macro range × 1 to × 20. A 1:6 'Apozoom' objective has recently been introduced for this set-up. Wild-Leitz also offer a similar automatic system in the macro range on their 'M420' zoom macroscop. It is debatable whether the macrozoom lenses used on these systems can out-perform the individually computed Leitz or Nikon macro lenses, although the photomacroscop would seem to win over the 'Aristophot' and 'Multiphot' in terms of convenience of operation, combined with the relative lack of experience required to obtain reasonable results.

### Special techniques

More specialist techniques are sometimes employed in the macrophotography of fossils. Stereophotography involves photographing the specimen in two slightly different attitudes differing by an angle of rotation of 7–10° (Fig. 1D). The resultant two photographs give a three-dimensional image when optically fused by means of a steroscope (Evitt 1949). Immersion of a specimen in a liquid such as alcohol, water, glycerin, or xylene is undertaken particularly if the fossil is of low relief, and where the distinction between the fossil and the surrounding matrix needs enhancement, and also to make clearer internal structures (Rasetti *in* Kummel & Raup 1965). Photographs taken in ultraviolet radiation at low inclinations also bring out features of low relief (e.g. Whittington 1985). Lastly, X-ray photography with the use of long exposures has been successfully employed on pyritized material (Stürmer *et al.* 1980). A combination of the above techniques is possible, as with stereo and X-ray photography.

### Processing and printing

A fine grained developer should be used for the film, to maintain detail. The enlarger should have a good quality lens and hold the film perfectly flat. Resin coated paper has advantages over traditional fibre-based paper in speed of development, fixing, and washing, and the fact that glazing is unnecessary — it can be simply air-dried if required. Multigrade paper (either fibre-based or resin coated) is convenient to use and enables very fine contrast control on the finished print by utilizing enlarger filters graduated to half a grade of monograde papers; it also makes redundant the potentially wasteful practice of having five boxes of different grade paper open simultaneously. Glossy paper provides a wider range of contrast and tone, and more detail than matt paper. Optimum use of space and prints of matching tone with parallel edges are necessary for an aesthetically pleasing plate (Fig. 1).

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## 6.2.4 Electron Microscopy

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Both the transmission (TEM) and scanning (SEM) electron microscopes have wide-ranging applications in palaeobiological research, including studies of skeletal microstructure and growth, functional morphology, and taphonomy.

### Transmission electron microscopy

The TEM produces an image by passing a beam of electrons through a specimen which must be very thin (90–250 nm) and must fit onto a 3.5 mm diameter microscope grid. Methods for investigating fossils using the TEM were developed in the early days of carbon replication. This technique involved coating a specimen with carbon, dissolving the specimen, and examining the carbon replica of the specimen surface in the microscope. Although much useful information could be gained using carbon replicas, the technique was relatively unpopular because of limitations on specimen orientation in the microscope, and the delicate nature of the replica. Before the advent of SEM, however, small specimens, such as coccoliths and diatoms, and fragments of larger specimens were routinely examined in this way.

Fossil plant and animal tissue is generally mineralized and unsuitable for direct study with the TEM. However, unmineralized tissue may be prepared for TEM examination by releasing it from the matrix using acids or other solvents. The released tissue is thoroughly washed in distilled water to remove any remaining acids or solvents, and is then dehydrated through a graded series of acetone solutions. After two changes in pure acetone, it is embedded in an epoxy resin. Sections are cut with a glass or diamond knife on an ultramicrotome, then mounted on grids, dried, and examined in the TEM (see Glauert 1974). Using this method Urbanek & Towe (1974) were able to produce some excellent micrographs of unstained graptolite tissue, and the palaeobotanical literature contains many similar examples.

## Scanning electron microscopy

The introduction of the SEM in 1968 gave palaeontologists an instrument of such versatility that 20 years later new techniques for investigation are still being developed. The SEM produces an image by bombarding the surface of a specimen held in a high vacuum with a stream of electrons. This provokes the generation of X-rays, secondary electrons, and backscattered electrons, which may be collected and processed to form a visual image of the specimen on a cathode ray tube (see Goldstein *et al.* 1981). The method is non-destructive, and some microscopes can accommodate specimens up to 10 cm in diameter.

Stereoscopic images can be prepared with SEM. Two photographs are taken at a separation of 8° and, when examined using a stereo viewer, these may give much additional information on the spatial arrangement of the specimen. Good examples of this application can be found in issues of *A Stereo-Atlas of Ostracod Shells* (British Micropalaeontological Society, London).

A disadvantage of the early SEMs was that all material to be examined had first to be coated with a thin layer of conducting metal such as gold, platinum, or aluminium. Many museum curators are unwilling to commit type or other valuable specimens to this treatment, despite the fact that some coatings can be subsequently removed (e.g. gold by treatment with cyanide). A device known as CFAS (charge free anticontamination system) is now available which allows uncoated specimens to be examined (Taylor 1986). The microscope chamber is pumped to a poorer vacuum than the gun and column, and a backscattered electron detector is used in place of the normal secondary electron detector to collect the signal. Specimens do not have to be glued or permanently attached to a stub, but are simply held on a metal plate with plasticine or a similar substance which does not contaminate the inside of the microscope. Clear micrographs of uncoated specimens can be obtained using CFAS (compare Fig. 1E, F).

The coating of valuable specimens may also be avoided by preparing replicas (Fig. 1C) for examination in the SEM. Hill (1986) investigated various replicating materials and concluded that cellulose acetate (which must be used with care on delicate material) gave the best results, whereas the more commonly used latex rubber gave poor results.

The method of attachment specimens to stubs is of paramount importance, especially if the specimen is later to be recovered for examination of the reverse side. Double-sided adhesive tape is commonly used because it is convenient and permits specimen removal using an organic solvent. However, this is not a recommended procedure; the volatile components of the adhesive tape evaporate in the microscope and deposit in the form of carbon on the inside of the column and apertures, giving rise to poor image resolution. A simple and inexpensive method for attaching microfossils (e.g. foraminifera, pollen, and spores) and small fragments of macrofossils is as follows: (1) cut dried processed film into small squares and glue it to stubs with the emulsion side of the film uppermost; (2) moisten a small area of the film with water using a fine paintbrush to soften the gelatin; and (3) manipulate the specimens onto this area and leave them to dry (after examination, removal or reorientation can be achieved using a wet paintbrush).

Permanent attachment of material to stubs should be made with epoxy resin (not the quick setting varieties, which may not set as hard as normal types). Only small quantities of epoxy should be used for small specimens, and special care should

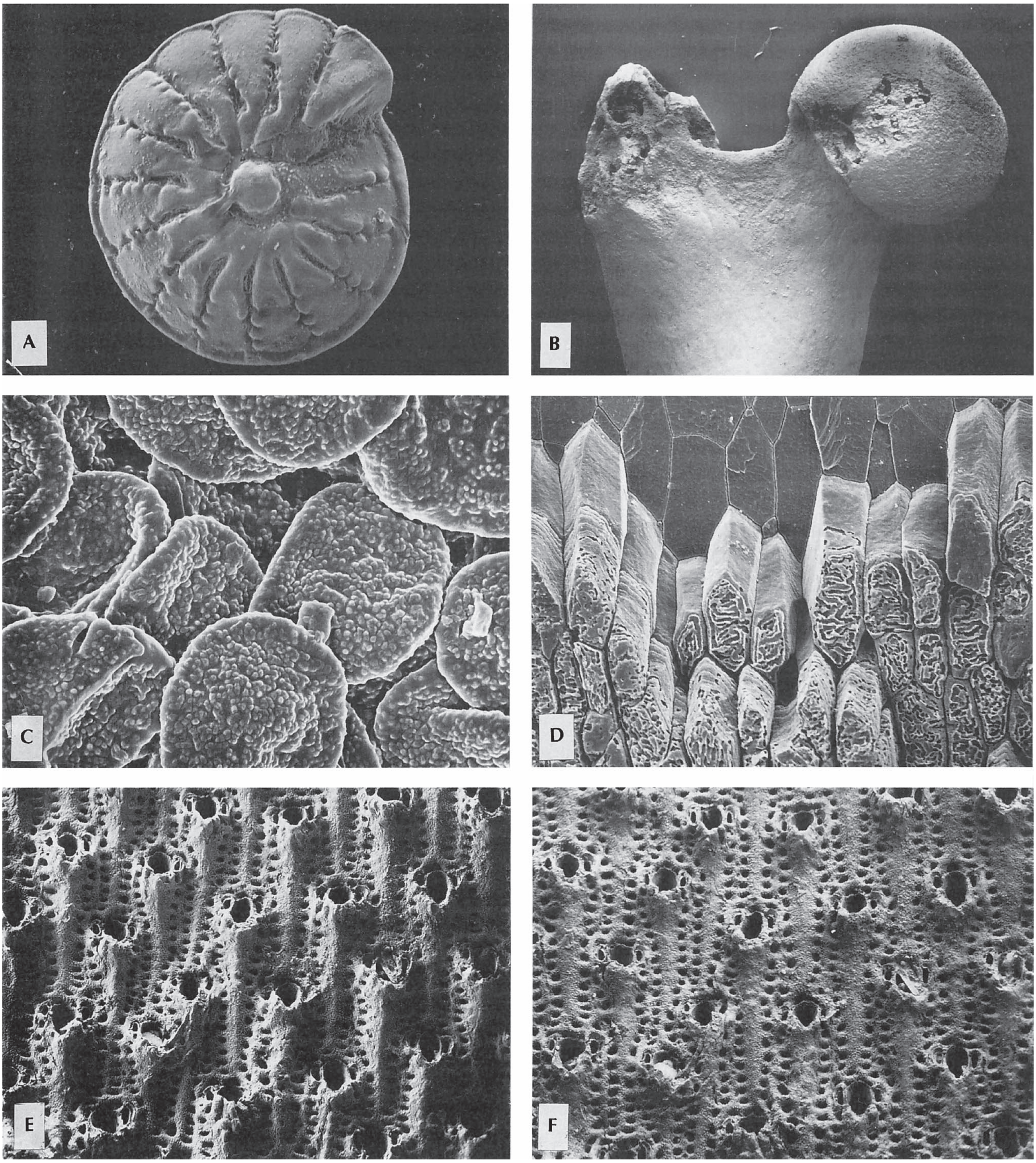


**Fig. 1** Scanning electron micrographs illustrating some of the diverse palaeobiological applications of the SEM. A, Umbilical view of the benthic foraminifer *Pseudorotalia yabei* (Ishizaki), a species from the Miocene of Borneo potentially useful in stratigraphy, × 33. (Micrograph courtesy of Dr J.E.P. Whittaker.) B, Proximal end of a rodent femur from a British Pleistocene cave site showing evidence of digestion by a predator, × 10. (Micrograph courtesy of Dr P.J. Andrews.) C, Dow Corning silicon rubber replica of *in situ* spores of the fern *Qasimia schyfsmae* (Lemoigne) from the Permian of Saudi Arabia, × 1000. (Micrograph courtesy of Dr C.R. Hill). D, fractured shell of the British Jurassic bivalve *Deltoideum delta* (Smith) showing prismatic microstructure with endolith borings, × 335. E,F, part of a colony of the bryozoan *Metrarabdotos moniliferum* (Milne Edwards) from the Pliocene of U.K. depicted as a conventional secondary electron image of the gold-coated specimen (E) and a backscattered electron image of the uncoated specimen (F) prepared using CFAS, × 13.

be taken with porous material which tends to absorb the adhesive and in some cases obscures surface detail. For very small fossils (e.g. diatoms), which are not practicable to mount individually, the following method is advocated: (1) abrade a clean stub with very fine wet and dry emery paper, wash thoroughly in an ultrasonic bath and dry; (2) rub epoxy resin into the abraded surface using a cocktail stick and remove the excess adhesive with a lint-free tissue such as 'vellin' to leave the epoxy only in the very fine grooves; and (3) onto this surface place the specimens which will adhere permanently.

Coccoliths are among the most difficult fossils to prepare, but dry material can be treated as above if the stub is very finely abraded and the excess epoxy wiped off very thoroughly. The most successful method for mounting coccoliths is simply to abrade a stub with very fine emery paper, wash, dry, and then pipette a suspension of material onto the stub; dry and coat before examining.

Many fossils in the SEM accumulate charge which degrades image quality. Charging may be related to the composition of the specimen, poor attachment to the stub, or inadequate coating. The use of CFAS, a backscattered electron detector, or reduction of the accelerating voltage may eliminate charging but often does so at the cost of poorer resolution. One of the most promising developments to help overcome the charging problem is a method of collecting and processing the signal prior to recording it, known as *scanstore*. The last and most successful method is the use of a Field Emission SEM. This instrument produces a thousand times more electrons than a conventional SEM and can be operated at very low voltages without apparent loss of resolution.

Quantitative and qualitative analysis of elements can be undertaken with suitably equipped SEMs (and also TEMs). Analysis is usually best carried out on flat specimen surfaces, but new computer controlled and corrected systems can allow analysis of rough surfaces.

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# 6.2.5 Determination of Thermal Maturity

J. E. A. MARSHALL

## Introduction

Fossils, in addition to their importance in biostratigraphy, are invaluable as indicators of *thermal maturity* or *rank*. The fossil groups used are exclusively microfossils and have to be organic (e.g. spores) or have an organic component in a mineralized wall (e.g. conodonts). Such microfossils indicate thermal maturity because their organic matter alters through progressive burial. As temperature increases with depth, hydrogen and oxygen are lost in excess to carbon, which changes physical properties such as colour, reflectivity, and fluorescence. Thus measurement of these properties is an estimate of the maximum temperature reached, although determination of exact values is complicated by factors such as time. Not all methods are of equal value for the different microfossil groups, or applicable throughout the geological column.

## Vitrinite reflectivity

The origins of thermal maturation studies lie in the investigation of coal rank and particularly the optical properties of coal revealed by incident light examination of polished blocks. (If light is shone on the polished coal surface a consistent amount is reflected back, proportional to burial depth.) The coal maceral adopted for measurement is *vitrinite*; the rank indicator is known as *vitrinite reflectivity* and is expressed as a percentage. Vitrinite is not restricted to coals and is found widely dispersed in dark mudrocks (but not carbonates). Measurement is made on a microscope equipped with a photometer and stabilized power sources; the sample is observed using oil immersion objectives to obtain sufficient contrast to resolve individual macerals. Measurements are made relative to a standard of known reflectivity for calibration. Reflectivity determination is routine, although difficulties can be encountered in identifying vitrinite and discriminating between types of vitrinite which behave differently during maturation. There is also the phenomenon of suppressed reflectivity values in amorphous organic matter (A.O.M.) kerogen rich in as opposed to woody dominated kerogen — the former showing systematically lower values. This effect must be considered when comparing samples, or in calibration against temperature.

The relationship between temperature and vitrinite reflectivity is not simple: time must be considered in addition to maximum temperature (time--temperature dependence remains a controversial subject, but the concensus is moving towards temperature as the single factor). Temperature values corrected for the effect of time can be estimated directly from a *Karweil type diagram* (Fig. 1) in which both are cross plotted against a series of reflectivity values. More complex models are also used, which involve a detailed burial history rather than a single heating event. In many instances vitrinite reflectivity is used as a thermal index without recourse to temperature conversion and, as such, is the most widely accepted indicator of hydrocarbon generation. Hydrocarbons, such as oil and gas, are generated by the action of heat on kerogen over time, so vitrinite reflectivity values may be used to define the major phases of generation. In general, reflectivity values below 0.5% show that no hydrocarbons have been generated, whilst the range 0.5–1.3% defines the oil window where the bulk of hydrocarbons are produced. Gas production continues above 1.3%.

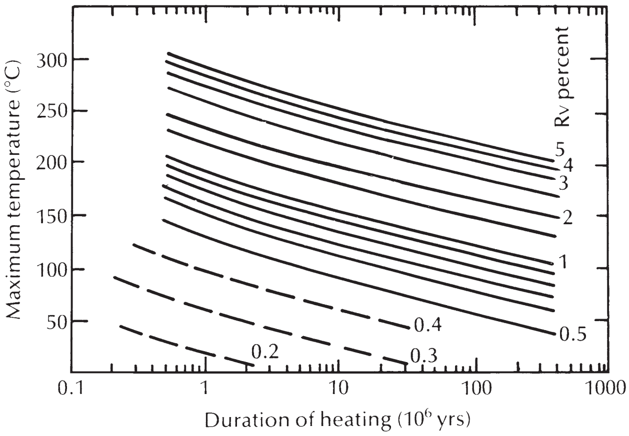


**Fig. 1** A Karweil type diagram from which maximum temperature can be determined from known vitrinite reflectivity and estimated duration of heating/burial. (From Bostick *et al.* 1979.)

## Spores and pollen

*Colour.* The colour of spores and pollen is the second most important index of organic maturity after vitrinite reflectivity. When determining colour in spores and pollen it is important always to select taxa of similar construction, as variation occurs in any assemblage. It is good practice to select simple spores and pollen with a 'single' unpigmented wall and without prominent sculpture; the sacci of bisaccate pollen satisfy these criteria and are ubiquitous in most Permian to Recent sediments. Colours are estimated on a visual scale (Fig. 2) by reference to a set of spore/pollen standards (most of which have been produced by commercial laboratories and are therefore not widely available because of cost and confidentiality).

The range of colour in spores is continuous and the scale boundaries are imposed arbitrarily. The colours are also difficult to describe in words so that, without recourse to standards, these scales can only be crudely applied. They are also frequently non-linear when compared to both depth of burial and other maturity indicators; brown and darker colours become unpredictable in their occurrence, rendering the scales of limited value at higher temperatures. The influence of time is important since changes in colour are not instantaneous. Thus a time–temperature cross plot like that used for vitrinite can be employed (Fig. 3) to estimate maximum temperature. The correlation of colour against vitrinite reflectivity in different depositional basins does not give a constant relationship since these materials behave differently kinetically. Differing geological histories result in different durations of thermal input and each basin has a somewhat different correlation.

*Fluorescence.* The walls of spores and pollen (in common with plant cuticle, acritarchs, dinoflagellate cysts, and certain types of A.O.M.) fluoresce in the visible spectrum when excited with ultraviolet light. Fluorescence colour (Fig. 2) varies both with organic matter composition and thermal maturity. The generation of these colours requires a sophisticated microscope with an incident ultraviolet light

| Spore colour | SCI | TAI | Rv (SCI) | RCH | Spore fluorescence colour & spectra |
|---|---|---|---|---|---|
| Colourless–pale yellow | 1 | | 0.3 | | Blue–green |
| Pale yellow–lemon yellow | 2 | 1.5 | 0.4 | 0.5 | 400 700 Green–yellow |
| Lemon yellow | 3 | 2.2 | 0.5 | | |
| Golden yellow | 4 | | 0.6 | 0.7 | Yellow |
| Yellow orange | 5 | 2.4 | 0.7 | 1.0 | Yellow–orange |
| Orange | 6 | | 0.8 | | |
| Orange brown | 7 | 2.6 2.8 | 0.9 | 1.2 | |
| Dark brown | 8 | 3.0 | 1.0 | 1.4 | Orange–red |
| Dark brown–black | 9 | 3.5 | | | Brown |
| Black | 10 | 4.0 | 1.5 | 2.0 | No further fluorescence |

**Fig. 2** A comparison of the Spore Colour Index (SCI) and Thermal Alteration Index (TAI) scales with verbal colour description. Vitrinite Reflectivity (Rv), Chitinozoan Reflectivity (Rch), spore fluorescence colours, and spectra are also included. The latter are measured over the range 400–700 nm and normalized to the same relative intensity. (From Otterjahn *et al.* 1974; Fisher *et al.* 1980; Smith 1983.)

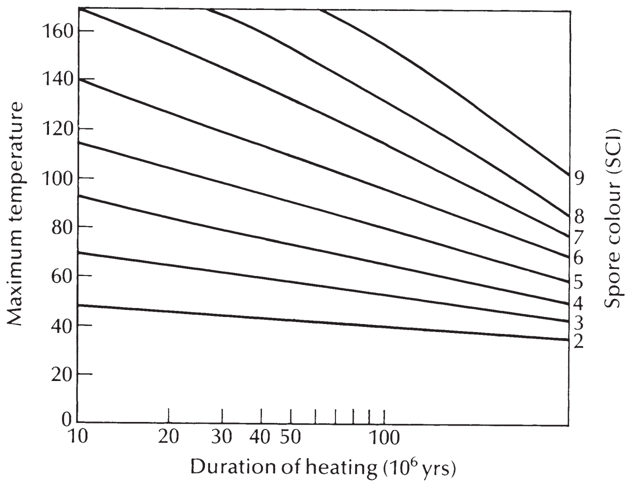


**Fig. 3** A Karweil type diagram from which maximum palaeotemperature can be determined from a known spore colour (SCI only) with an estimated duration of heating/burial. (From Cooper 1978.)

source and dichroic beam splitters. The colours are difficult to estimate (in comparison to spore colours in white light) as they are pastel shades and rather faint. Colour can also be quantified with a photometer/monochrometer that generates a curve relating intensity–wavelength (nm), for which the maximum peak height, width, and position change with maturity (Fig. 2). Quantitative fluorescence measurements are complicated by additional factors, such as intensity fading, microscope corrections, and uncertainty over absolute standards. The technique is therefore only employed in specialist laboratories.

## Conodonts

Conodonts have proved a popular group for determination of rank in Palaeozoic rocks due to the widespread adoption of a single colour scale and the availability of standards. The *conodont alteration index* (CAI) is an eight-point scale (Fig. 4) that covers the temperature range <50° to >700°C. It is thus applicable to the widest range of maturity, including schists, although above CAI 6 difficulties occur in the event of hydrothermal alteration. The essential difference between conodonts and other microfossils used in organic maturation studies is that conodonts are composed of a phosphatic mineral, with only trace amounts of organic matter. The initial colour changes (1–5) result from maturation of this

**Table 1** Use of fossils as indicators of organic maturity.

| Microfossil group | Reflectivity | Colour | Fluorescence | Geological range |
|---|---|---|---|---|
| Spores | * | *** | ** | Silurian–Recent |
| Pollen | * | *** | ** | Devonian–Recent |
| Acritarchs | | * | * | Precambrian – sub-Recent |
| Dinoflagellate cysts | | * | * | Triassic–Recent |
| Chitinozoans | * | | | Ordovician – Devonian |
| Conodonts | | *** | | Cambrian–Triassic |
| Vitrinite | *** | | | Silurian–Recent |

Note: * = minor application; *** = significant use.

material, whilst above CAI 6 the mineral itself recrystallizes with oxidation of the organic matter and becomes clear. The phosphatic composition generally restricts their recovery to carbonate rocks and low rank shales, whilst the trace amount of organic matter limits the colour changes so only two CAI points are available within the oil window. Like all colour scales it is a series of points imposed on a continuous colour series and difficult to express in words, so standards are required for serious work.

## Acritarchs

Acritarchs, like pollen and spores, undergo changes in wall colour with increasing maturity. They have not been as widely used because the colour changes are more subtle and difficult to determine on the thinner walled tests, whilst thicker walled forms are frequently pigmented with significant natural colour. Consequently, where their geological ranges overlap, pollen and spores are used in preference to acritarchs. In the Lower Palaeozoic, where spores and vitrinite are largely absent, acritarch colour (and fluorescence) become important (although conodont colour is also available for this interval). An acritarch colour alteration index has been produced (Fig. 4), with a five point scale based on colour changes in simple leiospheres.

## Chitinozoans

Polished sections through chitinozoan walls show reflectivity properties similar to the vitrinite maceral (a calibration is given in Fig. 2). Usage is still only at an initial stage but chitinozoans should provide early Palaeozoic researchers with a quantitative scale as precise as that of vitrinite. Chitinozoans have the advantage of being large and thus easily measured in comparison to acritarch walls; they can also be recovered from every type of sediment within which they occur, unlike conodonts. Problems with low numbers in polished whole-rock preparations can be solved by using polished thin sections.

## Other microfossil indicators of thermal maturity

Kerogen components, such as dinoflagellate cysts, plant cuticle, and most types of A.O.M., generally show colour and fluorescence changes with increasing rank in a similar way to spores and pollen, although changes relate differently to temperature. For various reasons they have not become established as routine thermal maturity indicators but can be used if required, and related approximately to the major points of existing scales. Situations where they are used include A.O.M. rich or distal

<table>
<tr><th>CAI</th><th>Temp. range (°C)</th><th>Conodont colour</th><th>AAI</th><th>Acritarch colour</th><th>Hydrocarbon generation</th></tr>
<tr><td>1</td><td><50–80</td><td>Pale yellow</td><td>1</td><td>Translucent–light yellow</td><td rowspan="2">Immature</td></tr>
<tr><td rowspan="2">1½</td><td rowspan="2">50–90</td><td rowspan="2">Very pale brown</td><td>2</td><td>Light yellow–pale yellow</td></tr>
<tr><td>3</td><td>Pale yellow–orange</td><td rowspan="3">Oil & wet gas</td></tr>
<tr><td rowspan="2">2</td><td rowspan="2">60–140</td><td rowspan="2">Brown–dark brown</td><td>4</td><td>Orange–dark brown</td></tr>
<tr><td rowspan="3">5</td><td rowspan="3">Black</td></tr>
<tr><td>3</td><td>110–200</td><td>Very dark greyish brown–dark reddish brown</td><td rowspan="7">Dry gas</td></tr>
<tr><td>4</td><td>190–300</td><td>Black translucent</td></tr>
<tr><td>5</td><td>300–480</td><td>Black opaque</td><td rowspan="5"></td><td rowspan="5"></td></tr>
<tr><td>6</td><td>360–550</td><td>Medium dark grey–medium grey</td></tr>
<tr><td>6½</td><td>440–610</td><td>Medium light grey–light grey</td></tr>
<tr><td>7</td><td>490–720</td><td>Very light grey–white</td></tr>
<tr><td>8</td><td>>600</td><td>Colourless or crystal clear</td></tr>
</table>

**Fig. 4** Correlation of conodont colour and acritarch colour with verbal colour descriptions, temperature ranges, and the main zones of hydrocarbon generation. (From Legall *et al.* 1981; Rejebian *et al.* 1987, by permission of the Geological Society of America.)

oxic marine kerogen facies which may either lack a terrestrial input, with no spores, pollen, or vitrinite, or have had it diagenetically modified and/or diluted.

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# 6.3 Museology

## 6.3.1 Collection Care and Status Material

P. R. CROWTHER

### Introduction

The fundamental aim of good fossil storage is to ensure the long-term survival of specimens, thus guaranteeing their future availability for study and display. The clean, ordered storage of specimens in a controlled environment is the physical basis of a good collection (Brunton *et al*. 1985; Rickards *in* Bassett 1979). The ability to view and handle fossils easily, the use of appropriate containers, and the logical ordering of specimens enables material to be found as required, often without recourse to a manual index or computerized documentation system (Section 6.3.2).

### Storage environment

Storage areas should be as free as possible from fluctuations in temperature and relative humidity (r.h.). Extremes and rapid changes of r.h. are the most common cause of damage to fossil material in museums. The vulnerability to oxidation of pyritized fossils and pyrite-bearing matrices ('Pyrite Disease') increases to unacceptable levels when r.h. rises above about 55%. Neutralization of affected material (Cornish *in* Crowther & Collins 1987) is no protection against future damage, which can only be prevented by keeping r.h. down. On the other hand, subfossil bone and some shale matrices shrink and crack when r.h. falls below about 45%. Rapid fluctuations of r.h. causes some clays and shales to swell and shrink alternately, leading to deterioration and loss. Monitoring and control of r.h. is therefore essential in geology storage areas, to keep conditions at 50 ±5% r.h. This is achievable either through full air conditioning or, more economically, through the use of portable dehumidification and humidification equipment. Conditioned silica gel can maintain small, sealed volumes (storage boxes or display cases) at whatever r.h. is required.

Temperature variation alone has little detrimental effect on fossil material, but because temperature is so intimately associated with r.h. (a fall in temperature causes r.h. to rise, and vice versa), its stabilization is essential for r.h. control. A combination of high r.h. and high temperature accelerates the hydrolysis of hemicellulose to acetic acid in the wood of oak or birch ply cabinets; this may attack calcareous fossils and matrices (the so-called 'Bynes Disease') and such woods are best avoided for cabinet construction.

Airborne dust is a particular and obvious menace to collections. It makes material difficult to examine and its removal is both time consuming and potentially damaging to fragile specimens. Dust proofing can be incorporated at several levels within a quality storage system: individual storage trays can be made deep enough to support acetate tops; storage drawers and boxes should have tightly fitting lids; and the mobile bays in a compactable racking system can be edged with seals which mesh together when picking aisles are fully closed.

## Storage furniture

The ordered physical storage of fossils in a controlled environment cannot be realized cheaply. The specialized storage requirements of 'difficult' categories of specimens dictate particular solutions, e.g. large vertebrates (Brunton *et al*. 1985; Gentry *in* Bassett 1979). Inside more generalized storage units, specimens should sit in paper-lined card trays (made of acid-free materials) to prevent abrasion and mixing. Storage unit design should be flexible regarding the use of drawers or shelves, and in the variety of drawer or shelf depths. They should incorporate good dust seals. Wooden cabinets are preferable (but not oak or birch ply for the reason given above) since they buffer against changes in r.h. and cushion vibration. Mobile, rail-mounted, compactable racking systems make the most effective use of limited space, but they require strong floors and inevitably subject their contents to more vibration.

## Status material

Article 72(g) of the 1985 *International Code of Zoological Nomenclature* (see Section 5.1.1) states that name-bearing types (holotypes, syntypes, lectotypes, and neotypes) are international standards of reference and are held in trust for science by those responsible for their safe keeping. Institutional responsibility in this regard is set out in the Code's Recommendation 72G as follows:

Every institution in which name-bearing types are deposited should:

**1** Ensure that all are clearly marked so that they will be unmistakably recognized as name-bearing types.

**2** Take all necessary steps for their safe preservation.

**3** Make them accessible for study.

**4** Publish lists of name-bearing types in its possession or custody.

**5** So far as possible, communicate information concerning name-bearing types when requested.

Failure to heed this code of practice hinders the progress of science and puts type material at risk. Any museum holding fossil type material should have a geologist on its permanent establishment; any university department or museum with types but no designated curator should deposit them elsewhere (Owen 1964). It is the responsibility of the name giver to ensure that types go to an appropriate repository, and it follows that editors must insist on authors carrying out this duty as a condition of publication. Indeed, taxonomic practice would be greatly enhanced if all status material (type, figured, and referred specimens) had to be registered in an appropriate institution as a condition of publication.

The question of how best to store status material has provoked some disagreement (Brunton *et al*. 1985, p. C25). Arguments that favour separating status material from the main collections include: meeting the ICZN and ICBN requirements regarding type specimen care; convenience of access; increasing its physical security in better quality storage by improving protection from theft and damage from fire, flood, etc.; and ease of evacuation in emergencies. Disadvantages of isolating such material include the risk that users might overlook its existence when working through the main collection; and that it might be totally destroyed in the event of a disaster affecting that one particular part of the store.

Whether type material should remain in its country of origin is another vexed question, although the ability of the home country to properly house and curate such material must be a primary consideration. Practices differ from nation to nation: Canada has legislation to ensure that types erected on Canadian material taken abroad for study are eventually repatriated; the Palaeontological Museum, Oslo, functions in effect as the National Museum for Norway and preferred policy is for all Norwegian primary type material to be held there (Bruton *in* Bassett 1979); the British Museum (Natural History) regards its holdings as international in scope, and considers it essential that related collections from different parts of the world are kept together, because palaeontology is a comparative science (see comment by Ball *in* Bassett 1979, p. 147).

Publication of a museum's holdings of status specimens should be given high priority, since the dissemination of such information to the world at large is one of the important responsibilities that goes with being a type repository. Many of the larger museums can utilize an in-house publication for this purpose (Section 6.4), while smaller repositories can still fulfil their obligations to the wider scientific community via specialist journals such as the *Geological Curator*.

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# 6.3.2 Collection Management and Documentation Systems

P. R. CROWTHER

## Introduction

All science depends on being able to 'repeat the experiment', to check the data on which conclusions drawn by others were based. In whatever way the fields of palaeobiology, biostratigraphy, taxonomy, evolutionary studies, etc. are delineated, each relies to a greater or lesser extent on our interpretation of the fossil record. It follows that fossil collections and their associated data represent the primary material evidence that underpins the intellectual structure of these elements of Earth science. The survival and availability of such collections is crucial to the advancement of knowledge, so that past results can be checked and new observational and analytical techniques can be applied. Without museum collections, palaeobiology could not exist.

The management of museum collections concerns the accessioning, control, cataloguing, use, and disposal of specimens. The accelerating awareness of the importance of collections management has been triggered by: pressures on museums to demonstrate accountability for their collections; modern security and audit requirements; and the higher standards of inventory control expected by governing authorities (Roberts 1988). Effective documentation is the key to collections management and is essential if the legitimate aspirations of museum users are to be met.

## Information storage and retrieval

A fossil without certain basic information (locality, stratigraphy, collector, etc.) is of little scientific value, however visually attractive it may be. Conversely, the most unprepossessing fossil fragment can continue to provide answers to new questions if it was effectively documented at the outset. A precise record of where, when, and how such a fossil was collected, and by whom, guarantees its future utility. All serious collectors have an obligation to science to ensure the long-term survival of their fossil material — which may represent an irreplaceable resource from a temporary exposure, and was perhaps collected at great public expense from a remote part of the globe.

The principle of being able to repeat an observation is as axiomatic to the large numbers of specimens associated with biometrics, population dynamics or phylogenetics as it is to the holotype concept in taxonomy. Today's collector/researcher can ensure the continued availability of primary source material — be it a unique type specimen or the thousands of measured specimens in a statistical study — by:

1 Allocating a unique identifying number to each specimen at the earliest opportunity.

2 Securely recording certain essential data about the specimen (locality, stratigraphy, collector name, collection date) and keying such a record to the specimen via its unique identifier.

3 Greatly improving the specimen's chances of survival and long-term availability for future study by depositing it in an appropriately staffed and funded museum.

This procedure ensures that the specimen's latent scientific potential is protected. The additional benefits that follow from producing specimen labels, classified catalogues, indexes (by donor, locality, age, etc.) are many, and certainly make a collection more accessible to the user. But they can all be created later as required, manually or by computer, if the essential collection data has been properly recorded. Museum collections are assemblages of facts in the form of specimens, specimen-related data (Light *et al.* 1986), and (increasingly) site-related data (Raup *et al.* 1987; Crowther & Wimbledon 1988). Many of these facts are available nowhere else; in the museum they remain available for re-examination, reinterpretation, and restructuring, over and over again (Waterston *in* Bassett 1979). The physical well-being of collections (Section 6.3.1) and the dissemination of information relating to those collections are both fundamental to the role of museums in Earth science today. An effective documentation system is the key to fulfilling such a role.

The theory of how best to permanently link a specimen with its essential data is well established in museology, using a unique number and a secure register of sequentially ordered data entries. Unfortunately, museum performance in this area has often left much to be desired, either through curatorial incompetence or (more usually) through understaffing and the tug of conflicting priorities.

The efficient retrieval of specimen data in a form capable of satisfying the needs of all museum users has proved an intractable problem. The traditional, manual approach is to maintain alongside the main register as many running card indexes (by taxon, locality, age, donor, etc.) as staff time allows. Any collection is to some extent 'self indexing' through the classified storage strategy adopted — by taxonomic group, stratigraphical division, geographical location, or (more likely) by a combination of these. But in reality many museums are unable to keep pace even with basic registration of specimens, and it is very rarely possible to resource a fully effective manual system.

## Computerized documentation systems

Computing techniques are having a major impact on both the scale and type of problems being attacked within contemporary palaeobiology (Section 6.1). Museums were quick to appreciate the potential of computer-based information technology for the sorting and selective retrieval of specimen-related data. Any conceivable index can be generated from a single input of specimen data, and interactive retrieval can be used to interrogate the database directly. Some museums with access to mainframe computers, either in-house or through computer bureaux, now have more than 15 years of experience to draw upon. The more recent development of the desk-top microcomputer, with its increasingly more powerful data-processing abilities and data storage capacity, has opened up the same advantages to a much wider spectrum of potential users. The sophisticated inputting, sorting, batch, and interactive retrieval routines that characterized the mainframe software packages of the nineteen-seventies can now be duplicated on a micro, while the storage capacity of hard discs enables typically lengthy museum specimen records to be held in sufficient numbers to cater for large collections. The availability of powerful relational database packages for microcomputers opens up exciting possibilities for the interactive interrogation of large complex files on low-cost hardware, in a way that would have seemed impossible just a few years ago. The capacity of the newest optical storage media makes it likely that within a very short time storage will cease to be any kind of limiting factor, even for the very largest collections.

The effectiveness of computerized information retrieval has had additional benefits on the way museums deal with specimen-related data. The information must be structured in a standard form before inputting, and the terminology applied to different data categories must be rigidly controlled if sorting procedures are to produce useful output. This inflicts higher standards of data recording on museums than has traditionally been the case. Taken to its logical extreme, the adoption of a single data standard by museums, combined with an agreed thesaurus for terminology control, opens up the exciting prospect of combining museum databases and of their remote interrogation by users. However, there is as yet little international agreement about the structuring of museum data, and the question of terminology control is at an even more rudimentary stage. The U.K. is probably as far advanced as any other country in this regard, with the Museum Data Standard of the Museum Documentation Association (MDA) now in widespread use by museums, whether they employ the MDA's manual recording cards and/or supporting software packages or choose to develop in-house applications of commercial database packages.

Full computerization of specimen records entails a massive short-term commitment of data preparation time, since it obviously involves keying in all the manual records accumulated during a museum's history. Crucially, it also entails structuring the data and terminology to conform with agreed standards — and rigorously checking the data input. This is beyond the staffing resources of most museums, and computerization is commonly restricted initially to upgrading inventories; detailed computer cataloguing is often limited to new material entering the museum. Nevertheless, the automatic scanning of manual records using developments of the 'optical character readers' already available open up the exciting possibility of direct input of typed or even handwritten records to a computer database, thereby drastically reducing data preparation time.

At a time when museums are coming under increasing pressure to make their reserve collections more accessible, new technology has an important role to play. As the efficient management of large taxonomic collections in the public domain becomes increasingly expensive, those responsible for such collections must become more adept at justifying their unique role to those who ultimately pay the cost through taxes or entrance charges. A database compiled for basic collections management purposes can be made available to the general visitor via interactive terminals, after only minor modifications to strip out sensitive information (donor address, insurance value, storage location, etc.). Linked to a video disc (which are already capable of holding 50 000 images), such a system could provide instant visual access on demand to a collection, yet involve no physical risk to the specimens themselves.

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# 6.3.3 Exhibit Strategies

R. S. MILES

## Introduction

The purpose of mounting exhibits is normally to communicate information, so this section looks at some of the principles behind successful *distance communication*. By distance communication we imply the existence of a gap, either in time or space, between the sender and receiver of a message. This mode of communication applies typically to exhibits, whether comprising single posters or entire museums. Classroom teaching, lectures and demonstrations, on the other hand, involve face-to-face communication, in which the sender is there in person. It is important to distinguish between these two modes of communication, because if the sender is not there to answer questions, an effort must be made, at the stage of designing the communication, to ensure that it is intelligible to its intended audience. Good communication is selected for a purpose, and has a sound logical structure. Successful communicators know their audience, and attend both to the content ('what to say') and the form ('how to say it') of their communications.

## The audience

The organizers of exhibits inevitably form a mental image of their audience. Ideally this is based on hard data, e.g. the audience's vocabulary, understanding, interest in the subject, and commitment to its study. Care must be taken to avoid creating a false image, either through professional self-interest or limited experience of the audience. Where sufficient data are not available, survey techniques similar to those found in market research can be used. Questionnaire design and sampling methods have been described by Loomis (1987) and Miles *et al*. (1988). Accurate knowledge of the audience helps the communicator to connect his or her message with the viewer's world, and use language that is matched to the viewer's requirements. It is also helpful to know about the audience's misunderstandings (or 'alternative conceptions'), for these may need to be removed before the desired information can be imparted. For example, an intuitively held Lamarckian view of evolution might block understanding of Darwin's theory of natural selection.

## Selection and structure of content

What to communicate, where to start, and how to continue? — in other words, the selection and ordering of the content — are basic questions in organizing any exhibit. Generally, there is more to say about a subject than the space or other resources allow, or the viewer's stamina permits, and there has to be some selection. The basis of this selection is a clear statement of purpose. For a group of exhibits this statement takes the form, at the broadest level, of a series of *aims*. But a more detailed statement of purpose is required for individual exhibits, and this is best provided by listing the *teaching points*, i.e. the facts, concepts, relationships, procedures, and so on that need to be communicated. Teaching points generally divide into key concepts and ancillary points. Thus some are included simply in order to define other concepts or to remove misconceptions, others to ensure the positive transfer of knowledge. Teaching points also help to promote clear communication among those responsible for exhibits, and provide a basis for judging the success of exhibits as pieces of communication (below).

The ordering or sequencing of content is done with the help of a strong central theme, to give a good flow of ideas and a framework that unifies the facts, theories, and so on that are spelled out in the teaching points. It is important to tell only one story at a time; to organize things so that the audience knows what is going on (e.g. where they are going and how long it will take to get there); and to make the status of each message clear (e.g. is it the main conclusion or a supporting argument, is it a question or an instruction?).

A common way of ordering ideas is to place them in a logical sequence, e.g. concept A is dealt with before concept B because concept A must be understood before concept B can be understood. However, it is often unwise to argue from first principles in exhibitions for the lay public, because of the need to attract and keep the viewer's interest and connect the message to his or her familiar world. Thus, if no particular sequence of concepts can be chosen on grounds of logical relations, it might still be better to deal with concept A before concept B, because on psychological grounds it is easier for the viewer to understand concept A before concept B (Fig. 1).

To help the audience know what is going on it should be told, in an introductory exhibit, what the exhibits are about and how they are organized. In large exhibitions it may be necessary to repeat such information in different places. In addition to conceptual orientation, it may also be necessary to provide topographic orientation, i.e. signposts, maps, and exhibit numbers. The aim is to indicate the correct route through the exhibits, and such orientation devices must be designed to make sense to viewers who have no prior understanding of the content and arrangement of the exhibits (Miles *et al*. 1988).

## Selection of media

Communications media are the physical means of transporting messages from the sender to the receivers. Some media are normally used in the static mode, e.g. three-dimensional objects, graphics, and text; others are used in the dynamic mode and undergo a change of state during operation, e.g. audiovisuals and interactive computers. Selecting the appropriate medium for a particular message is important, yet never easy. There are few rules to assist the selection procedure, and the assessment of setting-up and maintenance costs is likely to weigh as heavily as educational advantage.

If an exhibit is to communicate change over time or movement (e.g. continental drift), it is useful to use a dynamic medium, possibly a film or working model. But the basic exhibit media still remain

1. Diversity of life —— 2. Charles Darwin
3. Domestic selection
4. Species as taxonomic groups
5. Species as breeding groups
6. Reproductive potential
7. Environment
8. Inheritance + variation —— 9. Population genetics
10. Theory of natural selection —— 11. Types of selection
12. Allopatric speciation

**Fig. 1** Chain of concepts from an exhibition on *Origin of species* at the British Museum (Natural History), London. Logical dependency relations are found between concepts 12 and 10, 11 and 10, and 6, 7, 8, and 10 — although 6, 7, and 8 (the premises of the theory) could be in any order. Concepts 1–5 are ordered in relation to 6–12, and to each other, on psychological grounds.

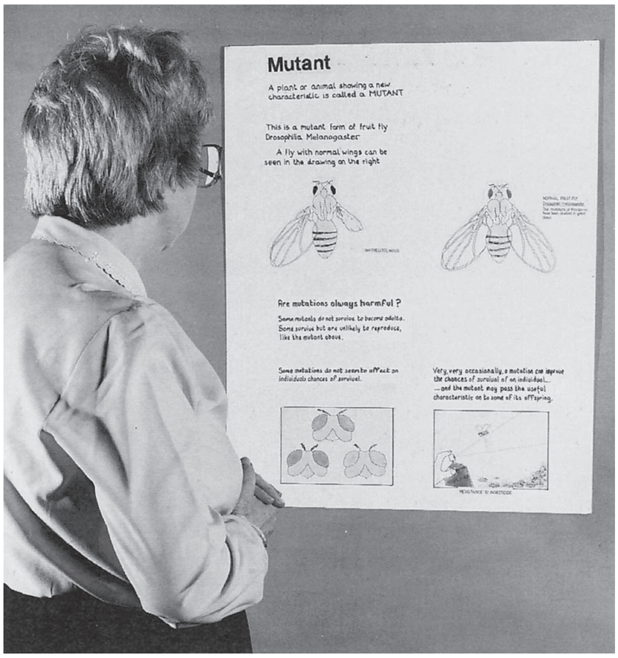


**Fig. 2** Mock-up of an exhibit used in developmental testing.

objects (real things, replicas, and models), graphics (illustrations, diagrams, and photographs), and text (text panels and labels), and these are often used in combination. Although traditional, these media nevertheless require skill and care if they are to be used effectively. Lighting, conservation (e.g. certain fossils decay if conditions exceed 60% relative humidity; print fades under ultraviolet rays), the selection of type and line lengths, and the integration of different media so that they work together, are just some of the things that have to be considered. For further information on all aspects of design, see Screven (1986), Hall (1987), and Miles *et al.* (1988).

Static object-cum-graphics exhibits elicit a relatively passive response from viewers, who are simply asked to look and read. However, educationalists have long understood that actively engaged learners are more likely to be successful than passive learners, which has led to the development of 'hands-on' exhibits that involve viewers in some sort of physical activity. This may be as simple as handling specimens, or as complex as operating interactive videodiscs. With larger exhibitions the more modern, dynamic media also give variety to the exhibits, which serves to maintain the viewers' interest. One caveat here: it is normally a good idea to employ professional help with complex media such as audiovisuals and computers. Such media are difficult to use well, and the exhibits are expensive to set up and maintain.

## Testing

It is difficult for the distance communicator to be sure that a message will be clearly understood without further explanation. Exhibit organizers who check on the effectiveness of their displays are often surprised at the variety of interpretations put on apparently simple and straightforward messages. The causes are to be sought in viewers' alternative conceptions, the different meanings attached to words, and the false perception of objects and graphics. The need to know the audience has been mentioned above; a further important way of lessening the chance of being misunderstood is to put exhibits through a process of developmental testing (also called *formative evaluation*).

The recommended procedure is called *cued testing*. Rough mock-ups of the exhibits are made. These may be handwritten, and photographs or drawings can often substitute for three-dimensional objects (Fig. 2). The mock-ups are then tried out on small samples of the intended audience (ten people are generally sufficient) with the help of a simple questionnaire. Designs can be quickly adjusted and the procedure repeated until satisfactory results are obtained. This is a qualitative approach involving no difficult statistics, and its worth has been demonstrated over and over again with a variety of audiences and institutions. For further information on the procedure, and for examples of questions used in testing, see Jarrett (1986). Broader aspects of evaluation, including the summative evaluation of completed exhibitions, have been covered by Loomis (1987) and Miles *et al*. (1988).

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# 6.4 Societies, Organizations, Journals, and Collections

J. NUDDS & D. PALMER

## International bodies

There are two international bodies whose areas of interest serve to link palaeobiologists world-wide.

*International Union of Geological Sciences* (IUGS). This is one of the three largest scientific unions in the world. It was founded in 1961 to facilitate international co-operation in geology and is affiliated directly to UNESCO. Much of its work is concerned with the establishment of international commissions and committees on various branches of geology, e.g. Commission on Stratigraphy (see Section 5.8), Committee on Geology Teaching, and its membership is composed mainly of international associations. There is, however, no commission on palaeontology, although the International Palaeontological Association (see below) is affiliated to the IUGS. *Episodes*, which replaced the *Geological Newsletter* in 1978, is the official organ of the IUGS.

*International Palaeontological Association* (IPA). This is the major international organization linking palaeontologists throughout the world. Originally titled the International Palaeontological Union (IPU), it was formed in 1933 in Washington, D.C., at the Sixteenth International Geological Congress, its aim being the collaboration and co-operation of international activity in palaeontology and stratigraphy. Membership was open to both societies and individuals. On becoming affiliated to the IUGS in 1966, the IPU was required to alter its name from 'Union' to 'Association', although this was not formalized until 1972.

Much of the IPA's activity is devoted to fostering smaller research groups (e.g. International Association for the Study of Fossil Cnidaria, Graptolite Working Group, etc.) and providing a forum for international co-operation between them (for list see Teichert & Yochelson 1985). The IPA also cosponsors relevant meetings and is currently composed of some 22 societies and nearly 500 individual members. *Lethaia* is its official organ (see below).

## Societies and organizations

There are over 500 extant geoscience organizations according to a directory published in *Geotimes* (1987, **32**(10); annually updated); some 30 or more are solely palaeontological but these do include several small local societies. Listed below are those relatively few international and major national palaeontological organizations, with information on their publications, etc. Also appended to this chapter (Appendix 1) is a more extended list of contact addresses for a number of other palaeontological organizations world-wide.

There are also many 'non-geological' societies whose interests and activities impinge upon palaeontology and result in meetings and publications of direct concern to the palaeontologist, e.g. the Linnean Society, the Systematics Association, the Royal Society of London, the Society of Economic Paleontologists and Mineralogists. Access to this literature is best gained through the standard Earth science and biological bibliographies, such as the *Bibliography and Index of Geology* and *Biological Abstracts*.

*Association of Australasian Palaeontologists (AAP).* This is a specialist group of the Geological Society of Australia and is responsible for a variety of publications. Its official journal is *Alcheringa* (see below), while the *Memoir* series (begun in 1983) have thus far been either thematic in nature or in honour of an Association member. The free annual newsletter, *Nomen nudum*, acquaints members with the activities of palaeontological colleagues throughout Australasia. Members of the AAP, who must also be members (ordinary, associate, or student) of the Geological Society of Australia, receive *Alcheringa* at a reduced rate, while the *Memoirs* are individually priced. Applications for membership should be made to: the Administrative Officer, Geological Society of Australia Inc., 606 A.N.A. House, 301 George Street, Sydney, New South Wales 2000, Australia.

*Palaeontological Association.* Founded in 1957 to promote research in palaeontology, the Association is based in London, U.K., but has a world-wide membership which is open to individuals, institutions, libraries, etc. on payment of the appropriate annual subscription. Institutional membership is only available by direct application, not through agents, while student membership is open to persons receiving full-time instruction at an institution recognized by Council. Applications for membership should be made to: the Membership Treasurer, Dr. H.A. Armstrong, Department of Geological Sciences, The University, South Road, Durham DH1 3LE, U.K. The Association holds an Annual Conference in December, and organizes review seminars, lecture meetings, and field excursions throughout the year. It publishes the quarterly journal *Palaeontology* (see below) and a quarterly *Newsletter*, which are issued free to all members of the Association; and *Special Papers in Palaeontology* (see below).

*Paleontological Society.* Founded in 1908, the Paleontological Society is based in the U.S.A. and produces a number of publications. Applications for membership should be made to the Secretary, Dr D.L. Wolberg, New Mexico Bureau of Mines, Socorro, NM 87801, U.S.A. All members receive the bi-monthly *Journal of Paleontology* (see below) and *Memoirs of the Paleontological Society* (see below). Members may also receive the quarterly journal *Paleobiology* (see below) at a reduced subscription. (*Paleobiology* Subscriptions, P.O. Box 1897, 810 East 10th St., Lawrence, KS 66044, U.S.A.). The Society also publishes two series of topical publications: *Short Course Notes* are published each year as part of the University of Tennessee Studies in Geology Series, for distribution at the Society's annual short course, held with the Annual Meeting of the Geological Society of America; the *Special Publications* series includes the proceedings of symposia sponsored by the Society at its regional meetings. Both are available from The Paleontological Society, Department of Geological Sciences, University of Tennessee, Knoxville, TN 37996–1410, U.S.A.

*Palaeontographical Society.* Founded in 1847, the Society exists for the purpose of figuring and describing British fossils in its *Monographs* (see below). Subscriptions are due on 1st January each year. Membership applications should be made to the Secretary, Mr S.P. Tunnicliff, British Geological Survey, Keyworth, Nottingham NG12 5GG, U.K. All members receive the Annual volume, which consists of a number of complete or part monographs. Members also receive 25% discount on all in-print and reprinted publications, and 33% discount on micro-edition publications, which may be ordered through the Secretary.

*British Micropalaeontological Society (BMS).* Founded in 1970, the Society's aim is to further the study of micropalaeontology. Meetings and demonstrations are held regularly throughout the year and the BMS now publishes a number of both serial and occasional publications. Membership is open to individuals and to libraries on payment of the appropriate annual subscription. Membership applications should be made to the Treasurer, Dr. I.P. Wilkinson, British Geological Survey, Keyworth, Nottingham NG12 5GG, U.K. Publications include the *Journal of Micropalaeontology* (see below) and

*The British Micropalaeontologist* (a newsletter) which are issued free to all members; and *A Stereo-Atlas of Ostracod Shells* (see below).

*Paleontological Research Institution (PRI).* Founded in 1932, the PRI is based in Ithaca, New York, and publishes two series of palaeontological monographs, *Bulletins of American Paleontology* and *Palaeontographica Americana* (see below). These give authors a relatively inexpensive outlet for the publication of significant longer manuscripts. In addition, it reprints rare but important older works from the palaeontological literature. The PRI headquarters in New York houses a large collection of invertebrate type and figured specimens, an extensive collection of well documented fossil specimens, and a comprehensive palaeontological research library. For additional information contact Director, Dr W.D. Allmon, 1259 Trumansburg Road, Ithaca, New York 14850–1398, U.S.A.

*Society of Vertebrate Paleontology (SVP).* Founded in 1941, membership of the U.S.A. based SVP is open to anyone 18 years of age or over who is interested in any aspect of fossil vertebrates. Applications for membership and all matters regarding subscriptions should be directed to the Secretary-Treasurer, Dr Robert M. Hunt Jr., Division of Vertebrate Paleontology, W436 Nebraska Hall, University of Nebraska, Lincoln, Nebraska 68588–0514, U.S.A. The Society produces a *News Bulletin* and supports the *Journal of Vertebrate Paleontology*.

## Journals

Scientific literature of all kinds continues to grow enormously (Menard 1971), with current estimates of some 50 000 journals published world-wide. The quickest entrée into this bibliographic 'ocean' is to first clarify exactly what is wanted, and then to ask a sympathetic and trained librarian for help. Failing this, the standard bibliographical procedure has to be followed, starting with bibliography of bibliographies, such as Mackay (1973). For current Earth science literature (especially in the English language) the monthly *Bibliography and Index of Geology* is most widely used and draws its data from nearly 3000 journals, plus books, etc. However, this and other major bibliographical sources are only available in specialist libraries. Fortunately, recent advances in library information technology have made such bibliographies available 'on line' e.g. GeoRef (see Hall & Brown 1987).

Palaeontology is essentially a historical science with fossils as its raw material, and taxonomic procedure and zoological nomenclature as its means or code of conduct (see Section 5.1). The fundamental principles or criteria by which this 'business' is conducted include the concept of the *type specimen* and *type series* (which has essentially to be suitably housed and conserved — safe and yet accessible; see Section 6.3.1) and the historical priority of authorship and description (provided it fulfils certain agreed standards of text, illustration, and publication, in order to promote stability and universality in the scientific naming of animals).

One of the main implications of this taxonomic prerequisite for palaeontology is that it requires an historically cumulative literature. Since the validity of previously published nomenclature extends back by convention as far as 1757, the student potentially requires access to well over 200 years of published work. Many of the older sources are rare books or monographs and journals that had very limited editions and were not widely circulated (Thornton & Tully 1971; see also the journal *Archives of Natural History*, published by the Society for the History of Natural History). This historical principle is characteristic of all the taxonomically-based natural sciences but is not a feature of the physical sciences or many of the newer, rapidly growing and 'high profile' subsciences (Menard 1971). In many of these areas literature over 25 years old is 'unshelved' and considered redundant. Only a 'core' of the most cited journals are regarded as important — about 4000 for the whole of science as far as the *Science Citation Index* is concerned, of which only 12 are purely palaeontological.

The literature profile required for the study of palaeontology is fundamentally different. This is demonstrated by sample citations drawn from papers published in recent issues of the journals *Geologica et Palaeontologica, Journal of Paleontology, Palaeontology*, and *Paleobiology*. A further sample of biological papers from the weekly interdisciplinary science journal *Nature* was taken for comparison. The citations from each journal were ordered historically and assembled to produce cumulative relative frequency curves (Fig. 1). These clearly separate into two groups: one includes a significant proportion of older work (10% pre-1910); the other cites very little nineteenth century or older work (less than 2% pre-1910). The difference between the two patterns stems directly from the former group being primarily specimen oriented, i.e. taxonomically-based work, which requires recognition of historical

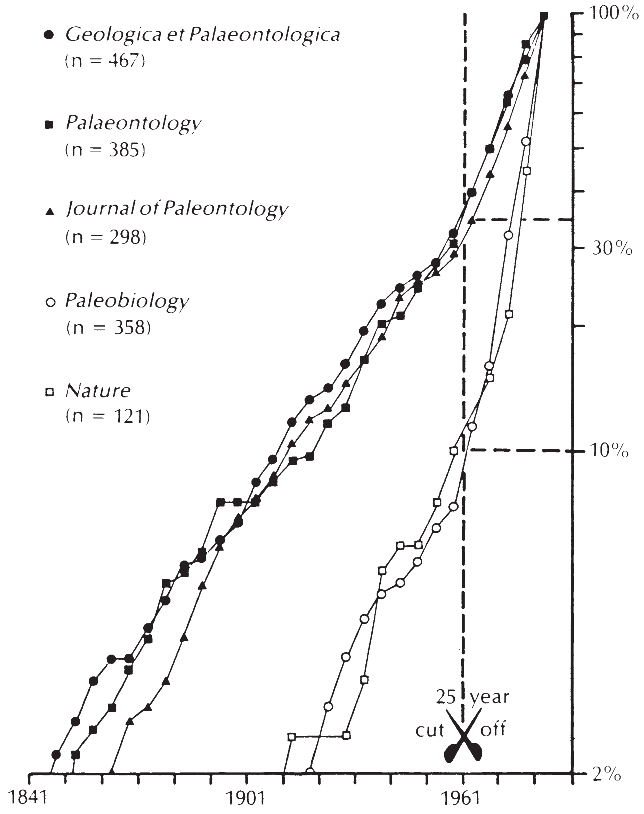


**Fig. 1** Proportional cumulative curves (log-linear scale) of sample bibliographic citations from recent issues of five science journals, arranged historically.

priority. The latter group (*Paleobiology* and the *Nature* sample) includes little in the way of purely taxonomic work but rather documents more theoretical and thematic research. Nevertheless, this group still shows an indirect reliance on older literature through the frequent citation of work published in the former group. If a 25 year cut-off (i.e. all pre-1960) were to be imposed on access to the type of literature at present currently being used for research that is published in the more taxonomically based journals, then at least 30% of the references would not be available.

Another important aspect of the literature used in palaeontological research is the remarkable diversity of published sources required. A small survey of 500 references from the bibliographies of the nine papers in *Palaeontology* **30(4)** (1987) consistently shows that, even with variable length citation lists (from 28–100 in sample), 50% are derived from different journals and 20% are non-periodical publications, so that only 30% are repeated journal citations. Furthermore, each successive paper cites a high proportion of different journals and only a small proportion of citations (10–20%) are common between any two or three papers.

On a world-wide basis there are nearly 100 purely palaeontological current serial publications, which vary enormously in their scope, print runs, cost, etc. Of these, about 20 are mentioned in some detail below and a further 70 listed in a more limited way in Appendix II of this chapter, along with a further 17 bibliographical publications in Appendix III. Titles are listed in alphabetical order. The letter codes at the end of each citation in the following list refer to: A, the number of subscribers to the journal; B, the print run; C, the average number of pages per year; D, the page size; International Standard Serial Number (ISSN); and CODEN.

*Alcheringa.* This is the organ of the Association of Australasian Palaeontologists of the Geological Society of Australia (see above). Issued twice yearly, it first appeared in 1975 and covers all aspects of palaeontology, including taxonomy, biostratigraphy, micropalaeontology, vertebrate palaeontology, palaeobotany, palynology, palaeobiology, palaeoanatomy, palaeoecology, biostratinomy, biogeography, chronobiology, biogeochemistry, and ichnology. Review articles are welcomed and occasionally a single volume is devoted to a particular topic. Emphasis is placed on high quality illustrations. Manuscripts are published approximately one year after acceptance and should be sent to Dr J.W. Pickett, Specialist Services Section, Geological Survey of New South Wales, Mineral Resources Development Laboratory, PO Box 76, Lidcombe, New South Wales 2141, Australia.

Subscription information may be obtained from the Geological Society of Australia Inc., 606 A.N.A. House, 301 George Street, Sydney, New South Wales 2000, Australia. Members of the Association of Australasian Palaeontologists receive *Alcheringa* at a reduced rate. The journal is abstracted in *Current Contents, Geological Abstracts, GeoRef, Petroleum Abstracts*, and *Science Citation Index*.
A, 650; B, 1000; C, 344; D, 17 × 25 cm; ISSN, 0311–5518; CODEN, ALCHDB.

*Fossils and Strata.* A sister journal to *Lethaia* (see below), it was first issued in 1972 and comprises an internationally distributed series of monographs and memoirs in palaeontology and stratigraphy. It is issued irregularly in *Numbers*; by the end of 1991 31 had appeared. While *Lethaia* is a fully international journal, *Fossils and Strata* provides an outlet for more comprehensive systematic and regional descriptions dealing with areas in the five countries of Norden, or written by palaeontologists and stratigraphers from these countries. Contributions by colleagues in other countries may also be included as far as this series is deemed to be an appropriate medium. Articles can normally be accepted only if they are heavily subsidized by the national Research Council in their country of origin, or by other funds. Most papers are in English, but they may be in French or German. Manuscripts, which are published approximately four to five months after acceptance, should be sent to S. Bengtson, Institute of Palaeontology, PO Box 558, S-75 122 Uppsala, Sweden.

Issues are individually priced and may be ordered from the publishers, Universitetsforlaget, Postboks 2959, Tøyen, Oslo 6, Norway. Members of the IPA (see above) are offered discount prices on all issues. The journal is abstracted in *Biological Abstracts*, *British Geological Literature*, *Geological Abstracts*, and *GeoRef*.
B, 1000; C, 124 (per number); D, A4; ISSN 0024−1164.

*Geobios*. Published with the cooperation of the *Centre National de la Recherche Scientifique*, it first appeared in 1968 and is issued bi-monthly. It publishes papers of international interest on all aspects of palaeontology, stratigraphy, and palaeoecology. Articles may be in English or French. Manuscripts are published two to six months after acceptance and should be sent to *Geobios*, Centre des Sciences de la Terre, Université Claude-Bernard, 27–43 Boulevard du 11 Novembre, 69622 Villeurbanne, France.

Subscription information may be obtained from the Secretary at the above address. The journal is abstracted in *Biological Abstracts*, *Bulletin Signalétique*, *Pascal Folio*, *Current Contents*, *Geological Abstracts*, *GeoRef*, *Geoscience Database*, and *Referatiunyi Zhurnal*.
A, 528; B, 650; C, 900−1000; D, 21 × 27 cm; ISSN 0016−6995; CODEN, GEBSAJ.

*Geologica et Palaeontologica*. Published in Marburg, it appears annually and was established in 1967 to publish articles on all aspects of geology and palaeontology from all over the world. Articles may be in either English, German, or French. Manuscripts are published about one year after acceptance and should be sent to Redaktion von Geologica et Palaeontologica, Fachbereich Geowissenschaften der Philipps-Universität, D-3550 Marburg/Lahn, Lahnberg, Germany. This journal is Abstracted in *Bibliography and Index of Geology*, *Pascal Folio*, and *Viniti I Moskva*.
A, 92; B, 600; C, 192; D, A4; ISSN 0072−1018; CODEN, GPALA2.

*Journal of Micropalaeontology*. The British Micropalaeontological Society (see above) published the first volume in 1982 and produces two issues per year. It carries papers on any aspect of micropalaeontological research, world-wide, and includes studies on Recent forms also. It tends to be dominated by taxonomy and palaeoecology. Manuscripts are published from three months to one year after acceptance and should be sent to Dr M.C. Keen, Department of Geology, University of Glasgow, Lilybank Gardens, Glasgow G12 8QQ, U.K.

The journal is issued free to all members of the Society (see above).
A, 800; B, 1000; C, 240; D, 21 × 27 cm; ISSN 0262−821X.

*Journal of Paleontology*. The main publication of the Paleontological Society (see above), it was first issued in 1927 and appears bi-monthly. All aspects of palaeontology are dealt with, but taxonomy, palaeoecology, biostratigraphy, and evolution tend to dominate. Papers are published approximately six months after acceptance and should be sent to Don C. Steinker, Department of Geology, Bowling Green State University, Bowling Green, OH 43403, U.S.A.

The journal is issued free to all members of the Paleontological Society (see above) and is abstracted in *Biological Abstracts*, *Current Contents*, *British Geological Literature*, *Geological Abstracts*, *GeoRef*, *Indian Science Review*, *Petroleum Abstracts*, and *Science Citation Index*.
A, 2773; B, 3150; C, 1320; D, 21.5 × 28 cm (formerly 17.5 × 24 cm); ISSN 0022−3360; CODEN, JPALAZ.

*Journal of Vertebrate Paleontology*. Founded in 1980 (first issue 1981) at the University of Oklahoma, since 1984 it has been supported by the Society of Vertebrate Paleontology (see above). Published quarterly, it accepts papers on all theoretical and applied aspects of the palaeontology of chordates, especially their origins, evolution, anatomy, taxonomy, biostratigraphy, palaeoecology, palaeogeography, and palaeoanthropology. Manuscripts are published approximately 18 months after acceptance and should be sent to either Richard Cifelli, Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma 73019, U.S.A. (mammals) or Hans-Dieter Suess, Vertebrate Palaeontology, Royal Ontario Museum, Toronto, Canada M5S 2C6 (other vertebrates).

The journal is issued free to all members of the Society of Vertebrate Paleontology (see above) and is abstracted in *Biological Abstracts* and *GeoRef*.
A, 1000; B, 1200; C, 400; D, 21.6 × 27.9 cm; ISSN 0272−4634; CODEN, JVPADK.

*Lethaia*. The official organ of the IPA (see above) and sponsored by the National Councils for Scientific Research in Denmark, Finland, Norway, and Sweden, *Lethaia* was first issued in 1968 and is published quarterly. It includes articles of international interest in palaeontology and stratigraphy. Articles on the morphology and anatomy of fossil plants and animals should be of general interest to palaeontologists, and articles on systematic palaeontology should deal with the higher units in systematics or key forms on which concepts of classification are based. New features, new forms, and significant changes in the known distribution of fossil organisms also constitute important criteria for the acceptance of articles. Palaeobiology, particularly palaeoecology, and ecostratigraphy are the core topics of the journal. Articles on stratigraphy should meet the same requirements for general interest and deal with stratigraphic principles, correlations of at least continental-wide importance, stratotype areas of key character, new occurrences or revisions which establish major features in palaeogeography, etc. *Lethaia*, with its sister journals *Boreas* and *Fossils and Strata* (see above), forms part of a publishing system with special ambitions to apply modern techniques in scientific publication. Most papers are in English, but they may be in French or German. Manuscripts are published approximately one year after acceptance and should be sent to the Editors of *Lethaia*, Department of Palaeozoology, Swedish Museum of Natural History, Box 50007, S-104 05 Stockholm, Sweden.

Subscription information may be obtained from the Norwegian University Press (Universitetsforlaget AS), PO Box 2959, Tøyen, Oslo, Norway.

The journal is abstracted in *Biosciences Information Service of Biological Abstracts*, *British Geological Literature*, *Current Contents*, *Geological Abstracts*, *GeoRef*, *Current Awareness in Biological Sciences*, *Contributions to Coastal, Ocean, Lake and Waterway (CERE)*, and *Science Citation Index*.
A, 1200; B, 1500; C, 384; D, 17 × 25 cm; ISSN 0024−1164; CODEN, LETHAT.

*Micropaleontology*. Published by the Micropaleontology Press (American Museum of Natural History) since 1955, it appears quarterly and covers the stratigraphy, systematics, morphology, palaeobiology, and palaeoecology of all micro-organisms with hard parts. The journal is relevant to Earth sciences, oil exploration, and oceanography and is dominated by foraminiferans, ostracodes, radiolarians, and nannoplankton. Manuscripts, which are published just 13 weeks after acceptance, should be sent to Dr J. Van Couvering, Micropaleontology Press, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, U.S.A.

Subscription information may be obtained from Micropalaeontology Subscriptions, Dept. MPT, Box 3000, Denville, New Jersey 07834, U.S.A. The journal is abstracted in *Biological Abstracts*, *Chemical Abstracts*, *Geological Abstracts*, *GeoRef*, *Ocean Abstracts*, *Petroleum Abstracts*, and *Science Citation Index*. There is also an irregular monograph series *Micropaleontology Special Publication* (1976; ISSN 0160−2071) and bibliographical series (see *Ellis and Messina Catalogues* below).
A, 1000; B, 1300; C, 388; D, 21.6 x 27.9 cm; ISSN 0026−2803; CODEN, MCPLAI

*Palaeontographica*. Published by E. Schweizerbart'sche Verlagsbuchhandlung of Stuttgart, this major international monograph series was initiated in 1846. It is divided into two series, A and B, the former dealing with palaeozoology and stratigraphy, the latter with palaeobotany. In both series five volumes (i.e. ten numbers) are produced every year. This journal has established a world-wide reputation for the highest standards of monographic treatment and accepts papers on all fossil groups of all ages. Papers may be in English, German, or French. Publication usually occurs within a year of acceptance and manuscripts for Series A should be sent to Prof. Dr W. Haas, Institute für Paläontologie der Universität, Nussallee 8, D-5300 Bonn 1, Germany; for Series B send to Dr H. J. Schweitzer at the same address.

Subscription information may be obtained from the publishers (see above) at Johannesstrasse 3A, D-7000 Stuttgart 1, Germany. The journal is abstracted in *Biological Abstracts*, *British Geological Literature*, and *GeoRef*.
C, 855; D, 23 × 29 cm; ISSN 0375−0442 (Series A), 0375−0299 (Series B); CODEN, PGABA8(A), PABPAD(B).

*Palaeontographical Society Monographs.* Monographs of the Palaeontographical Society (see above) were first published in 1848 (for 1847). Each annual volume consists of a number of complete or part Monographs. They are confined to descriptions of British fossils, restricted geographically, stratigraphically, or taxonomically. The Palaeontographical Society sets very high standards for its monographs and the interval between acceptance of an offered title and publication may be many years. Manuscripts and should be sent to either Dr. J. Hutt, Edinvillie, Gartly, Huntly, Aberdeenshire AB5 4RS, U.K. or Dr A.T. Thomas, Department of Geological Sciences, University of Birmingham, PO Box 363, Birmingham B15 2TT, U.K.

The annual volume is issued free to all members of the Palaeontographical Society (see above). Non-members may purchase the publications of the Society at the listed prices from The Natural History Museum, Cromwell Road, London SW7 SBD, U.K. The journal is abstracted in *Biological Abstracts*, and *GeoRef*.

A, 700–750; B, 900; D, approx. quarto; ISSN 0376–2734; CODEN, PLTSAJ.

*Palaeontologica Sinica.* Published by the Institute of Vertebrate Palaeontology and Palaeoanthropology, Academia Sinica and the Nanjing Institute of Geology and Palaeontology, Academia Sinica, this well established Chinese publication first appeared in 1922. It is the major monograph series for China and two or three numbers appear annually, each being a single substantial paper. Systematic studies are often complemented by palaeoecological, palaeobiogeographical, and biostratigraphical studies of the relevant taxa, and palaeoanthropology, palaeozoology, and palaeobotany receive equal coverage. Papers are in Chinese with an English translation. They may take up to two years to be published after acceptance and should be sent to the editor, Chang Mei-Li, Nanjing Institute of Geology and Palaeontology, Academia Sinica, Chi-Ming-Ssu, Nanjing, People's Republic of China. The journal is abstracted in *GeoRef*.

A, 1200; B, 2000; C, 250; D, 19 × 26 cm; ISSN 0375–054X (Series A); 0375–0531 (New Series B–Invertebrates of China), 0578–1604 (Series C).

*Palaeontology.* The journal of the Palaeontological Association (see above), it first appeared in 1957 and is issued quarterly. This widely-read international journal publishes papers on all aspects of palaeontology from all areas of the world and includes Recent material of palaeontological relevance. Review articles are particularly welcome, and short papers can be published rapidly. Preference is given to works of more than local significance. A high standard of illustration is a feature of the journal. Manuscripts, which are published one year to 18 months after acceptance, should be sent to Prof. D. Edwards, Department of Geology, University of Wales College of Cardiff, Cardiff CF1 3YE, U.K.

The journal is issued free to all members of the Association (see above for details) and is abstracted in *Biological Abstracts, GeoRef, Science Citation Index*, and *GeoSciTech* (online).

A, 1400; B, 2150; C, 785; D, 19 × 24.5 cm; 1SSN 0031–0239; CODEN, PONTAD.

*Paläontologische Zeitschrift.* The official journal of Paläontologische Gesellschaft, it was first issued in 1914 and appears quarterly. Papers appear in English or German on all aspects of systematic palaeontology, palaeoecology, and palaeobiogeography. Manuscripts are published from nine months to one year after acceptance and should be sent to Dr R. Werner, Forschungs-Institut Senckenberg, Senckenberganlage 25, 6000 Frankfurt am Main, Germany. The journal is abstracted in *Biological Abstracts*, *British Geological Literature*, and *GeoRef*.

A; *c*.1000; B, 1500; C, 350; D, 16 × 24 cm; ISSN 0031–0220; CODEN, PAZEAW.

*Paleobiology.* This is a quarterly journal of the Paleontological Society (see above) which first appeared in 1975 and specializes in articles dealing with biological palaeontology. The emphasis is on biological or palaeobiological processes and patterns, including speciation, extinction, development of individuals and of colonies, natural selection, evolution, and patterns of variation, abundance, and distribution in space and time. Papers concerning Recent organisms are considered appropriate if they are of interest to palaeontologists. Taxonomic papers are welcome if they have broad applications. Book reviews can also be submitted or invited. Manuscripts should be sent to *Paleobiology*, Department of Geology, University of Cincinnati, Cincinnati, OH 45221, U.S.A.

Although published by the Paleontological Society (see above), a subscription to *Paleobiology* is in addition to the Society's dues. The journal is abstracted in *Biological Abstracts*, *Current Contents*, *GeoRef*, *Petroleum Abstracts*, and *Science Citation Index*.

B, 2500; C, 471; D, 17.5 × 25.5 cm; ISSN 0094–8373; CODEN, PALBBM.

*Paleontological Journal.* Published four times a year by Scripta Technica (a subsidiary of John Wiley & Sons), it first appeared in 1967. It consists of translations in English of papers from the Russian-language journal *Paleontologicheskiy zhurnal*, published by the U.S.S.R. Academy of Sciences. It deals with the anatomy, morphology, and taxonomy of extinct animals and plants, their phylogenetic relationships, distribution, ecology, origin, and evolution, as well as the biostratigraphy of Eastern Europe and Asia. Each issue consists of papers selected from one issue of *Paleontologicheskiy zhurnal*, and appears approximately 16 weeks after original publication. The editor is Matthew H. Nitecki, Geology Department, Field Museum of Natural History, Chicago, Illinois, U.S.A.

Subscription information can be obtained from the *Paleontological Journal*, Subscriptions Department, John Wiley & Sons, 605 Third Avenue, New York, NY 10158, U.S.A. The journal is abstracted in *Biological Abstracts* and *GeoRef*.
C, 562; D, 18 × 25.5 cm; ISSN 0031–0301 (Russian version, 0031–031X); CODEN, PJOUAK.

*Palynology.* Published by the American Association of Stratigraphic Palynologists (AASP, founded 1967), it appeared in 1977 and is issued annually. Papers are published on all aspects of Quaternary or pre-Quaternary palynology from all over the world, but are dominated by contributions relating to North America. Each volume includes the proceedings of the previous annual meeting. Manuscripts should be submitted to David K. Goodman, Arco Oil and Gas Co., Research Centre, 2300 West Plano Parkway, Plano, Texas 75075, U.S.A.

*Palynology* is issued free to all members of the AASP; subscription information may be obtained from the Treasurer at the above address. An irregular *Contribution Series* (ISSN 0160–8843) and quarterly *Newsletter* (ISSN 0192–7299) are also published. The journal is abstracted in *Biological Abstracts*, *British Geological Literature*, *Geological Abstracts*, *GeoRef*, and *Petroleum Abstracts*.
C, 962; D, 21.6 × 27.9 cm; ISSN 0191–6122.

*Pollen et Spores.* Published with the co-operation of the *Centre National de la Recherche Scientifique*, it was first issued in 1959 and appeared quarterly until 1989. It published papers on all aspects of palynology on a world-wide basis, either in French or English.

Subscription information BP 2015, 34024 Montpellier Cedex, France. The journal was abstracted in *GeoRef*.
A, 400; B, 800; C, 600; D, 15.5 × 24 cm; ISSN 0375–9636; CODEN, POSPAQ.

*Review of Palaeobotany and Palynology.* One of several international geoscience journals published by Elsevier Science Publishers, PO Box 211, 1000 A E, Amsterdam, The Netherlands, it was first published in 1967, and there are eight issues a year. The main language is English but texts may also be submitted in French and German. The scope of the journal covers the whole of palaeobotany and palynology. Manuscripts should be sent to the Editorial Office, *Review of Palaeobotany and Palynology*, P.O. Box 1930, 1000 BX Amsterdam, The Netherlands. The journal is abstracted in *Biological Abstracts*, *British Geological Literature*, *Current Contents*, *Geological Abstracts*, *GeoRef*, *Pascal Folio*, *Petroleum Abstracts*, and *Science Citation Index*.
ISSN 0034–6667; CODEN, RPPYAX.

*Revue de Micropaléontologie.* First published in 1958, this French journal appears quarterly and accepts articles, congress and symposia reports, and book reviews dealing with any aspect of micropalaeontology, especially taxonomy and stratigraphy. Articles may be in English, but are usually in French. Manuscripts are published from nine to 18 months after acceptance, and should be sent to *Revue de Micropaléontologie*, Maison de la Géologie, 79 Rue Cl. Bernard, 75005 Paris, France.

Subscription information may be obtained from the same address. The journal is abstracted in *British Geological Literature*, *GeoRef*, *Pascal Folio*, and *Petroleum Abstracts*.
A, 550; B, 700; C, 266; D, 21 × 27 cm; ISSN 0035–1598; CODEN, RMCPAM

### Museums

On a world-wide scale there are a great number of institutions which house palaeontological collections of importance. The directory *World Palaeontological Collections* (Cleevely 1983) lists some 500 named collections, of which over 200 are in the U.K. Cleevely's invaluable work builds on several previous compilations and includes discussions on problems of compiling such directories, a brief history of earlier guides to geological collectors with brief bibliographies on the history of palaeontology, fossil collecting, collections and their published catalogues, and other relevant reference sources. Listed in Appendix IV are the main international and national museums with major fossil collections. Many important regional and university museums have had to be excluded and the reader is referred to Cleevely for a more complete listing. There is a bias towards British museums and Cleevely's geographical ordering has been followed.

## References

Cleevely, R.J. 1983. *World Palaeontological Collections*, British Museum (Natural History) and Mansell Publishing, London.

Hall, J.L. & Brown, M.J. 1987. *On-line bibliographic databases* (4th edn). ASLIB, London.

MacKay, J.W. 1973. *Sources of information for the literature of Geology. An introductory guide*. Geological Society of London, Bath.

Menard, H.W. 1971. *Science: growth and change*. Harvard University Press, Cambridge, Ma.,

Teichert, C. & Yochelson, E.L. 1985. The International Palaeontological Association: historical perspective. *Episodes* **8**, 252–256.

Thornton, J.L. & Tully, R.I.J. 1971. *Scientific books, libraries, and collectors. A study of bibliography and the book trade in relation to science* (3rd edn) and *Supplement 1969–75* (1978). The Library Association, London.

## Appendix I: Palaeontological organizations—supplementary list

American Association of Stratigraphic Palynologists. (Founded, 1967; membership, 400) G.D. Wood, Amoco Production Co., PO Box 3092, Houston, TX. 77253, U.S.A. Publications: *Palynology*, *Contribution Series*, *Newsletter*.

Asociación Paleontológica Argentina. (Founded, 1955; membership, 400) Maipu 645, 1 Piso, Buenos Aires, Argentina. Publication: *Ameghiniana*.

Association Paléontologique Française. Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, 8 rue Buffon, 75005 Paris, France.

Austrian Paleontological Society (Österreichische Paläontologische Gesellschaft). (Founded 1966; membership, 166) Institut für Paläontologie der Universität, Universitätsstrasse 7/11, A-1010 Vienna, Austria. Publication: *Beiträge zur Paläontologie von Österreich*.

Bernard Price Institute for Palaeontological Research. University of Witwatersrand, Johannesburg 2001, South Africa. Publication: *Palaeontologia Africana*.

Botanical Society, Paleobotany Section. Gar W. Rothwell, Department of Botany, Ohio University, Athens, OH 45701, U.S.A. Publication: *Bibliography of North American Paleobotany*.

Cushman Foundation for Foraminiferal Research. Museum of Comparative Zoology, Invertebrate Paleontology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, U.S.A. Publications: *Journal of Foraminiferal Research*, *Special Publications*.

Forschungsinstitut und Natur-Museum Senckenberg. Senckenberg-Anlage 25, D-6000 Frankfurt am Main 1, Germany. Publication: *Senckenbergiana Lethea*.

International Federation of Palynological Societies. D.M. Jarzen, National Museum of Natural Sciences, Paleobiology Division, Ottawa, Ontario K1A OM8, Canada.

Palaeobotanical Society. 53 University Road, Lucknow, India. Publication: *Geophytology*.

Palaeontological Society of China. (Founded, 1929; membership, 1200) Nanjing Institute of Geology and Palaeontology, Chi-Ming-Ssu, Nanjing 210009, People's Republic of China. Publications: *Acta Palaeontologica Sinica*, *Acta Micropalaeontologica Sinica*.

Palaeontological Society of India. 98 Mahatama Gandhi Marg, Lucknow, India. Publication: *Journal of the Palaeontological Society of India*.

Palaeontological Society of Japan (Nippon Koseibutsu Gakkai). (Founded, 1935; membership, 720) Department of Geology, Kyushu University, Fukuoka (Hakata) 812, Japan. Publications: *Transactions and Proceedings*, *Special Papers*, *Fossils*.

Paläontologische Gesellschaft. (Founded, 1912; membership, 950) Forschungsinstitut Senckenberg, Senckenberg-Anlage 25, D-6000 Frankfurt am Main 1, Germany. Publication: *Paläontologische Zeitschrift*.

Palynological Society of India. (Founded, 1965; membership, 205) 24B/5 Original Road, New Delhi 110005, India. Publication: *Journal of Palynology*.

Schweizerische Paläontologische Gesellschaft. (Founded, 1921; membership, 198) Birkhaeuser Verlag, PO Box 133, CH-4010 Basel, Switzerland. Publication: *Schweizerische Paläontologische Abhandlungen*.

Sociedad Española de Paleontologia. Enadmisa, Doctor Esquerdo 138, 28007 Madrid, Spain. Publications: *Revista Española de Paleontologia*, *Revista Española de Micropaleontologia*.

Società Paleontologica Italiana. Instituto di Paleontologia, Via Università n. 4, 41100 Modena, Italy. Publication: *Bollettino della Società Paleontologica Italiana*.

Vsesoyuznoe Paleontologischekoe Obshchestvo. Leningrad, U.S.S.R. Publication: *Trudy Sessii*.

## Appendix II: Serial publications — supplementary list

These Serial publications are listed in the following format: name of publication; International Standard Serial Number (ISSN); first year of publication; type of publication (P, periodical; MS, monograph series); periodicity (qu, quarterly; bi-m, bi-monthly; irreg, irregular; ann, annual; bi-ann, bi-annual); language(s) of text and summaries; parent body (society, institute, or publisher) and address; distributor (if different from parent body) and address; current (1989) editor (ed. 1989); circulation (circ); average number of pages per year (pp/yr); size of pages (cm); indexing, abstracting, and online services; CODEN; and other publications from the same parent body.

*Acta Micropalaeontologica Sinica*. ISSN 1000–0674; 1984–; P; qu; Chinese, summaries in English; Palaeontological Society of China; Science Press, Beijing; distributed by China International Book Trading Corporation (Guoji Shudian), PO Box 2820, Beijing, Peoples Republic of China; 450 pp/yr; 14 × 22 cm; indexed in *Biol. Abstr.*, *GeoRef*; see also *Acta Palaeontologica Sinica*.

*Acta Palaeobotanica*. ISSN 0001–6594; 1960–; P; qu; Polish, summaries in English; Pánstwowe Wydawnictwo Nankowe Oddzial, Kraków, Poland; indexed in *GeoRef*; CODEN, APBCAG.

*Acta Palaeontologica Polonica*. ISSN 0567–7920; 1956–; P; qu; English, French, Polish, summaries in Polish and Russian; Instytut Paleobiologii PAN, Aleja Zwirki i Wigury 93,02–089 Warsaw, Poland; ed., J. Dzik; circ 700; 440 pp/yr; 12.6 × 19.6 cm; indexed in *Biol. Abstr.*, *Bull. Sig.*, *GeoRef*, *Ref. Zhur.*, *Zoo. Rec.*, CODEN, APGPAC.

*Acta Palaeontologica Sinica*. ISSN 0001–6616; 1953–; P; bi-m; Chinese, summaries in English; Palaeontological Society of China; Institute of Scientific and Technological Information of China, China Publications Centre, Chegongzhuang Xilu 21, PO Box 339, Beijing, Peoples Republic of China; 700 pp/yr; 15.5 × 22.5 cm; indexed in *Biol. Abstr.*, *GeoRef*; CODEN, KSWHAT; see also *Acta Micropalaeontologica Sinica*.

*Ameghiniana*. ISSN 0002–7014; 1957–; P; qu; English and Spanish, summaries in English and Portuguese; Associación Paleontológica Argentina, Maipu 645, Primer Piso 1–5047, 1006 Buenos Aires, Argentina; ed, G.J. Scillato Yane; circ. 1000; indexed in *Biol. Abstr.*, *GeoRef*; CODEN, AMGHB2.

*Annales de Paléontologie*. ISSN 0753–3969; 1982– (Vol. 68, no. 1); P; qu; French, summaries in English; Masson et Cie, 120 bd. St. Germain, 75280 Paris Cedex 06, France; ed., B. Badre, Laboratoire de Paléontologie des Vertébrés & Paléontologie humaine, Université Paris VI, 4 place Jussieu, 75230 Paris Cedex 05, France; circ 700; 350 pp/yr; 12 × 19 cm; indexed in *Biol. Abstr.*, *Bull. Sig.*, *GeoRef*, *Pascal Folio*. Merger of *Annales de Paléontologie: Vertebrés* (ISSN 0570–1627) 1964– and *Annales de Paléontologie: Invertebrés* (ISSN 0570–1619).

*Beiträge zur Paläontologie von Österreich*. 1976–; P; irreg; German and English; Österreichische Paläontologische Gesellschaft; Paläontologisches Instituts der Universität Wien; distributed by Kommissionsverlag Universitätsstr. 7/11, A-1010 Vienna, Austria; indexed in *Biol. Abstr.*, *GeoRef*; CODEN, BPOEDX.

*Bolletino della Società Paleontologica Italiana*. ISSN 0375–7633; 1960–; P; qu; Italian Council for Scientific Research, Piazzale A. Moro 7, 00185 Rome, Italy; subscription information from Soc. Paleontologica Italiana, c/o Istituto di Paleontologia, Via Università n.4, 41100 Modena, Italy; circ 800; indexed in *Biol. Abstr.*, *GeoRef*; CODEN, BSPIAY.

*Bulletin of the British Museum (Natural History)*, Geology Series. ISSN 0007–1471; 1949–; MS; irreg; English; The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.; circ 700; 300 pp/vol; 14.4 × 21.5 cm (B4); indexed in *Biol. Abstr.*, *GeoRef*, *Zoo. Rec.*; CODEN, BUBMAO.

*Bulletins of American Paleontology*. ISSN 0007–5779; 1895–; MS; bi-ann; English. Palaeontological Research Institution, 1259 Trumansburg Rd, Ithaca, New York 14850–1398, U.S.A.; ed., P.B. Hoover; circ 500; indexed in *Biol. Abstr.*, *GeoRef*; CODEN, BAPLAJ; see also *Palaeontographica Americana*.

*Cahiers de Micropaléontologie*. ISSN 0068–5054; 1965–; MS; irreg; French, summaries in English; Editions du CNRS, 15 Quai Anatole France, F–75700 Paris, France; indexed in *Brit. Geol. Lit.*, *Geo. Abstr.*, *GeoRef*.

*Communicaciones Paleontologicas: Museo Nacional de Historia Natural*. 1970–; P; irreg; Spanish, summaries in English; Museo Nacional de Historia Natural, Casilla de Correos 399, Montevideo, Uraguay.

*Contributions from the Institute of Geology and Palaeontology, Tohoku University*. ISSN 0082–4658; 1921–; irreg; Japanese, summaries in English; Tohoku University, Institute of Geology and Palaeontology — Tohoku Daigaku Rigakubu Chishitsugaku Koseilbutsugaku Kyoshitsu, Aobayama, Sendai 980, Japan; circ 750, indexed in *Biol. Abstr.*, *GeoRef*.

*Contributions from the Museum of Palaeontology: University of Michigan*. ISSN 0097–3556; 1924–; irreg; English; University of Michigan, Museum of Paleontology, Museums Building, Ann Arbor, MI 48109, U.S.A.; ed., G.R. Smith; circ 500; indexed in *Biol. Abstr.*, *GeoRef*; CODEN, UMMPA3; see also *University of Michigan Museum of Paleontology: Papers on Palaeontology*.

*Contributions to Canadian Palaeontology, Geological Survey of Canada, Bulletin*. ISSN 0068–7626; 1988–; P; irreg; English, summaries in French; Geological Survey of Canada, 601 Booth St., Ottawa, Canada KIA OE8; ed., L. Reynolds; 18.6 × 23.7 cm; indexed in *GeoRef*; CODEN, CGSBAN.

*Fieldiana: Geology*. ISSN 0096–2651; 1985–; irreg; English; Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605–2496, U.S.A.; ed., T. Plowman; circ 450; indexed in *Biol. Abstr.*, *Chem. Abstr.*, *GeoRef*.

*Folia Geobotanica et Phytotaxonomica*. ISSN 0015–5551; 1966–; P; qu; English, French, German, summaries in English and German; Ceskoslovenska Akademie Ved, Botanicky Ustav, Vodickova 40, 11229 Prague 1, Czechoslovakia; distributed by Junk, B.V., Lange, Voorhout 9–11, The Hague, Netherlands; circ 1100; indexed in *Biol. Abstr.*, *Geo. Abstr.*, *GeoRef*; previously *Folia Geobotanica et Phytotaxonomica Bohemoslavaca*; CODEN, FGPHAP.

*Geologica Hungarica, Series Palaeontologica*. ISSN 0374–1893; 1928–; irreg; English, French, German, Hungarian, Russian. Magyar Allami Foldtani Intezet, Budapest, Hungary; distributed by Collets Holdings Ltd., Denington Estate, Wellingborough, U.K.; indexed in *Biol. Abstr.*, *GeoRef*; CODEN, GHPADH.

*Geophytology*. ISSN 0376–5156; 1971–; P; English; Palaeobotanical Society, 53 University Road, Lucknow 7, India; circ 240; indexed in *Biol. Abstr.*, *GeoRef*; CODEN, GPHTAR.

*Journal of Foraminiferal Research*. ISSN 0096–1191; 1971–; P; qu; English; Cushman Foundation for Foraminiferal Research, Museum of Comparative Zoology, Invertebrate Paleontology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, U.S.A.; ed., P. Loubere; circ 800; indexed in *Biol. Abstr., S.C.I., Br. Geol. Lit., Geo. Abstr., GeoRef;* CODEN JFARAH; see also *Special Publication: Cushman Foundation*.

*Journal of Palynology*. ISSN 0022–33979; 1966–; P; English; Palynological Society of India; distributed by Today and Tommorow's Printers, 24 B/5 Original Road, New Delhi 110005, India; ed, P.K.K. Nair; circ 400; indexed in *Biol. Abstr., GeoRef*.

*Journal of the Palaeontological Society of India*. ISSN 0552–9360; 1956–; P; English; distributed by Indian Books and Periodicals Syndicate, B-5/62 Dev. Nagar P.O. Road, Karol Bagh, New Delhi, 110005, India; circ 1000; indexed *GeoRef;* CODEN, PLS1BJ.

*Marine Micropaleontology*. ISSN 0377–8398; 1976–; P; qu; English; Elsevier Science Publishers, PO Box 211, 1000 AE Amsterdam, The Netherlands; indexed in *Biol. Abstr., Curr. Cont., Geo. Abstr., GeoRef, Mar. Sci. Cont. Tab., S.C.I.;* CODEN, MAMIDH.

*Memoir (Paleontological Society)*. ISSN 0022–3360; 1968–; MS; irreg; English; see under Paleontological Society; ed. D.C. Steinker, Dept. Geology, Bowling Green State University, Bowling Green OH 43403, U.S.A.; circ 3000; 74 pp/issue; 21.5 × 28 cm; indexed in *Biol. Abstr., GeoRef;* CODEN, PSMECR; see also *Journal of Paleontology* and *Paleobiology*.

*Memoir of the Association of Australasian Palaeontologists*. ISSN 0810–8889; 1983–; irreg; English; Geological Society of Australia, 606 A.N.A. House, 301 George Street, Sydney, New South Wales 2000, Australia; see also *Alcheringa*.

*Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology*. Academia Sinica, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing 28, Peoples Republic of China; CODEN, CKKKD7; see also *Palaeontologia Sinica* and *Vertebrata Palasiatica*.

*Michigan State University: Museum Publications, Paleontological Series*. 1972–; irreg; English; Michigan State University Museum, East Lansing, MI 48824, U.S.A.; circ 1500.

*Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*. ISSN 0077–7749; 1870–; irreg (3 nos/vol, 2–3 vols/yr); German and English; E. Schweizerbart'sche Verlagsbuchhandlung, Johannesstr. 3A, D-7000 Stuttgart 1, Germany; circ 650; 15.5 × 23.3 cm; indexed in *Biol. Abstr., Chem. Abstr., GeoRef, Petrol. Abstr.;* CODEN, NEJPAP; see also *Monatshefte* below.

*Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*. ISSN 0028–3630; 1900–; monthly; German and English; E. Schweizerbart'sche Verlagsbuchhandlung, Johannesstr. 3A, D-7000 Stuttgart 1, Germany; circ 768; 14.7 × 22 cm; indexed in *Biol. Abstr., Chem. Abstr., GeoRef, Petrol. Abstr.;* CODEN, NJGMA2; see also *Abhandlungen* above.

*New South Wales Geological Survey Memoirs: Palaeontology*. ISSN 0077–8699; 1888–; MS; irreg; English; Dept. of Mineral Resources, Box 5288, Sydney, New South Wales 2001, Australia; ed, H. Basden; circ 400; indexed in *GeoRef*.

*New Zealand Geological Survey: Palaeontological Bulletin*. ISSN 0078–8589; 1913–; MS; irreg; English; D.S.I.R. Science Information Publishing Centre, PO Box 9741, Wellington, New Zealand; ed., I. Mackenzie; circ 800; indexed in *Biol. Abstr., Geo. Abstr., GeoRef., Petrol. Abstr.;* CODEN, PBZGAB.

*Palaeobotanist*. ISSN 0031–0174; 1952–; 3/yr; English; Birbal Sahni Institute of Palaeobotany, 53 University Road, Lucknow 7, India; ed., M.N. Bose; circ 400; indexed in *Biol. Abstr., GeoRef, Indian Sci. Abstr.;* CODEN, PLBOAJ.

*Palaeogeography, Palaeoclimatology, Palaeoecology*. ISSN 0031–0182; 1965–; P; 4 parts/vol, 5 vols/yr; English, French and German; Elsevier Science Publishers, PO Box 211, 1000 AE Amsterdam, The Netherlands; eds, P. de Deckker, C. Newton & F. Surlyk; circ 1400; 19 × 26 cm; indexed in *Biol. Abstr., Brit. Geol. Lit., Bull. Signal., Chem. Abstr., Curr. Cont., Geo. Abstr., GeoRef, Ocean Abstr., Pascal Folio, Petrol. Abstr., S.C.I.;* CODEN PPPYAB.

*Palaeontographica Americana*. ISSN 0078–8546; 1916–; MS; irreg; English; Paleontological Research Institute, 1259 Trumansburg Road, Ithaca, New York 14850, U.S.A.; ed., P.R. Hoover; circ 400; 21.8 × 28 cm; indexed in *Biol. Abstr., Geo. Abstr., GeoRef;* CODEN, PALAAI; see also *Bulletins of American Paleontology*.

*Palaeontographica Canadiana*. ISSN 0821–7556; 1983–; MS; irreg; Joint Committee on Paleontological Monographs of the Canadian Society of Petroleum Geologists and the Geological Association of Canada, Dept. of Earth Sciences, Memorial University, St. John's, Newfoundland A1B 3X5, Canada; ed., R. Ludvigsen; circ 600; 115 pp/no; 21.5 × 28 cm; indexed in *GeoRef*.

*Palaeontologia Africana*. ISSN 0078–8554; 1953–; P; irreg; English; Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, 1 Jan Smuts Avenue, Johannesburg 2001, South Africa; ed., M.A. Raath; circ 600; 17.5 × 24.5 cm; indexed in *Biol. Abstr., GeoRef;* CODEN, PBPRAS.

*Palaeontologia Jugoslavica*. ISSN 0552–9352; 1958–; P; qu; Serbo-Croatian, English, French, German; Jugoslavenska Akademija Znanosti i Umjetnosti, Brace Kavurica 1, 41000 Zagreb, Yugoslavia; ed., Malaz; indexed in *Biol. Abstr., GeoRef., Zent. Math.;* CODEN, PLJUA9.

*Palaeontologia Polonica*. ISSN 0078–8562; 1929–; MS; irreg; English, summaries in Polish; Polish Academy of Sciences, Institute of Paleobiology, Al. Zwirki i Wigury 93, 02–098 Warszawa, Poland; distributed by Ars Polona-Ruch, Krakowskie Przedmiescie 7, 00–068 Warszawa, Poland; 15.4 × 23.6 cm; indexed in *Biol. Abstr., GeoRef;* CODEN, PLPOAL.

*Palaeovertebrata*. ISSN 0031–0247; 1967–; P; qu; French, English, German, Spanish; Laboratoire de Paléontologie, Place Eugene Bataillon, 34060 Montpellier Cedex, France; ed., B. Sige; circ 200; indexed in *Bull. Signal., GeoRef;* CODEN, PLVTAW.

*Palaios*. ISSN 0883–1351; 1986–; P; bi-m; English; Society of Economic Paleontologists and Mineralogists, PO Box 4756, Tulsa, OK 74159–0756, U.S.A.; ed., D.J. Bottjer; circ 2000; 17.6 × 25.2 cm; 600 pp/yr; indexed in *GeoRef*.

*Paléobiologie Continentale*. ISSN 0750–7488; 1970–; Université des Sciences et Techniques, Laboratoire de

Paléobotanique, Montpellier, France; CODEN, PACODI.

*Paleobios*. ISSN 0031–0298; 1967–; MS; irreg; English; Museum of Paleontology, University of California, Berkeley, CA 97420, U.S.A.; ed., M.G. Kellog; circ 1000; indexed in *GeoRef*. CODEN, PLB1AZ.

*Paleontología y Evolución*. ISSN 0211–609X; 1979–; Spanish; Instituto de Paleontología, Barcelona, Spain.

*Paleontologia Mexicana*. ISSN 0185–478X; 1954–; MS; irreg; Spanish; Universidad Nacional Autónoma de México, Instituto de Geologia, Ciudad Universitaria, 04510 México; indexed in *GeoRef*; CODEN, MUGPA9.

*Paleontologicheskiy Sbornik* (*L'vov*). ISSN 0131–2634; 1961–; Russian; Izdatel'stvo L'vovskogo Universiteta, U.S.S.R.; indexed in *GeoRef*; CODEN,PALSA4.

*Quartärpaläontologie*. ISSN 0138–3116; 1975–; irreg; English, French, German, Russian; Institut für Quartärpaläontologie, Akademie-Verlag Berlin, Leipziger Str. 3–4, 1086 Berlin, Germany; ed., H.D. Kahlke; indexed in *GeoRef*; CODEN, QUARDW.

*Revista Española de Paleontologia*. 1986–; P; Spanish and English; Sociedad Española de Paleontologia, Museo Nacional de Ciencias Naturales, c/José Gutiérrez Abascal 2, 28006 Madrid, Spain; circ 100; A4; see also *Revista Española de Micropaleontologia* below.

*Revista Española de Micropaleontologia*. ISSN 0556–655X; 1969–; P; 3/yr; Spanish; Enadmisa, Doctor Esquerdo 138, 28007 Madrid, Spain; circ 700; indexed in *Biol. Abstr., GeoRef*; CODEN, RTEMB5; see also *Revista Española de Paleontologia* above.

*Revue de Micropaléontologie*. ISSN 0035–1598; 1958–; P; qu; French and English; Maison de la Geologie, BP 11–705, 75224 Paris Cedex 05, France; ed, M. Neumann; circ 700; 270 pp/vol; 21 × 27 cm; indexed in *Brit. Geol. Lit., GeoRef, Pascal Folio, Petrol. Abstr.*; CODEN, RTEMB5.

*Revue de Paléobiologie*. ISSN 0253–6730; 1982–; P; French and English; Muséum d'Histoire Naturelle de Genève, 1 Route de Malagnou, CP 434, 1211 Geneva 6, Switzerland.

*Rivista Italiana di Paleontologia e Stratigrafia*. ISSN 0035–6883; 1895–; P; qu; Italian, English, French, and German; Dipartimento di Scienze Terra, Universita Milano, Via Mangiagalli 34, Milan, Italy; circ 450; indexed in *Biol. Abstr., Geo. Abstr., GeoRef, Petrol. Abstr.*; CODEN, RPLSAT. Also *Memoria* ISSN 0375–9784; MS; Italian, summaries in English; CODEN, RVPMA5.

*Sbornik Geologickydi Ved. Paleontogie* (= Journal of Geological Sciences, Palaeontology). ISSN 0036–5297; 1949–; irreg; Czech, English, German, and summaries in Czech and Russian; Ustredni Ustav Geologicky, Malostranske nam. 19, 118 21 Prague 1, Czechoslovakia; distributed by Artia, PO 790 VE Smeckach, Prague 1, Czechoslovakia; circ 600; indexed in *Bull. Sig., GeoRef, Ref. Zhur.*; CODEN,SGPABC.

*Schweizerische Palaeontologische Abhandlungen*. ISSN 0080–7389; 1874–; MS; irreg; German, French, English, and Italian; Schweizerische Paläontologische Gesellschaft; distributed by Birkhaeuser Verlag, PO Box 133, CH-4010 Basel, Switzerland; ed, B. Engesser; indexed in *Biol. Abstr., GeoRef*; CODEN, SPAAAX.

*Senckenbergiana Lethaea*. ISSN 0037–2110; 1919–; P; 6/yr; German, French, and English; Senckenbergische Naturforschende Gesellschaft, Senckenberganlage 25, D-6000 Frankfurt 1, Germany; distributed by Verlag Dr Waldemar Kramer, Bornheimer Landwher 57A, D-6000 Frankfurt 60; ed., H. Malz; circ 850; indexed in *Biol. Abstr., Brit. Geol. Lit., Chem. Abstr., GeoRef*; CODEN, SLETAE.

*Smithsonian Contributions to Paleobiology*. ISSN 0081–0266; 1969–; MS; irreg; English; Smithsonian Institute Press, PO Box 1579, Washington, DC 20013, U.S.A.; circ 3000; 21.5 × 28 cm; indexed in *Biol. Abstr., GeoRef*; CODEN, SPBYA8.

*Special Papers — Palaeontological Society of Japan*. ISSN 0549–3927; CODEN, SPPAB7; see also *Transactions and Proceedings of the Palaeontological Society of Japan* below.

*Special Papers in Palaeontology*. ISSN 0038–6804; 1967–; 2/yr; English, Palaeontological Association (see above); distributed by Marston Book Services, Osney Mead, Oxford OX2 0EL, U.K.; circ 300; *c*. 160 pp/no; 19 × 24.5 cm; indexed in *Biol. Abstr., GeoRef*. CODEN, SPPAB7.

*Special Publication*: *Cushman Foundation for Foraminiferal Research*. ISSN 0070–2242; 1952–; irreg; English; Cushman Foundation for Foraminiferal Research. Museum of Comparative Zoology, Invertebrate Paleontology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, U.S.A. ed., S.J. Culver; circ 600; indexed in *Biol. Abstr., GeoRef*; CODEN, SPCFAO; see also *Journal of Foraminiferal Research*.

*Stereo-Atlas of Ostracod Shells*. ISSN 0952–7451; 1973–; bi-ann; English; British Micropalaeontological Society; ed., D.J. Siveter, Department of Geology, The University, Leicester LE1 7RH, U.K.; circ 400; 160 pp/yr; 23.8 × 30.8 cm; indexed in *GeoRef*.

*Transactions and Proceedings of the Palaeontological Society of Japan*. ISSN 0031–0204; 1935–; P; qu; English, summaries in Japanese; Palaeontological Society of Japan (Nihon Koseibutsu Gakkai), c/o Japan Academic Societies Centre, 2-4-16 Yayoi, Bunkyo-ku, Tokyo 113, Japan; eds, I. Hayami & I. Obata; circ 550; indexed in *Biol. Abstr., GeoRef., Petrol. Abstr.*; CODEN, TPPJAA.

*Trudy Paleontologicheskogo Instituta*. ISSN 0376–1444; 1932–; P; Russian; Akademiya Nauk SSSR, Paleontologicheskiy Institut, Profsoyuznayas 113, S-117321 Moscow, U.S.S.R.; indexed in *GeoRef*; CODEN, TPIAAG.

*Tulane Studies in Geology and Palaeontology*. ISSN 0041–4018; 1962–; qu; English; Tulane University, Department of Geology, New Orleans, LA 70118, U.S.A.; eds, H.C. Skinner & E.H. Vokes; circ 1000; indexed in *Chem. Abstr., GeoRef, Petrol. Abstr.*; CODEN, TSGEB6.

*University of Kansas Paleontological Contributions*: *Articles*. ISSN 0075–5044; 1947–; MS; irreg; English; CODEN, KUPABM. *Monographs* ISSN 0278–9744; 1982–; MS; irreg; English. *Papers* ISSN 0075–5052; 1965–; MS; irreg; English; CODEN,KCPA3. University of Kansas, Paleontological Institute, 121 Lindley Hall, Lawrence, KS 66045, U.S.A.; ed., R.L. Kaesler; circ 1500; indexed in *Biol. Abstr., Geo. Abstr., GeoRef*.

*University of Michigan Museum of Paleontology*: *Contributions*. ISSN 0041–9834; 1924–; irreg; English. *Papers on Paleontology*. ISSN 0148–3838; MS; irreg; English; CODEN, PPUMD3. University of Michigan, Museum of Paleontology, Ann Arbor, MI 48109, U.S.A; circ 500;

indexed in *Biol. Abstr.*, *GeoRef.*

*Utrecht Micropaleontological Bulletins*. ISSN 0083–4963; 1969–; MS; irreg; English; CODEN, UTMBAA. *Special Publications*. ISSN 0165–2753; MS; irreg; English; CODEN, UMBPDJ. Rijksuniversiteit tu Utrecht, Dept. of Stratigraphy and Paleontology, c/o T. van Schaik, Budapestlaan 4, 3584 CD Utrecht, The Netherlands; indexed in *GeoRef.*

*Vertebrata Palasiatica*. ISSN 0042–4404; Academia Sinica, Laboratory of Vertebrate Paleontology, Beijing, China; indexed in *GeoRef.*, *S.C.I.*; CODEN, VEPAAU; see also *Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology* and *Palaeontologica Sinica*.

*Voprosy Mikropaleontologii*. ISSN 0507–3693; 1956–; Russian; Akademiya Nauk Ordena Trudovogo Krasnogo Znameni Geologicheskiy Institut, Moscow, U.S.S.R.; indexed in *GeoRef*; CODEN, VMIKAD.

*Voprosy Stratigraffi i Paleontologii*. ISSN 0134–8698; 1975–; Russian; Izdatelstvo Saratevskogo Universiteta, Saratov, U.S.S.R.

## Appendix III: Bibliographical publications

For an explanation of abbreviations, please see Appendix II.

*Bibliographie Palynologie*. ISSN 0766–5679; 1975– (supplement to *Pollen et Spores*); French; eds, M. Van Campo, M. and C. Millerand, Laboratoire de Palynologie, Université des Sciences et Techniques du Languedoc, 34060 Montpellier Cedex, France; indexed in *GeoRef.*

*Bibliography and Index of Geology*. ISSN 0098–2784; 1969–; monthly; English; ed., G.N. Rassam, American Geological Institute, 4220 King St., Alexandria, VA 22302–1507, U.S.A.; circ 900; available online, CISTI, DIALOG, Orbit Information Technologies. Formed by merger of *Bibliography of North American Geology and Bibliography and Index of Geology Exclusive of North America*.

*Bibliography and Index of Micropaleontology*. ISSN 0300–7227; 1972–; monthly; English; ed., S. Carroll, Micropaleontology Press, c/o American Museum of Natural History, Central Park West at 79 St., New York, NY 10024, U.S.A.; circ 250; available online, CISTI.

*Bibliography of Fossil Vertebrates*. ISSN 0272–8869; 1940–; ann; English; Society of Vertebrate Paleontology, c/o Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007, U.S.A.; indexed in *GeoRef.*

*Bibliography of North American Paleobotany*. Botanical Society of America, Paleobotanical Section; ed., G.W. Rothwell, Dept. Botany, Ohio University, Athens, OH 45701, U.S.A.

*Biological Abstracts*. ISSN 0006–3169; 1927–; monthly; English; BioSciences Information Service (BIOSIS), 2100 Arch Street, Philadelphia, PA 19103–1399, U.S.A.; available online, BRS, CISTI, Central Institute for Scientific and Technical Information, DIMDI, Data-Star, DIALOG, European Space Agency, JICST, Mead Data General, STN International; indexed in *Anim. Breed. Abstr.*, *Ind. Vet.*, *JAMA*, *Popul. Ind.*, *Rev. Plant Path.*, *VITIS*, *Vet. Bull.*

*British Geological Literature*. ISSN 0140–7813; 1972–; qu; English; ed. N. Edwards, Bibliographic Press Ltd., 52 Little Paddocks, Ferring, Worthing, West Sussex BN12 5NH, U.K.; circ 300.

*Bulletin Signalétique. Bibliographie des Sciences de la Terre 227: Paléontologie*. ISSN 0300–9335; 1972–84; French; Editions du CNRS, 23 rue du Maroc, 75019 Paris, France; see *Pascal Folio*.

*Catalog of Fossil Spores and Pollen*. ISSN 0148–642X; 1957–; 3/yr; English; ed., W. Spackman, Pennsylvania State University, Coal Research Station, Deike 517, College of Earth and Mineral Sciences, University Park, PA 16802, U.S.A.; circ 600.

*Catalogue of Conodonts*. Irreg; English; ed., W. Ziegler, E. Schweizerbartsche Verlag, Johannesstr. 3-A, D-7000 Stuttgart 1, Germany.

*Current Contents/Life Science*. ISSN 0011–3409; 1958–; English; Institute for Scientific Information, 3501 Market St., Philadelphia, PA 19104, U.S.A.; and 132 High St., Uxbridge, Middlesex UB8 1DP, U.K.; available online, BRS; indexed in *Abstr. Bull. Inst. Pap. Chem.*, *Abstr. Hyg. Compumath*, *Ind. Sci. Rev.*, *SSCI*, *Sci. Cit. Ind.*

*Ellis and Messina Catalogues of Micropaleontology*. English; ed., S.E. Carroll, Micropaleontology Press, c/o American Museum of Natural History, Central Park West at 79th St., New York, NY 10024, U.S.A.; including *Catalogue of Diatoms, Catalogue of Foraminifera, Catalogue of Ostracoda*.

*Geological Abstracts*: *Palaeontology and Stratigraphy*. ISSN 0268–8018; 1986–; bi-m; English; ed., A. Cruikshank, Geo Abstracts Ltd., Regency House, 34 Duke St., Norwich NR3 3AP, U.K.; circ 300.

*Geotitles*. 1969–; English; monthly; Geosystems, PO Box 40, Didcot, Oxfordshire OX11 9BX, U.K.; available online, DIALOG; formerly *Geotitles Weekly*.

*Pascal Folio. Part 47*: *Paléontologie*. 1985–; 10/yr; French (Bureau de Récherches Geologiques et Minieres); Centre National de la Récherche Scientifique, Centre de Documentation Scientifique et Technique, Service des Abonnements, 26 rue Boyer, 75971 Paris 20, France; supersedes *Bulletin Signalétique*.

*Referativnyi Zhurnal*. ISSN 0486–2309; 1954–; monthly; Russian; Vsesoyoznyi Institut Nauchno-Technicheskoi Informatsii (VINITI), Baltiiskaya ul. 14, Moscow A-219, U.S.S.R.; subscription information for Mezhdunarodnaya Kniga, Dimitrova ul. 39, 113095, Moscow, U.S.S.R.; indexed in *Chem. Abstr.*

*Zentralblatt für Geologie und Palaeontologie. Teil II. Palaeontologie*. ISSN 0044–4189; 1807–; 7/yr; German; eds, A. and E. Seilacher, E. Schweizerbart'sche Verlagsbuchhandlung, Johannesstr. 3A, D-7000 Stuttgart 1, Germany; indexed, *Chem. Abstr.*

*Zoological Record*. ISSN 0084–5604; 1864–; English; eds, H.G. Vevers & M.A. Edwards (Zoological Society of London), BioSciences Information Service (BIOSIS) U.K., Garforth House, 54 Micklegate, Boston Spa, Yorkshire YO1 1LF, U.K.; indexed, *Helminthol. Abstr.*; available online, BRS, DIALOG.

## Appendix IV: Museums housing major fossil collections

### Europe

*Austria*
Vienna: Naturhistorisches Museum, Wien, Burgring 7, A-1014, Vienna

*Belgium*
Brussels: Institut Royale des Sciences Naturelles de Belgique, 31 Rue Vautier, B-1040 Brussels

*Czechoslovakia*
Prague: Národni Muzeum, Václavské náměsti, 1700, Prague 1

*Denmark*
Copenhagen: Dansk Geologisk Forening, Mineralogisk Museum, 7 Øster Voldgade, 1350 Copenhagen K

*France*
Lyons: Université de Lyon I, Départment des Sciences de la Terre, 43 Boulevard du 11 Novembre, 69622 Villeurbanne Cedex
Paris: Muséum National d'Histoire Naturelle, Jardin des Plantes, 57 Rue Cuvier, 75281 Paris Cedex 05

*Germany*
Berlin: Humboldt Universität, Museum für Naturkunde, Palaontologisches Museum, Invalidenstrasse 43, 104 Berlin
Frankfurt am Main: Senckenberg Naturmuseum, 25 Senckenbergan-Anlage, D-6000, Frankfurt am Main 1 (Publication: *Senckenbergiana Lethaea*)
Munich: Bayerische Staatssammlung für Paläontologie und Historische Geologie, Richard Wagner-Strasse 10, D-800 München 2

*Ireland, Republic of*
Dublin: National Museum, Geology Department, Merrion Row, Dublin 2

*Italy*
Florence: Museo di Paleontologia dell'Università di Firenze
Milan: Museo Civico di Storia Naturale di Milano, Corso Venezia 55, 1-20121 Milano
Verona: Museo Civico di Storia Naturale di Verona, Lungadige Porta Vittoria 9, I–37100 Verona

*Netherlands*
Haarlem: Teylers Museum, Damstraat 21, Haarlem
Leyden: Riijksmuseum van Geologie en Mineralogie, Hooglandse Kerkgracht 17, NL-2312 HS, Leyden

*Norway*
Oslo: Universitets Paleontologiska Museum, Sars Gate 1, Oslo 5

*Poland*
Warsaw: Muzeum Ziemi PAN, Polish Academy of Sciences, Palaeozoological Division, Al. Na Skarpie 20-26, PL-00-488, Warszawa

*Spain*
Madrid: Museo Nacional de Ciències Naturales, Paseo de la Castellana 84, Madrid 6

*Sweden*
Lunds: Lunds Universitet, Palaeontologiska Institutionen, Fack, 221 01 Lund 1
Stockholm: Naturhistoriska Riksmuseet, Stockholm 50
Uppsala: Zoologiska Museum, Palaeontological Institut, Universitet i Uppsala

*Switzerland*
Basel: Naturhistorisches Museum, Augustinergasse, 2, CH-4000 Basle
Geneva: Muséum d'Histoire Naturelle, route de Malagnou, 1211 Geneva 6 (Publication: *Revue de Paléobiologie*)
Lausanne: Musée Géologique, Palais de Rumine, 1005 Lausanne

*United Kingdom*
Birmingham: University Museum, Department of Geological Sciences, PO Box 363, Birmingham B15 2TT
Cambridge: Sedgwick Museum, Downing Street, Cambridge CB2 3EQ
Keyworth: British Geological Survey, Keyworth NG12 5GG
London: British Museum (Natural History), Cromwell Road, London SW7 5BI. (Publication: *Bulletin of the British Museum* (*Natural History*), *Geology Series*)
Manchester: Manchester Museum, The University, Oxford Road, Manchester M13 9PL
Oxford: University Museum, Parks Road, Oxford OX1 3PW
Edinburgh: Royal Scottish Museum, Chambers Street, Edinburgh EH1 1JF
Edinburgh: British Geological Survey, Murchison House, West Mains Road, Edinburgh EH9 3LA
Glasgow: Hunterian Museum, Glasgow University, Department of Geology, Glasgow G12 8QQ
Cardiff: National Museum of Wales, Cathays Park, Cardiff CF1 3NP
Belfast: The Ulster Museum, Botanic Gardens, Belfast BT9 5AB

*U.S.S.R.*
Leningrad: Vsesoyuznyi Nauchno-Isledovatel'skij Geologicheskij institut (VSEGEI), Srednij prospekt 74, SU 199026, Leningrad
Kiev: Scientific Nature Research Museum, Academy of Sciences, Ukraine RSR
Moscow: Palaeontological Institute, Academy of Sciences, Profsoyuzhayes 113, S-117321 Moscow (Publication: *Trudy Paleontologicheskogo Instituta*)
Novosibirsk: Institute of Geology and Geophysics, Siberian Branch of the Academy of Sciences, SU-630090 Novosibirsk

### North America

*Canada*
Drumheller, Alberta: Tyrrell Museum of Palaeontology, P.O. Box 7500, Alberta TOJ OYO

Ottawa: National Museum of Canada 1767, Geological Survey of Canada, 601 Booth Street, Ottawa, Ontario K1A OE8
Toronto: Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6

*U.S.A.*
Ann Arbor: Museum of Paleontology, University of Michigan, Ann Arbor, MI 48109 (Publications: *Contributions; Papers on Paleontology*)
Cambridge: Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138
Chicago: Field Museum of Natural History, Roosevelt Road and Lake Shore Drive, Chicago 5, IL 60605 (Publication: *Fieldiana: Geology*)
East Lansing: Michigan State University Museum, East Lansing, MI 48824 (Publication: *Museum Publications Paleontological Series)*
Los Angeles: County Museum of Natural History, Exposition Boulevard, Los Angeles, CA 90007
Newhaven: Peabody Museum, Yale University, New Haven, CT 06520
New York: American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024 (Publication: *Micropaleontology*)
Pittsburgh: Carnegie Museum of Natural History, 440 New York Forbes Avenue, Pittsburgh, PA
Washington: Smithsonian Institution, U.S. National Museum of Natural History, Washington DC 20560 (Publication: *Smithsonian Contributions to Paleobiology*)
Utah: University of Utah, Salt Lake City, UT 84112
U.S. Geological Survey: E-501 National Museum of Natural History, Washington DC 20560

## South America

*Argentina*
Buenos Aires: Museo Nacional Historia Naturales, Avenida Angel, Gallardo 470, Casilla de Correo 220, 10-Suc 5, 1405 Buenos Aires
La Plata: Museo de La Plata, Paseo del Bosque 1900, La Plata

*Brazil*
Rio de Janiero: Museu Nacional, Quinta da Boa Vista, 20942 Rio de Janiero

*Chile*
Santiago: Museo Nacional de Historia Natural, Cosilla 787, Santiago

*Uruguay*
Montevideo: Museo Nacional de Historia Natural, Casilla de Correos 399, Montevideo (Publication: *Communicaciones Paleontologicas*)

## Australasia

*Australia*
Brisbane: Queensland Museum, Gregory Terrace, Fortitude Valley, Brisbane, Queensland 4066
Canberra: Bureau of Mineral Resources, PO Box 378, Canberra City, ACT 2601
Melbourne: National Museum of Victoria, 285–321 Russell Street, Melbourne, Victoria 3000
Sydney: Australian Museum, 6–8 College Street, Sydney, New South Wales 2000

*New Zealand*
Lower Hutt: D.S.I.R. New Zealand Geological Survey, PO Box 30 368, Lower Hutt

## Africa

*Kenya*
Nairobi: Institute for African Prehistory, National Museum, PO Box 40658, Nairobi

*South Africa, Republic of*
Cape Town: South African Museum, PO Box 61, Cape Town

## Asia

*China, Peoples Republic of*
Beijing: Natural History Museum, 126 Tien Chiao Street, Beijing 2
Beijing: Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, PO Box 643, Beijing 28 (Publications: *Memoirs*)
Beijing: The Geological Museum, Ministry of Geology, Xisi, Beijing
Nanjing: Institute of Geology and Paleontology, Academia Sinica, 39 East Beijing Street, Chi-Ming-Ssu, Nanjing 210008, Jiangsu

*India*
Calcutta: Geological Survey of India, 27 Jawaharlal Nehru Road, Calcutta 700 016

*Israel*
Jerusalem: Department of Geology, Institute of Earth Sciences, Hebrew University, Jerusalem 91904

*Japan*
Tokyo: University Museum, University of Tokyo, 7-3-1 Hongo, Tokyo 113
Tokyo: Department of Palaeontology, National Science Museum, 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo 184

*Sri Lanka*
Colombo: Colombo National Museum, P. O. Box 854 Sir Marcus Fernando Mawatha, Wanbo 7

*Taiwan*
Taipei: Department of Geology, Taiwan Museum, 2 Siang Yang Road, Taipei

# 6.5 History of Palaeontology

## 6.5.1 Before Darwin

J. C. THACKRAY

### Sixteenth century beginnings

Geological objects have attracted attention since early times by their striking colours, textures, and shapes. They have been treasured as curiosities and for their medicinal or magic powers. In classical and medieval surveys such objects were described in alphabetical order, and stories recounted of their powers and virtues.

With the rennaissance of the sixteenth century came a change in approach. Georgius Agricola (1494–1555), a physician and apothecary in the mining town of Chemnitz in Saxony, surveyed the whole range of such objects — *fossils* as he called them all — in *De Natura Fossilium* (1546). He devised a classification, based on physical properties such as hardness, ability to take a polish, and lustre, which was a considerable advance on the earlier arrangements. Agricola believed that fossils were formed by a concreting fluid which circulated within the Earth.

Twenty years later, the Swiss physician Conrad Gesner (1516–1565) published *De Rerum Fossilium Lapidum et Gemmarum* (1565). This was the first book on fossils to be illustrated (Fig. 1). The large number of woodcuts allowed much more secure identification of the objects described than even Agricola's careful descriptions. It is also significant that Gesner based his descriptions on objects in his own collection and those of his friends. This was the start of the long connection between private and institutional collections and research.

Gesner divided his geological objects into 15 classes, based on their form or material. He recognized classes containing objects like plants or herbs, like parts of animals, like things in the sea, and like geometrical forms. His descriptions include the opinions of previous authors, the meaning and origin of the name, an account of the medicinal properties and the powers and virtues of the stone, and in some cases an opinion as to its origin. Gesner was not particularly concerned to separate organic fossils from the inorganic. He was trying to explain the 'stoniness' that was the common feature of all his objects, and to explain the wide range of resemblances that he observed. It is difficult for a twentieth century palaeontologist to look at geological objects with fresh eyes, and appreciate what a hard task this was (Rudwick 1972, Ch. 1).

Italy was the centre of interest in fossils in the late sixteenth and early seventeenth centuries. Ulisse


**Fig. 1** Illustrations of fossils published by Conrad Gesner in *De Rerum Fossilium* (1565, opposite pp. 62 and 126).

Aldrovandi (1522–1605) in Bologna, Francesco Calceolari (*c.* 1521–*c.* 1606) in Verona, and Ferrante Imperato (1550–1625) in Naples all built up large collections of natural and manufactured objects which included large numbers of geological specimens. All three published large and well-illustrated catalogues of their collections (Torrens 1985).

A fourth collection was housed in the Vatican in Rome. Michele Mercati, who was Curator in the fifteen-sixties, prepared a catalogue which, although plates were engraved, was not published until the eighteenth century. Mercati, like Aldrovandi and others, believed that the stones in his collection, whether they were shaped like flying birds, shells, leaves, or bones, had grown within the rock by some animative or vegetative spirit.

One of the plates from Mercati's unpublished catalogue was used nearly 100 years later by the Danish physician Niels Stensen (1638–1686) to illustrate the first detailed demonstration that a particular stone could indeed be organic in origin (Fig. 2). Stensen dissected the head of a giant shark in Florence in 1666. He was already familiar with the fossils called 'tongue stones' found in large numbers in Malta, and their resemblance to the teeth of his shark convinced him that they were indeed part of an ancient shark. His short published account of these teeth (1667) was very different from the writings of 100 years earlier. Stensen paid no attention to the magical powers or virtues of the fossils, and was not concerned with previous opinions on their origin. He listed a series of facts, and then the conjectures based on these facts, almost like a mathematical theorem. His conclusion was not dogmatic; he merely indicated the lack of proof that the objects are not organic in origin (Scherz 1958).


**Fig. 2** The head of a dissected shark, engraved for Michele Mercati and published by Niels Stensen in *Elementorum Myologiae Specimen* (1667).

## Seventeenth century England

Stensen's work on the shark's teeth, and his later book on fossils in general, were translated into English by Henry Oldenburg, Secretary of the Royal Society. The Society, led by its Curator Robert Hooke, was the centre of a debate on the origin of fossils which lasted for 50 years from 1660. Discussion was focused much more clearly than it had been a century before onto the problem of whether the petrified bones, shells, and teeth found in the rocks were organic remains or not. The two techniques brought to bear on the problem were: study of the Bible and other sacred writings; and observations on the fossils themselves and their position in the Earth (Porter 1977; Ch. 2).

Robert Hooke (1635–1703) took up one side of the debate in his lectures to the Royal Society. He maintained that it was inconceivable that fossil shells could have been formed for no purpose. As the purpose of a shell is to protect a mullusc, and the purpose of a tooth is to bite, it followed that fossil shells, bones, and teeth must be the remains of ancient animals. He realized that a few of these animals, such as ammonites, appeared to be extinct, and that the stoniness of the fossils could be explained by percolating waters. The position of fossils on inland hills and mountains he explained by the action of earthquakes, raising and lowering the land.

Martin Lister (*c.* 1638–1712), a London physician, took the opposite view. He had published a book on living molluscs, and so appreciated much more clearly than Hooke that most fossils from Britain did not exactly resemble living animals. He could not accept the extinction of an animal species, and therefore rejected the organic origin of fossils. Two other observations confirmed his belief. He saw that many of the objects were just impressions, showing no sign of any shell, and that particular rock types appeared to have produced particular shells.

Another great naturalist, John Ray (1627–1705), was much less decided. He could see the arguments on both sides. On the one hand, it seemed incredible that the detailed similarities between living and fossil shells, even extending to microscopic structure, should be merely fortuitous. On the other hand, the extinction of, e.g. the ammonites, suggested an imperfection in God's original Creation which was also incredible. Ray did suggest that perhaps fossil species might not be extinct, but living in unexplored oceans, but this did not totally satisfy him. The other problem was to account for the position of the fossils. It was generally accepted that the Flood was the only event which had affected the surface of the Earth since its formation six thousand years before, but Ray knew that fossils were not strewn over the land surface, but were embedded in rock layers. A flood deep enough to submerge the Alps was hard to explain rationally (Raven 1942, Ch. 16).

One of the great collectors of the day, John Woodward (1665–1728), had no doubts. He published an *Essay towards a Natural History of the Earth* (1695) which confidently disposed of all these objections. He announced that fossil shells and bones were the remains of antediluvial animals that, together with the materials of the Earth's surface, had been churned up by the Flood, settling out into layers in order of their specific gravities. He accepted Ray's suggestion that unfamiliar forms would one day be found alive.

## Eighteenth century advances

With the coming of the eighteenth century, the great fossils debate 'ran out of steam' in Britain. Hooke, Ray, Lister, and others were either dead or aged, and there were no naturalists of comparable stature in the younger generation. Further developments took place on the continent of Europe, in the first instance through the work of Johann Scheuchzer (1672–1733), a keen supporter of John Woodward. He translated Woodward's theory into Latin and argued strongly both for the organic origin of fossils and for the importance of Noah's Flood as a geological agent. Thus in *Piscium Querelae et Vindiciae* (1708) fossil fish themselves protested at being considered inorganic, and in *Homo Diluvii Testis* (1726) the remains of a very rare antediluvian human were described. The title page of his great book on fossil plants, *Herbarium Diluvianum* (1709), shows Noah's Ark floating on the receding waters as shells and debris are thrown up on the shore in the foreground to become today's fossils (Jahn *in* Schneer 1969).

By the middle of the century there was widespread agreement that 'extraneous fossils', as petrified bones and shells had become called, were indeed the remains of ancient animals and plants. Many of the objects which had puzzled earlier naturalists were now described in detail, and their origins made clear. Belemnites, thought to be thunderbolts in earlier days, were successfully interpreted as cephalopods by Erhart in 1724; echinoids were monographed by Klein in 1734, and coelenterates and other invertebrates by Buttner in 1714. By the time Linnaeus published his *Systema Natura* in 1735 fossils were treated and named as living things.

Many eighteenth century naturalists continued to attribute the distribution of fossils to the action of a single flood, in spite of the difficulties of explaining their relationship to strata and their regional variability. But others considered the explanation to be more complex. The belief grew that the Earth must be much older than the few thousand years of the traditional biblical chronology. C.L. Compte de Buffon (1707–1788) showed by experiment that the Earth must have taken tens or even hundreds of thousands of years to cool from its molten origin to its present state. In *Des Epoques de la Nature* (1778) he described seven chapters of Earth history, the later ones characterized by the deposition of particular rock groups and populated by different animals and plants. Human history was relegated to the last and shortest of the epochs (Haber 1959).

## Early nineteenth century Paris

The problem of whether or not any animals had become extinct was tackled head on by Georges Cuvier (1769–1832), Professor of Anatomy at the Musée National d'Histoire Naturelle. He studied the skeletons of African and Indian elephants and showed that they were consistently different from each other, and should therefore be placed in different species. Both species were different from the bones of the mammoth from the gravels of Northern Europe, and from the mastodon of North America, which were nonetheless clearly elephants. Here at last was a demonstration of the former existence of species which surely were not still alive and unnoticed (Fig. 3).

As Cuvier's work progressed he described the remains of a whole zoo of extinct vertebrates: the giant sloth of South America, the mastodon of North America, a hippopotamus, rhinoceros, and so on. It seemed to him that the only possible cause for the extinction of this fauna was a sudden and widespread 'revolution of the globe'. Cuvier had several lines of evidence for the nature of this event. He found a number of bones bearing attached oysters and other marine organisms, which suggested that the sea-level had risen, and the fact that beds containing fossil bones tended to be in low-lying areas indicated that the waters had not covered the hilltops. Since many of his bones were well preserved, the flood could not have been violent enough to transport them very far, but had nonetheless been rapid enough to drown the animals where they stood (Rudwick 1972, Ch. 3).

Cuvier's colleague at the Museum, Jean Baptiste Lamarck (1744–1829), held a very different view of the history of animal life, and one that brought him into conflict with Cuvier. Lamarck worked in the Jardin des Plantes for many years, before taking over invertebrate animals at the Museum. He believed that the animal and plant kingdoms exhibited an endless series of gradations, and that classification into species was only an artificial device. He believed that animals constantly changed their form as they reacted to changing environments. These changes continually moved them up a ladder of life which stretched from the lowly invertebrate at the base to the mammals and man at the top. Extinction played no part in this scheme.

Cuvier's ideas developed further as he came to study fossil bones from the gypsum quarries at Montmartre. When reconstructed, these appeared much less like living mammals than the bones from the gravels. Some combined characters from two or more living families, while others were quite unfamiliar. The key to the puzzle came as the stratigraphy of the Paris Basin was worked out and it was realized that the gypsum beds were older than the gravels. This stratigraphic work was carried out by Cuvier himself in association with Alexandre Brongniart (1770–1847) and published in the *Journal des Mines* in 1808. In this monograph the strata above the Chalk were described in terms of their lithologies, and then subdivided with reference to the fossils they contained. A whole series of distinct faunas seemed to have appeared successively. In the *Preliminary Discourse* to his *Recherches sur les Ossemens Fossiles de Quadrupedes* (1812), Cuvier gave a general account of Earth history, based on his stratigraphic and palaeontological work, in which he showed that the generally quiet and tranquil conditions on Earth had been interrupted periodically by 'revolutions' of a type not seen at the present day; these had affected large areas of the world and had largely destroyed the existing fauna each time they occurred.

Cuvier's ideas were accepted and developed by Adolphe Brongniart (1801–1876), Alexandre's son. He published *Historie des Vegetaux Fossiles* (1828), in which four successive floras were distinguished.

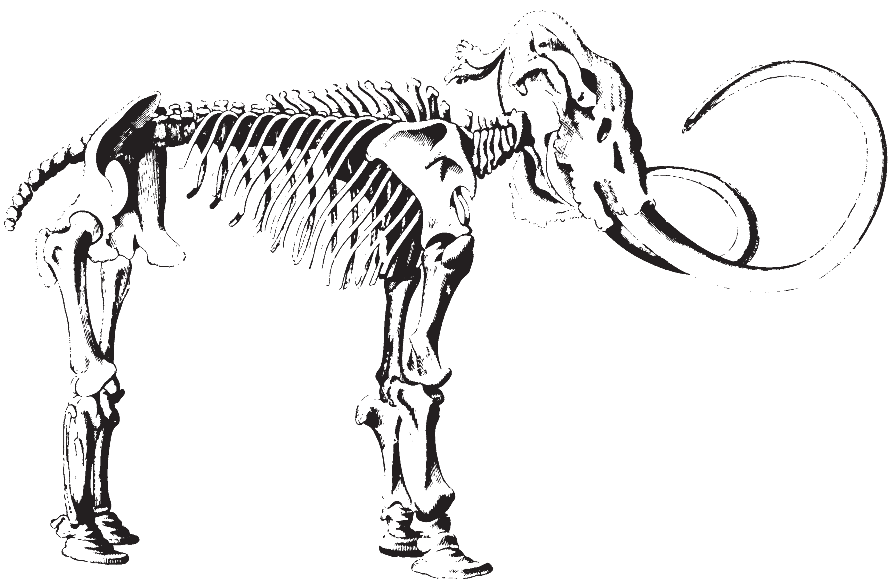

**Fig. 3** Skeleton of a mammoth discovered on the Lena River, Siberia, published by Georges Cuvier in *Recherches sur les Ossemens Fossiles*, 4th edn (1834–1835, plate 11).

He made the point that there was a clear progression through these four floras, from the Carboniferous cryptogams, through the gymnosperms of the Mesozoic and the angiosperms of the Tertiary, to the varied plants of the present day. He related this progression, and the parallel one he saw in the animal record, to the gradual decrease in the level of carbon dioxide in the atmosphere, with changing climate and sea-level also having a secondary effect (Bowler 1976, Ch. 2).

### Early nineteenth century Britain

Stratigraphic work was being carried out in Britain, at about the same time as in France, by a contemporary of Cuvier's, William Smith (1769–1839). Smith was a land drainer, mineral surveyor, and canal engineer who lived in and around Bath in the west of England for much of his life. As early as 1796 Smith had realized that fossils could be used to identify strata more securely than lithology (Fig. 4). He used this discovery to construct a table of strata together with a sketch geological map of England and Wales in 1799, although only in 1815 was his great geological map published (Eyles *in* Schneer 1969). His methods became widely known in England through the writings of John Farey, Joseph Townsend, and particularly James Parkinson (1755–1824).

Parkinson was a London physician and one of the founders of the Geological Society in 1807. This Society was largely chemical and mineralogical in its earliest years, but rapidly took up stratigraphic studies using fossils until, by the mid-eighteen-twenties, this was almost its exclusive concern. These studies, by men such as Thomas Webster, William Conybeare, and Gideon Mantell, were useful contributions to the steadily growing store of regional geological knowledge, which almost incidentally provided descriptions of previously unknown fossils. With the work of Murchison in Wales and the Welsh Borders in the eighteen-thirties, a whole new invertebrate fauna was brought into view. The Geological Society eventually took over

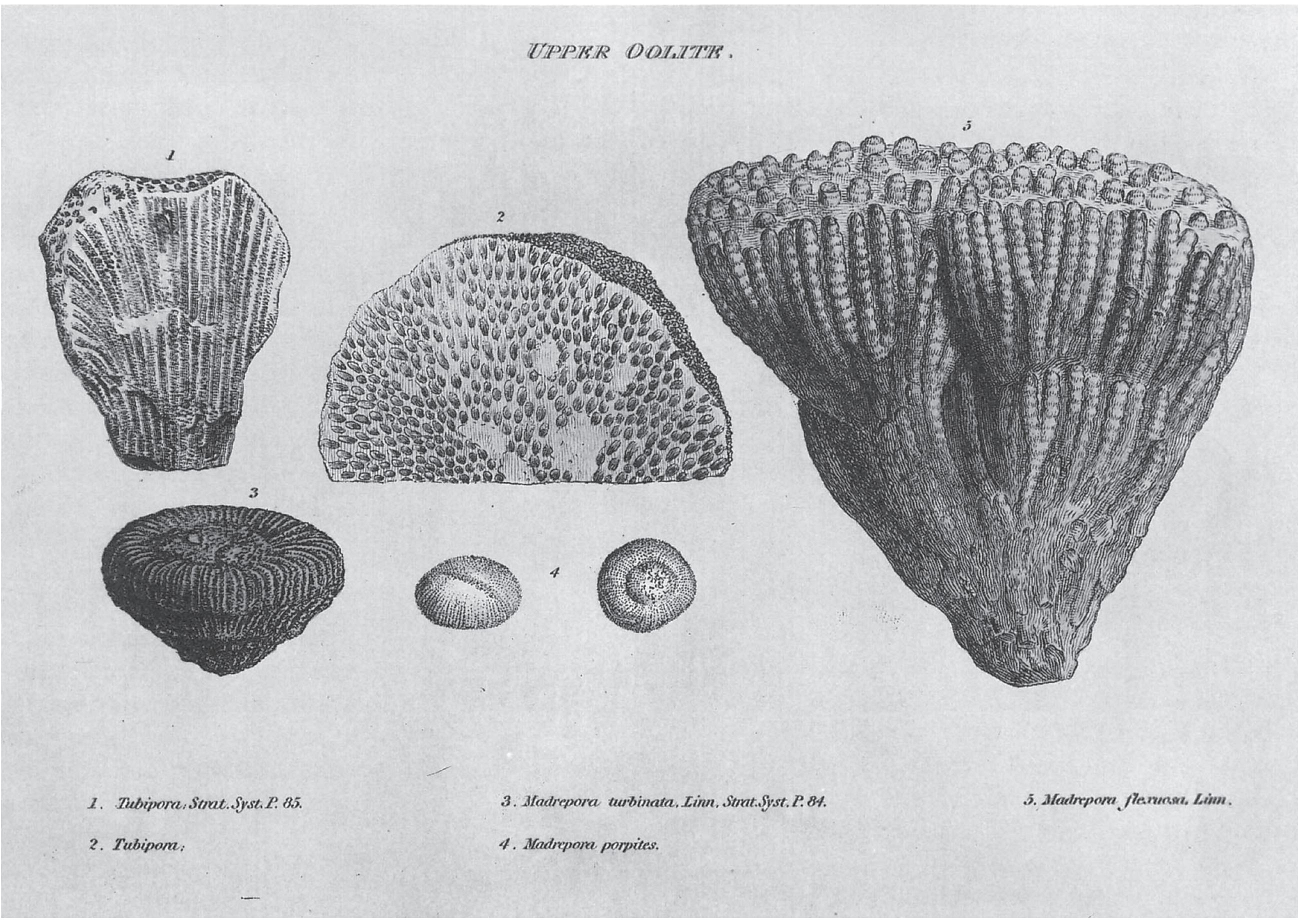


**Fig. 4** Fossils of the Upper Oolite illustrated by William Smith in *Strata Identified by Organized Fossils* (1819, opposite p. 29).

from the Museum in Paris as the principal forum for palaeontological debate.

Although William Smith was hailed as 'the father of English geology', the influence of Cuvier was also very strong. His ideas on the relationship of fossils to Earth history came to England through the translation of his *Preliminary Discourse* by Robert Jameson (1774–1854). The book was entitled *Theory of the Earth*, which linked it in people's minds with the earlier theories of Woodward and Ray. In his notes Jameson tied Cuvier's chronology to the Bible in a way that its author had never done. He identified Cuvier's final revolution with Noah's Flood, and emphasized the dramatic and destructive power of the events. In doing this he reflected the characteristic theological slant of much British geology of this period.

The leading exponent of the Deluge in Britain was William Buckland (1784–1856), Professor of Geology and Mineralogy at the University of Oxford (Fig. 5). Although his main lines of evidence concerned erratic blocks and the shape of valleys, he was strongly influenced by the researches he carried out on bone caves in Yorkshire and elsewhere. Kirkdale Cave was discovered in 1821 and interpreted by Buckland, after careful study of the living animals, as the den of hyenas, whose long occupancy was ended by the Deluge. Along with this emphasis on Biblical chronology came a belief that the Earth and everything in it was designed for man. Buckland viewed the history of life within this tradition in his *Bridgewater Treatise* (1836), putting forward not only the sort of progression that Brongniart had advocated but also the idea that God had a guiding hand in adapting life in the best possible way to changing conditions (Rupke 1983, Ch. 2).

It is a salutory reminder of the state of palaeontological knowledge in the eighteen-thirties that another distinguished geologist and a pupil of Buckland, Charles Lyell (1797–1875), could argue that there was no sign of progression in the fossil record. He appealed, like Darwin later, to the poverty of collections and the lack of knowledge of many parts of the world, to show that negative evidence was no evidence. He made much of the discovery of mammals in the Oolitic rocks and of a reptile in the Devonian. He denied that early fossil fish, such as those found by Hugh Miller in Scotland, were any 'lower' than modern forms. This argument was used to back up his view that there was no evidence for the range of life, climate, environments, and geological processes ever being any different from those of the present day. Lyell also believed that personal religious belief must be kept quite separate from the study of fossils or any other aspect of geology (Bartholomew 1976).

**Fig. 5** Portrait of William Buckland published as the frontispiece to his *Bridgewater Treatise, Geology and Mineralogy*, 3rd edn (1858).

Many features of Lyell's geology appealed to Charles Darwin (1809–1882). He read Lyell's *Principles of Geology* (1830–1833) while on the Beagle, and found it an excellent basis for interpreting the features he saw on his voyage. Lyell befriended him on his return and gave Darwin entrée to the Geological Society, where he met the experts he needed to work on his collections. Darwin's later writings on evolution, which were to influence all subsequent work on fossils, were not based on the study of the fossil record. In 1859 he was able, just like Lyell in 1830, to blame the inadequacy of the fossil record for not providing evidence to back up his theory.

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## 6.5.2 Darwin to Plate Tectonics

P. J. BOWLER

### Introduction

Fossil discoveries continued apace in the late nineteenth century, but the theoretical foundations of palaeontology were transformed by the advent of evolutionism. For several decades the attempt to reconstruct the development of life on Earth using fossil and other evidence was the most active area of evolutionary biology, although this programme encouraged a distinctly non-Darwinian view of how the process worked. In the twentieth century palaeontologists somewhat belatedly adapted to the synthesis of Darwinism and genetics, and began to grapple more actively with the geographical dimension — although for many years they opposed the theory of continental drift.

### New discoveries, 1860–1940

The impetus given to fossil collecting in the early nineteenth century was sustained in later decades by more extensive mining activities and by the opening up of new areas of the Earth to scientific exploration. In Europe and America major new museums were founded to exhibit and interpret the discoveries to the public and as centres of research. The British Museum (Natural History) in London and the American Museum of Natural History in New York are obvious examples of museums that built up their reputations at this time. By the early twentieth century many large cities had similar institutions, giving rise to considerable rivalry in the establishment of good collections. Many of the new discoveries helped to fill in the outline of the history of life created by Cuvier and his followers, greatly extending knowledge of the dinosaurs and other groups which had originally been established on the basis of small numbers of incomplete specimens. The popularity of evolution theory focused particular attention on fossils that could be identified as 'missing links', again fuelling the rivalries of collectors and institutions.

The Miocene fauna of Pikermi, Greece, was studied by Albert Gaudry in the eighteen-sixties. His work threw new light on the proboscidean *Deinotherium* and on many other forms, leading Gaudry to support the concept of a continuous evolutionary development linking the known Eocene and Pleistocene faunas (Rudwick 1976; Buffetaut 1987). The discovery of an *Archaeopteryx* specimen with feathers at Solnhofen, Bavaria, in 1861 aroused intense excitement, especially after it was acquired (at vast expense) by the British Museum (Natural History) and subsequently described by T.H. Huxley as an intermediate between reptiles and birds. A second specimen was discovered in 1877. The unearthing of almost complete *Iguanodon* specimens at Bernissart, Belgium, in 1878 showed that these dinosaurs were bipedal, not quadrupedal as originally reconstructed (Colbert 1971). A mounted specimen in Brussels gave a new awareness of the appearance of dinosaurs from 1883 onwards. Other important collections of fossil reptiles came from the Jurassic Oxford Clay of Peterborough in Cambridgeshire and from Transylvania, the latter studied by the colourful and eccentric baron Franz Nopsca.

In North America, the opening up of the West led to a veritable 'war' between collectors such as O.C. Marsh and E.D. Cope. Their discoveries of Jurassic dinosaurs from Colorado in the eighteen-seventies greatly extended knowledge of the 'Age of Reptiles' and formed the basis of impressive museum displays. Marsh's discovery of toothed birds in Kansas supported the evolutionary link already suggested by *Archaeopteryx* (Fig. 1). Marsh also collected a series of fossils in Nebraska throwing light on the

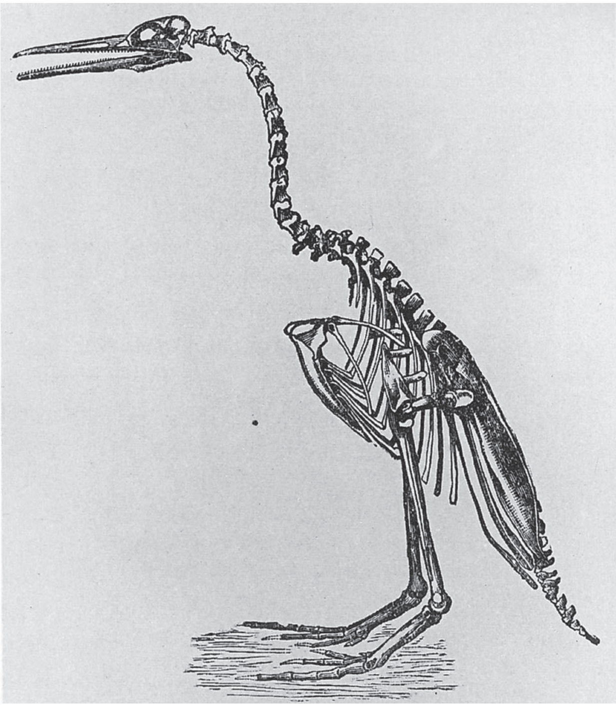

**Fig. 1** *Hesperornis regalis* (Marsh). (From Huxley, T.H. 1888. *American addresses*. Appleton, New York, p. 52.)

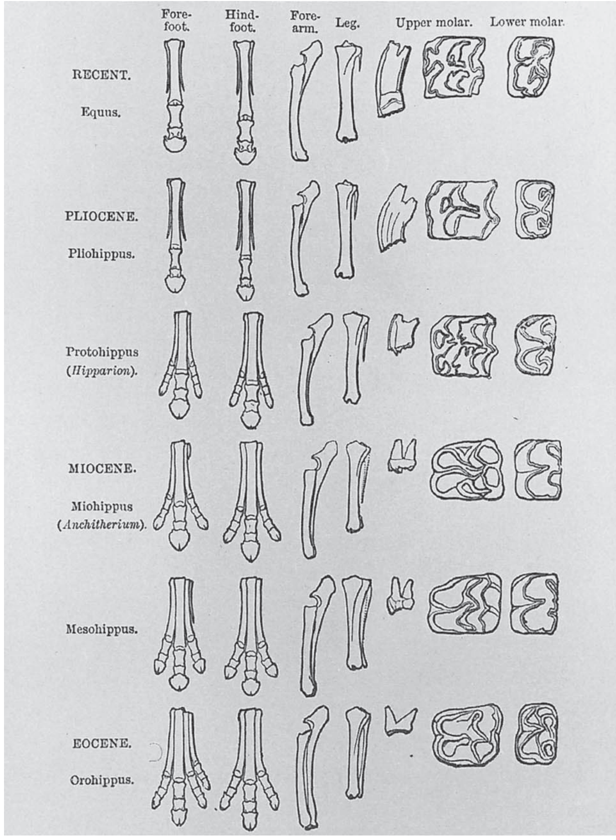


**Fig. 2** Modification of the teeth and lower limbs of the horse family, after Marsh. (From Wallace, A.R. 1889. *Darwinism*. Macmillan, London, p. 388).

**Fig. 3** The neanderthal cranium. (From Huxley, T.H. 1863. *Man's place in Nature*. Williams and Norgate, London, p. 139.)

evolution of the modern horse, culminating with the four-toed '*Eohippus*' in 1876. The fossil sequence was described as 'demonstrative evidence of evolution' by T.H. Huxley (Fig. 2). In the early twentieth century, H.F. Osborn described gigantic early mammals from the American west, including the titanotheres.

Of particular interest to the public were fossils relating to the origin of mankind (Reader 1981). In 1857 the discovery of a cranium at Neanderthal in Germany aroused much controversy but was eventually accepted as an early human form with some ape-like characters (Fig. 3). For some time considered as a possible ancestor of modern humans, the neanderthals were reinterpreted in the early twentieth century by Marcellin Boule, Arthur Keith, and others as a parallel and distinct human family driven to extinction by our own forebears. Eugene Dubois' discovery of '*Pithecanthropus erectus*' (now *Homo erectus*) in Java during the eighteen-nineties revealed an even earlier human form, again dismissed by many as a side-branch of our family tree. Thinking on human origins was to some extent thrown off course by the notorious Piltdown fraud of 1912, in which a human cranium and an ape jaw were attributed to an intermediate '*Eoanthropus*'. This reinforced the generally popular assumption that the expansion of the brain was the chief driving force of human evolution, making it easier to dismiss *Pithecanthropus*, with its small brain and upright posture, as irrelevant. Raymond Dart's discovery of the first australopithecine at Taungs, South Africa, in 1924 was again dismissed because of the refusal to admit that a small-brained hominid could have achieved bipedalism. Dart was also ignored because of the widespread opinion that mankind must have evolved in central Asia, not Africa (although expeditions to Asia did reveal more *Homo erectus* specimens, at first known as *Sinanthropus* or Peking man). The australopithecines only began to be taken seriously after Robert Broom's discoveries of the nineteen-thirties.

## Palaeontology and evolution theory

The search for 'missing links' ensured that evolutionism gave an added zest to fossil hunting, but it would be a mistake to overemphasize the impact of Darwin's theory on palaeontology. The description of fossils was still seen as a branch of morphology, with little attention being paid to intraspecific variation or the possibility of local effects on populations. Palaeontologists were thus not in the best position to appreciate the most original aspects of Darwin's theory. They had, in any case, begun to look for patterns of development in the fossil record long before the *Origin of species* appeared in 1859. The element of discontinuous change stressed by early catastrophists had begun to decline in the eighteen-fifties. H.G. Bronn and Richard Owen had begun to emphasize that there were 'laws of development' to be seen linking the fossils within each class, while the general idea of progressive evolution had been circulated as early as 1844 by Robert Chambers in his popular and controversial *Vestiges of the natural history of Creation* (Bowler 1976). It was recognized that the development of life included branching and what is now called adaptive radiation, but there was a preference for depicting the 'tree of life' with a central trunk leading through to the human race as the pinnacle of creation. The debate sparked off by Darwin's *Origin* certainly catalysed the scientific community's conversion to evolutionism, but the impetus for most palaeontological evolutionism came from transformations within the 'developmental' view of life's history already taking shape in the pre-Darwinian era. A few important figures, of whom J.W. Dawson of Montreal is the best example, continued to promote a discontinuous and hence anti-evolutionary view of the fossil record. But in general the acceptance of a loosely-defined evolutionism came naturally to most palaeontologists, for whom the new approach was little more than an extension of the earlier search for abstract laws of development.

Many evolutionists saw their principal task as the reconstruction of the history of life on Earth using the fossil record, supplemented by evidence from comparative anatomy and embryology. In Germany, Ernst Haeckel popularized this version of 'Darwinism' in books such as his *History of Creation* (1876). Even T.H. Huxley only began to make active use of evolutionism in the study of fossils after reading Haeckel — his original support for Darwin was purely tactical (Desmond 1982). Palaeontologists now began to arrange the known specimens of each group into the most plausible evolutionary series, and of course to look for the missing links. Haeckel's recapitulation theory — the claim that ontogeny recapitulates phylogeny — was widely accepted by palaeontologists looking for clues as to the 'shape' of the pattern they should expect to find. In these circumstances, it is hardly surprising that many of their views on the mechanism of evolution were distinctly non-Darwinian in character. Haeckel himself was a Lamarckian, recognizing that the inheritance of acquired characters provided a better theoretical basis for recapitulation than natural selection. Many so-called 'Darwinists' might be better called pseudo-Darwinists, since their commitment was to evolutionism rather than to natural selection. In the later nineteenth century many palaeontologists became actively opposed to the selection theory (Bowler 1983, 1986). In America, an active school of neo-Lamarckism flourished from the eighteen-seventies onwards, led by the vertebrate palaeontologist E.D. Cope and the invertebrate palaeontologist Alpheus Hyatt. They too supported recapitulation and claimed that evolution occurred by regular extensions to the process of individual growth. Arrangements of fossils into apparently linear sequences, as in the case of the horse family (Fig. 2) helped to create an impression that evolution was too regular a process to be explained in terms of random variation and selection.

The fascination with 'laws of development' led many biologists to reject Darwin's claim that adaptation was the chief guiding force of evolution. They believed that factors internal to the organism would drive variation in a particular direction whatever the demands of the environment. On this model, one could expect parallel lines of evolution to advance steadily in the same direction over vast periods of time. In Britain such a view was expounded by Owen's disciple St. George Mivart, who became one of Darwin's most active critics. Nor were Owen and Mivart mere speculators, since they recognized the possibility of mammal-like reptiles ahead of Huxley. Many palaeontologists supported the concept of *orthogenesis* (parallel evolution) driven by internal forces. Hyatt's arrangements of fossil cephalopods were widely accepted as classic examples of nonadaptive evolution. Vertebrate palaeontologists thought that many extinct species had developed grossly maladaptive characters before finally succumbing, one example being the antlers of the 'Irish elk'. Such ideas were still being promoted through into the nineteen-thirties by eminent palaeontologists such as H.F. Osborn. Osborn's subordinates at the American Museum of Natural History — including W.D. Matthew and W.K. Gregory — tried to sustain less extreme anti-Darwinian positions, but were still in a minority.

It would be easy to dismiss the palaeontologists' support for non-Darwinian concepts such as recapitulation, Lamarckism, and orthogenesis, as an aberration in the history of evolutionism, but this is a misconception engendered by our modern preference for the selection theory. In the late nineteenth century, non-Darwinian palaeontologists were in the forefront of evolutionary research, and they helped to shape the popular conception of what evolutionism is all about. Their views were instrumental in circumventing the application of Darwinian principles to human origins: no one thought of specifying an adaptive scenario to explain why humans separated from apes, since it was assumed that the primates were governed by an inherent trend toward brain-growth. The popularity of parallel evolution helped to ensure that many hominid fossils were dismissed as the products of independent lines of evolution unconnected with our own origins. Such views remained acceptable to palaeontologists and palaeoanthropologists well into the twentieth century, long after they had been overtaken by changing attitudes elsewhere in biology (Bowler 1986).

The emergence of genetics at the turn of the century ensured that most experimental biologists soon came to repudiate Lamarckism, but palaeontology remained a morphological discipline and resisted the new trends. The 'Mendelian revolution' would eventually complete what Darwin had been unable to achieve: the destruction of the developmental world view characteristic of nineteenth-century morphology. But not until the nineteen-forties did palaeontologists begin seriously to take note of the new developments. It was G.G. Simpson's *Tempo and mode in evolution* of 1944 that forced the discipline to confront what has become known as the modern synthetic theory of evolution. The re-

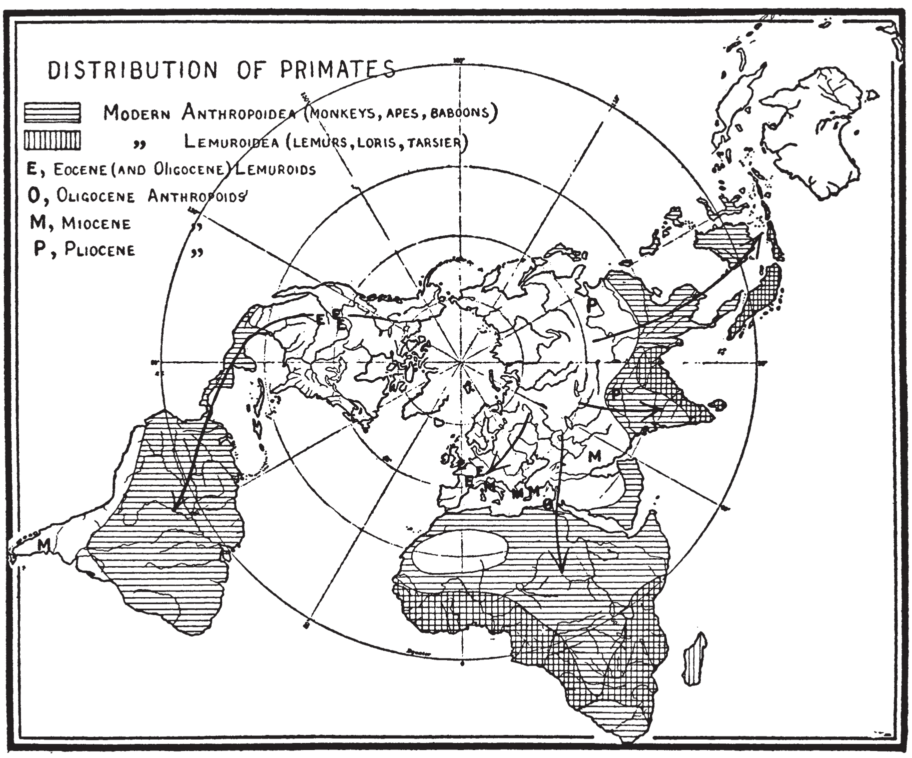


**Fig. 4** Dispersal of the primates. (From Matthew, W.D. 1939. *Climate and evolution*. New York Academy of Sciences, p. 46.)

sult was a transformation in the kind of questions studied by palaeontologists in the postwar era. Parallelism and orthogenesis were replaced by adaptive scenarios and a greater concern for microevolution in local populations.

### Palaeontology and geography

Although nineteenth-century palaeontologists were chiefly concerned with the creation of patterns of evolutionary development, their increasing knowledge of the world-wide distribution of fossils forced them to grapple with the geographical perspective. Darwin's theory drew attention to the apparently anomalous distribution of some modern forms and explained the phenomenon as the result of migrations in earlier geological epochs. Biogeographers postulated 'land bridges' in the past joining various parts of the Earth's surface. Palaeontologists also began to make use of this concept — Haeckel, for instance, suggested that the lack of fossil hominids could be explained by assuming that our ancestors had lived on the lost continent of Lemuria, now sunk in the Indian Ocean. When it was recognized that the Palaeozoic faunas of South America and South Africa were identical, it was natural to postulate a land bridge across the Atlantic which had sunk in the Mesozoic to allow the two continents' faunas to diverge. In thus ignoring the possibility of continental movement, palaeontologists merely followed the lead given by physical geologists.

Thinking on the geographical distribution of life in the Tertiary was deeply influenced by the Canadian-American palaeontologist W.D. Matthew, whose *Climate and evolution* of 1914 took the permanence of the existing continents for granted. Matthew saw central Asia as the heartland of mammalian evolution, from which waves of successively higher forms spread out to the rest of the world (Fig. 4). This theory was even extended to human origins, generating a widespread reluctance to take the discovery of hominid fossils in Africa seriously. When the possibility of continental drift was proposed by Alfred Wegener and a handful of followers, palaeontologists were in the forefront of opposition during the nineteen-twenties and nineteen-thirties. Charles Schuchert, in particular, defended the traditional concept of land bridges. Even G.G. Simpson wrote actively against continental drift in the nineteen-forties. The advent of plate tectonics in the postwar years thus represented a second major theoretical revolution to which palaeontologists had to respond. Land bridges were abandoned and the continental movements postulated by geologists have become major features of our current explanations of the evolution and distribution of life on Earth.

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## 6.5.3 Plate Tectonics to *Paleobiology*

J. W. VALENTINE

### Introduction

During the period 1960–1975, palaeontology underwent a vigorous and lasting expansion of concerns and goals. While some of the roots of this expansion lay in earlier times, the formalization of concepts and the definition of problems that have grown into major features of palaeontological research occurred during this period. From its inception as a science, palaeontology has drawn upon both geological and biological sciences, and its findings have been applied to problems in each of those fields. It is thus appropriate briefly to mention major trends and events in biology and geology that became of particular importance to palaeontology.

## Trends in earth science

The period was dominated by the rise of the plate tectonic paradigm (for a short historical account see Hallam 1973). Scattered but inconclusive evidence that the continents had held different geographical relations in the past had been adduced over several decades, but in the nineteen-fifties palaeomagnetic studies provided strong support for this hypothesis. Then in the nineteen-sixties the basis of differential movements of crustal segments was clarified. Hess (1962) suggested that oceanic crust was generated at deep ocean ridges and consumed in trenches, and palaeomagnetic studies of the sea floor soon provided supporting evidence. There followed a flood of geophysical experiments and observations leading to the development of the theory of plate tectonics by the close of the nineteen-sixties. During this period also, the need was felt for direct exploration of the ocean floor, and in 1964 a major initiative was launched to take deep cores of that floor (Joint Oceanographic Institutions for Deep Earth Sampling — JOIDES). This project led to the establishment of the Deep Sea Drilling Program (DSDP), the Reports from which had reached volume 27 by the close of 1974. The results of the drilling programme supported the implications of the geophysical data. Continents, continental fragments, and islands had ridden with the moving sea floor plates in which they were embedded. By 1973 many features of the relative positions of major continental masses were well enough worked out for palaeogeographic maps that covered most of Phanerozoic time (Smith *et al. in* Hughes 1973) to be constructed.

## Trends in life science

Developments that affected palaeontology included a great rise in interest in the ecological disciplines, fuelled in part by concern over man's impact on the environment. Field exploration and experimentation were enlarged and extended into ecosystems, such as the pelagic and deep-sea realms, which had been poorly known and indeed misunderstood. Studies were particularly intense on factors regulating the ecological and evolutionary controls affecting the demography and distribution of natural populations, and on the principles that regulate the stability and diversity of ecosystems. Evolutionary studies were much concerned with processes of genetic change within lineages, and with speciation (e.g. Mayr 1963; Dobzhansky 1970) and with the significance of neutral mutations in evolution (see Kimura 1983); and a beginning was made in evolutionary aspects of development from a molecular perspective (Britten & Davidson 1971).

## Early history of life

Palaeontology in 1960–1975 flourished in response to its own traditional concerns and at the same time was increasingly influenced by contemporary events in earth and life sciences. Among the outstanding examples of palaeontological research were those which illuminated the fossil record of Archaean and Proterozoic life and of the earlier metazoan radiations. During the nineteen-sixties it became generally appreciated that stromatolites dating from the Archaean were marine algal structures. In 1965 a microbiota of presumed prokaryotes was described from the Gunflint Iron Formation, about two billion years old, which began a series of studies that revealed a microbial record extending back well into the Archaean (Section 1.2). This led to important syntheses of the geological and palaeontological evidence of Precambrian environments. A major element in the resulting hypotheses was that biogenic oxygen levels, representing a balance between supply via photosynthesis and consumption via oxidation of iron and other reduced substances, had risen across a variety of critical concentrations during the Proterozoic to permit the evolution of increasingly complex and active organisms.

The appearance of soft-bodied metazoan fossils in Late Precambrian rocks in the Ediacara Hills, South Australia was confirmed and the fauna described. Faunas in Europe, Africa, Asia, and North America, some known earlier and some now described, were identified as being similar to the Ediacaran assemblage, and the concept of a Late Precambrian metazoan fauna spanning perhaps 100 million years became established (Section 1.3). At the same time, it was proposed that there was a fauna, consisting chiefly of small enigmatic fossils, many phosphatic, that followed Ediacaran time but preceded the appearance of trilobites and echinoderms in the Early Cambrian. Elements of this fauna had long been known, but its distinctive position became clarified through descriptions of late Precambrian–Cambrian sections in Siberia and by synthesis of this stratigraphic data with records from Europe (Sections 1.4, 5.2.5). Also during the late nineteen-sixties and early nineteen-seventies, the soft-bodied fauna of the Burgess Shale of British Columbia was recollected and opened to restudy and re-evaluation; it proved to be far less clearly allied to living taxa than had been supposed (Section 3.11.2).

From these studies the early history of life began to be written; life extended billions of years back in time, presumably beginning in an essentially anoxic environment. A radiation of soft-bodied metazoans preceded Cambrian time (Section 1.3), but nevertheless the abrupt appearance of metazoan phyla during the Early Cambrian did not appear to be an artifact, but to represent a true evolutionary episode of singular magnitude, producing many novel body plans.

## Systematics and biostratigraphy

Researches on mineralized skeletal fossil groups of the Phanerozoic continued apace, with noteworthy activity in early Palaeozoic echinoderms, Permian brachiopods, early fishes, and taxa involved in the reptile–mammal transition. The organization and revision of scattered systematic and stratigraphic data into multivolume treatises, begun in previous years, continued, and these data were subjected to a further level of summarization in reviews of geological ranges of taxa, with assessments of changing diversifications, extinctions, and standing diversity levels, especially those of higher taxa in terms of their familial representation (Harland *et al.* 1967). Critical reviews of the methodology and application of biostratigraphy signalled increasing rigour in this area. Practical advances in biostratigraphy included the major refinement of zonations of late Mesozoic and Cenozoic rocks arising from study of micro- and nannofossils recovered from DSDP cores.

## Palaeoecology and palaeobiogeography

Against this background of intense activity along well established trends, palaeontological subdisciplines that were in their infancy grew into major fields. Palaeoecology (Section 4) and palaeobiogeography (Section 5.5) are outstanding examples. As both industrial and academic programmes were employing palaeoecologists, a stream of students trained in biological as well as geological sciences was attracted to palaeontology, and many of the students had ecological interests. Early work focused on environmental reconstructions, thus contributing to geological interpretations; there was, however, growing interest in population and community palaeoecology and biogeography. Fossil assemblages were increasingly appreciated as representing the remains of biotic communities, and their description in this light tended to bring them to life and to fill them with new interest. Accordingly the interpretation of palaeocommunities and their palaeoenvironmental contexts became a common research goal, and the burgeoning literature of population and community biology was co-opted to serve as the basis for many theoretical aspects of the fossil record (e.g. Shopf 1972; Valentine 1973). Trace fossils, reflecting as they do the activities of organisms, proved to be sensitive environmental indicators of special importance, for they commonly occur in sediments otherwise devoid of fossils, and ichnology grew into a thriving subdiscipline (Sections 4.11, 4.19.4, 4.19.5). Still another branch of palaeontology expanded with the study of nannofossils and microfossils from DSDP and other deep-sea cores. The cores yielded planktic forms from surface and near-surface waters and benthic forms from the deep-sea benthos. Subjected to palaeoecological, biogeographical and isotopic analyses, these fossils permitted reconstruction of ancient ocean climates, current systems, biological productivity, and other features which contributed to the rise of the discipline of palaeoceanography.

The advent of plate tectonic theory provided a basis for the reconstruction of palaeobiogeographies that resembled historical reality on a global scale more or less throughout the entire Phanerozoic. The result was startling. Biodistributional patterns that had been attributed to either dispersal across 'land bridges' and 'stepping stones' (e.g. to bridge the early Mesozoic Atlantic Ocean), or to narrow biodistributional barriers between distinctive faunas (e.g. to explain the juxtaposition of American and European-type assemblages in the Early Cambrian of Northeastern America), were suddenly clarified. The 'land bridges' as envisioned did not exist, but rather the continents themselves had been juxtaposed during the Early Mesozoic; and the Cambrian barrier had once been an ancient ocean, long since subducted (see also Section 5.12) In addition to solving biodistributional puzzles of this sort, palaeogeographical reconstructions implied that environmental conditions, marine and terrestrial alike, must have varied in response to plate tectonic processes. Islands, continental fragments, and entire continents had moved between climatic zones and had been variously aggregated and dispersed. Not only would the climates of mobile geographical elements change as they entered new latitudes, but the climates themselves, and the circulation patterns of atmosphere and ocean, would be affected. Distributional and associational patterns in the fossil record could now be placed in environmental contexts by evidence independent of the fossils themselves, and palaeoecology could now be concerned not only with the interpretation of local assemblages, but also with their contexts in regional and global patterns (Hughes 1973). It became possible in principle not only to apply and test theoretical notions from population and community ecology to fossils, but to formulate and test theoretical principles from fossil evidence.

### Evolutionary studies

The growing confidence in applications of fossil data to biological theory was also exemplified in evolutionary studies. The patterns of morphological change observed among fossils did not always meet the expectations of many evolutionary models, and Eldredge & Gould *in* Schopf (1972) proposed that morphological changes within evolving lineages were concentrated at morphospeciation events, and that between such events change was slight — an alternation of morphological change and stasis that they termed 'punctuated equilibrium'. As these authors pointed out, long-term trends in morphological change could be attributed to the differential success of lineages that happen to exhibit change in a particular direction favoured by subsequent events, and need not indicate a history of phyletic evolutionary trends. Furthermore, the abrupt appearance of higher taxa in the record might indicate a punctuational origin. As for the fate of higher taxa, the accumulated data of their waxing and waning over Phanerozoic time led to studies of fossil taxonomic diversity (Section 5.3) and to theoretical models to account for their observed behaviours and for evolutionary change in general. In the Red Queen hypothesis (Section 2.5), for example, it was argued that adaptive improvement in a given lineage must perforce reduce adaptation in others, and when evolutionary processes acted to overcome this disadvantage, they produced adaptive deterioration in still other lineages; thus evolution must occur merely to maintain the status quo. From such hypotheses, the field of macroevolution was reborn within palaeontology.

As the concerns of palaeontology broadened, textbooks appeared that stressed these new interests (e.g. Raup & Stanley 1971) and new professional journals were established (*Palaeogeography, Palaeoclimatology, Palaeoecology*, from 1965; *Lethaia*, from 1968) that featured palaeobiological contributions. The journal *Paleobiology* appeared in 1975, marking the close of this period. During 1960–1975, palaeontology had become vastly enriched and diversified in a virtual 'evolutionary radiation' and within its many branches lay the potential for further fruitful expansion.

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## 6.5.4 The Past Decade and the Future

A. HOFFMAN

### Introduction

The scope of palaeontology is very broad, for it covers the entire history of life on Earth. Therefore, the spectrum of research strategies must also be very wide. During the nineteen-seventies, however, a gap appeared (and has continued to grow in the nineteen-eighties) between two major approaches to palaeontology. On the one hand, the traditional approach — *palaeontography* — tends to emphasize the description of fossils and the reconstruction of extinct life as the basis for establishing a classification of organisms that reflects their phylogeny. The description of fossils and their distribution in the rocks is obviously important also for biostratigraphic correlation. On the other hand, many palaeontologists have boldly undertaken to search for general rules that may govern the causal process(es) responsible for the pattern of life, or the appearance and order of the biosphere. In this approach — which might be called *theoretical palaeobiology* — the empirical data of palaeontology are primarily employed for generating and testing theoretical hypotheses about the laws of organic and biotic evolution. The growing gap between palaeontography and theoretical palaeobiology has been the most conspicuous feature of the last decade in the history of palaeontology, but it must be closed in the future.

## Palaeontography

That the palaeontographical approach is here regarded as traditional does not imply that such research is conducted today in the same way as it was in the last century, or even 20 years ago. New analytical tools have come into common use: electron microscopy, biogeochemistry, mineralogy, and even crystallography of fossils, etc. Incomparably more attention has been paid recently to the functional morphology of extinct organisms. The geological setting of fossils has also come more into focus, as recent developments in sedimentology allow quite detailed information about the habitat of extinct organisms to be deduced from the rock record. Palaeocommunity analysis has reached its peak as the means of describing the biotic environment of life forms in the geological past. In spite of such innovations and shifts in emphasis, however, the major achievements of this research strategy could conceivably have been made 20 years ago: discovery of the conodont animal, reinterpretation of many Ediacaran fossils, reconstruction of tabulates as sponges rather than corals, etc. Perhaps even more importantly, the main questions being asked within the conceptual framework of the palaeontographical approach have remained largely the same as before: What did extinct organisms look like, and how did they live? What is the shape of 'the tree of life' which links together the genealogies of all organic groups, both extinct and extant? What was the ecological and biogeographical structure of the biosphere in the geological past?

To answer such questions using palaeontological data requires a methodology of historical reconstruction. This is the subject of the ongoing theoretical debates in palaeontography: the paradigm method of functional morphology versus constructional morphology in the reconstruction of organisms (Section 4.1), cladistic versus stratophenetic methods in the reconstruction of phylogeny (Section 5.2), etc. The rival methodologies refer also to contrasting perspectives on various problems in evolutionary biology: the relative roles of selection and constraint in phenotypic evolution (Sections 2.2, 2.3), the commonness of convergent and parallel evolution, etc. Thus, the palaeontographical approach to the history of life cannot be separated from theoretical considerations; yet within its conceptual framework, theory is not a goal in itself.

## Theoretical palaeobiology

Just the opposite is the case with theoretical palaeobiology. In this approach, the emphasis is on the questions: Why is the shape of 'the tree of life' as it is? How does the process of evolution operate? What are the universal laws of organic and biotic evolution? The approach is therefore distinctively nomothetic. These questions are certainly not new; they were not posed for the first time in the nineteen-seventies. Palaeontology at an earlier peak (at the turn of the century and even well into the second quarter of the twentieth century) largely focused on these problems. Abel, Cope, Hyatt, Osborn, Wedekind, and Schindewolf all followed the nomethetic approach, regarding the fossil record primarily as the main source of empirical data relevant to these questions — at a time when the term *palaeobiology* was first coined. But the methodological rigour of modern theoretical palaeobiology, with its emphasis on pattern recognition and explanation through quantitative modelling and hypothesis testing, is entirely new. The beginnings of this research strategy can be traced back at least to Brinkmann (1929) but the onset of its explosive development is symbolically represented by the appearance of Schopf's *Models in paleobiology* (1972) and the founding of the journal *Paleobiology* in 1975. In retrospect, these publishing events seem to have been crucial in shaping the research area of theoretical palaeobiology.

Since about 1975, the research effort of theoretical palaeobiology has been primarily organized around four subject areas of major controversy (for review and references see Hoffman 1988). In each case, the controversy chiefly concerned a proposal that some specifically macroevolutionary processes — irreducible to the microevolutionary processes envisaged by the neo-Darwinian paradigm of evolution — are responsible for the origin of the macroevolutionary patterns described by palaeobiologists.

**1** *Punctuated equilibrium.* The concept of *punctuated equilibrium* seems to have attracted most attention, among palaeontologists as well as among other scientists and the general public. Perhaps the main cause for the heated debate on punctuated equilibrium has been the ambiguity of and repeated changes in the meaning of this concept since its original formulation by Eldredge & Gould *in* Schopf (1972). Its proponents and advocates have presented and argued for quite a number of substantially different versions (sometimes more than one within the body of a single article). In its 'weak' version, punctuated equilibrium is primarily meant as a contrast to so-called phyletic gradualism (i.e. the view that phenotypic evolution proceeds continuously in the same adaptive direction and at a constant rate). Punctuated equilibrium then means that the rate and direction of phenotypic evolution vary along a considerable proportion, or even an overwhelming majority, of phyletic lineages. When so understood, punctuated equilibrium is entirely trivial because this has never — since the advent of the neo-Darwinian paradigm — been seriously doubted by evolutionary biologists or palaeontologists.

The 'strong' version of punctuated equilibrium includes two assertions: (1) that phenotypic evolution never proceeds gradually, or that no significant evolutionary change is achieved by accumulation of small adaptive steps; and (2) that all phenotypic evolution is associated with speciation events. This latter assertion cannot be tested in the fossil record because, apart from a few instances of indisputable lineage splitting, speciation must be equated in palaeontology with considerable phenotypic change. The first assertion, however, has been repeatedly tested and refuted. In spite of a myriad of empirical problems, several cases of significant gradual evolution have been convincingly documented (Section 2.3). An even more radical variant of this 'strong' version of punctuated equilibrium is nevertheless tenable: that even an apparently continuous sequence of fossil populations may in fact consist of a discontinuous series of extinct species, because continuity is always assumed rather than proven. This variant, however, explicitly enters the realm of metaphysics.

The 'moderate' version of punctuated equilibrium emphasizes the occurrence, and even commonness, of stasis in the evolutionary history of each phyletic lineage. When stasis is understood as the complete evolutionary stasis of the entire phenotype, this proposition is untestable because the fossil record provides data concerning only a small sample of anatomy while evolution may as well occur in soft-body anatomy, physiology, or behaviour. When stasis is understood to be the absence of change in some morphological characters, it certainly appears to be a widespread phenomenon. It may be due to a variety of microevolutionary processes, and it then perfectly fits the neo-Darwinian paradigm. To emphasize this phenomenon borders upon triviality. In principle, stasis may also be due to some constraints on morphological evolution which actively resist a change favoured by natural selection. The claim, however, that this is in fact the main mechanism of morphological stasis is unsupported by any evidence.

Thus, the debate on punctuated equilibrium has not led to the finding of any new evolutionary rules. It has, however, considerably raised the standards of palaeontological research on evolutionary rates and produced much fascinating empirical data on phenotypic evolutionary rates in a wide variety of fossil organisms.

**2** *Species selection.* The results of the controversy on *species selection* are quite different. Since its first formulation (Stanley 1975) the concept of species selection has evolved as much as punctuated equilibrium, with which it was initially linked (Section 2.6). It is clear by now, however, that if species selection is meant to designate something more than just a net effect (on the supraspecific level) of natural selection at the individual level, then it must be defined as a causal process changing the relative speciosity of various clades due to selection for or against their heritable species-level properties. It also must be distinguished from species drift, i.e. the accidental change in species richness of various clades due to the vagaries of their environment or pure chance. Under such a definition, species selection is not related at all to punctuated equilibrium. It indeed represents a macroevolutionary process that can, potentially, operate in nature, but not one actual example of species selection has yet been convincingly documented. The debate on species selection has thus resulted in expanding the scope of potential evolutionary forces which can, in theory, be invoked to explain macroevolutionary patterns, but the empirical research it stimulated has not been particularly productive.

**3** *Taxonomic diversification.* Much palaeobiological discussion has been devoted to the problem of taxonomic diversification of the biosphere in the Phanerozoic. The very nature of the fossil record makes it difficult to establish the empirical pattern of change in global taxonomic diversity through geological time (Section 2.7). Assuming, however, that this pattern can be at least approximately represented by a global-scale compilation of the stratigraphic ranges of taxa at a supraspecific level, and at the time resolution of the geological stage, Sepkoski (1978) undertook a bold attempt at its causal explanation by a deterministic model. A variety of theoretical models have been subsequently proposed to account for these empirical data. Sepkoski's more complete equilibrium model of diversity-dependent diversification of three great evolutionary faunas which have displaced one another via biotic interactions seems to have attracted most attention (Section 1.6). However, a nonequilibrium model envisaging diversity-dependent diversification as driven by evolutionary novelties and mass extinctions may withstand the test of empirical data even better. These models explain the macroevolutionary pattern of taxonomic diversification in the Phanerozoic by reference to a set of specifically macroevolutionary rules, operating at a supraspecific level of biological organization. However, a simple stochastic model representing the pattern of taxonomic diversification as a net result of two independent random walks — one concerning the average rate of speciation, the other the average rate of species extinction per geological state — cannot be rejected as a null hypothesis. This model portrays the pattern of global taxonomic diversification as nothing but a by-product of a myriad of microevolutionary processes operating simultaneously upon a vast number of species in very many environments. Its apparent success, however, may also imply that the empirical pattern of diversity change through geological time is too heavily loaded by statistical noise to allow identification of the underlying causal process(es).

**4** *Mass extinctions.* Perhaps the most spectacular debate in modern theoretical palaeobiology concerns mass extinctions (Section 2.12). When taken in conjunction with the hypothesis that the Cretaceous–Tertiary mass extinction was caused by an extraterrestrial impact, the concepts of mass extinction periodicity (Raup & Sepkoski 1984) and biological distinctness from background extinction (Jablonski 1986) have led to the view that mass extinctions represent a separate class of macroevolutionary phenomena, caused by a separate category of macroevolutionary processes. Hence, a general theory of mass extinctions has been sought. Some palaeobiologists have even declared that this new perspective on mass extinctions refutes the neo-Darwinian paradigm of evolution. When considered in more detail, however, the components of this new perspective do not appear to be demonstrated beyond any reasonable doubt. The statistical test which was taken to indicate extinction periodicity seems to be biased toward this result. Moreover, a simple stochastic model is also capable of reproducing the empirical pattern of extinction peaks through time. Except perhaps for the Permian–Triassic crisis, the individual mass extinctions turn out to be clusters of events rather than single catastrophes, and there is no evidence to support the claim that they were all due to similar causes. Both hypotheses of an extraterrestrial causation of the Cretaceous–Tertiary boundary event and of a biological difference between the regimes of mass and background extinction are viable, but other rival hypotheses are at least equally plausible.

Thus, any attempt to develop a general theory of mass extinctions must be judged precarious. In terms of its theoretical consequences, the research on mass extinctions may therefore be regarded as fruitless, at least for the moment. On the other hand, it has been enormously productive in terms of empirical data, for it has stimulated much innovative work — palaeontological, microstratigraphical, sedimentological, geochemical, and mineralogical — at the stratigraphical horizons considered to represent times of mass extinction.

*Other topics.* These four major debates in theoretical palaeobiology of course do not cover the entire area of its research interests. Much consideration has also been given in the last decade to topics such as the evolutionary implications of the ecological organization of the biosphere. The laws of community evolution have been sought but thus far not found (Section 4.17), not only because the conceptual framework of community palaeoecology is at present too cloudy, but perhaps also because such laws are rather unlikely to exist, as ecologists continue to remind palaeobiologists (Futuyma; Underwood; *both in* Raup & Jablonski 1986). Van Valen's (1973) Red Queen hypothesis has directed much palaeobiological research toward analysis of the significance of diffuse coevolution for evolution in ecosystems (Section 2.5). Thus far, however, the results are largely inconclusive (Hoffman & Kitchell 1984).

## The future

In spite of considerable efforts undertaken within the framework of theoretical palaeobiology, no new biological laws, or even inductive generalizations, have been demonstrated by studies on the history of the biosphere. Perhaps there are no macroevolutionary rules which could be detected by palaeobiologists; if so, the nomothetic approach of theoretical palaeobiology would be counterproductive — but, of course, we cannot possibly know whether or not this is indeed the case. Or perhaps the palaeontological data presently available for palaeobiological analyses are inadequate because they are collected entirely within the framework of palaeontography, for purposes other than testing general hypotheses about the process(es) of evolution. If so, a substantial improvement in the empirical database is badly needed — but such an improvement will only be possible when the gap between theoretical palaeobiology and palaeontography is closed.

In either instance, however, a change in emphasis for palaeontology appears to be inevitable. Palaeontology has become much more fascinating (and also fashionable) in the last decade than it used to be. It owes this success largely to theoretical palaeobiology, because in the eyes of many scientists and public alike the essence of science is to seek general laws. No wonder that palaeontography has often been looked upon as a rather dull, though admittedly necessary, companion of theoretical palaeobiology. Yet palaeontology is first and foremost a historical science. Palaeontologists are primarily historians of the biosphere and must focus on reconstructing history. The history of the biosphere, however, may not be shaped according to a set of general biological laws. Karl Popper's (1945) *Poverty of historicism* should long have been obligatory reading for palaeontologists. The emphasis of palaeontological research must shift back to the study of unique, historical biological events and chains of events; it must follow the idiographic approach. Only then should we attempt to seek inductive generalizations about the evolution of lineages, the waxing and waning of clades, mass extinctions and explosive radiations of taxa, etc.

Research on particular events and sequences of events, however, should meet the new standards introduced to palaeontology during the last dozen years or so. Models of these phenomena should be developed and rigorously tested, quantitatively whenever possible. To this end, a detailed stratigraphic framework and a coherent taxonomic system are absolutely crucial. This is not only an empirical challenge but also a theoretical one; for while cladistics may provide a methodology for systematics, its application to taxa of variable geological age is not a simple matter, and the methodology of biostratigraphy seems to be rather undervalued and consequently underdeveloped.

Perhaps even more importantly, however, palaeontology must ultimately break down the barriers that have for long separated it from many other disciplines within the earth and life sciences. In the last decade, these barriers have already begun to collapse. On the one hand, palaeontologists are beginning to look to molecular and cell biology for a better understanding of fossil organisms (Section 2.1). This may lead to the demonstration that morphogenesis of the skeletal parts — which are the objects of palaeontological study — is under much stronger environmental controls than traditionally accepted. Were it so, the implications for palaeontological interpretation of fossil morphologies and their variation in space and time would be tremendous. On the other hand, palaeontologists are beginning to view the biosphere as a component of a global system which encompasses life, ocean, air, and the lithosphere. This trend is reflected by the growing interest among palaeontologists in stable isotope geochemistry, palaeoceanography, and palaeoclimatology (Section 4.19). The promise of these disciplines for the history of the biosphere lies in their potential to shed new light on the workings of the global system and hence, indirectly, on the state of the biosphere.

For the future of palaeontology, I thus envisage a more humble focus on reconstruction of the history of life, rather than on attempts to discover the laws of this history; but I also envisage a considerable expansion of the scope of palaeontology to include all aspects of the history of life on Earth, rather than solely the history of particular lineages, clades, or communities. To this end, however, we must always be very explicit about the biological entities we undertake to describe and reconstruct — whether we talk of genotypes, phenotypes, or single traits, whether of phena, biological species, or phyletic lineages, whether of taphocoenoses, ecological communities, or taxocoenoses — and we must also be explicit about the limitations of our biological interpretations. Otherwise, palaeontology will inevitably fall back to the stage of mere story-telling.

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