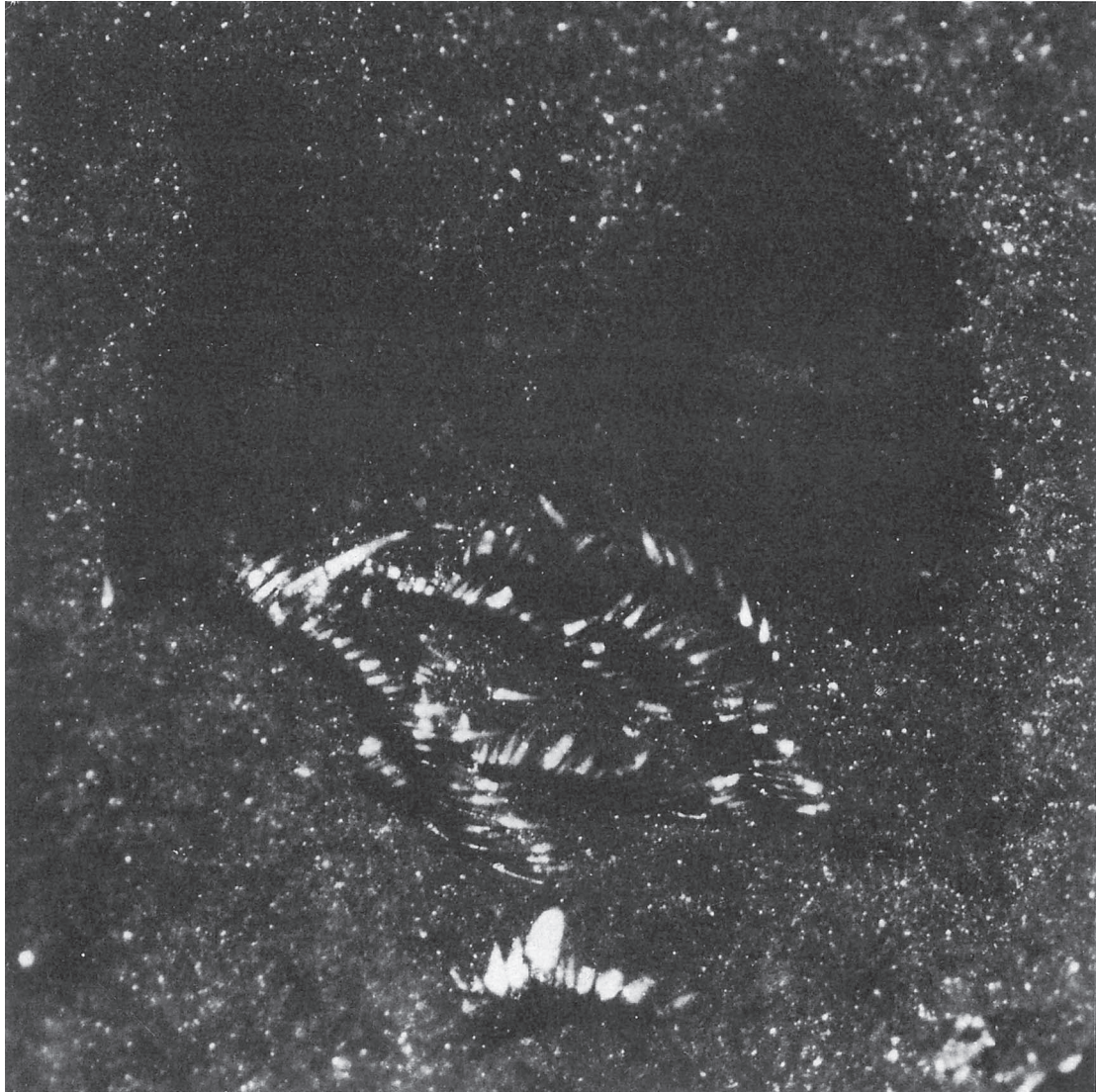


5

TAXONOMY, PHYLOGENY, AND BIOSTRATIGRAPHY



The head region, including part of the apparatus, of the first conodont animal discovered preserving soft tissues — from the Lower Carboniferous Granton Sandstones, $\times 60$. (Photograph courtesy of J.K. Ingham.)

5.1 Rules of Nomenclature

5.1.1 International Codes of Zoological and Botanical Nomenclature

M. E. TOLLITT

Introduction

Nomenclature is the international currency of communication among biologists. It enables any given taxon to be recognized world-wide by a unique name. An obvious premise for this is that all names must be in a single language. In both zoology and botany this was originally Latin; in zoology at least it now incorporates so many non-Latin words that it can only be called 'the language of nomenclature'.

The basic principle underlying both zoological and botanical nomenclature is the concept of priority as determined by the date of publication. However, the rules for determining priority in the two disciplines differ in important respects. These differences go back to 1842 when the British Association for the Advancement of Science set up a committee to draft a single code on biological nomenclature from which the botanists withdrew. The resulting 'Stricklandian Code' was of seminal effect in palaeozoology and neozoology but not in botany. The subsequent divergence in the historical development of the two codes since that time (see McNeill & Greuter *in* Ride & Younes 1986; Ride *in* Ride & Younes 1986) is such that each is considered separately here.

International Code of Zoological Nomenclature

The zoological Code faces enormous problems from the sheer size of its subject matter. Well over a million species, fossil and extant, have been described and several thousand new ones are described each year, with over a thousand new genera. The facility with which new matter can be published and the speed of development of new production technologies makes fixing the date of publication of a work ever more difficult (Ride *in* Ride & Younes

1986). Names are admitted into zoological nomenclature if they satisfy the criteria of availability (Articles 10–20). These are a set of objective tests that are usually easy to apply. Basically a name, to be available, must be published (in the sense of Articles 8 and 9) after 1757, accompanied by a description, and in accordance with the Principle of Binominal Nomenclature.

The operation of the present Code (International Commission on Zoological Nomenclature 1985; with 88 Articles and 83 Recommendations) relies on six basic principles: Binominal Nomenclature, Priority, First Reviser, Co-ordination, Homonymy, and the Principle of Name-bearing Types.

1 *The Principle of Binominal Nomenclature* (Article 5) demands that a species name must be a combination of two names — a binomen. For convenience the starting point for zoological nomenclature is arbitrarily taken to be 1 January 1758, with the two earliest wholly binominal works, the tenth edition of Linnaeus' *Systema Naturae* and Clerck's *Aranei Svecici*, deemed to have been published on that date.

2 *The Principle of Priority* (Article 23) simply states that the oldest available name for a taxon is its valid name. However, names established for collective groups and ichnotaxa do not compete in priority with other genus-group names.

3 *The Principle of the First Reviser* (Article 24) enables the precedence of one name over another to be determined when normal priority cannot be established, as in the case of simultaneous publication. The First Reviser is essentially the first author to cite together names (or nomenclatural acts) published on the same date, or different original spellings of the same name, and to have chosen one of them over the other. Contrary to popular belief 'page priority' plays no part in determining precedence.

4 *The Principle of Co-ordination* (Articles 36, 43, 46) states that within the family group, genus group, or species group, a name established for a taxon at any rank in that group is deemed to have been simultaneously established with the same author and date as for taxa based on the same name-bearing type at other ranks in the group. The rationale for this principle lies in the subjective nature of the decision

to allot sub- or super-taxonomic rank to a family, genus, or species. There is clearly no objective difference between taxa all based on the same name-bearing type — thus the establishment of one implies establishment of the other or others.

5 The Principle of Homonymy (Article 52) ensures that every taxon governed by the Code (i.e. from subspecies to superfamily) has a unique name different from any other. The senior name of one or more homonyms is the valid name; the junior homonym must have its name replaced. However, in certain circumstances (Article 59) secondary homonyms produced by the transfer of species from one genus to another can be restored.

6 The Principle of Name-bearing Types (Article 61) states that each nominal taxon (i.e. a nomenclatural as opposed to a taxonomic taxon; see below) has, actually or potentially, its name-bearing type. Thus the name-bearing type of a nominal family-group taxon is a nominal genus, that of a nominal genus-group taxon a nominal species and that of a nominal species-group taxon either a holotype, lectotype, neotype, or syntype series. By this means a zoologist distinguishes between the animal named and the mere name, thus combining nomenclatural rigour with taxonomic flexibility. The nominal taxon has been the subject of much discussion in comparing zoological with botanical nomenclature since the latter relies on the type of a name rather than the type of the organism named (see Melville *in* Ride & Younes 1986).

International Code of Botanical Nomenclature

The botanical Code (Voss *et al.* 1983; with 73 Articles and 60 Recommendations) also relies on six basic principles:

Principle I. Botanical nomenclature is independent of zoological nomenclature. Thus, identically spelled names can exist validly under each code. The corresponding rule in zoology (Article 1c) has not the status of a Principle.

Principle II. The application of names of taxonomic groups is determined by means of nomenclatural types.

Principle III. The nomenclature of a taxonomic group is based upon priority of publication. This principle is concomitant with the Principle of Priority in the zoological Code and is based on the same rationale.

Principle IV. Each taxonomic group with a particular circumscription, position, and rank can bear only one correct name, the earliest that is in accordance with the Rules, except in specified cases. This Principle is analogous with the Principle of Homonymy in the zoological Code.

Principle V. Scientific names of taxonomic groups are treated as Latin regardless of their derivation.

Principle VI. The Rules of nomenclature are retroactive unless expressly limited.

Operational procedures in zoological nomenclature

As there can be only one international code of rules for any given system of scientific nomenclature, so there can be only one body to administer it and deal with difficulties encountered by zoologists in applying it. For zoologists this is the *International Commission on Zoological Nomenclature*, established in 1895.

The Commission's first task was to produce a new set of rules to supersede not only the Stricklandian Code, but also a number of other codes of limited scope that had developed in the interim. The authority of the Code depends on the willingness of palaeozoologists and neozoologists to accept and use it. It can never wholly correspond to the needs of all its clients, for they have total freedom to express their taxonomic opinions as they choose. The fact that most of them seek to do so in ever more complicated ways tends to produce more complicated rules of nomenclature, and this generates a tension between those responsible for the Code (the Commission) and its users, who would naturally prefer the Code to be as simple as possible.

The Commission thus has two basic responsibilities: (1) it must prepare modifications to the Code to meet newly perceived requirements (leading eventually to a new edition of the Code), and (2) it must deal with problems caused by mismatches between the rules and published nomenclatural acts. Its area of operation covers all names from subspecies to superfamily published since 1757. In this second area of responsibility the Commission has plenary powers to suspend, under prescribed conditions (Article 79) the application of any provision of the Code where, in its view, such application would disturb stability or universality or cause confusion. In this, and in all its actions, the Commission

is governed by its Constitution, which is considered an integral part of the Code (Appendix F).

To achieve these responsibilities the Commission must sustain an open dialogue with palaeozoologists and neozoologists everywhere. It does this by personal contact, correspondence, and through its quarterly publication, *The Bulletin of Zoological Nomenclature*. This contains formal applications to the Commission for the solution of particular nomenclatural problems, or for changes to the Code; comments on these applications; and the eventual decisions of the Commission.

The Commission's decisions (termed Opinions) in individual cases are final (though always open to review if found to be incomplete or defective). Its decisions (termed Declarations) on proposed amendments to the Code or Constitution are provisional until they have been approved by the body to whom the Commission reports, the Section on Zoological Nomenclature of the International Union of Biological Sciences.

Operational procedures in botanical nomenclature

In comparison with zoological nomenclature, botanical nomenclature is more highly structured in its operations, thereby giving it a broader and more secure power base.

Modification of the botanical Code can only be made by the plenary session of an International Botanical Congress acting on proposals approved by the Nomenclature Section of the Congress which meets beforehand and which any botanist present at the Congress is free to attend. Nomenclatural activity between Congresses is in the hands of a General Committee, an Editorial Committee for the Code, a number of 'Permanent Nomenclatural Committees' dealing with particular plant groups covered by the Code, and a number of *ad hoc* committees set up to report to the next Congress.

The International Association for Plant Taxonomy (IAPT) plays a key role in botanical nomenclature with a special section of its journal, *Taxon*, given over to the publication of nomenclatural matters, such as proposals to conserve names, amend the Code, etc. The final plenary session of each Botanical Congress adopts any proposals of the Nomenclature Section to amend the Code and approves the names for conservation or rejection.

The decentralized organizational structure of botanical nomenclature has a number of advantages. It does not suffer from the acute financial problems

that have dogged zoological nomenclature. Spreading of the workload has meant that costs have been equally spread. Moreover, the broad organizational base has meant that in recent years the botanical Code has been universally accepted amongst the botanical community.

References

- International Commission on Zoological Nomenclature. 1985. *International Code of Zoological Nomenclature*. Adopted by the XXth General Assembly of the International Union of Biological Sciences, 3rd edn. International Trust for Zoological Nomenclature, London.
- Ride, W.D.L. & Younes, T. (eds) 1986. *Biological nomenclature today*. International Union of Biological Sciences Monograph Series, No. 2.
- Voss, E.G., Burdet, H.M., Chaloner, W.G., Demoulin, V., Hiepko, P., McNeill, J., Meikle, R.D., Nicolson, D.H., Rollins, R.C., Silva, P.C. & Greuter, W. (eds) 1983. *International Code of Botanical Nomenclature*. Adopted by the Thirteenth International Botanical Congress, Sydney, August, 1981. Bohn, Scheltema and Holkema, Utrecht; W. Junk, The Hague.

5.1.2 Disarticulated Animal Fossils

R. J. ALDRIDGE

Introduction

Names in zoological nomenclature are given to complete animals. In palaeontology knowledge of these animals is gained almost without exception from only incomplete remains, most commonly biomineralized skeletons. There are few problems in taxonomic treatment or nomenclature where the preserved fossil material forms a major part of the living animal, but difficulties potentially arise when the skeleton comprised multiple components of differing morphology that became disarticulated and scattered on the death of the animal and decay of the soft tissue. These components may not be recognized as belonging to the same animal, or there may be uncertainties or differences of opinion regarding the complete skeletal composition. Some authors have consequently advocated a system of *parataxonomy* to accommodate fragmentary remains. A *parataxon* was defined by Melville (1979, p. 14) as 'a taxon based on a fragment or detached

organ of an animal which can be classified at genus-group and species-group levels by comparison with other fragments or detached organs, but cannot be assigned to the same taxa at those levels as the whole animal to which they belong'. In practice, parataxonomy is outside the orthotaxonomy of the same group of organisms, being based on a particular, fragmentary, sort of material (Bengtson 1985).

The success of workers on fragmentary remains, particularly specialists in conodonts, in pursuing the taxonomy of their groups without recourse to parataxonomy, has resulted in the latter not being admitted to the *International Code of Zoological Nomenclature* (Section 5.1.1). Under Article 23(f) (i) of the Code, the Principle of Priority is held to apply 'even if any part of an animal is named before the whole animal'. The procedures adopted in the nomenclature of fragmentary fossils and of the partially or completely known skeletons of which they were components can be illustrated by reference to current practice in conodont taxonomy.

Conodonts and parataxonomy

Conodonts were soft-bodied marine animals which possessed a feeding apparatus constructed from microscopic phosphatic elements; their stratigraphical range is Upper Cambrian–uppermost Triassic. The fossil record of the group consists almost entirely of disjunct elements, which are normally recovered through mechanical or chemical disaggregation of rock samples. Collections made in this way may contain elements from several different coexistent species. Rarely, complete or partial apparatuses of individual animals are found preserved intact on bedding planes (Fig. 1) or as fused clusters in acid-insoluble residues, giving direct evidence of the apparatus composition of some species. The apparatuses of many other species have been partly or completely reconstructed using morphological and distributional criteria, and most conform to a limited number of structural plans.

Until the mid nineteen-sixties each morphologically distinct element type was given its own binomen, following an initial belief by some specialists that every animal contained elements of only one type. However, specimens of complete apparatuses on bedding planes, first discovered in 1934, prove that each individual contained several components of up to eight different types. A dual nomenclature developed, with separate names for completely preserved apparatuses existing alongside the names for the element types. This procedure is outside the



Fig. 1 Complete apparatus of a single conodont animal preserved on a bedding plane; specimen x-6377, University of Illinois, from the Carboniferous of Illinois ($\times 32$).

Code and becomes unworkable in practice when applied to partially known apparatuses or to those reconstructed through studies of isolated elements. At an international symposium held in 1971, conodont specialists agreed to dispense with dual nomenclature and to follow the Principle of Priority in naming multielement, apparatus-based taxa.

Nomenclature of apparatus-based taxa follows two steps: consideration of the valid specific name and consideration of the appropriate generic name (Fig. 2). For many apparatus-based taxa, some or all of the component elements may already bear separate names. The valid specific name for the apparatus-based taxon is the oldest of these names, provided that the holotype bearing that name can be demonstrated to belong or probably belong to the apparatus-based species under consideration. This can usually be assessed by the examination of other elements found in association with the holotype. In cases where the oldest name was allocated to a characteristic element of the apparatus, no difficulties arise. Where the oldest species name is borne by a specimen representing an element of conservative morphology, repeated in many species, then the nature of the other elements associated with the

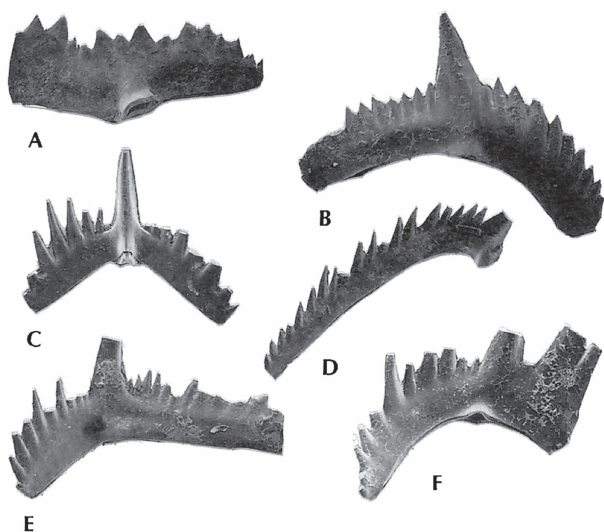


Fig. 2 Element types in the reconstructed Silurian conodont apparatus of *Ozarkodina confluens* (Branson & Mehl 1933) $\times 33$. Originally, Branson & Mehl gave each element type a separate name: A, *Spathodus primus*; B, *Ozarkodina typica*; C, *Trichognathus symmetrica*; D, *Prioniodus bicurvatus*; E, *Hindeodella confluens*; F, *Plectospathodus flexuosus*. As all six species names were published in the same paper, their relative precedence was determined by Jeppsson (1969), who as First Reviser (see Section 5.1.1) chose the name *confluens*; the other five are subjective junior synonyms. The appropriate generic assignment is not to *Prioniodus*, the oldest name, nor to *Hindeodella*, the next oldest. The Ordovician type species of *Prioniodus* has a different apparatus from that of *confluens*, while the apparatus of the Devonian type species of *Hindeodella* is unknown. *Spathodus* and *Trichognathus* are junior homonyms of older names and were not replaced until after 1933. *Ozarkodina* and *Plectospathodus* were both erected in 1933, with *O. typica* and *P. flexuosus* as their type species, and either might be used as the generic name; *Ozarkodina* was selected by Lindström (1970).

holotype is crucial. If these are unknown and cannot practicably be determined by re-collecting the type horizon, then the oldest name is treated as a *nomen dubium* and the next oldest available name comes under consideration.

The procedure for allocating an appropriate generic name is similar. In this case, the oldest generic name borne by any element included in the apparatus is selected, provided that the type species of that genus can be demonstrated to be congeneric or probably congeneric with the apparatus-based taxon under consideration. If the type species is not congeneric or is based on an element from an unknown apparatus, then the next oldest available name is considered. Exceptions to this procedure occur when the apparatus-based taxon can be shown

to belong to an established apparatus-based genus with an older name. If none of the elements provides an appropriate generic name, and there is no prior name available from congeneric species, a new name is required.

Stability of nomenclature is achieved through the determination of the apparatus structures of the holotypes of each species and of the type species of each genus. Until this is attained for all existing names, a few that have been treated as *nomina dubia* may become available as knowledge about their apparatuses is acquired, and they may prove to be senior synonyms of names currently in use. In the absence of unequivocal knowledge of all apparatuses, there will always be some taxa that are known or believed to represent only part of the skeleton, other parts of which may carry different names. For these, Bengtson (1985, p. 1354) introduced the term *sciotaxon*, defined as a 'taxon that is considered to represent the same real taxon as another taxon based on material of a different nature'. This concept has application in all groups where fossil representatives are commonly fragmental.

References

- Bengtson, S. 1985. Taxonomy of disarticulated fossils. *Journal of Paleontology* **59**, 1350–1358.
- Branson, E.B. & Mehl, M.G. 1933. Conodont studies, no. 1. *The University of Missouri Studies* **8**, 1–72, 4 pls.
- Jeppsson, L. 1969. Notes on some Upper Silurian multi-element conodonts. *Geologiska Föreningens i Stockholm Förhandlingar* **91**, 12–24.
- Lindström, M. 1970. A suprageneric taxonomy of the conodonts. *Lethaia* **3**, 427–445.
- Melville, R.V. 1979. Further proposed amendments to the International Code of Zoological Nomenclature Z.N.(G.) 182. *Bulletin of Zoological Nomenclature* **36**, 11–14.

5.1.3 Disarticulated Plant Fossils

B. A. THOMAS

Introduction

Whole plants are only very rarely preserved in the fossil record. The vast majority of plant fossils are organs, or pieces of organs, that were shed in life,

broken off, or detached after death. There have been several successful reconstructions of whole plants but these are exceptions rather than the rule. Therefore, the major problem confronting anyone studying plant fossils is how to name and classify these very different fragments. Naming is in essence identifying and it constitutes what is called nomenclature. Principle IV in the *International Code of Botanical Nomenclature* states 'Each taxonomic group with a particular circumscription, position, and rank can only bear one correct name, the earliest that is in accordance with the Rules, except in specified cases' (see also Section 5.1.1). Such a principle is much more difficult to follow with fossils than with living plants for observations are limited almost exclusively to morphological and anatomical characters.

Palaeobotanists use a system of nomenclature for isolated organs, whereby the leaves, stems, roots, and various parts of reproductive organs receive different generic and specific names. Such a system enables information to be assembled not only for species lists but for evolutionary, ecological, and stratigraphic purposes. Even so, there are many problems which may be approached in various ways. Papers in Spicer & Thomas (1986) summarize the interrelated problems and the methods of using the available information.

Organ genus and form genus

Much debate has centred on the concept of the genus as applied to plant fossils and on the use of the *organ genus* and *form genus* (see Chaloner *in* Spicer & Thomas 1986 for discussion). Organ genera are based on fossil organs that can be assigned to families and higher taxa. Form genera are based on less well understood fossils that cannot be assigned to families. Any fossils that are completely known as whole plants can be assigned to genera as if they were living plants. Based on this conception, the use of nomenclatural priority should ensure a workable system, and generic keys may then be constructed for identification purposes (e.g. Thomas & Meyen 1984).

Modern names for plant fossils

There is a case for using modern names for some plant fossils when their diagnostic suites of characters fall within a characteristic range of variation of comparable organs of living genera or species, e.g. *Ginkgo*, *Metasequoia*, and many of the Tertiary

genera of leaves and seeds (Collinson *in* Spicer & Thomas 1986). However, the use of a modern binomen for a fossilized organ must not be taken to imply that the whole plant had the same botanical characteristics as the living genus or species. Unsubstantiated extrapolations via whole plants to their past phylogeny, ecology, and environmental parameters might be completely incorrect.

Organic connection between taxa

Sometimes organs that have received different generic names are found in organic connection, e.g. the Carboniferous lycophyte cone with *Lepidostrobo-phyllum* megasporophylls has been found attached to leafy shoots assignable to *Lepidophloios* and megaspores *Cystosporites* recovered from the cones. By such means whole plants may be reconstructed (Fig. 1).

Occasionally two genera may be shown to represent parts of the same plant, even though they are preserved in different ways, e.g. petrified fragments of the stem of the compression *Archaeopteris* have the same anatomy as the wood *Callixylon*. This gave Beck (1960) the concept of the Progymnosperms.

Even though it may seem unnecessary to retain the various generic names, it is best to do so. Even if an organic connection between some species is known, there is no certainty that all species of these genera will be shown to have been connected in this way. Indeed, as organs are likely to have evolved independently, there is every reason for keeping both names, especially if they might well have different stratigraphic ranges.

Evolution and change

Early evolutionary radiation of any group will produce organisms that share a mixture of morphological characters. Only later will they be sufficiently distinct to be recognized as taxa. Spicer and Burnham (independently *in* Spicer & Thomas 1986) have suggested methods of using systems of grouping specimens into morphological forms, thereby having an alternative, but parallel, scheme to the generally used Linnaean system. Hughes (e.g. *in* Spicer & Thomas 1986) has similarly suggested an alternative data handling scheme for early angiosperm-like pollen.

Classification

The use of the binominal system of nomenclature

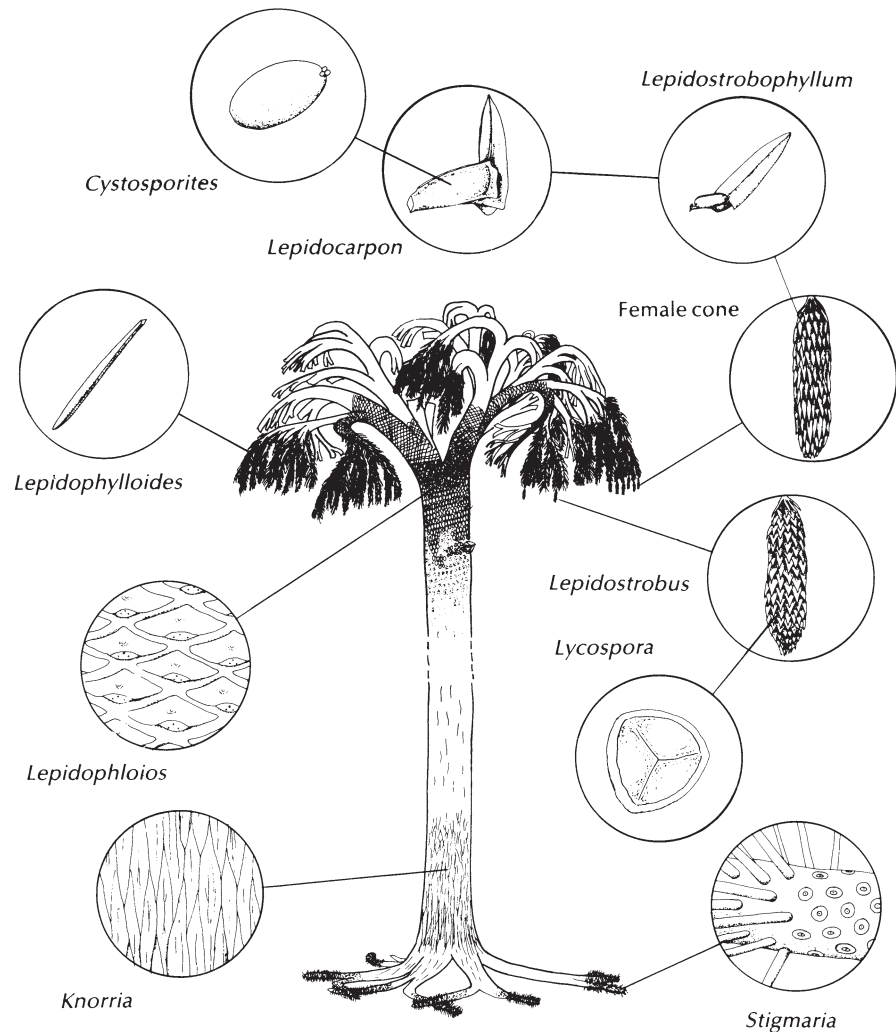


Fig. 1 Whole plants are rarely fossilized intact, so reconstructions, such as this Carboniferous arborescent lycophyte, are based on evidence from detached plant parts, each of which usually has its own name. *Knorria* is the name given to old wrinkled bark, and *Lepidophloios* one name given to fossils of leaf-cushion covered stem. Leaves are referred to as *Lepidophylloides* and the rhizophore rooting system as *Stigmaria*. Microsporangiate cones (*Lepidostrobus*) yield *Lycospora* microspores. The megasporangiate cone has *Lepidostrobophyllum* sporophylls with one functional megaspore (*Cystosporites*) per sporangium. Comparable permineralized megasporangiate sporophylls are called *Lepidocarpon*. (From Thomas & Spicer 1987.)

for dispersed plant organs reflects a comparison of their morphologies. This has been extended above the generic level to classify plant fossil organs into families, orders, and subdivisions, with each classification depending on the views of the author. Many plant organs do not fit into such families and are put into an *incertae sedis* 'unknown' category. Another approach is to use *satellite taxa*, which suggest affinity to those genera in a family or order (Thomas & Brack-Hanes 1984).

References

- Beck, C.B. 1960. The identity of *Archaeopteris* and *Callixylon*. *Brittonia* **12**, 351–368.
- Spicer, R.A. & Thomas, B.A. (eds) 1986. *Systematic and taxonomic approaches in palaeobotany*. Systematics Association, Special Volume 31. Clarendon Press, Oxford.
- Thomas, B.A. & Brack-Hanes, S.D. 1984. A new approach to family groupings in the lycophytes. *Taxon* **33**, 247–255.

Thomas, B.A. & Meyen, S.V. 1984. A system of form-genera for the Upper Palaeozoic lepidophyte stems represented by compression-impression material. *Review of Palaeobotany and Palynology* **41**, 273–281.

Thomas, B.A. & Spicer R.A. 1987. *The evolution and palaeobiology of land plants*. Croom Helm, London.

5.1.4 Trace Fossils

S. R. A. KELLY

Introduction

The status of trace fossil names has had a complex history (Basan 1979). The 1985 *International Code of Zoological Nomenclature* (Section 5.1.1) marks an

important step in the official recognition of the need for a code of ichnological nomenclature, by taking under its wing some aspects of the problems of ichnology. Many difficulties were clearly anticipated by Bromley & Fürsich (1980), however, and any user of the Code should be aware of the main two:

1 Trace fossils may be made by the activity of any organism, whether animal, plant, or protist. The restriction of trace fossils to animals in the Code is an unnecessary limit to ichnology, and future use must indicate that trace fossils were *not* just produced by animals.

2 Traces of extant organisms can appear identical to those produced by fossil predecessors. There is no logical need to isolate Recent from fossil traces. Recent traces are incipient potential trace fossils; some, like borings and abrasions on hardgrounds, are already lithified.

Whilst it is useful to have some reference to trace fossils in formal biological codes of nomenclature, these are probably not the best places for the inclusion of a 'Code of Ichnological Nomenclature' which is itself non-biological yet involves all biological kingdoms. There is a strong argument for the establishment of an independent ichnological code (Sarjeant & Kennedy 1973; Basan 1979), to be administered by an international body and run principally by palaeontologists (whose interest it would mainly serve). Whilst this is an ideal aim for the future, the present article attempts to provide guidelines for the ichnotaxonomist today.

Principles of ichnology

Most of the background to ichnology has been described by Ekdale *et al.* (1984). Bromley & Fürsich (1980) outlined six principles fundamental to trace fossil nomenclature:

1 Trace fossils are structures produced in sediments and hard substrates (either organic or inorganic in origin) by the activity of organisms (animals, plants, and protists).

2 The nomenclature of trace fossils is based solely upon the morphological characteristics of the structure.

3 A particular structure may be produced by the work of two or several different organisms living together, or in succession, within the structure.

4 The same individual or species of organism may produce different structures corresponding to different behaviour patterns.

5 The same individual or species of organism may produce different structures corresponding to identical behaviour but in different substrates, e.g. in sand, in clay, or at sand–clay interfaces.

6 Identical structures may be produced by the activity of systematically different trace-making organisms, where behaviour is similar.

Establishing an ichnological name

Two codes should be consulted when establishing or revising ichnological names. The names, authorship, and dates of most trace fossils are covered by the 1985 zoological Code (Section 5.1.1). Other examples may be dealt with using the proposed ichnological code of Sarjeant & Kennedy (1973).

Formal trace fossil names are form taxa and comprise an ichnogenus, ichnospecies (both italicized), and author with date (placed in brackets when the name has been altered subsequent to its original establishment), e.g. *Rusichnites grenvillensis* (Dawson, 1864); *Cruziana grenvillensis* (Dawson, 1864). The names should be treated in a similar way to Linnaean binominal zoological names. A suitable idiomorphic (i.e. showing full, uninhibited morphological development) holotype should be designated, figured, and placed in a suitable institutional collection (Section 6.3.1). A name proposed for an ichnotaxon does not compete in priority with one established for an organism, even for one that may have formed the ichnotaxon. The principle of homonymy applies to all levels of ichnotaxa. The 1985 zoological Code regarded the type species as unnecessary with regard to trace fossils, although arguably such a concept is useful to provide a reference species when creating others.

Supraichnogenetic nomenclature

The 1985 zoological Code indicated that only family-level names should be used for trace fossils at formal supraichnogenetic level. In practice, higher level groupings of trace fossils are almost always informal. Häntzschel (1975) used only the following divisions: Trace Fossils, Borings, Coprolites, and Trace Fossils or Medusae Incertae Sedis. Ekdale *et al.* (1984) outlined various classifications applied to trace fossils. Bio- and ichnotaxonomic classifications are commonly confused, but should always be kept separate. Typical higher classifications include:

1 *Biotaxonomic classification*. Whilst it is possible to identify with accuracy the constructor of some trace

fossils or traces in the absence of the body concerned, in many cases this is highly speculative (see Principles 3–6 above). Subjective.

2 Preservational classification. The relationship between the trace and its position in or on the sediment. Full relief (exichnia/endichnia), epirelief (epichnia), hyporelief (endichnia). Objective.

3 Biological behavioural classification. Resting, crawling, grazing, feeding, dwelling, escape, coprolitic, faecal, pseudofaecal, excavation, regurgitation, plant penetration structures; even stromatolitic structures are included by some workers. Subjective.

4 Palaeoenvironmental classification. Ichnofacies distributions with relation to depth, energy, salinity; soft versus hard substrate traces.

Undesirable names and constructor–trace relationships

In creating new names, palaeontologists should ensure that the selected name does not infer a particular architect, constructor, or tracemaker. However, existing names, such as *Teredolites*, which are undesirable because they imply erroneously a particular occupant or creator (in this example, *Teredo*), are nevertheless valid names and should be retained for the purposes of nomenclatural stability.

Great care is needed by the palaeontologist to separate the concepts of trace fossils and their supposed creators. Ichnotaxa should be treated as non-biological form names *only* and their association with named organisms should be a matter of careful

discussion, especially when there is no body fossil present. Even if there is a body fossil present, it may not be that of the original constructor.

Exclusions

Trace fossil names should not be applied to such fossil evidence as internal or external moulds or impressions, casts or replacements, prod and bounce marks of shells or organisms acting as transported clasts and not propelling themselves. Such structures do not represent biological activity.

References

- Basan, P.B. 1979. Trace fossil nomenclature: the developing picture. *Palaeogeography, Palaeoclimatology, Palaeoecology* **28**, 143–167.
- Bromley, R.G. & Fürsich, F.T. 1980. Comments on the proposed amendments to the International Code of Zoological Nomenclature regarding ichnotaxa. *Bulletin of Zoological Nomenclature* **37**, 6–10.
- Ekdale, A.A., Bromley, R.G. & Pemberton, S.G. 1984. *Ichnology, the use of trace fossils in sedimentology and stratigraphy*. Society of Economic Paleontologists and Mineralogists, Tulsa, Ok.
- Häntzschel, W. 1975. Trace fossils and problematica. In: C. Teichert (ed.) *Treatise on invertebrate paleontology. Part W. Miscellanea, Supplement 1*, 2nd edn. Geological Society of America, Boulder, Co., and University of Kansas Press, Lawrence, Ka.
- Sarjeant, W.A.S. & Kennedy, W.J. 1973. Proposal of a code for the nomenclature of trace fossils. *Canadian Journal of Earth Sciences* **10**, 460–475.

5.2 Analysis of Taxonomy and Phylogeny

5.2.1 Overview

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Taxonomy is the science of classification of organisms. This involves both the naming of taxonomic units, including rather dry nomenclatural aspects

which are as much legal as scientific, and the analysis of morphological characters forming the basis of that nomenclature, which can be one of the most important foundations from which larger inferences are made. On the assumption that evolution has occurred, taxonomy has been much intertwined with *phylogenetics*, concerned with the description of evolutionary relationships. Because fossils have been assumed to be the proof (or at least the

exemplars) of evolution, the interplay between taxonomy and phylogeny has perhaps been more intimate in palaeontology than in the taxonomy of living organisms. This has led to problems which are not trivial ones just to do with names. Some of these problems are discussed in this section. The rules governing the naming of organisms are not considered in detail, although they do have importance in attempting to ensure nomenclatorial stability and uniform usage throughout the scientific community (Section 5.1).

Taxonomic basis of palaeontological theories

Good taxonomy is the basis on which practically all other palaeontological generalizations rely; bad taxonomy will result in ill-founded and misleading theories. This can sometimes be a problem because the theorists are usually not the same people as the taxonomists. The former may even regard taxonomists as a bit of a nuisance and as 'nit pickers' (some are!), while taxonomists may regard their generalizing colleagues as taking unjustified liberties with poor data. None the less, taxonomy and most palaeontological generalizations are inextricably linked:

1 Palaeogeographic theories based on fossil taxa always rely upon maps, or clusters of similar taxa. The analysis of patterns will only be as good as the taxonomy of the organisms included in the data. For example, palaeogeographic maps are often reconstructed from the distribution of genera, but if these genera are unnatural groupings of species, any conclusions drawn from the maps are bound to be ambiguous.

2 Synecological generalizations from the fossil record, whether concerned with the history of 'communities' through time (Section 4.17), or attempts to construct whole biota from *Lagerstätten* (Section 3.11), rely on correct taxonomic assessment of their components. The famous Middle Cambrian Burgess Shale fauna from western Canada (Section 3.11.2) has been reworked from the taxonomic standpoint in the last two decades. This has revealed important features at the community level which were not apparent from the original descriptions by C.D. Walcott, e.g. the prominence and diversity of worms of the Phylum Priapulida when compared with the Recent.

3 Analysis of patterns of diversification (Section 2.7) and extinction (Sections 2.12 & 13) is considered one of the ways in which the fossil record contri-

butes uniquely to biological history. The reality of such patterns depends critically on the taxonomic underpinning. Some supposed evolutionary 'bursts' correspond well with the activities of particularly diligent monographers. Recently Patterson & Smith (1987) have shown how much of the data for supposed 26 million year extinction cycles of families (Section 2.12.3) are inadequate in one way or another — notably by including examples of 'taxonomic pseudoextinction' (Briggs *et al.* 1987) where an apparent extinction is only the product of taxonomic practice. It should not be claimed — as some extreme sceptics might — that there *are* no patterns of extinction or radiation in the fossil record. There surely are. The important point is that taxonomy is crucial to discriminating those patterns correctly.

Why fossils pose particular problems for the taxonomist

Fossils do not always fit comfortably into classifications based on the living fauna and flora (Cracraft & Eldredge 1979). Linnaean taxonomic categories are applied to both fossils and their living relatives, and occasional suggestions that they be replaced by something else for fossils have not found favour. The problems posed by fossils stem both from the nature of the material itself and from the introduction of the time dimension into taxonomy.

The information obtainable from fossils is limited, whereas, in principle, that from living organisms is inexhaustible. Many fossils are fragmentary, nearly all lack traces of the soft anatomy, they may be distorted, and so on. Classifications of living organisms are now influenced by biochemical studies, immunology, DNA analysis — and at the other end of the scale by behavioural information — virtually all of which is not available from fossil material. Modern taxonomic studies often compare relationships deduced from the molecular level with cladograms based on 'classical' whole-organism morphology; where agreement between the two is good, the relationships are likely to be well founded. With fossils such independent testing is not available. Soft anatomy can, of course, be inferred from hard parts, but this may be a difficult procedure when the fossil group in question is entirely extinct.

Although such preservational limitations are obvious, the influence of the temporal dimension is subtler. If there were no fossil record, the Recent fauna and flora would consist of discrete species-level taxonomic units, each of which could be characterized genetically, and analysed by cladistic

methods into a hierarchy of relationships with the rest. The historical component — including the phylogenetic steps leading to the Recent taxa — would be inferred directly from the cladograms. The existence of the fossil record means that there is direct evidence for the *timing* of branching events. Some zoologists use the fossil record only with this intent; for such scientists the importance of *Archaeopteryx* is not as an ‘intermediate’ between birds and Reptilia (itself a paraphyletic group), but as a chronometer dating the earliest record of some derived characters shared by all birds, e.g. feathers. This viewpoint is shared by many cladists (Section 5.2.2). Such workers tend to place the fossils in the appropriate position on their cladograms but eschew according the extinct forms the formal (often high-level) taxonomic recognition they have received in the past.

It is not surprising that fossil forms often show combinations of primitive characters in relation to their living relatives. Despite the claims of some creationists, the distribution of characters in the fossil record overwhelmingly supports the notion of descent with modification. It is this very property which has created further problems for the taxonomist. In past years, palaeontologists have noted the general similarity of fossils living at the same geological time period — and such groups have been dubbed with names, which have now become familiar in the literature (the so-called mammal-like reptiles would be an example). In this case the notion of time has become linked directly with the taxonomy. The problem is that the nature of the ‘similarity’ was not analysed by the original taxonomists — it merely seemed appropriate that primitive and ancient forms ‘belonged together’. Much of the argument about taxonomy and fossils over the last few years is essentially about the question of what to do with such groups, which are based on shared primitive characters — and often have a similar stratigraphic age as well.

From the phylogenetic point of view, units of classification (orders, families, genera, etc.) can be one of three things: *monophyletic*, descended from a single common ancestor, and including all its descendants; *polyphyletic*, an artificial group descended from more than one ancestor (usually classified together because of a striking but superficial similarity); or *paraphyletic*, descended from a common ancestor, but not including all descendants. This last named category is the one that causes the trouble in palaeontological classifications, because it includes the units based on primitive

similarity — the limbs, as it were, of the evolutionary tree, without the branches and twigs. Few people today would seriously defend a classification that includes polyphyletic taxa — the story of taxonomic progress is often the story of the dismantling of polyphyletic taxa, like the old phylum which included all the superficially worm-like animals. Cladists attempt to reduce units of classification to monophyletic groups (Wiley 1981); other systematists continue to recognize paraphyletic taxa, sometimes with the reservation that it is in lieu of anything better. Cladistic analysis does not formally recognize ancestors, and the particular problem of reconciling the fossil record with such analyses is that palaeontologists, and especially invertebrate palaeontologists, recognize ancestors with some frequency.

Direct phylogenetic information from the fossil record

Palaeontologists frequently describe *lineages* connecting two or more fossil taxa, which are supposed to represent hypotheses about their evolutionary relationships. Invertebrate palaeontologists, in particular, often have a prolific fossil record, with thousands of specimens from a formation or area on which to base such lineages, which are usually represented as some kind of evolutionary tree. Ancestral species are often included in such trees. Discussion of many of the macroevolutionary phenomena that form the subject of chapters in this book depends on the acceptance of the reality of these trees. Invertebrate groups yield trees that can be tested against future occurrences of species, and as such are properly scientific constructs. Foraminiferal phylogenies, for example, are tested every time a new borehole is put down. The detailed way in which such trees are constructed varies from worker to worker, but usually involves a stratigraphic sequence of samples (the *stratophenetic* method; Section 5.2.4), from which species are recognized. The species are then arranged in phyletic sequence, which may or may not involve branching events where an ancestral species splits into two descendants. Gradualistic change is slow and continuous, punctuational change is rapid (often apparently instantaneous as seen in the rocks); both probably occur in the fossil record, with the latter predominating. In gradualistic lineages there are problems about the arbitrariness of applying names to segments of a spectrum, but such niceties probably do not deserve the attention they have

received. Punctationally derived species are usually clearly defined entities, which should be morphologically capable of diagnosis and limited stratigraphically. Examples of such trees can be found in the literature of ammonites, graptolites, trilobites, brachiopods, and microfossils in general, but rarely in vertebrates other than mammals. These species–species lineages almost invariably involve rather small changes in skeletal morphology.

Another kind of ‘evolutionary’ tree is to be found in the palaeontological literature. This kind is much less precise than the ones just described, often relates to higher-level taxa than species (genera, families or even higher taxa), and has been a more characteristic product of vertebrate workers. The fossil record of vertebrates is sporadic and capricious. Most records of higher taxa are separated by stratigraphic and morphological gaps, and there is little chance of reading evolutionary history directly from sequence. However, trees have been constructed from the succession of forms purporting to record ‘advancement’ of morphology through time; early forms have been described as ancestors in such phylogenies. This kind of loose treatment is worth distinguishing from stratigraphic species lineages, because the chances of finding an entirely appropriate ancestor in this kind of sequence are small. ‘Ancestor’ in this sense is used as a kind of shorthand for ‘early representative retaining many primitive features’; it is this usage which has been strenuously criticized by cladists, and with some justice. One has only to look at the recent history of the discoveries relating to the evolution of *Homo* and its relatives to see how each early discovery is claimed as some kind of ‘ancestor’, but at the same time how each major discovery has contributed to turning a simple, straight-line ape–man transition into a more complex, branched tree.

Many (perhaps most) palaeontologists continue to use their phylogenetic trees as a basis for taxonomy. Some of these palaeontologists strive also to make their higher taxa monophyletic. But of course the recognition of ancestors poses a set of problems for which there is no formal solution. If a fossil species lies at the ‘origin’ of two monophyletic genera, to which is it assigned, or is it not assigned to either? It may not be clear which are primitive and which are derived characters, because fossil species are often discriminated on tiny features without *a priori* polarity. If a cluster of such species is otherwise united by shared, primitive (symplesiomorphic) features, to recognize that group as a genus inevitably results in a paraphyletic grouping.

In short, the better and more complete the fossil record is (i.e. the more fully the evolutionary history is spelled out in the rocks), the more problematic becomes the strict application of cladistic classification ‘rules’. This paradox is important in understanding the controversy between cladists and stratopheneticists which has burgeoned in the last few years.

Cladistics, stratigraphy and the reconstruction of phylogenetic history

The impact of cladistics on systematics has been profound and beneficial. Cladistics has provided a rational basis for classification which can encompass both the animal and plant kingdoms, based on objective assessment of character distributions. This has done much to dispel the subjective and often authoritarian approach to systematics that has pertained in the past — where the recognition of a genus, for example, depended on whether the expert happened to have felt that a species ‘deserved’ generic status. This is not the place to elaborate the mechanics of cladistic classification, which is treated below (Section 5.2.2). Cladistics was developed initially by neontologists and enthusiastically adopted by vertebrate palaeontologists at an early stage. As stated above, it is the vertebrate fossil record which is in general subject to the largest (morphological, stratigraphic) ‘gaps’ and the woolliest trees, and cladistic analysis of relationships provided both a new objectivity, and a new sophistication of computer-based techniques.

Hennig, the originator of cladistic analysis, was clear that his intent was historical: the branches on the cladograms represented real, historical speciation events (Hennig 1966). The cladogram was, in a sense, a model of evolutionary history. For the insects with which Hennig worked there was but little fossil record, and a careful working of living taxa was the most productive approach to phylogenetics. Darwinian evolution is a theory — a conceptual framework in which biological thinking operates. A further development of cladistics (‘pattern’ or ‘transformed’ cladistics) was to remove this theory-laden presumption from the procedure: classification should be based *entirely* on the pattern of distribution of characters in the cladogram, without regard to any presumed evolutionary history. This attempt at objectivity has been misrepresented by certain creationists as ‘scientists do not believe in evolution’, whereas the point was to make any system of belief irrelevant to the objectivity of the

character analysis. But what place could fossils have in this new objectivity? Fossils are, at the least, fragments of history; can they have any place in a classification system which attempts to minimize the historical component from its construction?

The present status of these questions depends very much on the philosophical stance of the investigator. In the first place there is no doubting the power and breadth of cladistic techniques in taxonomy across all classes of organisms; there is no other method of such universal applicability. It is perhaps not surprising that those who developed the methods of analysis should defend them with the fervour of those defending the true faith, and castigate dissenters forthrightly. There have been equally strong disagreements within this *coterie* about which analytical technique is likely to yield the most robust results. None the less it is clear that there are several possible attitudes to the fossil record even among people who would call themselves cladists, valuing as they do the technique of analysis for its explicitness, objectivity with regard to characters, and ready testability from new data. In an attempt to be fair to the diversity of opinion on present attitudes to taxonomy and the fossil record I have tried to summarize the differing philosophical positions into a few categories.

1 Pattern cladists. Such workers contend that fossils have contributed very little to theories of relationship based on Recent organisms (Patterson 1981). The contribution of fossils lies in determining the antiquity of groups, but seldom if ever in discrimination of relationships, which fossils have in the past often confused more than clarified. These workers allow fossils their palaeobiogeographical importance, and, on occasion and in lieu of anything better, admit palaeontological evidence in the determination of character polarity. The historical, narrative contribution that fossils may make, based on sequence, is effectively eliminated.

2 Evolutionary cladists. Under this category come workers who use essentially the same cladistic methods to analyse relationships as the pattern cladists, but regard the fossil record as of importance in *testing* those relationships (Hill & Camus 1986). They would regard congruence between the sequence of branching nodes on the cladogram and the stratigraphic appearance of the appropriate taxon in the fossil record as an important part of the scientific method, and to this extent directly acknowledge the temporal dimension that fossils offer. In the examples worked, which have only a moderate fossil record, there is a surprisingly good

match between the sequence on cladogram and sequence in rock.

3 Phylogenetic historians. This category of worker regards the *reason* for analysing character distribution as the reconstruction of the phylogenetic history of the organisms analysed. Such workers regard genealogy as a fact — and, as such, capable of being reconstructed. They distinguish between the fact of genealogy and the theory of evolutionary mechanism (including Darwinism, Neutral theory and the like); the latter is testable from trees, but should in no sense be incorporated *a priori* in their construction. These workers admit both cladistic and stratigraphic analysis into the methodology of phylogeny construction (Fortey & Jefferies 1982) according to circumstances. Both methods are regarded as models of phylogenetic history. For fossil groups with good, stratigraphically controlled fossil records, a stratophenetic approach is appropriate; for groups with a poor fossil record cladistic methods give results which more closely approach the reconstruction of historic branching events.

4 Stratigraphic palaeontologists and stratopheneticists. Such workers rely heavily on stratigraphic sequence to deduce phylogenetic relationships, which are drawn out as 'trees'. Ancestral species, and paraphyletic taxa are not uncommon in classifications drawn from such trees. These palaeontologists often allow stratigraphy to be the arbiter of primitive and derived character states. Many (but certainly not all) workers with this approach tend to operate at the species–species level on their trees. Genera tend to become 'branches' of the trees, but in some cases (in the foraminiferal lineage *Globigerinoides* to *Orbulina*, for example; see Banner & Lowry in Cope & Skelton 1985) different generic names are applied to different steps in a single lineage: this probably represents the perfect antithesis to the cladistic approach to classification.

It should be added that there are many more palaeontologists who conform to none of these categories, but continue to operate with rather vague notions of 'affinity'. However, any of the four attitudes listed above represents a valid scientific approach, even though the champions of one method or another might deny it! It is noticeable that the attitude to phylogeny does seem to relate to the kind of scientific problem which is under examination. Pattern cladists tend to be those who study groups with a sporadic fossil record (fishes, spiders), and whose intention is to clarify relationships of living organisms, while at the other ex-

treme the stratigraphic palaeontologists tend to be those who study groups with arguably complete fossil records (ammonites, foraminifera, graptolites, bivalves), and whose main concern is the correlation of rocks. At the moment there is little acknowledgement of the role of either extreme by the other, and hence taxonomy is polarized. On the one hand, cladists are making new sense of classification — especially at high level — and focusing attention upon characters rather than subjective notions in the definition of groups. They are also minimizing the contribution of fossils and simply do not 'see' ancestors. On the other hand, stratigraphic palaeontologists continue to describe trees at low taxonomic level — and include what they regard as proven ancestors — but fail to recognize the contribution that a cladistic analysis might make to the logical ordering of their higher level classifications. Whether a compromise can be struck, perhaps approximating to one of the historical approaches, remains to be seen.

References

- Briggs, D.E.G., Fortey, R.A. & Clarkson, E.N.K. 1987. Extinction and the fossil record of the arthropods, In: G.P. Larwood, (ed.) *Extinction and survival in the fossil record*. Systematics Association Special Volume No. 34, pp. 171–209. Clarendon Press, Oxford.
- Cope, J.C.W. & Skelton, P.W. (eds) 1985. *Evolutionary case histories from the fossil record*. Special Papers in Palaeontology No. 33.
- Cracraft, J. & Eldredge, N. (eds) 1979. *Phylogenetic analysis and paleontology*. Columbia University Press, New York.
- Fortey, R.A. & Jefferies, R.P.S. 1982. Fossils and phylogeny — a compromise approach. In: K.A. Joysey & A.E. Friday (eds) *Problems of phylogenetic reconstruction*. Systematics Association Special Volume No. 21, pp. 197–234.
- Hennig, W. 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana.
- Hill, C.R. & Camus, J.M. 1986. Evolutionary cladistics of marattialean ferns. *Bulletin of the British Museum (Natural History)*, Botany Series **14**, 219–300.
- Patterson, C. 1981. Significance of fossils in determining evolutionary relationships. *Annual Review of Ecology and Systematics* **12**, 195–223.
- Patterson, C. & Smith, A.B. 1987. Is the periodicity of extinction a taxonomic artefact? *Nature* **330**, 248–252.
- Wiley, E.O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. Wiley Interscience, New York.

5.2.2 Cladistics

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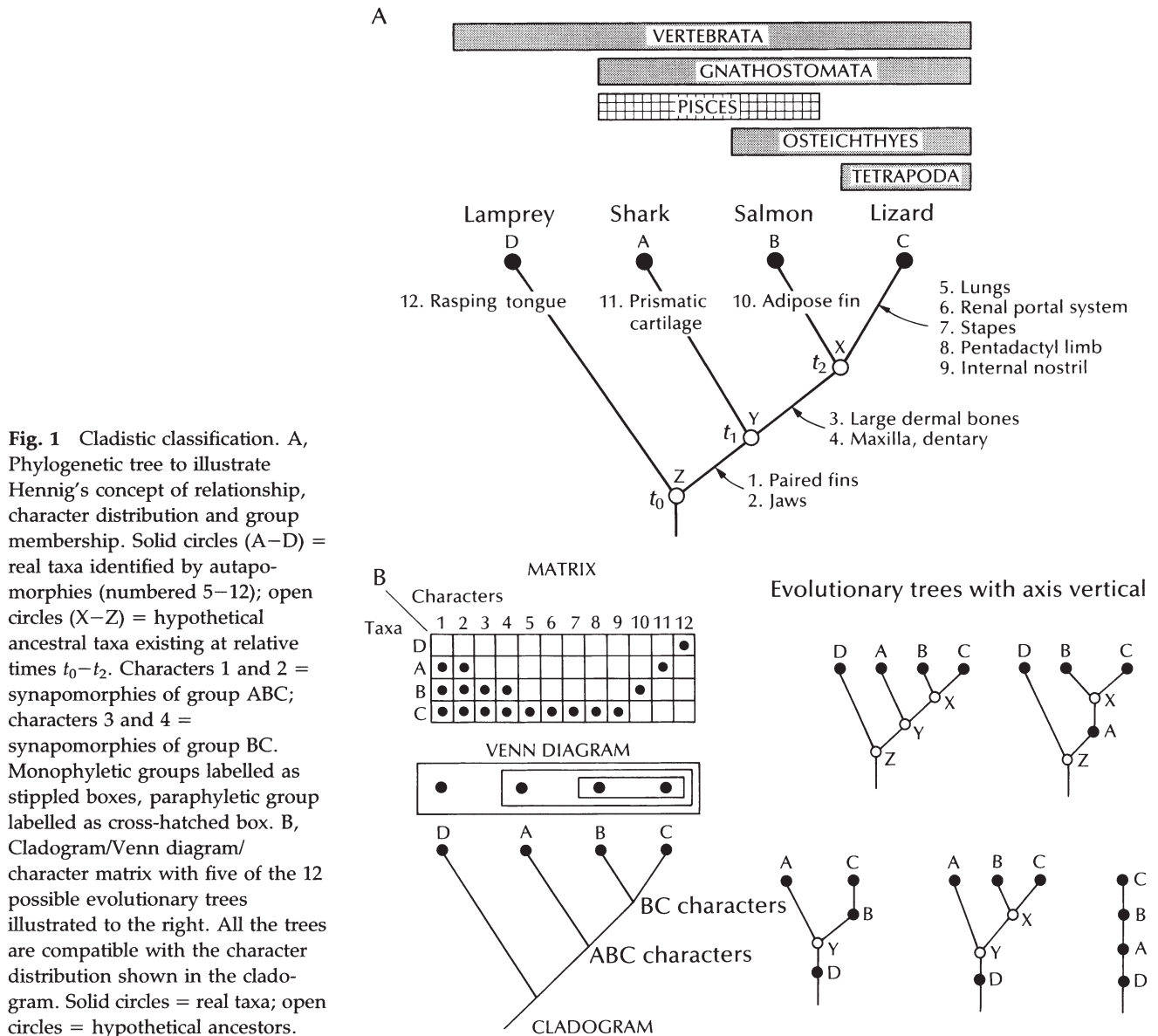
Introduction

Cladistics is a method of biological classification which, in its purest form, seeks to group taxa into sets and subsets based on the most parsimonious distribution of characters. The results of analysis are expressed in *cladograms* which are atemporal (Fig. 1B, left) showing only the distribution of characters and representing a general pattern with which several evolutionary trees might be compatible. A highly readable contemporary account is given by Wiley (1981). Cladistic methods were originally formulated by Hennig (1966) under the name 'Phylogenetic systematics'. Hennig explained his ideas within an evolutionary framework. This account treats cladistics in an historical way, leading from its evolutionary formulation to the more general theory.

Hennig's contribution was to offer a precise definition of relationship and to outline how relationship might be detected. Hennig's concept of relationship is relative and is illustrated in Fig. 1A. Taxa B and C are more closely related to each other than either is to a third taxon, A, because B and C share a common ancestor, X at time t_2 , not shared with any other taxon. Similarly A is more closely related to B+C than to D because these taxa share a unique common ancestor, Y at time t_1 . B and C are called *sister-groups*; A is the sister-group of the combined taxon B+C. The aim of cladistic analysis is to search for the sister-group hierarchy, and express the results in branching diagrams called cladograms.

Synapomorphy, symplesiomorphy and autapomorphy

Sister-groups are discovered by finding shared derived characters (*synapomorphies*) inferred to have originated in the latest common ancestor. Synapomorphies can be thought of as evolutionary novelties or as homologies. From Fig. 1A characters 3 and 4 are synapomorphies suggesting that the lizard and the salmon shared a unique common ancestor X at time t_2 . Shared primitive characters (*symplesiomorphies*) are characters inherited from more remote ancestry and are irrelevant to the



problem of relationship of the lizard and the salmon. Thus, the shared possession of characters 1 and 2 in the salmon and the lizard would not imply that they shared a unique common ancestor because these attributes are also found in the shark. Characters 1 and 2 are more universal and may be useful at a higher hierarchical level to suggest common ancestry, Y at time t_1 .

It is important to recognize that synapomorphy and symplesiomorphy describe the status of characters *relative to a particular problem*. Thus, characters 3 and 4 are synapomorphies when one is interested in the relationships of the salmon or the lizard, but symplesiomorphies if the problem involves the relationships of different species of lizards or different species of salmon. Hennig recognized a third

distribution: those characters unique to one species or group, such as characters 5–9 in the lizard, 10 in the salmon, 11 in the shark, and 12 in the lamprey. These he called *autapomorphies*, which in Fig. 1A define the terminal taxa A–D.

The characters used to discover relationship are derived characters or character-states and this implies acceptance of transformation (absence \rightarrow presence, or condition $a \rightarrow a'$). Hennig suggested several criteria by which polarity of transformation may be recognized. The two most frequently used are ontogenetic transformation and outgroup analysis (see Ax 1987). The latter is most applicable to palaeontological studies, and may be briefly stated: when a character exists in a variable state within the group under study, the condition that is also

found outside the group is the plesiomorphic state. Cladistic analysis is concerned with ordering these derived states into transformation series and this is done by choosing the arrangement of taxa that is congruent with the greatest number of characters. An alternative way of expressing this is that the most parsimonious solution is sought. There are a number of computer algorithms available to help in this task (Platnick 1987).

It has been argued that it is inappropriate to apply the principle of parsimony to an exercise seeking to reconstruct phylogenetic relationship; after all, evolution may not have followed the most parsimonious course. In cladistic analysis the most parsimonious solution is sought because this is the only universal criterion by which different hypotheses of relationship might be evaluated. This has been dubbed methodological parsimony. To accept a solution which is other than parsimonious requires additional assumptions which themselves require independent justification.

Types of groups

As a result of the relative definition of relationship, Hennig identified three types of groups:

1 A *monophyletic* group contains the latest common ancestor plus *all and only all* its descendants. In Fig. 1A such groups would be BC(X), ABC(Y), DABC(Z). In the particular example the monophyletic groups would be called Osteichthyes, Gnathostomata and Vertebrata respectively.

2 A *paraphyletic* group is one remaining after one or more parts of a monophyletic group have been removed. Group AB (Pisces) is a paraphyletic group: one of the included members (B) is genealogically closer to C which is not part of the group Pisces.

3 A *polyphyletic* group is one defined on the basis of convergence, or by non-homologous characters assumed to have been absent in the latest common ancestor. A group AC containing the shark and the lizard, based on the possession of internal fertilization would be considered a polyphyletic group. Internal fertilization is certainly a derived character within vertebrates and might be indicative of a monophyletic group. But a grouping based on this feature is not congruent with any other character distributions. Rather, it is incongruent with a group BC suggested by two characters (3, 4). A polyphyletic group represents a non-parsimonious solution, and the characters by which we recognize it are non-homologous, false guides to relationship.

Most systematists would agree with the desir-

ability of recognizing monophyletic groups and respect the artificiality of polyphyletic groups. It is paraphyletic groups which are the source of debate, particularly with palaeontologists.

Paraphyletic groups

Cladistic classification insists that only monophyletic groups be included, as recognized on the basis of synapomorphy. Paraphyletic groups obscure relationships because they are not real in the same sense, they do not have historical reality and they cannot be recognized by a synapomorphy. Reptilia, for instance, is a paraphyletic group recognized by having synapomorphies (amniotic membranes, cleidoic egg) of a larger group (Amniota) but lacking the synapomorphies of two contained amniote subgroups — birds (feathers) and mammals (hair). Reptiles are distinctive only because they lack characters. The 'defining attributes' of such a paraphyletic group are symplesiomorphies (shared primitive features) only.

Evolutionary classification (Section 5.2.3) allows the inclusion of paraphyletic groups with the justification that extra evolutionary information is conveyed. That extra information is seen to be evolutionary divergence. From Fig. 1A then, evolutionary systematists consider it justified to retain Pisces as a paraphyletic group and separate off the lizards (Tetrapoda) in a collateral group to emphasize the many autapomorphies (characters 5–9) of this latter group. In a cladistic classification such divergence would be expressed through the *number* of autapomorphies.

Paraphyletic groups are popular in palaeontology (Patterson 1981) because they are traditionally the ancestral groups (fishes ancestral to tetrapods, reptiles ancestral to birds and mammals, inarticulate brachiopods ancestral to articulate, regular echinoids ancestral to irregular echinoids). These paraphyletic groups are based on absence of characters of the presumed descendants. The problem is compounded in fossils because conditions of soft anatomy used in the classification of Recent representatives cannot be checked; nor can it ever be certain whether absence of features is real or a preservational artifact. In other words, nothing can be found to support an ancestral/paraphyletic group.

A special case of ancestral/paraphyletic groups frequently occurs in palaeontology: the extinct, presumed ancestral group. Hennig called these *stem-groups*, and well known examples include

Rhipidistia, Cotylosauria, Pelycosauria, and Therapsida. All of these groups are paraphyletic, and are defined on the absence of features of the presumed Recent descendants. When analysed in a cladistic fashion, such groups usually turn out to be composed of successively more derived taxa (some showing more synapomorphies with the Recent group). Thus, a stem-group to the Euechinoidea, such as the Palaeozoic 'Perischoechnoidea', can be resolved into a series of sister-group relationships of increasingly derived taxa (Smith 1984). By breaking up such a paraphyletic group into real historical entities (successive monophyletic taxa) some insight is gained into the sequence of character acquisition, from which may be deduced something about biological evolution.

The use of paraphyletic groups also introduces problems when trying to express ideas of relationship in a Linnaean taxonomy. Paraphyletic groups such as Reptilia and Inarticulata have equal rank with their presumed descendants (Aves and Mammalia, Articulata) in an attempt to emphasize the morphological divergence of the descendants. This implies that all members of the Reptilia are each other's closest relatives. But this is not so since, amongst reptiles, crocodiles are known to be closer to birds than to lizards or turtles. Paraphyletic groups therefore introduce an asymmetry between the Linnaean classification and ideas of phylogeny.

Cladistics and Linnaean classification

It is for these reasons that cladists try to apply equal rank to sister-groups. For cladists the classification and the cladogram are the same thing. The Linnaean classification for Fig. 1A would be:

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Group ABCD
  Subgroup D
    Subgroup ABC
      Infragroup A
        Infragroup BC
          B
          C

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It has been mentioned above that for many fossil groups currently thought of as paraphyletic stem-groups, it may be possible to divide them into a series of successively more cladistically derived taxa. Potentially, this could provide problems because, to express every sister-group pairing, a very large number of ranks might be needed. There are, however, several conventions that can be adopted to circumvent this problem (Wiley 1981) including the

use of a rank *plesion* for fossil taxa (Patterson & Rosen 1977).

Cladograms and trees

Cladistic classification, as explained so far, is concerned with searching for sister-groups and expressing the results of that search in classifications where sister-groups are given equal rank. When Hennig formulated his phylogenetic system he did so in strictly evolutionary terms. His branching diagrams were phylogenetic trees with an implicit time axis in which hypothetical ancestors were located at the nodes; the nodes represented speciation or cladogenetic events with evolutionary transformation taking place along the branches. It soon became apparent, however, that Hennig's phylogenetic trees or cladograms were more general than originally thought.

It is possible to view a diagram such as Fig. 1A as a strict cladogram, with no time axis, representing instead a pattern of distribution of characters. The nodes denote a hierarchy of synapomorphies and the relationship can be represented as a Venn diagram of sets and subsets in which there is no implication of ancestry and descent (Fig. 1B). Given the character information contained in this Venn diagram, there are a number of equally compatible evolutionary trees that embody the concepts of ancestry and descent with modification. Five such trees are shown in Fig. 1B (right). One, and only one, has the same topology as the cladogram and this is the one in which the nodes represent hypothetical ancestors. The others contain one or more real ancestors. Choice between these trees depends on factors other than the distribution of characters, which is the only empirical content. Selection of one tree in preference to others may depend on a willingness to regard one taxon as ancestral to the others. Alternatively, the possibility of certain trees involving real ancestors might be denied because of an unfavourable stratigraphic sequence. The important point is that while evolutionary trees are very precise statements of singular history, their precision is gained from criteria other than character distributions; these trees cannot be justified on characters alone. It is possible that stratigraphic data, combined with independent stratigraphic testing (assessments of completeness and suitability of sedimentation) may restrict the choice of trees.

Cladograms, on the other hand, are statements of general pattern testable by applying more data and are useful for, amongst other tasks, the analysis of

biogeographic history (Nelson & Platnick 1981; Section 5.4).

References

- Ax, P. 1987. *The phylogenetic system*. Wiley Interscience, New York.
- Hennig, W. 1966. *Phylogenetic systematics*. 2nd edn. 1979. University of Illinois Press, Urbana.
- Nelson, G. & Platnick, N. 1981. *Systematics & biogeography: cladistics and vicariance*. Columbia University Press, New York.
- Patterson, C. 1981. Significance of fossils in determining evolutionary relationships. *Annual Review of Ecology and Systematics* **12**, 195–223.
- Patterson, C. & Rosen, D.E. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History* **158**, 81–172.
- Platnick, N.I. 1987. An empirical comparison of microcomputer parsimony programs. *Cladistics* **3**, 121–144.
- Smith, A.B. 1984. *Echinoid palaeobiology*. George Allen & Unwin, London.
- Wiley, E.O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. Wiley Interscience, New York.

5.2.3 Evolutionary Systematics

A. J. CHARIG

Introduction

'Evolutionary systematics' should not be confused with 'phylogenetic systematics'. It is an accident of history that the words 'evolutionary' and 'phylogenetic', despite their virtual synonymy, have come to be associated with two very different methods of reconstructing phylogeny and classifying organisms. Charig (1982) recognized this as a possible source of confusion and misunderstanding and suggested that the generally applied evolutionary approach, otherwise called 'conventional' or 'orthodox', might instead be referred to by the wholly non-descriptive but also wholly unambiguous name 'Simpsonian systematics'; this was intended to be a tribute to the late G.G. Simpson, once the leading exponent of that approach.

Early classifications of biological organisms, exemplified by that of Linnaeus, arranged the

species hierarchically — into nested sets — according to their possession of characters held in common (shared characters). The characters used were essentially anatomical. Such a procedure was generally easy when the only species considered were those living today, most of which are clearly definable through their genetic isolation. But the discovery of fossil forms that were intermediate in their characters between two or more extant groups, coupled with the general acceptance of the concept of organic evolution, together led systematists to change their purely typological approach into something more 'evolutionary'. It seemed reasonable to base the classification upon phylogenetic (i.e. genealogical) relationships: the closer the phylogenetic relationship between two species, the closer should they be to each other in the classificatory hierarchy. Thus the assessment of phylogenetic relationships was still based mainly, if not exclusively, upon characters held in common.

However, it is clear that hierarchies constructed upon different shared characters are often incompatible with each other. It is therefore logically impossible that *all* shared characters indicate a close phylogenetic relationship; in some cases apparent identity of characters must be due to homoplasy (parallelisms, convergences and reversals) and can have little phylogenetic significance. Recognition of the phylogenetically correct hierarchy *may* be assisted by determination of the polarity of evolutionary trends and by choosing the hierarchy that appears most frequently (maximal congruence or parsimony).

Phylogeny and classification

At this point it is important to ensure that the distinction between phylogeny and classification be clearly understood. *Phylogeny* is the history of the evolution of living organisms; it is the pattern of the evolutionary pathways by which the millions of organic species, past and present, have arisen. It is an objective reality; the organisms actually evolved in a particular way. Yet our knowledge of phylogeny is very imperfect; our attempted reconstructions of it may differ greatly from each other, and we cannot be sure which (if any) is correct. *Classification*, on the other hand, is the arrangement of living organisms into a meaningful and practical hierarchy, a system of reference. It *need not* be connected with the phylogeny in any way. It should permit the cataloguing of organisms (in, say, a museum collection or a textbook), assist

the memory and enable the prediction of certain attributes; it may also, though not necessarily, indicate the presumed phylogenetic relationships. It is entirely man-made and subjective, so that systems of classification may vary between authorities even more than do the attempted reconstructions of phylogeny.

The only connection between phylogeny and classification is the fact that the two forms of classification most commonly used today, the evolutionary and the stratophenetic, are based primarily upon the perceived phylogeny; and it is obvious that the stratophenetic approach (Section 5.2.4) can be used only by palaeontologists. Also based on phylogeny, but *exclusively* on that, are certain varieties of cladistic classification — the ‘phylogenetic systematics’ of Hennig (1966) and the ‘phylogenetics’ of Wiley (1981); their practitioners will be referred to below as ‘phylogenetic cladists’. In contrast, ‘transformed cladistics’ (Platnick 1980) (now more usually called ‘pattern cladistics’; Beatty 1982) does not even require that evolution should have taken place (Section 5.2.1); nor do phenetic classifications.

The making of an evolutionary classification therefore consists of two major stages: the reconstruction of the phylogeny and, based on that phylogeny, the actual setting up of a formal classification.

Reconstruction of phylogeny

Phylogeny is represented graphically as a dendrogram (‘family tree’). Parts of the tree will probably remain unknown, with unresolved polytomies, and our knowledge of much of the rest is likely to be — to a varying extent — uncertain. There are, essentially, two ways of reconstructing it. One is by analysing the distribution of characters among the species concerned (‘cladistic analysis’, the basic method used by phylogenetic cladists; Section 5.2.2). The other is by analysing the distribution of species in the strata (the basic method employed by stratopheneticists, who of course include in their ranks only palaeontologists; Section 5.2.4). However, the phylogenetic cladist is generally prepared to confirm and/or supplement his cladistic analysis with stratophenetic evidence, and vice versa; further, both the phylogenetic cladist and the stratopheneticist may obtain additional evidence on the phylogeny from the embryology and ontogeny of extant organisms, and from the geographical distribution of organisms both Recent and fossil. (It should be noted that there are *some* cladists who,

in their attempted reconstruction of the phylogeny, consider it improper to supplement or confirm the cladistic analysis in any way.) Evolutionary systematists resemble the less doctrinaire cladists in that they use a judicious combination of both basic methods, with character distribution analysis as their primary method; thus, if the data permit, they will confirm and supplement their results by means of evidence from the fossil record (i.e. stratophenetically), from embryology and ontogeny, and from geographical distribution.

It must be said that, in the past — when *all* systematists might have been described as ‘evolutionary’ — they were not rigorous enough in their application of character distribution analysis; they often tried to unite two groups as ‘sister-groups’ (i.e. originating from an immediate common ancestor) on the evidence of shared characters that were sadly inappropriate. The characters were sometimes ‘primitive’, what the cladists call *plesiomorphous*, and were therefore found in other (or even all) members of the group in question. They might sometimes have been homoplastic, with their presence in the two groups being due to parallelism, convergence or an evolutionary reversal, rather than to an immediate common ancestry. Although such problems may often be clarified by a demonstration of polarity or maximal congruence, that had not been done. Reductions and losses, frequently employed as shared characters, could be included here as possible cases of homoplasy; it is only rarely that reductions can be compared to ascertain precise similarity, and losses never. Further, shared characters were sometimes vague and ill-defined, or too broadly defined to be used properly as indicators of close phylogenetic relationship (e.g. ‘warm-blooded’). Unfortunately many present-day phylogenetic taxonomists, of both schools, are still guilty of such sloppy work.

Erecting a classification

The second component of evolutionary systematics, the actual setting up of a formal classification, consists of the arbitrary division of the phylogenetic tree into segments, subsegments and so on; each segment constitutes a taxon, the origin of which is defined by the first appearance of an *evolutionary novelty* (Fig. 1). Thus the Class Reptilia begins with the first appearance of the amniote egg. Some of the radiating lineages within that class have become entirely extinct (e.g. Ornithischia, Ichthyosauria) while others have survived to the present day (e.g. Testudinata, Squamata). Yet other lineages (e.g.

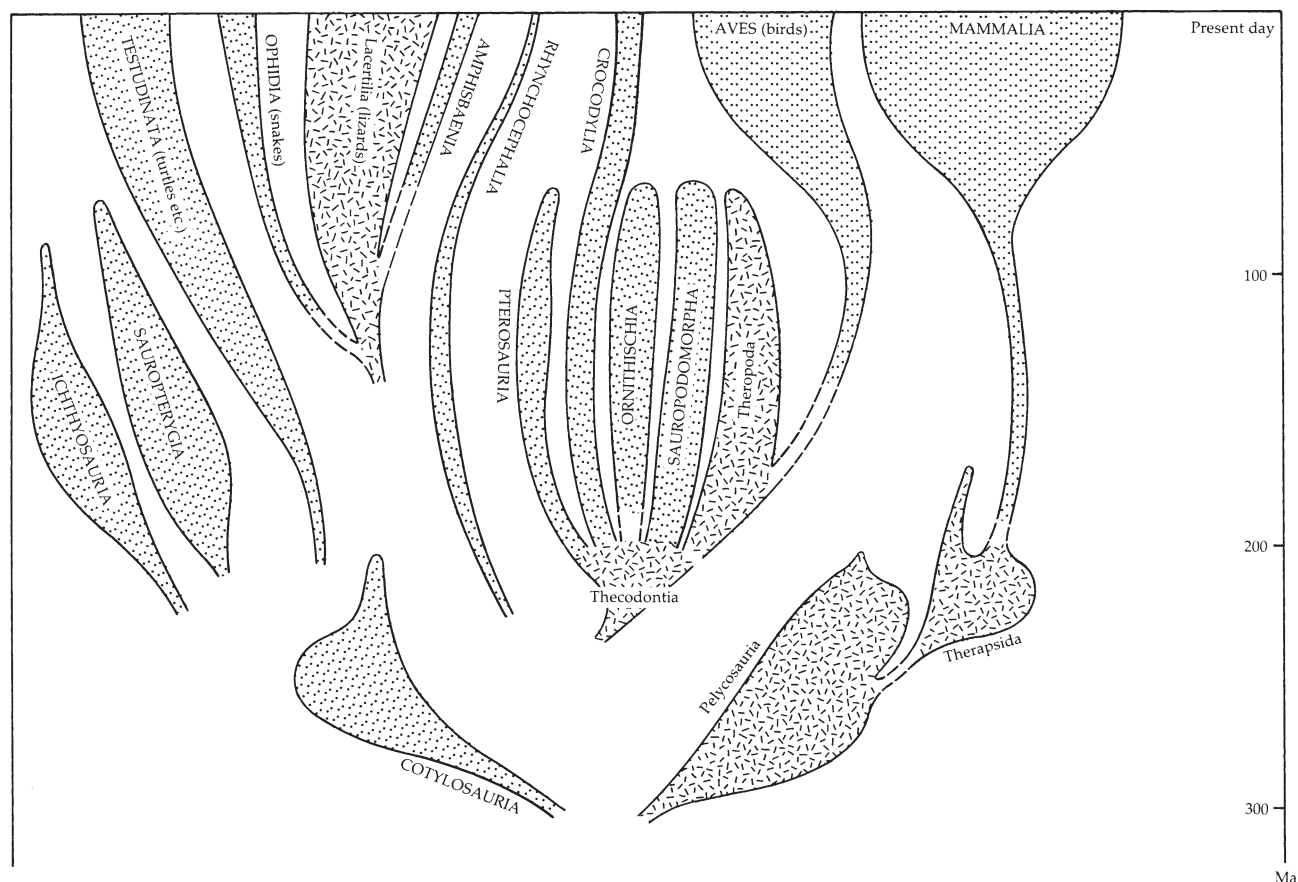


Fig. 1 A greatly simplified family tree ('spindle diagram') of the Amniota. Paraphyletic taxa are dash-stippled and named in lower case lettering. Each gives rise to at least one other taxon. Not named on the diagram are: Reptilia = everything except Aves and Mammalia; Archosauria = Thecodontia + all descendant groups except Aves; Synapsida = Pelycosauria + Therapsida. Holophyletic taxa are dot-stippled and named in upper case lettering. They give rise to nothing else.

Theropoda, Therapsida), however, have evolved into forms so different that the part of the lineage in question is subjectively considered to merit placement in separate classes (Aves, Mammalia respectively), the initiation of each being marked by the first appearance of its own characteristic evolutionary novelty. Thus the reptiles may be defined as tetrapods that possess an amniote egg but have not yet acquired either a functional dentary-squamosal jaw articulation (the possession of which defines a mammal) or feathers (defining birds).

This means that a taxon of given rank may be deemed to have evolved from another taxon of the same rank, so that Class A may be regarded as ancestral to Class B. A corollary of this is that Class A, since it does not include Class B, does not include *all* its own descendants, i.e. it is not a complete *clade*; it is not *holophyletic* (Ashlock 1971; = 'monophyletic' *sensu* Hennig) but is *paraphyletic*. All stem-

groups, all ancestral groups are *ipso facto* paraphyletic; good examples are Reptilia (excluding Mammalia and Aves), Synapsida (excluding Mammalia), Archosauria (excluding Aves) and Thecodontia (excluding all other archosaurs). Cladists abhor and deride paraphyletic taxa, saying that they 'cannot be characterized', 'do not have historical reality', and 'obscure close relationships' (see, for example, Section 5.2.2); they forget that the relationship is 'close' only if it be defined in cladistic terms! Evolutionary systematists, on the other hand, consider that paraphyletic taxa *can* be characterized (in mathematical parlance, as 'complement sets') and they find them extraordinarily useful, especially when discussing ancestry.

The seemingly endless argument over the desirability or otherwise of admitting paraphyletic taxa into the classification is, in fact, the old argument over the relative merits of the 'horizontal' and 'verti-

cal' classifications, to which there can be no definitive solution. When a radiating group is split into its separate components, should a 'stem-group' be left at the base of the radiation, or should the split be extended as far back as possible towards the origin of the group? Alternatively, putting the problem into human terms: to whom is one more closely related, a first cousin, or a direct descendant a hundred generations on? The evolutionary systematist's answer is the first cousin, the cladist's is the direct descendant — no matter how many generations removed. It all depends, of course, on the meaning attached to 'relationship'. But at least it cannot be denied that one shares a much greater proportion of genetic material with the first cousin.

Advantages and disadvantages of evolutionary systematics

The method of phylogeny reconstruction used by evolutionary systematists is much the same as that used by phylogenetic cladists (it employs all the available evidence, of whatever category); it differs from it mainly in that there is no requirement to force a series of dichotomous resolutions from every multiple split, even where the available evidence does not justify such resolution. In the past, alas, the method has generally been applied too loosely, too unscientifically; and even today, all too frequently, the same is still true. However, provided that it is used with proper intellectual rigour, as advocated by Hennig, the method is still the best available.

This method of classification possesses several advantages over the now fashionable cladistic method. It is essentially the most practical method, the most useful for a wide variety of purposes, and it contains the greatest amount of information; one might instance the hiving-off from a large taxon (e.g. Reptilia) of a daughter-group (Aves) into a separate taxon of equivalent rank (Class) in order to indicate extreme evolutionary divergence. (It is true that this to some extent obscures the simple phylogenetic content of the classification, but that information is still available, in unambiguous graphic form, in the dendrogram.) The structure of the evolutionary classification permits the discussion of ancestor–descendant relationships, whereas cladistic classifications regard all taxa as terminal in position and consider only sister-group relationships. Moreover, the very fact that evolutionary classifications are drawn up in an arbitrary fashion confers upon them the necessary degree of uniform-

ity and stability that is lacking in cladistic classifications; the latter vary enormously from worker to worker and, according to the cladistic creed, they are obliged to change with every alteration to the perceived phylogeny. Finally, there is the important point that evolutionary classifications are used far more widely than any other.

References

- Ashlock, P.D. 1971. Monophyly and associated terms. *Systematic Zoology* **20**, 63–69.
- Beatty, J. 1982. Classes and cladists. *Systematic Zoology* **31**, 25–34.
- Charig, A.J. 1982. Systematics in biology: a fundamental comparison of some major schools of thought. In: K.A. Joysey & A.E. Friday (eds) *Problems of phylogenetic reconstruction*. Systematics Association Special Volume No. 21, pp. 363–440.
- Hennig, W. 1966. *Phylogenetic systematics*. 2nd edn 1979. University of Illinois Press, Urbana.
- Platnick, N.I. 1980. Philosophy and the transformation of cladistics. *Systematic Zoology* **28**, 537–546.
- Wiley, E.O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. Wiley Interscience, New York.

5.2.4 Stratophenetics

P. D. GINGERICH

Stratophenetic analysis is an approach to understanding the ancestor–descendant or genealogical relationships of organisms and groups of organisms preserved in the fossil record. The approach is based on: (1) quantitative assessment of morphological (*phenetic*) similarity, interpreted in the context of (2) independent evidence of geological age (furnished by *stratigraphy*). Morphology is important because it is what we can see and study directly in living organisms, and the material record of life in the past is morphological. Time is important because genealogy is sequential. Stratigraphy is the discipline that correlates short sequences of life's history ordered by superposition in local geological sections, building longer composite histories for continents and seaways. Geography too plays a role in phylogenetic inference because organisms propagate within the spatial confines of their geographical ranges.

The goal of stratophenetics, like that of cladistics (Section 5.2.2), is more than a phenetic assessment of affinity or a classification of organisms based solely on morphological similarity. Stratophenetics and cladistics both seek to clarify genealogical relationships. Stratophenetics differs from cladistics in placing more emphasis on time and in seeking ancestor–descendant relationships explicitly. These are expressed in phylogenetic trees rather than cladograms. The ultimate goal is to know the history of life. It is sufficient, in the interim, that stratophenetics continues to augment and extend a well established outline of this history based on fossils, identifying gaps as well as continuity in the historical record.

General approach

The term *stratophenetic(s)* was coined to characterize palaeontological procedures commonly used in studying phylogenetic relationships in the fossil record (Gingerich 1976, pp. 15–16). These procedures were long employed without a name (see Colbert 1963; Rowell 1970; and others) because the logic seemed self-evident and no competing approaches were advocated by palaeontologists. Responding to the development of phenetics and cladistics by neontologists, Simpson (1976) listed a summary of ‘eclectic’ or ‘evolutionary’ systematic procedures, but Simpson’s procedures and indeed the names he used to describe them seem unduly broad and vague (but see Section 5.2.3).

A stratophenetic approach to phylogeny involves four steps:

1 *Within-locality or within-sample organization.* Quantitative study of morphological variation in each locality sample of the organisms under study, to identify clusters of specimens belonging to species or other operational taxonomic units (populations, genera, families, etc.) based on morphological similarity at one time and place. A taxon exists only in relation to another, and each taxon in a given time interval or locality must differ by a measurable amount from all others before it can be recognized as distinct.

2 *Stratigraphic organization.* Superposition of localities within local stratigraphic sections and correlation of localities between sections. Correlation is based on sequential change observed in fossils, palaeomagnetic signatures, radiometric dating, and any other geological evidence. Stratigraphic superposition determines the polarity of character

transformations observed in a sequence of fossils. Superposition in each local section is determined before correlation between sections. Thus superposition and polarity are independent of correlation.

3 *Stratophenetic linking.* Operational taxonomic units in adjacent time intervals are linked together by their overall morphological similarity, beginning with intervals that have the most taxonomic units and linking those in subjacent (earlier) or superjacent (later) intervals. When a taxon overlaps no other in an adjacent interval, the search for a similar ancestor or descendant is extended to the next subjacent or superjacent interval, and this process may be repeated. Ideally, there is more overlap in the ranges of variation of taxa linked between two adjacent intervals than there is in the ranges of variation of taxa within the same interval. No attempt is made to restrict similarity to shared derived features at this stage because there is no way to determine *a priori* which characteristics are primitive and which are advanced, and there is no way to determine *a priori* which advanced features are uniquely derived and which evolved convergently.

Stratophenetic linking can be approached, as Rowell (1970) has done, by looking at species in a multivariate morphometric space with principal component I (or I and II) as a horizontal axis (or axes), lifting species to their appropriate stratigraphic levels on a vertical axis, and drawing connections between similar forms in successive intervals of time. The most *economical* pattern of linking is the one requiring the minimum number of evolutionary lineages connecting all taxa, and the most *complete* pattern is the one with the fewest empty intersections of a lineage passing through a time interval.

4 *Hypothesis testing.* Patterns of stratophenetic linking are phylogenetic hypotheses that are tested each time a new specimen, a new locality sample, or a new taxon is discovered that belongs to the group under study. *Robust* patterns are those that change little as new discoveries are made.

Classification based on phylogeny requires two additional steps:

5 *Grouping.* Operational taxonomic units are grouped into sets of similar forms corresponding to higher taxonomic units (genera, families, etc.). These groups are constrained to include all intermediates in the minimum spanning tree of stratophenetic linking.

6 *Diagnosis:* Groups are distinguished from each

other using combinations of characteristics unique to each group. Shared derived characteristics are particularly important in diagnosing groups from ancestral stocks that preceded them in time. Shared derived diagnostic characteristics are identified *a posteriori* by their distribution on the minimum spanning stratophenetic tree.

Stratophenetic linking at the species level

Within-locality organization, stratigraphic organization, phenetic linking, and hypothesis testing are all illustrated in Fig. 1, which outlines the North American radiation of eight species of Carpolestidae and nine species of Plesiadapidae (archaic primates) found in a 1400 m stratigraphic section on Polecat Bench (and shorter sections measured nearby) in northwestern Wyoming. Solid lines represent the means and probable ranges of seventeen species-level taxa (*Elphidotarsius florenceae*, *Pronothodectes jepi*, etc.) recognized in studies by Rose (1975) and Gingerich (1976). Species differ principally in size, but they also differ in other morphological characteristics (dental formula, enamel crenulation, incisor form, etc.). Within-locality organization involves grouping specimens

representing all species-level taxa within each fossil-bearing locality; stratigraphic organization involves correlating all localities bearing the same or closely similar taxa and arranging these in stratigraphic order for comparison.

Phenetic linking of similar species-level taxa in adjacent intervals is shown with dashed lines in Fig. 1. The result suggests that there is a single carpolestid lineage and a single plesiadapid lineage below 500 m, while two carpolestid daughter lineages and two plesiadapid daughter lineages are present in some intervals above 500 m. Each pattern is economical in that the relationships of all species in each family require no more lineages than the maximum number of coexisting taxa; and each pattern is reasonably complete in that there is only one extended interval (800–1200 m) where lineages lack representative specimens or intermediate taxa.

The patterns shown in Fig. 1 are tested every time a new carpolestid or plesiadapid is found in northwestern Wyoming. There have been *c.* 80 new specimens found since 1976. These are superimposed in Fig. 1 as solid circles and associated integers. All fall within or near the dashed lines of the original patterns of linking, indicating that the original stratophenetic hypotheses of relationship

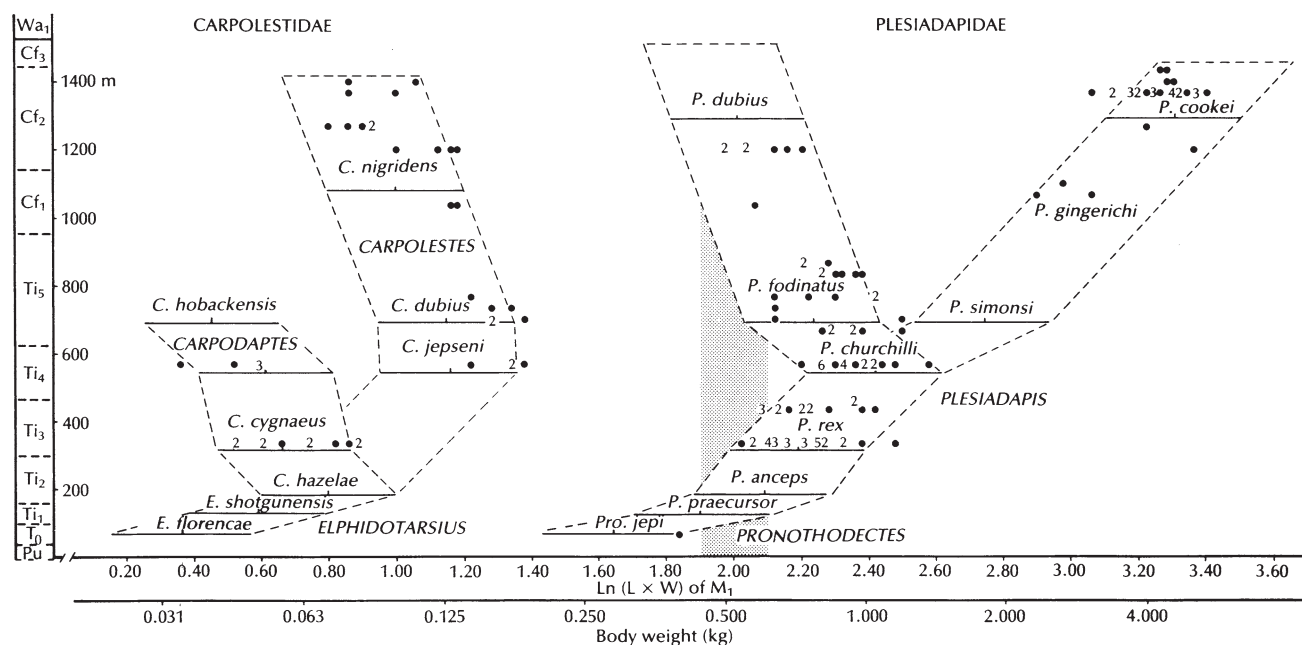


Fig. 1 Pattern of stratophenetic linking in early Cenozoic Carpolestidae and Plesiadapidae. Evolution of tooth size (logarithm of length multiplied by width of first lower molar) and, by inference, evolution of body size (estimated weight in kilograms) are given on the horizontal axis, but the pattern of linking shown here is based on all characteristics preserved in carpolestid and plesiadapid fossils. The vertical axis is a metre level in one master stratigraphic section in northwestern Wyoming (U.S.A.). Standard subdivisions of the Palaeocene and Early Eocene time-scale are also shown. The phylogenetic hypothesis shown here has proved to be robust in that new discoveries (solid circles and associated integers representing multiple specimens) have required little change in the basic pattern of linking. (From Gingerich 1976, 1980, with additions.) Reproduced, with permission, from the *Annual Review of Earth and Planetary Science*, Vol. 8 © 1980 by Annual Reviews Inc.

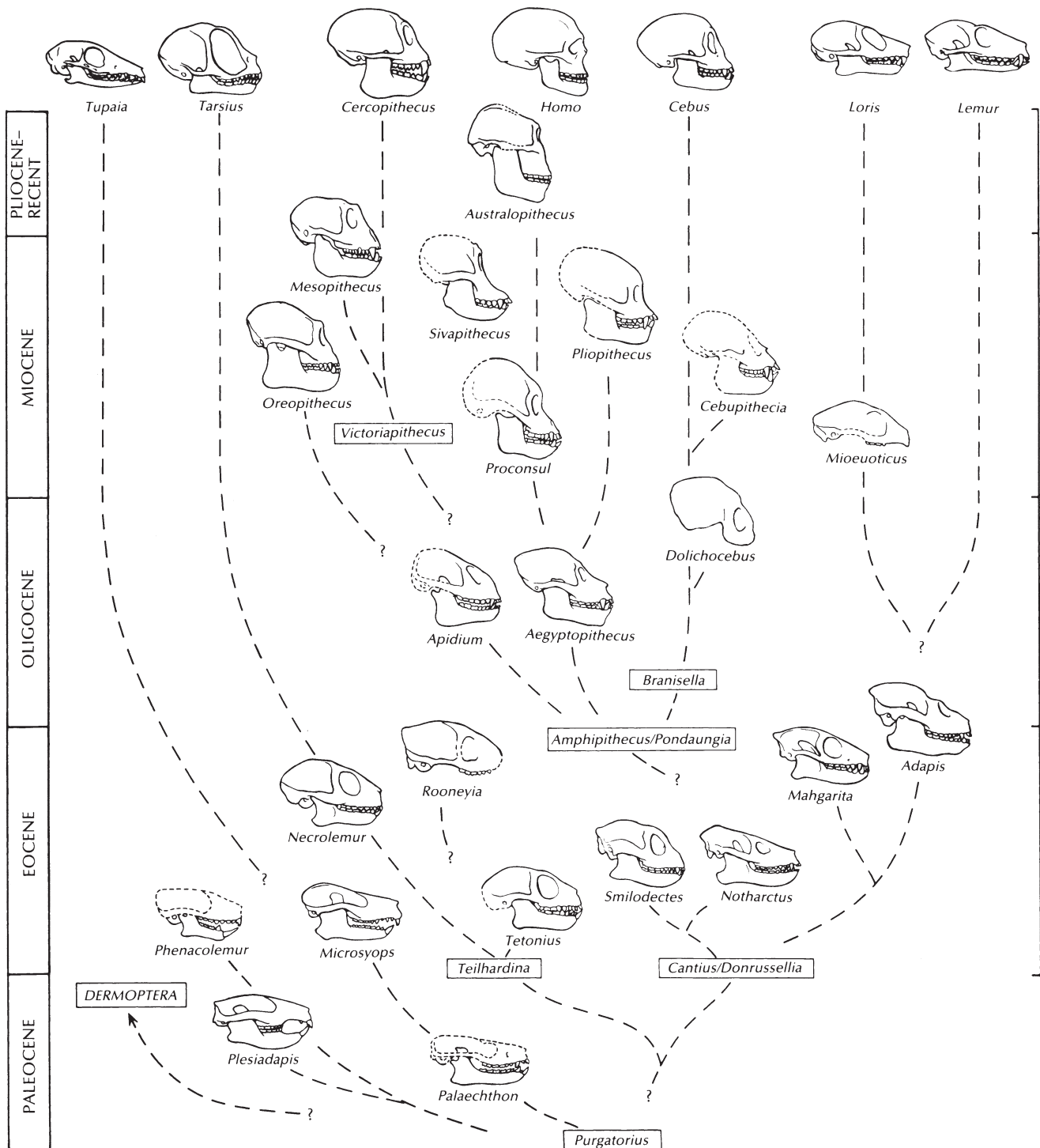


Fig. 2 Stratophenetically constructed outline of primate phylogeny. Morphology (form) is arrayed on the horizontal axis, and the vertical axis encompasses Cenozoic time. Fossil primates known from partial or complete skulls are ordered in form and in time relative to other known fossils. Note that the extant superfamilies Cercopithecoidea, Hominoidea, and Ceboidea are represented by a relatively dense fossil record, while there are many gaps in the historical record of Tupaioidea, Tarsioidea, Lorioidea, and Lemuroidea. Linkages marked by queries require additional evidence. (From Gingerich 1984.)

are robust and require little modification to accommodate the new evidence found to date.

It is worth noting that the patterns of strato-

phenetic linking shown here are *divergent upward*, i.e. contemporary lineages are found to join at their bases rather than their tops. The important and

long-known generalization that phylogenetic trees diverge rather than converge through time is an empirical result of stratophenetic analysis.

Stratophenetics and cladistics at higher taxonomic levels

Stratophenetics and cladistics can be viewed as alternative approaches to the reconstruction of phylogeny. Which approach is more appropriate in any particular instance depends on the nature of the historical record available for the group under study. Where there is a dense and continuous fossil record available for a group of closely similar species, like the example discussed above (Fig. 1), it is appropriate to analyse the evidence stratophenetically. Numerous intermediate forms provide evidence of transition, and the taxa differ in so few characteristics that it would be difficult to make meaningful cladistic inferences.

At the opposite end of the spectrum, there are groups of organisms (e.g. some insects, bony fishes, perching birds) for which the fossil record is notably discontinuous and includes only a fraction of the morphological diversity observed to be living today. Here stratophenetic analysis can contribute little, and cladistic inference may be warranted. Cladistic inference is rarely carried out in a vacuum, however, and it is usually appropriate to structure inferences to take advantage of broad outlines of relationship evidenced in the fossil record.

The evolutionary diversification of the mammalian order Primates (Fig. 2) is an example where the phylogenetic tree obtained from stratophenetic linking provides only an outline of the history of the group. Genera illustrating each of the seven superfamilies of living primates are arranged across the top of the diagram. Genera known from skulls in the fossil record, representing one of the living superfamilies or one of three extinct superfamilies, are positioned beneath their most similar living relatives in the appropriate interval of geological time. Stratophenetic linking based on all the evidence of morphological similarity (dashed lines) shows likely genealogical relationships at the family or superfamily level. Of the living groups, Tupaioidea may be related to Microsyopoidea and Plesiadapoidea, but there is a very large gap in their fossil record. Tarsioidea extend back into the Eocene (to *Necrolemur* and its allies), but here again there is a very large gap in the Late Cenozoic. Cercopithecoidea, Hominoidea, and Ceboidea have a reasonably dense fossil record in the Late

Cenozoic, and they appear to converge on *Apidium*-like and *Aegyptopithecus*-like forms in the Middle Cenozoic. Lorisioidea and Lemuroidea have poor fossil records, and they may or may not be derived from Eocene Adapoidea.

Consideration of all the morphological and geographical evidence in a stratigraphic context identifies parts of the historical record that are better known than others; such consideration identifies areas of questionable relationship (origin of lemurs and lorises, for example) that may repay a cladistic analysis carried out in the context of a stratophenetically based outline of primate history (Gingerich 1984). The scale is different, and the pattern of phylogeny is less complete, but the principles of stratigraphic organization and phenetic linking used to produce the outline of primate phylogeny shown here are the same as those used to link species of *Plesiadapis* in Fig. 1.

Conclusions

Stratophenetics differs from cladistics in placing more emphasis on time and in seeking ancestor–descendant relationships explicitly. These relationships may be at the species level, or more broadly drawn at higher taxonomic levels. Stratophenetics as a general approach to phylogeny at any taxonomic level seeks to identify taxa intermediate between others in form, in space, and in time, because intermediates provide the only positive evidence that a given transition occurred.

Stratophenetic outlines are phylogenetic trees constructed with time as an integral component. Phylogenetic trees are more informative than cladograms in relating the divergence of major taxonomic groups to geological time. In addition, stratophenetic outlines have heuristic value in identifying what we do *not* know (as well as what we know), thus identifying gaps in the historical record worthy of investigation. Time is a fundamental dimension in evolutionary studies, and a major goal of palaeontology should continue to be the study of the diversification of major groups of organisms in relation to geological time.

References

- Colbert, E.H. 1963. Phylogeny and the dimension of time. *American Naturalist* **47**, 319–331.
- Gingerich, P.D. 1976. Cranial anatomy and evolution of North American Plesiadapidae (Mammalia, Primates). *University of Michigan Papers on Paleontology* **15**, 1–140.

- Gingerich, P.D. 1980. Evolutionary patterns in early Cenozoic mammals. *Annual Review of Earth and Planetary Sciences* 8, 407–424.
- Gingerich, P.D. 1984. Primate evolution: evidence from the fossil record, comparative morphology, and molecular biology. *Yearbook of Physical Anthropology* 27, 57–72.
- Rose, K.D. 1975. The Carpolestidae, early Tertiary primates from North America. *Bulletin of the Museum of Comparative Zoology, Harvard University* 147, 1–74.
- Rowell, A.J. 1970. The contribution of numerical taxonomy to the genus concept. In: E.L. Yochelson (ed.) *Proceedings of the North American Paleontological Convention* 1, 264–293. Allen Press, Lawrence, Ka.
- Simpson, G.G. 1976. The complete palaeontologist? *Annual Review of Earth and Planetary Sciences* 4, 1–13.

5.2.5 Problematic Fossil Taxa

S. BENGTSON

Introduction

Fossils that cannot readily be placed in established phyla or major groups are commonly called *problematic*. The main problem of problematic fossils (or 'problematica') has often been perceived as one of ignorance, suggesting that if we only understood the nature of such a fossil better we could place it in a living taxon, but recent work has emphasized the potential value of problematic fossils as possible representatives of extinct major taxa. They could thus expand our concept of the diversity of life beyond those clades that have survived to the present day. A number of case studies and state-of-the-art summaries were presented by Hoffman & Nitecki (1986).

Extinct phyla

If a phylum has become extinct, its fossils are regarded as problematic. The converse is not always true (i.e. problematic fossils are not necessarily representatives of extinct phyla), and the question of phylum affinity is one of the most fundamental that can be asked about such fossils. In general, there has been a reluctance to identify extinct phyla. The reasons for this seem to be linked mainly with a tendency to regard the now living assemblage of phyla as a fundamental division of the world of

organisms. This viewpoint is not necessarily valid. Nevertheless, it may be impractical to use the phylum concept for classification of organisms belonging to the earliest phases of radiation of major clades.

Two aspects of phyla should be stressed. First, phyla themselves may be regarded as problematic taxa. They have come to circumscribe groups of organisms that are more or less obviously closely related to one another, the boundaries between phyla being drawn where the further relationship is unknown or uncertain. Second, phyla as currently recognized are almost exclusively based on living organisms. They are thus groupings of lineages that happen to have survived until now. Most fossil groups, even extinct ones, can be incorporated in such recent phyla with relative ease, and some may be admitted through a widening of the scope of a certain phylum. Problematic fossils are generally those that defy such straightforward taxonomic solutions; they become increasingly numerous with increasing geological age and are particularly characteristic of the Proterozoic and earliest Phanerozoic. This is consistent with the fact that all modern-day animal phyla appear to have been established no later than the beginning of the Phanerozoic.

Examples of problematic fossils

Some major fossil groups in the Palaeozoic are classic problematic fossils. For example, conodonts and graptolites — both of considerable biostratigraphic importance — were for a long time regarded as taxonomic conundrums. Discoveries of fine anatomical structures — preserved soft parts of conodonts, and the so-called 'cortical bandages' in graptolite periderm — have brought the solution closer to a consensus on the chordate affinities of the former (Dzik *in* Hoffman & Nitecki 1986; Aldridge 1987) and the hemichordate affinities of the latter (Urbanek *in* Hoffman & Nitecki 1986).

Other well known examples of diverse fossil groups of uncertain affinities are archaeocyathans, hyoliths, and tentaculites. These are also of some biostratigraphic importance, albeit more limited than in the case of conodonts and graptolites. Archaeocyathans are a diverse group of almost exclusively Lower Cambrian sedentary organisms typically forming a porous cup-shaped skeleton. They are usually considered as an extinct phylum, although their close similarity to sponges has recently been emphasized (Debrenne & Vacelet 1983).

Hyoliths and tentaculites had calcareous, cone-shaped conchs that show some resemblances to mollusc shells. They are placed by some specialists in the Mollusca, but may be regarded more properly as representatives of extinct phyla.

Most problematic fossils, however, are less diverse groups, sometimes represented only by a few species. Part of the reason for this may be artificial; rare fossils do not become intensively studied and are less likely to yield sufficient information to reveal their biological nature. But these problematic fossils may also represent clades of potential phylum status that did not survive to diversify. (Or, from a different viewpoint, they did not diversify enough to withstand chance extinction events.)

Many now living animals construct tubes as more or less permanent living structures. Such tubes often have a very simple morphology and reveal little about the soft parts that formed them. The fossil record features a multitude of tubular fossils, and many of them are problematic fossils. The earliest known metazoan biomineralizer, the Late Precambrian *Cloudina*, built calcareous tubes. Towards the beginning of the Cambrian there appeared in rapid succession a large number of tube-dwelling organisms which constructed tubes of different substances, both purely organic and reinforced with agglutinating mineral particles or various biominerals. Some of these tubes are sufficiently similar in form, composition, and structure to those of living organisms (such as annelids, pogonophorans, or foraminiferans) that a near affinity is probable, but in only a few cases are the similarities detailed enough for the affinity to be beyond reasonable doubt. Examples of well known problematic tubular fossils are the phosphatic hyolithelminths and the calcareous coleolids (cf. Fisher 1962). Neither of these groups is demonstrably monophyletic.

Many metazoan skeletons consist of numerous individual sclerites that normally dissociate upon the death of the animal. Such disarticulated fossils are another rich source of problematica throughout the Phanerozoic. The variety of skeletal elements in living organisms, however, is still very poorly known, and in some cases a closer comparison with spicules and sclerites of known organisms has been sufficient to solve the riddle of a problematic disjunct skeletal element. Nevertheless, a number of spicule- or sclerite-forming fossil organisms are sufficiently distinct in their mode of skeletalization that no homologies can be envisaged with known skeletal elements, and the organisms must be re-

garded as true problematica. Such fossils are particularly difficult to analyse, in that little information on the body shape and anatomical detail of the animal can normally be gathered from the dissociated sclerites, and no comparisons with better known related forms are possible. The occasional finds of complete articulated skeletons are of paramount importance in solving these problems.

Spicular constructions characterize not only metazoans, but also metaphytes and protists. The skeleton of receptaculitids and cyclocrinids consists of calcareous units radiating from an axis. These two groups are classic Palaeozoic problematica that have drifted among metazoans (particularly sponges), protists and metaphytes (particularly calcareous algae) in their search for a phylogenetic home. Current thought interprets them as calcareous algae, the cyclocrinids being particularly close to the dasyclads (Nitecki *in* Hoffman & Nitecki 1986; Beadle 1988).

Calcareous algae have also been a popular 'home' for a large number of more or less nondescript calcareous structures, much to the despair of algologists (Babcock *in* Hoffman & Nitecki 1986). Most of these fossils have been investigated only in petrographic thin sections, and the total morphology is poorly known, although their mineralogy may in fact be better understood than that of morphologically more distinct fossils.

With the realization that many modern sponges (the coralline sponges, or 'sclerosponges') may in fact secrete basal calcareous skeletons, some laminated calcareous fossils (notably the stromatoporoids) were with apparent success reinterpreted and reassigned from problematic coelenterate-like fossils to the sponges (Wood 1987). Such a solution was also proposed by some workers for the tabulates, commonly regarded as corals. That the latter proposal was over-enthusiastic has recently been demonstrated by the find of preserved polyps in a Silurian favositid (Copper 1985).

Micro- and nannofossils throughout the Late Precambrian and Phanerozoic include a large number of problematic remains. The organic microfossils include several diverse groups of considerable stratigraphic use but of unknown systematic affinity. The acritarchs are an admittedly heterogeneous assemblage of cyst-like organic microfossils, thought to represent algal eukaryotes. They are uniquely important for biostratigraphy in the Precambrian, where fossils of biostratigraphic potential are otherwise almost absent. Chitinozoans are flask-like, operculate, organic microfossils, often inter-

puted as the remains of metazoan eggs but in essence of unknown systematic affinity. They are known from the Cambrian to the Devonian and are of particular stratigraphic usefulness in the Lower Palaeozoic.

The analysis of problematic fossils

When dealing with problematic fossils one is faced with a complex situation in which the most difficult problem may be to find a sufficient number of characters interpretable in terms of homology. Obviously there can be no strict formula to follow in order to assess whether a problematic fossil belongs to a certain phylum or not, but it may be helpful to use the following set of questions as a checklist:

- 1 What are the observable characters of the fossil?
- 2 What were the original characters of the animal when preservational and diagenetic factors have been taken into account?
- 3 What constructional and functional significance can be attributed to the characters?
- 4 Can these characters be interpreted as homologous to characters formed by members of any known phylum?
- 5 Are any of these possibly homologous characters unlikely to have arisen by convergence due to constructional or functional factors?
- 6 If a character cannot be, or is not likely to be, homologous with any characters in known phyla, can it be a derived character that evolved secondarily from a member of a known phylum?
- 7 Does the fossil show affinities with any other fossils from the same or any other period of time? Repeat questions 1–6 for this combined group.
- 8 If the fossil (group) can be interpreted on the basis of its characters as belonging to a known phylum, what are the consequences for the evolutionary history of the phylum?
- 9 If the fossil (group) cannot be interpreted as belonging to a known phylum, what testable hypotheses may be formulated regarding its biological nature and phylogenetic origin?

These steps do not outline a proper phylogenetic analysis but may serve as preparatory measures for one. Their main purpose is to serve as a safeguard against casual misidentifications.

The significance of problematic fossils

Problematic fossils point to inadequacies in our interpretations of the fossil record. Although one

should always attempt first to find a place for a problematic fossil in the known phylogeny of organisms, it is crucial to realize that the established taxonomic system is heavily biased towards the clades that have survived until today. The potential importance of extinct major groups is nowhere better illustrated than in the dichotomy between Glaessner (1984) and Seilacher (1984) in their interpretation of the Late Precambrian Ediacaran biota (Sections 1.3, 2.13. 1). Glaessner has championed a style of interpretation which assumes that this biota may be classified within the established taxonomic framework of living animals. Seilacher has argued that the Ediacaran biota represents a separate branch of multicellular organisms that became extinct at the end of the Precambrian. The two poles of the issue thus embody totally different understandings of the history of the animal kingdom. The dichotomy is more philosophical than methodological in nature, but any crucial test of the opposing concepts will have to take a large number of factors (taphonomic, preservational, physiological, behavioural, etc.) into account.

Problematic fossils may thus be seen as challenges to our concepts of the diversity of the organic world in geological time. Whether they are problematic simply because we do not understand their nature sufficiently, or because they represent unknown branches of the evolutionary tree of life, they need to be studied with the utmost care and open-mindedness. It is particularly important not to force a cosmetic solution onto the scientific problem that they present by simply assigning them to the least dissimilar known phylum.

References

- Aldridge, R.J. 1987. Conodont palaeobiology: a historical review. In: R.J. Aldridge (ed.) *Palaeobiology of conodonts*, pp. 11–34. Ellis Horwood, Chichester.
- Beadle, S.C. 1988. Dasyclads, cyclocrinids and receptaculitids: comparative morphology and paleoecology. *Lethaia* **21**, 1–12.
- Copper, P. 1985. Fossilized polyps in 430-Myr-old *Favosites* corals. *Nature* **316**, 142–144.
- Debrénne, F. & Vacelet, J. 1983. Archaeocyatha: is the sponge model consistent with their structural organization? In: W.A. Oliver, W.J. Sando, S.D. Cairns, A.G. Coates, I.G. Macintyre, F.M. Bayer & J.E. Sorauf (eds) *Recent advances in the paleobiology and geology of the Cnidaria*, pp. 358–369. *Palaeontographica Americana*, No. 54.
- Fisher, D.W. 1962. Small conoidal shells of uncertain affinities. In: R.C. Moore (ed.) *Treatise on invertebrate paleontology. W. Miscellaneous*, pp. W98–W143. Geological Society

- of America, Boulder, Co., and University of Kansas Press, Lawrence, Ka.
- Glaessner, M.F. 1984. *The dawn of animal life*. Cambridge University Press, Cambridge.
- Hoffman, A. & Nitecki, M.H. (eds) 1986. *Problematic fossil taxa*. Oxford Monographs on Geology and Geophysics No. 5, 267 pp. Oxford University Press, New York.
- Seilacher, A. 1984. Late Precambrian and early Cambrian Metazoa: preservational or real extinctions? In: H.D. Holland & A.F. Trendall (eds) *Patterns of change in Earth evolution*, pp. 159–168. Springer-Verlag, Berlin.
- Wood, R. 1987. *Biology and revised systematics of some late Mesozoic stromatoporoids*. Special Papers in Palaeontology, No. 37.

5.3 Analysis of Taxonomic Diversity

A. B. SMITH

Diversity enters into many aspects of palaeobiology and particularly in the analysis of evolutionary patterns and ecological (community) structure. In evolutionary studies taxonomic diversity is measured by counting or estimating the number of taxa of a specific categorical rank known from a particular locality, lithological formation or time-span, and is generally taken as a proxy for morphological diversity. Ecological and biogeographical diversity are considered elsewhere (Sections 4.10, 4.16, 4.17).

Species diversity

A count of the number of species recorded from a rock unit or time-span will measure sampled diversity (Fig. 1A). However, there are many reasons why sampled diversity may not be a true reflection of absolute diversity (Raup 1976), the following being some of the more important:

- 1 Sampled diversity correlates with the amount of rock available for study, measured either as surface outcrop area (Fig. 1C) or estimated volume. The larger the outcrop area the greater is the diversity of species. However, surface outcrop area can only provide a crude approximation, since compilations do not distinguish between rocks of different facies. A large area of terrestrial Red Beds, for example, might have very much fewer fossils than a small outcrop of reefoidal limestone.
- 2 There is variation in the extent to which regional diagenesis and metamorphism destroy fossils from the rock record.
- 3 The number of palaeontologists involved in describing fossils from particular geological periods is

not uniform (Fig. 1B); some time periods have attracted more attention than others. Whether diversity of species from specific time periods is directly related to the number of workers that have studied the rocks of that period, or whether the number of workers is proportional to the extent of rock outcrop is unresolved. The fact that most species are recorded from single localities or local areas (Smith & Patterson 1988) suggests that it is availability of surface outcrop of the correct lithofaces that is important.

4 The distribution of Lagerstätten (Section 3.11) affects apparent diversity. Deposits that preserve the soft-bodied biota provide a more complete glimpse of community structure and diversity. They create apparent peaks in diversity that are artifacts, produced because weakly skeletalized taxa are not preserved at other times; most workers avoid this problem by excluding such taxa from their analyses.

In the analysis of global diversity through time, further biases may be introduced because of inaccuracies in the time-scale used (particularly crucial in normalized data), and the predominance of data from North America and Europe. All these problems have meant that the global history of species diversity is difficult to reconstruct, even for specific groups. (See Padian & Clemens *in* Valentine 1986, for an excellent discussion of what can and cannot be deduced about changing diversities for the terrestrial habitat.)

Five different approaches to estimating global species diversity through time have been proposed (see Signor *in* Valentine 1986, and the references therein).

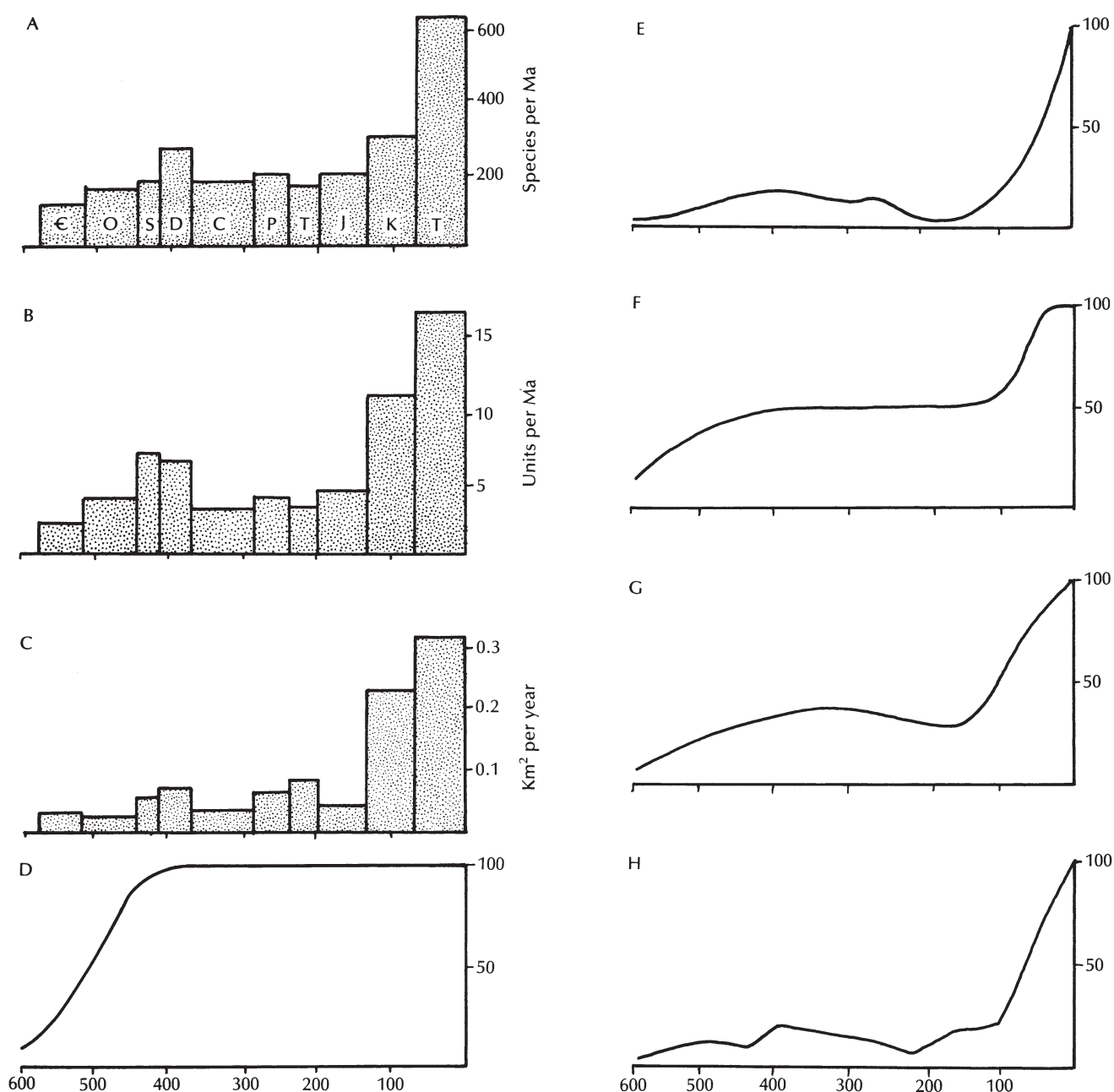


Fig. 1 Global species diversity through the Phanerozoic. A, Sampled species diversity. B, Palaeontological interest units for each time interval. C, Map area of rock outcrop for each time interval. D–H, Estimated global species diversity as a percentage of present day diversity: D, equilibrium model; E, empirical model; F, species richness model; G, consensus model; H, sampling model. (A and C from Raup 1976; B and D from Sheehan 1977; D–H from Signor *in* Valentine 1986.)

1 Equilibrium model (Fig. 1D). Gould and others proposed this model on the basis of the shape of spindle diagrams representing number of genera included in higher taxa. They considered that the position of the 'centre of gravity' in such diagrams indicates whether a group is in equilibrium or not. Since taxa from the Ordovician onwards appear to

be in equilibrium using this criterion, they concluded that species richness could have been constant since then. This conclusion was supported by Sepkoski's factor analysis of higher taxonomic groupings (Orders, Families).

2 Empirical model (Fig. 1E). Valentine estimated the ratio of genera in families for each time period and

then assumed that the same ratio held true for number of species in genera. Extrapolation from sampled generic diversity indicated that species diversity had increased by an order of magnitude since the middle Palaeozoic.

3 Species richness model (Fig. 1F). Bambach proposed that species richness could be estimated by looking at specific, well-preserved communities through time and extrapolating from them. From a hundred such communities he concluded that species diversity was relatively stable during the Palaeozoic, but changed dramatically (particularly in nearshore habitats) after the Mesozoic.

4 Consensus model (Fig. 1G). Sepkoski and others combined diverse lines of evidence to produce a consensus model. They used sampled species, generic, familial, and trace fossil diversity, together with Bambach's within-habitat species diversity, and found a significant correlation between all five. The common element found was interpreted as signal.

5 Sampling model (Fig. 1H). Signor developed a method of estimating actual species diversity from sampling theory. He assumed that the frequency distribution of species at a particular geological horizon was log-normal. He used Raup's geological mapped area (Fig. 1C) and estimated volume of rock, and Sheehan's estimate of palaeontological interest units, as measures of sampling intensity for each period (Fig. 1B). The total number of Cenozoic species was estimated and used to calibrate estimates for earlier geological periods.

Each method has its own advantages and disadvantages. The empirical, equilibrium, and consensus methods all rely on higher taxa being commensurate and equivalent entities. This is clearly not so (see below) and generic and familial data, though less prone to sampling problems than species data, suffer from other (taxonomic) biases. Bambach's species richness model does not rely on higher taxonomic diversity but does depend very heavily upon the specific fossil assemblages chosen for analysis (Hoffman 1985). Only Signor's analysis seems truly to take sampling bias into account, but even this has had to make a number of uncorroborated assumptions.

Species diversity has increased during the Phanerozoic but, because so many biases and problems beset the estimation of global diversity through time, little else is certain about the precise pattern of this change. Diversity-dependent models of global species diversity seem unsupported at present,

both on theoretical and empirical grounds (Cracraft 1985; Hoffman 1985). So long as species-level data primarily reflect the abundance of fossiliferous strata and non-monophyletic data plague taxonomic compilations, assessments of global diversity through time will remain problematic.

Diversity of higher taxa

Since the analyses of Simpson (1952) on vertebrate diversity and Valentine (1969) on marine invertebrates, it has been customary to infer evolutionary patterns from the diversity patterns of higher taxonomic categories such as Order or Family. Both of these authors found that the higher the taxonomic rank analysed the earlier in time was maximum diversity achieved. Taxonomic rank is, however, an arbitrary concept and rank can be given for a number of independent reasons (e.g. to accommodate diversity at species level, for paraphyletic 'ancestral' groups, for perceived morphological distinction, either real, or misconstrued). Higher taxa appear earlier in the geological record because: (1) the Linnaean system of nomenclature is hierarchical and, as shown by Raup (1983), higher groups must appear earlier in the record than the majority of their subgroups; and (2) traditional taxonomic practice has created paraphyletic higher taxa for dustbin groups comprising primitive early members.

Higher taxonomic categories are a poor indicator of species diversity if we accept Signor's sampling model (Signor *in* Valentine 1986). This is because most higher taxa are currently non-monophyletic — the creation of *ad hoc* classifications. Ranges and durations of higher taxonomic groups are less affected by sampling bias than species are, but are more affected by taxonomic procedures. Monophyletic groups are real but constitute only a small proportion of currently defined higher taxa. The rest represent groupings made by taxonomists on an arbitrary basis. Clearly, patterns derived from the analysis of largely non-monophyletic data will reflect the predilections of taxonomists and not real biological patterns.

Diversity and extinction

Peaks and troughs in diversity through time are sometimes interpreted as evidence for 'adaptive radiation' or 'mass extinction' (Section 2.12.3). However, rarely is sampling bias adequately taken into account. Taxa can disappear from the fossil record

for three reasons: (1) through biological extinction; (2) through sampling failure; and (3) through taxonomic name change. The first, biological extinction, is obviously what we wish to measure and only monophyletic groups can become extinct biologically. Paraphyletic groups, unless they include a monophyletic element that survives beyond the first appearance of the derived sister-group, disappear through taxonomist's convention and polyphyletic groups are artificial groupings without reality. Paraphyletic grades, created when a taxonomist subdivides a monophyletic group into two or more subgroups resulting in 'ancestral' groups defined on absence of characters (Section 5.2.2), generally terminate by pseudoextinction. Sampling failure can to some extent be taken into account through analysis of Lazarus taxa (Section 3.12). If there has been no change in name, Lazarus taxa are easily recognized, but taxonomists may have used gaps in the record as convenient places to divide a plesiomorphic 'ancestral group' from a derived monophyletic portion and only through cladistic analysis can such pseudoextinctions be identified.

References

- Cracraft, J. 1985. Biological diversification and its causes. *Annals of the Missouri Botanical Gardens* **72**, 794–822.
- Hoffman, T. 1985. Island biogeography and palaeobiology: in search for evolutionary equilibria. *Biological Reviews* **60**, 455–472.
- Raup, D.M. 1976. Species diversity in the Phanerozoic: a tabulation. *Paleobiology* **2**, 279–288.
- Raup, D.M. 1983. On the early origins of major biological groups. *Paleobiology* **9**, 107–115.
- Sheehan, P.M. 1977. Species diversity in the Phanerozoic: a reflection of labor by systematists? *Paleobiology* **3**, 325–328.
- Simpson, G.G. 1952. Periodicity in vertebrate evolution. *Journal of Paleontology* **26**, 359–370.
- Smith, A.B. & Patterson, C. 1988. The influence of taxonomic method on the perception of evolutionary patterns. *Evolutionary Biology* **23**, 127–216.
- Valentine, J.W. 1969. Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time. *Palaeontology* **12**, 684–709.
- Valentine, J.W. (ed.) 1986. *Phanerozoic diversity patterns*. Princeton University Press and American Association for the Advancement of Science, Princeton.

5.4 Vicariance Biogeography

L. GRANDE

Introduction

Biogeography is the study of distribution patterns of animal and plant taxa. It asks the question: 'In what specific geographical area of the Earth does (or did) a given taxon naturally occur?' *Vicariance* is a name for the process that occurs when a formerly continuous population is divided by the appearance of a barrier. The resulting isolated populations are thought by evolutionists to diverge (speciate) into *vicarious taxa* — taxa that are each other's closest relatives and initially occupy different (non-overlapping or allopatric) geographical areas within the original range of the ancestral species. *Vicariance biogeography* is therefore an historical study that assumes the present geographical distribution of organisms to be the result (at least in part) of an interplay between the biological evolution of taxa

and the physical evolution of the Earth's surface. It assumes that, if the history of life has paralleled the history of the Earth, then congruent biological and geological patterns of relationships should result.

Vicariance biogeography is thought to differ from some more traditional types of biogeographical studies (Section 5.5) because it does not look for dispersal (migration over a barrier) of a taxon as an explanation for its current distribution. Vicariance biogeographers do allow that the primitive cosmopolitanism of an ancestral taxon could have been achieved by enlarging its range through random processes or dispersal (e.g. seeds blown by the wind or carried by migratory birds), but differ from dispersalist biogeographers in their models for causal factors used to explain disjunct distributions and, ultimately, allopatric speciation.

Vicariance biogeography has become most popular during the last 20 years, but it dates back to several monographs by the late phytogeographer Leon Croizat (e.g. 1958, 1964). State of the art vicariance biogeographical techniques have been discussed in detail most clearly by Platnick & Nelson (1978), Nelson & Platnick (1980, 1981), Wiley (1981), and Brown & Gibson (1983, pp. 265–271).

Methodology

The method of vicariance biogeography is to search for general patterns of area relationships based on: (1) the relative relationships of endemic taxa; and (2) historical geology. Such a study might follow four steps:

1 *Collect primary data* about the relationships within one taxon. For example, we may find that in a family of teleost fishes containing three species (ABCidae in Fig. 1A) species A is more closely related to species B than to species C. With at least three taxa in our group we may discover a resolved pattern of relative taxonomic (i.e. phylogenetic) relationships based on a comparative anatomical study.

2 *Translate the biological group relationship into a pattern of area relationship.* For example (Fig. 1A), if species A is from area 1, B from area 2, and C from area 3, then teleost family ABCidae indicates that area 1 is more closely related to area 2 than to area 3.

3 *Look for a repeating pattern of area relationships.* For example, if plant family XYZaceae is found to have a pattern of phylogenetic relationships as shown in Fig. 1B, and species X is from area 1, Y from area 2, and Z from area 3, then plant family XYZaceae indicates that area 1 is more closely related to area 2 than to area 3 and repeats the pattern of area relationships shown independently by teleost family ABCidae. If several different groups of organisms indicate the same pattern of area relationships (e.g. Fig. 1C), the repeating pattern may reflect some general historical phenomenon. As the strength of the pattern increases, or as the complexity of the repeated pattern increases, the probability of finding congruent patterns of area relationship due to chance alone is diminished.

4 *Look for a non-biological (e.g. geological) event which gives the same pattern of area relationships,* and is thus a possible causal explanation for the repeating biological pattern. For example, if a large connected area (Fig. 2A) was subdivided by one barrier during Oligocene time (Fig. 2B) and later further subdiv-

ided by a seaway (Fig. 2C), then areas 1 and 2 would have a more recent common ancestry than areas 1 and 3 or areas 2 and 3. This geological history indicates that area 1 is more closely related to area 2 than to area 3, independent of any biological evidence (Fig. 2D). If a biological pattern of area relationships is very strong (repeated many times) vicariance biogeographers would predict that there is probably a general, non-biological (e.g. geological or environmental) explanation.

Use of fossils in vicariance biogeography

Fossils provide additional data which can increase the biogeographical range of a taxon in space or in time (e.g. coelacanths restricted to the western Indian Ocean today were once present in North America and elsewhere; fossil pike [Esocidae] in the Palaeocene indicate that the group dates back to at least 62 Ma). Fossils also reveal taxa unknown in the Recent biota (e.g. dinosaurs, ichthyodectiform fishes). Fossil *biotas* can contribute an additional methodological step that is potentially of use in vicariance studies, and this is *time control* (Grande 1985).

Vicariance biogeographers generally either use only Recent taxa as data, or a combination of Recent and fossil taxa. If it is accepted that some species disperse, then it must also be accepted that in some areas where sufficient dispersal has occurred, it may be difficult or impossible to recognize a predominant pattern of area relationships based on the present (Recent) fauna. The predominant area pattern may have been clear at one time but later obscured by conflicting area patterns due to dispersal and changing geology (e.g. removal of long-standing barriers). For example, a predominant area pattern that reflected some geological event during pre-Eocene time (Fig. 3A) may later have been obscured by a non-congruent pattern (Fig. 3B) superimposed during Oligocene time, producing an unresolved area pattern in the Recent biota (Fig. 3C). Fossil biotas, because they are datable, can provide time control, and therefore have the potential to identify area patterns (such as that shown in Fig. 3A) hidden in the Recent biota. By examining only Eocene biotas (assuming Eocene biotas are present in the geographical areas of concern in this example — western North America, western Pacific, and eastern Atlantic), the dispersal event (Fig. 3B) that masked the earlier pattern (Fig. 3A) in the Recent biota can be filtered from the data. If a biota's predominant area relationship pattern changes

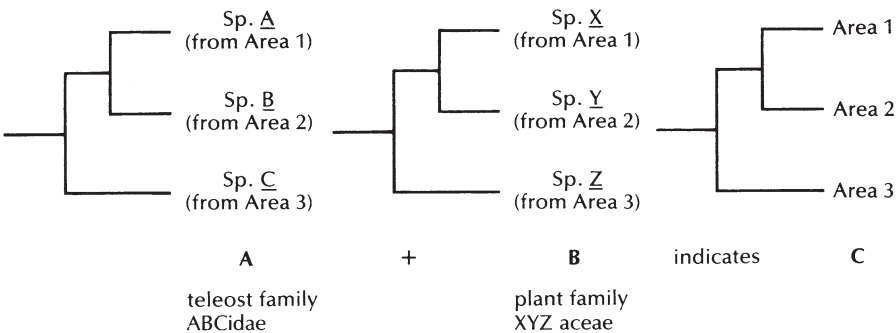


Fig. 1 Area cladogram (C) based on biological evidence (A and B).

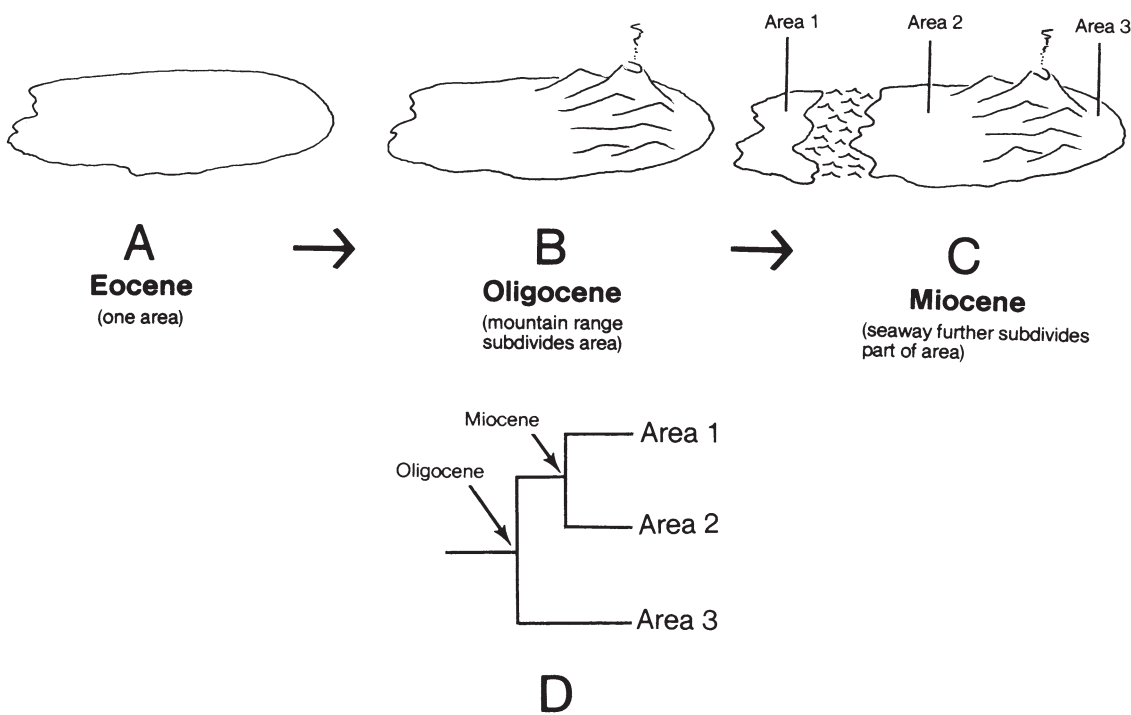


Fig. 2 Area cladogram (D) based on geological evidence (A, B, and C).

through time from resolved (Fig. 3A) to unresolved (Fig. 3C), then a geological explanation for the disappearance of the pattern (such as removal of a seaway, uplifting of a land bridge, or erosion of a mountain range allowing dispersal between previously isolated areas) can be sought.

To identify an area pattern hidden in an area of changing biogeographical affinity, underlying noise (which is due to older incongruent patterns) may also have to be filtered from the data. For example, to identify the predominant Eocene pattern in Fig. 3A, not only must the later Oligocene incongruencies be identified but also some older incongruencies may need taking into account. Such older incongruencies may be from more ancient groups

of organisms that conformed to much older geological and dispersal events. Older data can be filtered out by using only phylogenetically younger groups of organisms (e.g. teleost fishes, rather than garfishes or sturgeons in Fig. 4; see Grande 1985).

The geological history of the Earth has been very dynamic, and through a period of 100 million years, for example, a region's biogeographical affinities might have been affected by several different events. The use of time control on the data can help to sort out the components of a complex (i.e. changing through time) area pattern. Preliminary work (Grande 1985) indicates that time-controlled vicariance studies may be the only practical way to decipher certain complex biogeographical patterns.

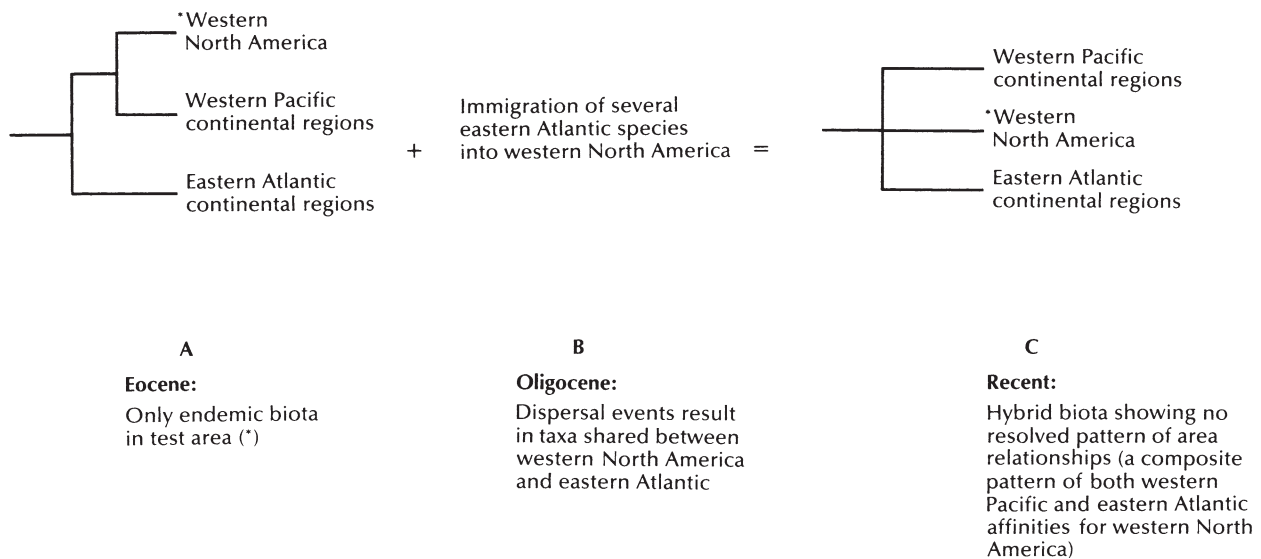


Fig. 3 Hypothetical model showing how a complex (not strictly vicariant) biogeographical history for a test area (western North America) can result in an unresolved pattern of area relationship in the Recent biota. Descendants of the dispersed taxa of B indicate transatlantic relationships, and obscure the earlier transpacific affinity of the test area. (After Grande 1985.)

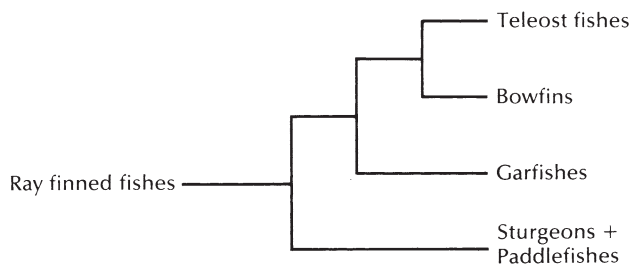


Fig. 4 Cladogram showing major groups of actinopterygian fishes.

Discussion

Vicariance biogeography represents an advance in the study of historical biogeography because of its emphasis on rigorous logic and quantitative analysis rather than using dispersal as an all-purpose explanation for any and all disjunct distributions of organisms. Some studies (Croizat 1958, 1964; Rosen 1975, 1978) have already shown that general patterns of area relationships based on biological organisms exist for discrete areas (i.e. Caribbean land areas) or at higher levels of generality (i.e. world-wide transoceanic). The full potential of this method is far from realized yet because detailed phylogenetic patterns of interrelationship are still unknown for most groups of organisms. Vicariance biogeogra-

phers hope that once the precise interrelationships of more groups of organisms are understood, the resulting phylogenetic patterns will conform to relatively few general patterns of area relationship. These general patterns could then give evolutionary biologists a fundamental new approach to understanding the evolution of the Earth and its biota.

References

- Brown, J.H. & Gibson, A.C. 1983. *Biogeography*. C.V. Mosby Co., St. Louis, Mo.
- Croizat, L. 1958. *Panbiogeography* (3 vols.). Published by the author, Caracas.
- Croizat, L. 1964. *Space, time, form: the biological synthesis*. Published by the author, Caracas.
- Grande, L. 1985. The use of paleontology in systematics and biogeography, and a time control refinement for historical biogeography. *Paleobiology* **11**, 234–243.
- Nelson, G. & Platnick, N.I. 1980. A vicariance approach to historical biogeography. *BioScience* **30**, 339–343.
- Nelson, G. & Platnick, N.I. 1981. *Systematics and biogeography: cladistics and vicariance*. Columbia University Press, New York.
- Platnick, N.I. & Nelson G. 1978. A method of analysis for historical biogeography. *Systematic Zoology* **27**, 1–16.
- Rosen, D.E. 1975. A vicariance model of Caribbean biogeography. *Systematic Zoology* **24**, 431–464.
- Rosen, D.E. 1978. Vicariant patterns and historical explanation in biogeography. *Systematic Zoology* **27**, 159–188.
- Wiley, E.O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. Wiley Interscience, New York.

5.5 Palaeobiogeography

C. R. NEWTON

Introduction

Palaeobiogeography is the study of the spatial distribution of ancient organisms, including analysis of the ecological and historical factors governing this distribution. Just as there is considerable overlap between the fields of ecology and biogeography, so there also exists a scientific continuum between certain aspects of palaeoecology and palaeobiogeography. Most palaeobiogeographical studies have dealt with distributions of individual taxa or with questions of global or regional provincialism.

Under the rubric 'palaeobiogeography' are two disparate subfields differing more in objectives than in methodology. *Applied palaeobiogeography*, representing the larger body of work, seeks to use the distribution of fossils as a tool for solving palaeogeographical, palaeoclimatological, or tectonic problems. In contrast, *palaeobiogeography* in the strict sense addresses the 'why and how' of the distribution of ancient organisms, including environmental, biological, and historical controls on habitable area (see also Section 5.4). Curiously enough, this second area of inquiry has been less explored, possibly because of the difficulty in deciphering process from pattern, with such a large number of variables and an admittedly imperfect fossil record (Section 3.12).

Methods in palaeobiogeography

Two competing schools have each developed methodologies to document and compare biogeographical and palaeobiogeographical patterns. *Cladistic biogeography*, which has borrowed heavily from the field of cladistic systematics (Section 5.2.2), uses area cladograms to consider the geographical relationships of species from monophyletic groups. The basic premise of this technique is that areas, like taxa, can be arranged in hierarchical groups that define levels of affinity between geographical regions. The most rigorous examples of cladistic biogeography have been based on taxonomic groups for which phylogenetic cladograms are also available. For example, Fig. 1 compares area cladograms for a variety of different animal taxa. The

remarkable concordance between area cladograms for the various taxa indicates a congruence of biogeographical processes, despite differing ecologies. Recognition and evaluation of such consistent patterns is a fundamental goal of both biogeography and palaeobiogeography. The central question, as stated by Nelson & Platnick (1981, p. 540) is: 'Might there be a single pattern of relationships (a general cladogram of areas) for all groups of organisms?' This intriguing question may serve as the focus for future cladistic palaeobiogeographical research.

Few cladistic palaeobiogeographical studies have thus far been conducted, largely because of constraints on databases suitable for cladistic analysis. Firstly, the prerequisite of rigorous phylogenetic cladograms severely limits the number of fossil groups and areas that can be analysed using cladistic biogeography (Jablonski *et al.* 1985). Secondly,

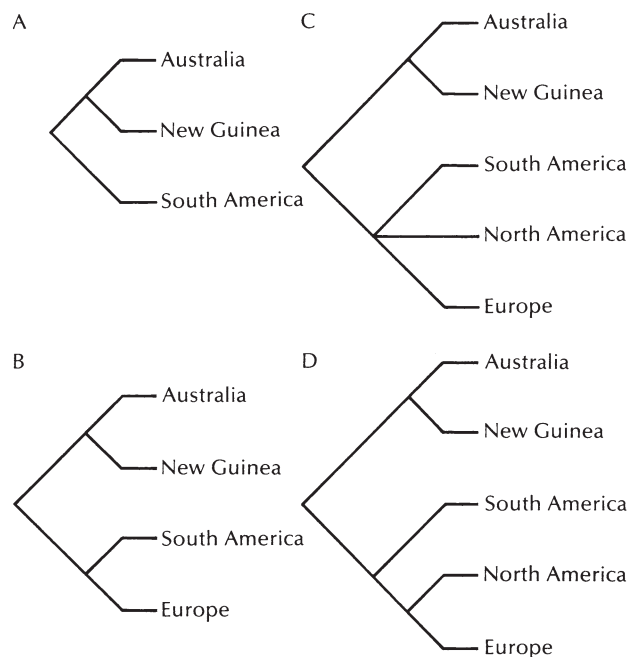


Fig. 1 Biogeographical area cladograms. A, For osteoglossine fishes and chelid turtles. B, For ratite birds. C, For galliform birds. D, For hylid frogs. Note the concordance of area cladograms for these groups of modern organisms. (From Patterson in G. Nelson & D.E. Rosen (eds) *Biogeography: a critique*. Copyright © 1981 Columbia University Press. Used by permission.

cladistic area analysis is relevant primarily for endemic taxa whose phylogenetic interrelationships are known; more widespread taxa or overlapping taxa occupying several regions are accommodated only with difficulty in the cladistic approach. This second restriction is at least as great as the first, because these latter groups constitute by far the majority of species (modern *and* ancient).

The competing school of *phenetic biogeography* emphasizes use of similarity coefficients or other quantitative techniques as applied to whole-fauna comparisons. This approach was pioneered by palaeontologist G.G. Simpson, in an attempt to quantify similarities between modern faunas. Two aspects of phenetics provide striking contrast with the cladistic biogeographical method. Firstly, although some phenetic biogeographers do use

phylogenetic relationships to aid in pattern interpretation, neither monophyly nor prior evolutionary studies are absolute prerequisites for phenetic biogeographical analysis. A second and more practical difference is that phenetic analysis is not confined to pattern analysis of endemic taxa, but can readily accommodate widespread species or species whose ranges include more than one area. This latter property makes phenetic methods simpler to apply for groups with complex, overlapping distribution patterns (e.g. Indo-Pacific molluscs).

Numerous similarity coefficients have been applied to phenetic biogeographical analysis, as well as to phenetic palaeobiogeographical analysis. Each of these numerical indices has idiosyncratic properties that affect biogeographical and palaeobiogeographical results (see Table 1, for some of the more

Table 1 Properties of selected similarity indices used in palaeoecology and palaeobiogeography.

Coefficient				
	1 As $N_1 \rightarrow N_2$	2 As $C \rightarrow 0$	3 As $C \rightarrow N_1$	4 If $\frac{N_1}{N_2} = \frac{1}{2}$ and $\frac{C}{N_1} = \frac{1}{2}$
1 Jaccard $\frac{C}{N_1 + N_2 - C}$	$\rightarrow \frac{C}{2E_1 + C}$	$\rightarrow 0$	$\rightarrow 1$	$\frac{1}{5}$
2 Simple matchings $\frac{C + A}{N_1 + N_2 - C + A}$	$\rightarrow \frac{C + A}{2E_1 + C + A}$	$\rightarrow \frac{A}{E_1 + E_2 + A}$	$\rightarrow 1$	$\frac{C + A}{5C + A} \left[\text{if } A = C, \text{ then } = \frac{1}{3} \right]$
3 Sørensen $\frac{C}{N_1 + N_2}$	$\rightarrow \frac{C}{2N_1}$	$\rightarrow 0$	$\rightarrow \frac{1}{2}$	$\frac{1}{6}$
4 1st Kulczynski $\frac{C}{N_1 + N_2 - 2C}$	$\rightarrow \frac{C}{2E_1}$	$\rightarrow 0$	$\rightarrow \infty$	$\frac{1}{4}$
5 2nd Kulczynski $\frac{C(N_1 + N_2)}{2(N_1 N_2)}$	$\rightarrow \frac{C}{N_1} [= \text{Simpson (8)}]$	$\rightarrow 0$	$\rightarrow 1$	$\frac{3}{8}$
6 Otsuka $\frac{C}{\sqrt{N_1 N_2}}$	$\rightarrow \frac{C}{N_1} [= \text{Simpson (8)}]$	$\rightarrow 0$	$\rightarrow 1$	$\frac{1}{\sqrt{8}}$
7 Correlation ratio $\frac{C^2}{N_1 N_2}$	$\rightarrow \frac{C^2}{(N_1)^2} [= (\text{Simpson (8)})^2]$	$\rightarrow 0$	$\rightarrow 1$	$\frac{1}{8}$
8 Simpson $\frac{C}{N_1}$	$= \frac{C}{N_1}$	$\rightarrow 0$	$\rightarrow 1$	$\frac{1}{2}$
9 Braun–Blanquet $\frac{C}{N_2}$	$\rightarrow \frac{C}{N_1} [= \text{Simpson (8)}]$	$\rightarrow 0$	$\rightarrow 1$	$\frac{1}{4}$
10 Fager $\frac{C}{\sqrt{N_1 N_2}} - \frac{1}{2\sqrt{N_2}}$	$\rightarrow \frac{C}{N_1} - \frac{1}{2\sqrt{N_1}}$ $\left[= \text{Simpson (8)} - \frac{1}{2N_1} \right]$	$\rightarrow -\frac{1}{2\sqrt{N_2}}$	$\rightarrow 1 - \frac{1}{2\sqrt{N_2}}$	$\frac{1}{\sqrt{8}} - \frac{1}{4\sqrt{C}}$

C = number of species common to both samples; E_1 = species present in less diverse sample; E_2 = species present in more diverse sample; A = species absent; N_1 = total number of species present in less diverse sample; N_2 = total number of species present in more diverse sample. (After Valentine 1973.)

commonly used similarity coefficients in phenetic analysis). The Simpson similarity coefficient, for example, is relatively insensitive to disparities in sample size and sampling intensity compared with the Sørensen coefficient, in which both N_1 and N_2 (species richnesses of two sites or areas) contribute information. It is not always a straightforward matter to compare results from different types of similarity comparisons. Some degree of standardization is, however, afforded by the widespread use of the Sørensen, Simpson, and Jaccard coefficients in both biogeographical and palaeobiogeographical studies. A variety of clustering techniques can be applied to the resulting similarity matrices (Fig. 2) in order to simplify relations between sites or areas, where the patterns are too complex to resolve by simple inspection (unfortunately, this is frequently the case).

One substantial contribution to the phenetic biogeographical school has been the proposal of new similarity indices whose probability distributions are known. A serious flaw in the Sørensen, Simpson, and Jaccard coefficients had been that their probability distributions were unknown and testing for significance of differences between various elements of the matrices was not possible. Alternative similarity indices with known probability distributions have been proposed independently by several different investigators (see review in Jablonski *et al.* 1985). The revised methodologies proposed by these workers have thus provided a means of rigorous statistical testing of biogeographical classifications, and have further provided a way of weighting biogeographical data to compensate for the overemphasis of widespread taxa that had formerly been typical of phenetic similarity comparisons.

Palaeobiogeographers have traditionally adopted phenetic rather than cladistic approaches to the recognition and comparison of ancient provinces. One reason for this is that the comparability of modern and ancient provinces using phenetic methods has been well established. This preference also stems from the restrictive prerequisites for cladistic analysis.

Palaeobiogeographical inference and interpretation

Recent challenges to the validity of the *ad hoc* explanations common in palaeobiogeography have brought about attempts to formalize procedures for

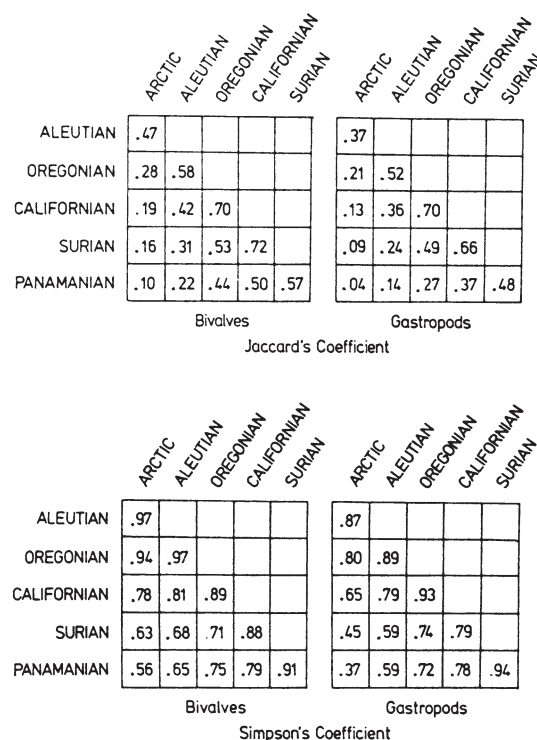


Fig. 2 Similarity matrices for bivalve and gastropod genera in different modern molluscan provinces, calculated using the Jaccard and Simpson coefficients. (From Campbell & Valentine 1977.)

biogeographical and palaeobiogeographical inference and interpretation. At issue are the largely anecdotal 'narrative explanations' traditionally used in these fields (Ball 1976). Critics have charged that the strictly inductive procedures and excessive reliance on Occam's razor have encouraged explanations which, though rational, are unique to individual case studies and hence have no predictive power (Ball 1976). Alternatives to the *ad hoc* mode of explanation have been put forth by proponents of both vicariance and dispersal biogeography.

Vicariance biogeography (Section 5.4) emphasizes the role of tectonic and other environmental processes in forming barriers that, in turn, cause geographical isolation and promote allopatric speciation. Proponents of vicariance biogeography have pointed out that a vicariant hypothesis can often be falsified by geological evidence; in contrast, claims for sweepstake and other chance dispersal are often not falsifiable (Platnick & Nelson 1978). The vicariant procedure of palaeobiogeographical or biogeographical hypothesis-testing proceeds first through a test for vicariant processes and then on to other explanations if vicariance is not sufficient or

is inconsistent with geological evidence. The structure of vicariant biogeographical analysis demands consideration of a minimum of three taxa and three geographical areas, so that two-taxa or two-area problems cannot be solved using this approach. Classic examples of vicariance events include closure of the Panamanian isthmus, separation of the major components of Pangaea, and opening of the Atlantic Ocean.

However, tectonic events are not the only controls on biogeographical patterns. *Dispersal biogeography*, an alternative mode of interpretation, stresses motility and reproductive strategies as primary controls on distribution patterns. Dispersalist interpretations can be found in case studies using both cladistic and phenetic methodologies for biogeographical pattern analysis, so that there is no simple link between method and interpretative mode. Despite charges by vicariists that dispersalist hypotheses cannot be falsified, in fact recent developments in palaeobiology have greatly strengthened the capabilities for testing dispersal hypotheses in palaeobiogeography.

Foremost among these developments are breakthroughs in interpreting larval strategies of fossil invertebrates. For molluscs, protoconch and prodisoconch morphology of gastropods and bivalves can often be used to differentiate planktotrophic (plankton-feeding) from non-planktotrophic veliger larval forms. Although this dichotomy does not exactly coincide with dispersal capability (for some

planktotrophic species have short residence times in the plankton and one lecithotrophic echinoderm does not settle for 30 days; Jablonski & Lutz 1980), in general planktotrophs are able to disperse more widely than non-planktotrophs. Some planktic larvae certainly disperse very widely as a consequence of oceanic gyres (Fig.3).

Geographical range and species longevity of fossil invertebrates correlate very well with inferred reproductive strategy, at least in some case studies. Studies of larval types in Cretaceous and Tertiary gastropod species of the Gulf of Mexico (Hansen 1980; Jablonski 1982) clearly indicate that non-planktotrophs had shorter durations than their planktotrophic counterparts (among Tertiary neogastropods, one million years versus five million years, respectively; Hansen 1980) (Fig. 4). Planktotrophy also correlates well with expanded geographical range of fossil gastropods; Jablonski (1982) found that among Cretaceous Gulf gastropods planktotrophs had median ranges of 1600 km, as compared with only 250 km for non-planktotrophs. Thus, identification of larval types may enable dispersalist models to be tested rigorously, particularly in those cases where closely related modern groups contain both planktotrophic and lecithotrophic representatives for morphological comparison.

Not all palaeobiogeographical dispersal hypotheses can be tested adequately. Perhaps the most difficult case to evaluate in the fossil record is the claim that the 'sweepstakes' or 'jump' modes of

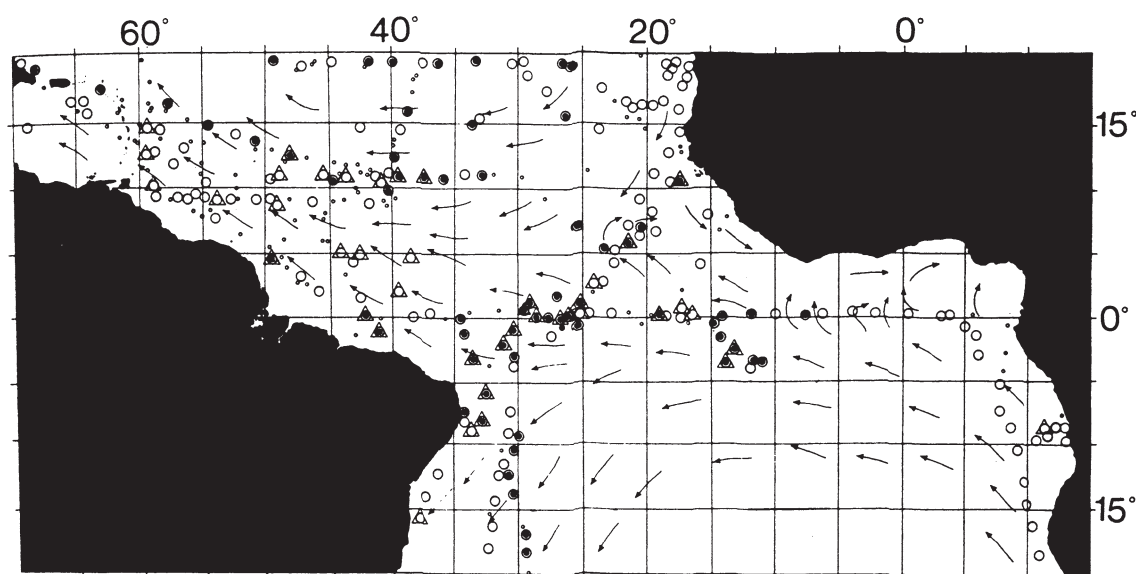


Fig. 3 Occurrence of veliger larvae of the gastropod family Architectonidae in plankton tows in the tropical Atlantic Ocean, with directions of surface currents indicated by arrows. Filled circles = *Philipppia krebsii*; triangles = *Architectonica nobilis*; open circles = other architectonids; smallest dots = sites where architectonids were absent. (From Scheltema in Gray & Boucot 1979.)

dispersal have played an integral role in the distribution of ancient organisms. These two dispersal modes both involve infrequent events and very small numbers of individuals that colonize sites far from the site of the parent population. Given the enormity of geological time, such improbable events have doubtless occurred. However, a palaeobiogeographical hypothesis that relies exclusively on this process is not particularly informative and cannot be falsified (Ball 1976; Platnick & Nelson 1978).

Biogeographical and palaeobiogeographical area distributions. A central issue in palaeobiogeography is the relation between biogeographical distribution and evolutionary rates in the fossil record. Flessa & Thomas (1985) have shown that *biogeographical area distributions* may yield 'hollow curves'. These distributions reflect the occurrence of taxa in one or more regions. As an example, Fig. 5 illustrates that most modern marine bivalve genera exist only in a few regions, whereas a few genera are extremely widespread. Modelling of biogeographical areas to produce this hollow curve suggests that the probability of geographical range expansion must increase with increasing geographical range; as Flessa & Thomas (1985, p. 367) commented, 'Like the rich getting richer, the cosmopolitans become more cosmopolitan'. The disparity between endemic and cosmopolitan taxa relates in some (but certainly not all) cases to contrasting reproductive strategies or modes of

locomotion (see discussion above concerning planktotrophs vs. non-planktotrophs in Cretaceous and Tertiary Gulf Coast faunas).

Hollow curves are also known for palaeobiogeographical area distributions. Fig. 4, from Hansen's (1980) work on Tertiary neogastropods, shows hollow curves for both planktotrophic and non-planktotrophic species, although the steeply negative slope characteristic of most hollow curves is far better developed among non-planktotrophs.

Latitudinal and longitudinal diversity gradients. Among the many biogeographical distributions known for modern organisms, two truly first-order patterns emerge. These are a pervasive *latitudinal diversity gradient*, in which most groups have maximum species diversities at low latitudes and decreasing diversity in temperate and polar regions; and a marine *longitudinal diversity gradient*, in which many taxa have highest diversities in the Indo-west Pacific region, with diminishing diversity away from this species-rich area. The origin and geological history of these present-day biogeographical patterns have inspired much debate. Of particular importance to palaeobiogeography is the question of whether these first-order patterns have persisted throughout Phanerozoic time or, alternatively, have arisen in response to late Cenozoic events and configurations.

The latitudinal gradient in marine and terrestrial

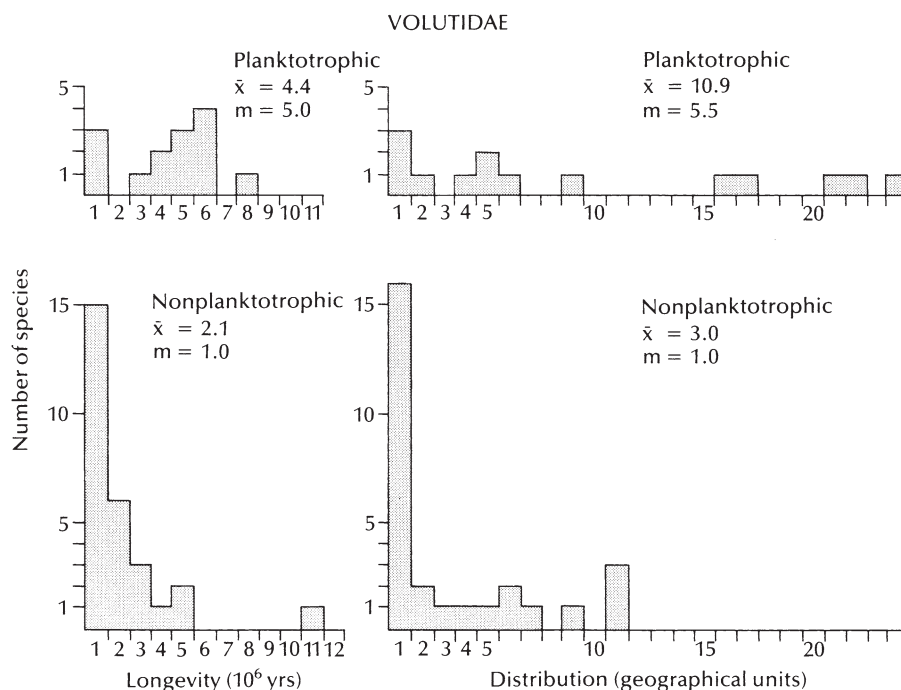


Fig. 4 Longevity and geographical distribution of Tertiary volutid gastropods from the Gulf Coastal Plain, illustrating that nonplanktotrophic gastropods have shorter species durations and more restricted geographical ranges. (From Hansen 1980.)

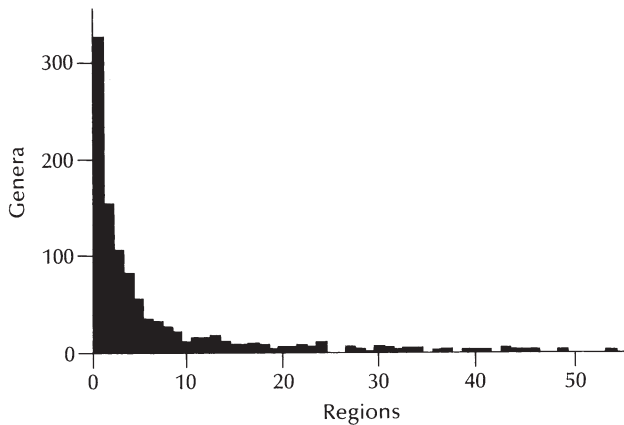


Fig. 5 Biogeographical area distribution of modern marine bivalve genera. (From Flessa & Thomas 1985.)

diversity apparently has persisted throughout much, if not all, of Phanerozoic time. It has been recognized in many palaeobiogeographical analyses, including studies on Cretaceous foraminifera (Fig. 6). One possible cause, the 'diversity-pump' hypothesis (Valentine 1984), involves extermination of high-latitude representatives of species during cooling events, leading to accumulation of higher diversities in lower-latitude portions of species' ranges. A further, special case of this temperature-mediated diversity model is the scenario of concomitant warming of the tropics and cooling of the poles, in which additional niches might be opened up at the boundary between tropical and subtropical zones; this mechanism is especially applicable to the last 20 million years (Valentine 1984). A third possible influence on the origin of the latitudinal diversity gradient is the long-term environmental stability of the tropics vs. the seasonal instability of temperate and polar regions.

The origin and geological longevity of the high-diversity region in the Indo-west Pacific and declining diversities away from this region are even more controversial. Some workers have linked the high Indo-west Pacific diversities with the overall warm, equable temperatures of the region and have associated the peripheral diversity declines with lowered sea-surface temperatures. Another option, the *vicariance-and-refuge* model, stresses the physiological dissection of the region and the presence of multiple, active tectonic blocks that have produced vicariant divergence within small, active-margin basins (Rosen 1984). If this latter model proves correct, then the Indo-west Pacific diversity high and longitudinal diversity gradient may well be an artifact of Cenozoic tectonic configurations.

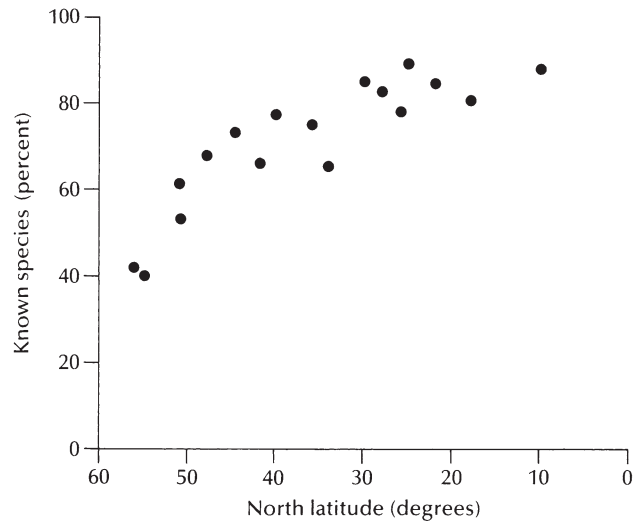


Fig. 6 Species diversity of latest Cretaceous (Maastrichtian) foraminifera as a function of palaeolatitude, illustrating a clear latitudinal diversity gradient. (From Stehli *et al.* 1969. Copyright 1969 by the AAAS.)

Pacific basin palaeobiogeography. Most palaeobiogeographical research (including the case studies cited above) emphasizes distribution patterns of organisms on continents or continental margins, particularly the major components of Pangaea. However, biogeographers have long been aware of the importance of islands in biogeographical distribution patterns. A.R. Wallace, for example, understood that islands often provide remarkable case studies for analysis of distributions and dispersal, and that the diversity and composition of island faunas depend greatly on the geological history of the island.

Several controversial studies of Pacific biotas have prompted a re-evaluation of the role of island faunas and floras in palaeobiogeography. Contrary to the prevailing notion that West Tethys was the predominant centre-of-origin for shallow-marine diversity during Mesozoic time, Kristan-Tollman & Tollman (1982 and subsequent papers) have suggested that oceanic islands provided 'stepping-stone' dispersal from the Americas westward to Europe. Tozer (1982) also reconstructed Triassic ammonoid biogeography using a model of tectono-stratigraphic terranes as islands widely dispersed in the Panthalassic (ancient Pacific) ocean. The mixed biogeographical affinities of some of these circum-Pacific terranes resemble the mosaic biogeographical patterns found in modern oceanic islands such as the Hawaiian chain (Newton 1987).

Applied palaeobiogeography. In some cases, palaeobiogeographical data can be used to resolve

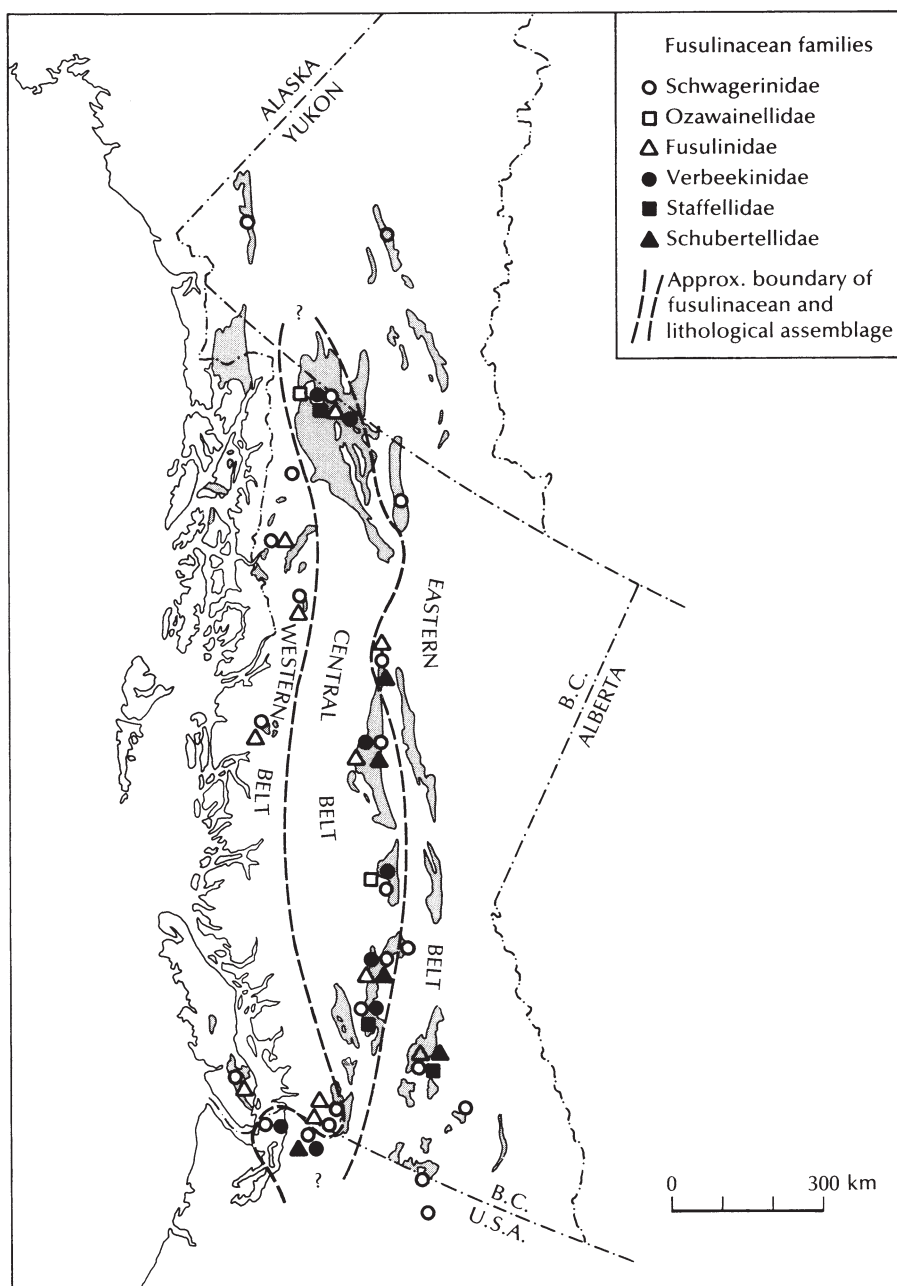


Fig. 7 Areal distribution of Permian fusulinaceans in the suspect-terrane belts of the western Canadian Cordillera. (From Monger & Ross 1971.)

geological problems, particularly those of a palaeoclimatic or tectonic nature (see also Section 5.11). For instance, the highly anomalous palaeobiogeographical patterns of fusulinaceans in the western Cordillera of North America provided the initial impetus for the concept of exotic or 'suspect' tectonostratigraphic terranes on the North Pacific rim (Fig. 7). Work on Jurassic ammonites has also suggested dramatic northward translation of many Cordilleran tectonostratigraphic terranes (Tipper 1981). These Jurassic studies are particularly noteworthy in that cratonal latitudinal zonations had

been well established for the ammonoids, so that Cordilleran tectonic displacement could be estimated. A very useful summary of Pacific faunal anomalies related to terrane displacements has been presented by Hallam (1986). In addition to work in the Pacific basin, applied palaeobiogeographical studies have contributed to tectonic models of separation of the Gondwana continents, and have also served as tests of pre-existing tectonic models in the complex Caribbean region.

As valuable as some of these studies have been, fauna-based palaeogeographical reconstructions

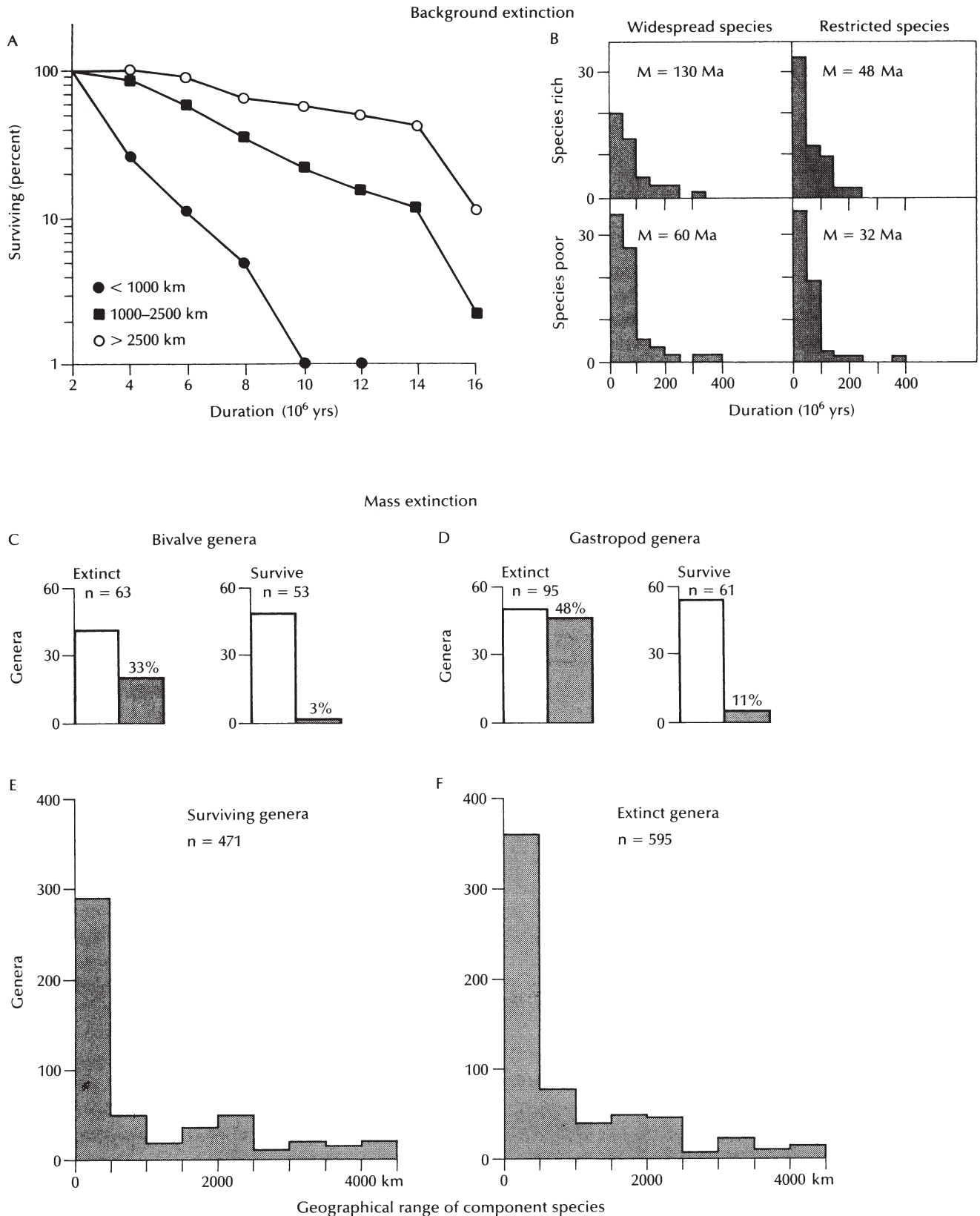


Fig. 8 Influence of areal distribution on the survivorship of species and genera of bivalves and gastropods during Cretaceous 'background' intervals and during the end-Cretaceous mass extinction. A, During non-extinction or 'background' intervals, broad geographical range correlates positively with species longevity. B, For 'background' intervals, widespread genera tend to have higher longevities than areally restricted genera. C and D, Histograms showing differential extinction of endemic genera (black) and survival of non-endemic genera (white). E and F, During the Cretaceous mass extinction, genera of survivors and victims had comparable patterns of species geographical distributions. (From Jablonski 1986.)

have sometimes been spectacular failures. Patterns of disjunct endemism, unevenness of sampling, and lack of adequate systematics have often led to erroneous interpretations or fruitless arguments. Because of these inherent shortcomings, fossil data without supplemental geological data cannot yield reliable tectonic reconstructions. None the less, with adequate sampling, an excellent systematic base, and an ecologically diverse group of fossils, some fruitful comparisons between expected and observed palaeobiogeographical distributions may be made (Newton 1987, 1988). One real advantage is that, despite other flaws, the palaeogeographical models that result from applied palaeobiogeography are usually testable, even if not always correct.

Palaeobiogeography and extinction. One of the most exciting and promising aspects of palaeobiogeography concerns the relationship between biogeographical area and extinction. Jablonski (1986) has shown that wide geographical range typically confers longer species longevities during 'background' intervals, but does not correlate well with longer lineage durations during mass extinctions (Fig. 8). This is similar to ecological traits such as larval planktotrophy, which, as discussed above, correlates well with species durations during steady-state or 'background' intervals but not during mass extinctions.

The positive correlation between large geographical range and minimal losses during mass extinctions also obtains at higher taxonomic levels. For example, Hallam (1981) showed that for Triassic bivalves, losses during the end-Triassic marine mass extinction were greater for those genera that were endemic (in this case, found in three or fewer regions) and lesser for those that were cosmopolitan (found in more than three regions). Further investigation of this intriguing link between palaeobiogeography and extinction may reveal much about the origin of mass extinctions (see also Section 2.12).

References

- Ball, I.R. 1976. Nature and formulation of biogeographical hypotheses. *Systematic Zoology* **24**, 407–430.
- Campbell, C.A. & Valentine, J.W. 1977. Comparability of modern and ancient marine provinces. *Paleobiology* **3**, 49–57.
- Flessa, K.W. & Thomas, R.H. 1985. Modelling the biogeographic regulation of evolutionary rates. In: J.W. Valentine (ed.) *Phanerozoic diversity patterns: profiles in macroevolution*, pp. 355–376. Princeton University Press, Princeton, N.J.
- Gray, J. & Boucot, A.J. (eds) 1979. *Historical biogeography: plate tectonics and the changing environment*. Oregon State University Press, Corvallis, Or.
- Hallam, A. 1981. The end-Triassic extinction event. *Palaeogeography, Palaeoclimatology, Palaeoecology* **35**, 1–44.
- Hallam, A. 1986. Evidence of displaced terranes from Permian to Jurassic faunas around the Pacific margins. *Journal of the Geological Society of London* **143**, 209–216.
- Hansen, T.A. 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology* **6**, 193–207.
- Jablonski, D. 1982. Evolutionary rates and modes in Late Cretaceous gastropods: role of larval ecology. *North American Paleontological Convention Proceedings* **1**, 257–262.
- Jablonski, D. 1986. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science* **231**, 129–133.
- Jablonski, D. & Lutz, R.A. 1980. Molluscan larval shell morphology: ecological and paleontological applications. In: D.C. Rhoads & R.A. Lutz (eds) *Skeletal growth of aquatic organisms*, pp. 323–377. Plenum, New York.
- Jablonski, D., Flessa, K.W. & Valentine, J.W. 1985. Biogeography and paleobiology. *Paleobiology* **11**, 75–90.
- Kristan-Tollman, E. & Tollman, A. 1982. Die Entwicklung der Tethystris und Herkunft ihrer Fauna. *Geologische Rundschau* **71**, 987–1019.
- Monger, J.W.H. & Ross, C.A. 1971. Distribution of fusulinaceans in the western Canadian Cordillera. *Canadian Journal of Earth Sciences* **8**, 262.
- Nelson, G. & Platnick, N.I. 1981 *Systematics and biogeography: cladistics and vicariance*. Columbia University Press, New York.
- Newton, C.R. 1987. Biogeographic complexity in Triassic bivalves of the Wallowa terrane, northwestern United States: oceanic islands, not continents, provide the best analogues. *Geology* **15**, 1126–1129.
- Newton, C.R. 1988. Significance of 'Tethyan' fossils in the American Cordillera. *Science* **242**, 385–391.
- Patterson, C. 1981. Methods of palaeobiogeography. In: G. Nelson & D.E. Rosen (eds) *Biogeography: a critique*, p. 482. Columbia University Press, New York.
- Platnick, N.I. & Nelson, G. 1978. A method of analysis for historical biogeography. *Systematic Zoology* **27**, 1–16.
- Rosen, B.R. 1984. Reef coral biogeography and climate during the Cainozoic: just islands in the sun or a critical pattern of islands? In: P.J. Brenchley (ed.) *Fossils and climate*, pp. 201–262. John Wiley, New York.
- Stehli, F.G., Douglas, R.G. & Newell, N.D. 1969. Generation and maintenance of gradients in taxonomic diversity. *Science* **164**, 947–949.
- Tipper H.W. 1981. Offset of an upper Pliensbachian geographic zonation in the North American Cordillera by transient movement. *Canadian Journal of Earth Sciences* **18**, 1788–1792.
- Tozer, E.T. 1982. Marine Triassic faunas of North America: their significance for assessing plate and terrane movements. *Geologische Rundschau* **71**, 1077–1104.
- Valentine, J.W. 1973. *Evolutionary paleoecology of the marine biosphere*. Prentice-Hall, Englewood Cliffs, N.J.
- Valentine, J.W. 1984. Neogene marine climate trends: implications for biogeography and evolution of the shallow-sea biota. *Geology* **12**, 647–650.

5.6 Biostratigraphic Units and the Stratotype/Golden Spike Concept

C. H. HOLLAND

Biostratigraphy

Biostratigraphy is the use of fossils in stratigraphic correlation. In stratigraphy, correlation is the heart of the matter. By its means local stratigraphic successions and the interpretations of these as sequences of events in geological history can be brought together in a regional or world-wide picture. In the Archaean and in the earlier part of the Proterozoic, where fossils are very rare, radiometric dating and such other features as structural episodes may provide the only available means of correlation. In contrast, in the very youngest rocks a whole variety of stratigraphic tools, including magnetostratigraphy and the study of climatic changes, may be brought to bear. In the Late Proterozoic and in most of the Phanerozoic, biostratigraphy provides often the only and almost always the most accurate method of correlation. In the Silurian, for example, biostratigraphic units with individual time ranges of only about one million years are available (Holland 1986). In the Mesozoic even greater precision is easily achieved. Such resolution is unobtainable from radiometric dating, useful though this may be in giving indications of placing in time and of the rates of processes.

Biostratigraphy has its origin in the pioneering work of W. Smith in the early part of the nineteenth century. As his land surveying took him farther afield from his base in Somerset in southwest England, Smith began to realize that, even though he might no longer use lithological characteristics to recognize his position in the stratigraphic succession, the contained fossils could be relied upon as indices. Thus was established one of the great principles of stratigraphy: that strata may be recognized by their 'organized fossils'. Smith was a practical man and it was only through later, more philosophical approaches that there came developments such as Oppel's use of zones (Hancock 1977). A general definition of the most frequently used kind of zone (which is better now always referred to as a biozone in contradistinction to the chronozone) is that it is a belt of strata characterized by an

assemblage of fossils, of which one abundant and characteristic form is chosen as an index.

Apart from the more generally applicable term *biozone*, there is really a whole family of qualified biozonal terms. The development of some of these and the attendant notions of equivalent time were clearly charted by Arkell (1933). The kinds of biozone now usually recognized include the assemblage biozone, acme biozone, total-range biozone, local-range biozone, concurrent-range biozone, and consecutive-range biozone (Section 5.7). Biozones continue to be used with great success and consistent correlation is achieved thereby. Yet some workers comment that their definition is often imprecise. The ultimate defence must be that the method does in practice work and the whole edifice of stratigraphy is really built upon it. It is important that those employing biozones define the units they are using.

Certain groups of fossils, notably the trilobites in the Cambrian, the graptolites in the Ordovician and Silurian, and the ammonites in the Mesozoic, have been used with such success that German stratigraphers, in particular, have been inclined to think of a primary orthostratigraphy based upon such a group and subsidiary parastratigraphy employing other fossils. In many circumstances, of course, such forms are not readily available and it is more important than ever to refer to whole faunas or floras. Perhaps the most striking development in more recent years has been the increasing importance of micropalaeontology in biostratigraphy, going far beyond the long established use of foraminiferans in Tertiary studies to the widespread employment of acritarchs, spores, chitinozoans, conodonts, and ostracodes. With macrofossils it is possible for the experienced worker to make some attempt at correlation even before laboratory examination can be undertaken. With microfossils, where initial preparation is required, this unfortunately is not possible.

For most stratigraphers across the world biostratigraphy does not stand alone as the only kind

of stratigraphy. Most would now recognize *lithostratigraphy* as another category. The *formation* is the fundamental unit in lithostratigraphy and this is essentially a mappable unit based upon the lithology of the rocks included within it. The necessity for such units became most apparent in situations where primary geological mapping was being undertaken in modern terms and often in difficult terrain; where the necessity to produce the geological map, which was likely to be of economic importance, left no possibility or no time for the niceties of palaeontology. There has been subsequent discussion as to the extent to which fossils may sometimes play a part in the recognition of lithostratigraphic units. Holland (1978) put the matter as follows. 'In fact the grey area between the black and white of lithostratigraphy and biostratigraphy may well be small. Biozones based, for instance, upon trilobites, graptolites, or ammonites will usually be readily distinguishable from fossiliferous formations. Groping towards a diagnosis in words, it seems that there is a kind of mathematical property of biozones involving sets or sequences'. Or, as Holland *et al.* (1978) put it: 'The use of fossils in lithostratigraphy is clear in those cases where they form part of the grossly recognisable lithology of the rock: as in coral beds, coquinas, plant beds, etc. There is, however, a less clear area closer to biostratigraphy, where lithostratigraphic units are defined, partly at least, by the identification of fossils. As such these units must remain readily recognisable and, in general, mappable.'

Global standard stratigraphy (chronostratigraphy)

There is a long and complex history of the evolution of stratigraphic classification as a whole. An important watershed within it came with a contribution by H.G. Schenck & S.W. Muller published in the U.S.A. in 1941. Here a distinction was made between timerock units such as the system and series, and time units such as the period and epoch. Ambiguously and unfortunately, the former were allowed to trail off from the series through the stage to the zone. It is these time-rock, time-stratigraphic or chrono-stratigraphic units which have caused much dissension in stratigraphy. The cause of the trouble is epitomized in Hedberg's (1954) statement: 'It [the time-stratigraphic unit] also is a material unit with a thickness and lateral extent measured in feet or metres, but its boundaries are theoretically independent of physical characters.

These boundaries are *time-surfaces*. . . ' How, it may reasonably be asked, can one recognize a stratigraphic unit whose boundaries are independent of physical characters?

The Stratigraphy Committee of the Geological Society of London pointed the way to the practice which is now being followed by the component bodies of the Commission on Stratigraphy of the International Union of Geological Sciences (Section 5.8) in establishing that chronostratigraphic units must be defined on the basis of internationally agreed boundary stratotype sections (Section 5.10). The base of each division is defined by a point in the section and this point has become known as the *golden spike*. The unique property of the golden spike (Fig. 1) is that here and here alone a defined point in rock is known (by definition) to coincide with a defined point in time. This reference point defines the base of the chronostratigraphic or global standard division in question. Its top is defined by the base of the division above. From the boundary stratotype the boundary is extended as accurately as possible using all available methods of correlation. These will usually be biostratigraphic. The important point is that, though the boundary so extended geographically through rock may approximate to equivalence with a boundary in time, it will probably never be known how closely this ideal is achieved. It is only at the golden spike that we can, by definition, be sure. Fig. 1 shows the way that a particular biostratigraphic unit may be used to carry a boundary in correlation. A flagrantly diachronous lithostratigraphic unit is added to the figure for completeness.

The term *global standard stratigraphy* is preferred to chronostratigraphy, both for its emphasis upon a unique internationally agreed standard and because it removes to some extent the unfortunate connotation with time. We (hypothetically) hammer golden spikes into rock, not into time. Parastratotype sections may be useful in some large regions or where the facies of the division is very different. These must be correlated as closely as possible with the standard stratotype and the latter must always have precedence in determining diagnosis. Regional chronostratigraphic divisions may be employed where, at the lower levels of the hierarchy, correlation is not possible with the stratotype for the global standard division in question. Their continued use in the wide territories of the U.S.S.R. is obviously thought to be helpful, particularly in the case of the regional stage or *gorizont* (Holland 1983). It is to be hoped that all such regional divisions will

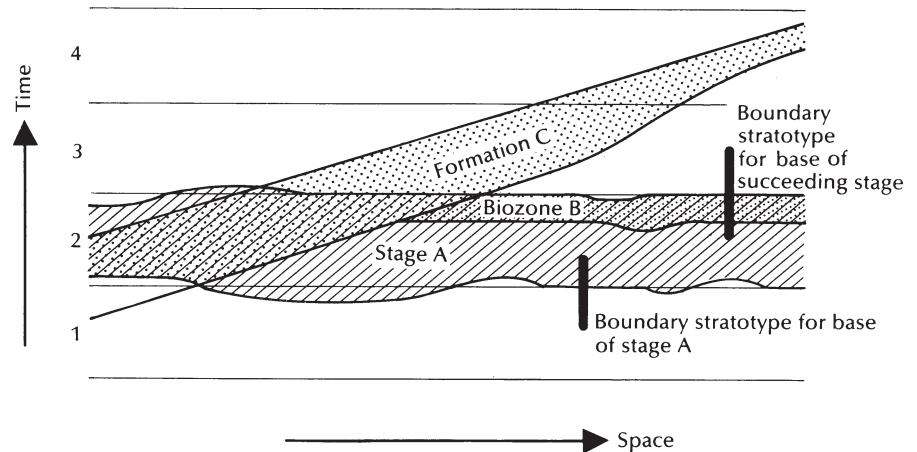


Fig. 1 Diagram to illustrate the role of the boundary stratotype in stratigraphy.

gradually disappear as correlation with the global standard becomes more and more comprehensive and more and more precise.

Disregarding the bemusing notion that global standard divisions are defined by time planes, there is a more serious problem affecting the widespread acceptance of global standard or chronostratigraphic units and the idea of the golden spike as employed in their definition. It springs from the history of stratigraphy as it has been practised in highly fossiliferous, ammonite rich Mesozoic rocks (Hancock 1977; Holland 1986).

Mesozoic stratigraphers have found it convenient to group their biozones into stages. Arkell (1956a), the doyen of Jurassic stratigraphers, saw the advantage of this as 'allowing several zones to be correlated in a general way over long distances when the zones individually are too precise'. Thus the stage in particular has become a contentious division in stratigraphy, some workers regarding it as that level in the global standard or chronostratigraphic hierarchy which comes below the series, others seeing it simply as a biostratigraphic unit involving the grouping of biozones. Mesozoic stratigraphers do appear to accept the necessity for internationally agreed schemes of biozones and stages and the necessity for internationally agreed stratigraphic divisions of a higher category, such as the system. Their sequence of ammonite biozones is now more or less standardized and, even if they cannot see their way to giving geographical names for these, they can provide boundary stratotypes for them. Thus their biozones would become chronozones, neatly falling into place in a global standard stratigraphy leading down from the system and then series, to the stage and then chronozone. In the

Palaeozoic there is as yet much less standardization of biozones, though Koren (1984) has pointed the way in her preliminary treatment of Silurian graptolite biozones. These may eventually become chronozones and thus take their place in a global standard hierarchy which is already becoming established by international agreement at higher levels. Fig. 2, for example, shows the agreed scheme for the Wenlock Series within the Silurian System (Bassett *et al.* 1975). This is the one place where two chronozones have already been properly defined, though the international machinery of standardization is not yet operating at this high level of resolution. The Whitwell Chronozone, its base defined at a boundary stratotype in the Welsh borderland, corresponds in range there to that of the *Cyrtograptus lundgreni* Biozone, one of very widespread recognition. The succeeding Gleedon Chronozone is similarly defined at a stratotype, but there comprises the ranges of both the *Gothograptus nassa* and *Monograptus ludensis* Biozones. These two chronozones make up the Homeric Stage, the upper of the two stages into which the Wenlock Series is now divided. It has not been adequately recognized that such a hierarchy of divisions is needed in order to express different degrees of precision in stratigraphy.

Fig. 3 summarizes the common procedures in stratigraphic classification within the Phanerozoic. With few exceptions it is only at the golden spike that there can be direct connection between lithostratigraphy and the global standard scheme. Usually, correlation will be achieved through biostratigraphy, as indicated by the thick arrow on the diagram. The additional time terms such as period and era are necessary only for purposes of language.

GLOBAL STANDARD STRATIGRAPHY			LITHOSTRATIGRAPHY	BIOSTRATIGRAPHY
SERIES	STAGE	CHRONOZONE		GRAPTOLITE BIOZONES
W E N L O C K	HOMERIAN	GLEEDON	Much Wenlock Limestone Formation	<i>ludensis</i>
			Farley — member of Coalbrookdale Formation	<i>nassa</i>
	SHEINWOODIAN	WHITWELL	Coalbrookdale Formation	<i>lundgreni</i>
				<i>ellesae</i>
				<i>linnarssoni</i>
				<i>rigidus</i>
				<i>riccartonensis</i>
				<i>murchisoni</i>
			Buildwas Formation	<i>centrifugus</i>

Fig. 2 Stratigraphic classification of the type Wenlock Series. (After Bassett *et al.* 1975.)

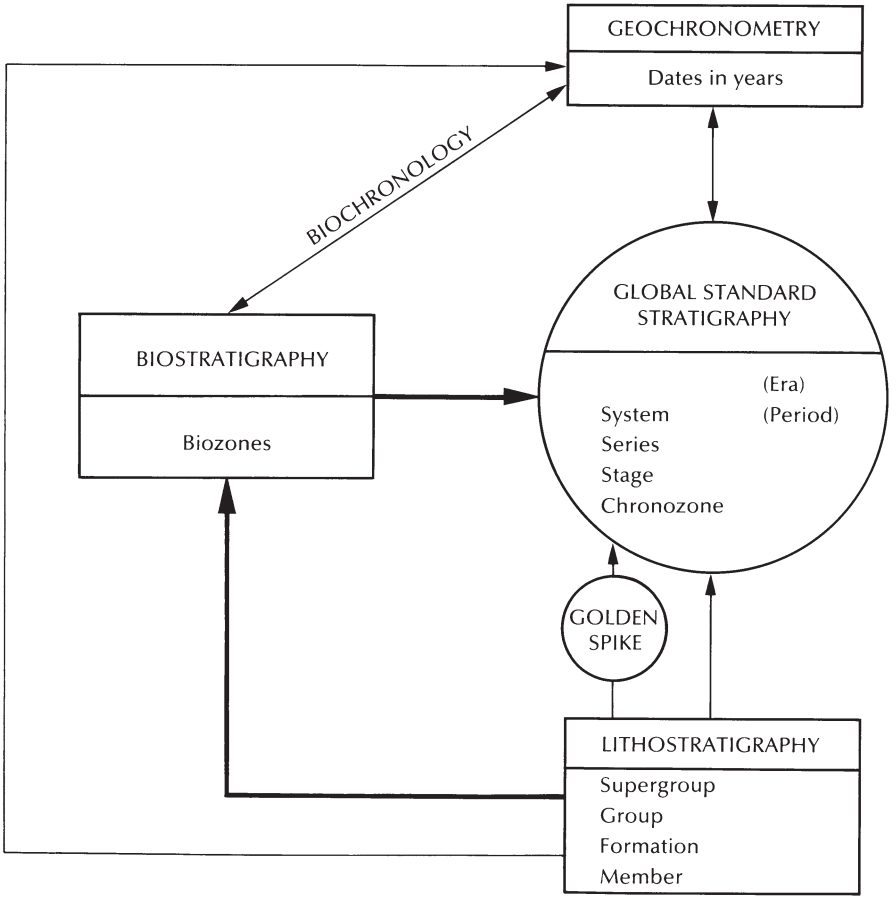


Fig. 3 Stratigraphic procedures.

Thus one cannot speak of dinosaurs living in the Jurassic System, but rather that they lived in the Jurassic Period.

Geochronometry achieved through radiometric dating is a different matter, though a connection between this and biostratigraphy is indicated on the figure as biochronology. The term *biochronology* is appropriate in those as yet rare cases in which a most detailed event stratigraphy allows the precise coupling of radiometric dates with biostratigraphy. E.G. Kaufmann and his colleagues have achieved this in the Western Interior Basin of North America, where within the Cretaceous some 400 bentonites or other volcanic related layers provide a succession of isochronous surfaces which have been dated by the potassium–argon method to give a resolution of fractions of a million years. This chronology is linked with a most detailed ammonite and bivalve biostratigraphy. Such fine tuning is unlikely to be frequently achieved, even at this particular level, and thus it remains important that an internationally agreed global standard stratigraphy is maintained.

Concluding comments

In summary, *biostratigraphic units* are bodies of strata characterized by their fossil content. As Arkell (1956b) put it: 'without the fauna a zone is nothing; a will-o'-the-wisp, without substance, unrecognisable'.

Global standard stratigraphic divisions (chronostratigraphic divisions) are bodies of strata representing divisions of the internationally agreed hierarchy including era, system, series, stage, and chronozone. Their definition depends upon selected marker points (golden spikes) in basal boundary stratotype sections (Section 5.10), the choice having been ratified by the International Union of Geological Sciences (IUGS) acting through its Commission on Stratigraphy (Section 5.8). In few cases as yet have international procedures achieved completion. The Subcommittee on Silurian Stratigraphy has a fully agreed scheme and in some other systems, such as the Devonian, matters are well advanced. In the meantime the names for the various systems are generally accepted. It is important that once the horizons for boundaries between global standard

divisions are chosen, and once the golden spikes in boundary stratotype sections are agreed and the whole matter ratified by the International Union of Geological Sciences, these decisions are accepted for the reasonable future, so that stability is assured and fundamental work can move ahead against a rational and clear background. It is important to recognize that no boundary stratotype is likely to be perfect in all respects. It is too much to expect that sections will be found which have all the desirable attributes. It is also important to recognize that there is some urgency about the matter and, above all, that nationalism has no place in stratigraphy.

References

- Arkell, W.J. 1933. *The Jurassic System in Great Britain*. Oxford University Press, Oxford.
- Arkell, W.J. 1956a. *Jurassic geology of the world*. Oliver and Boyd, Edinburgh.
- Arkell, W.J. 1956b. Comments on stratigraphic procedure and terminology. *American Journal of Science* **254**, 457–467.
- Bassett, M.G., Cocks, L.R.M., Holland, C.H., Rickards, R.B. & Warren, P.T. 1975. The type Wenlock Series. *Report of the Institute of Geological Sciences* **75/13**.
- Hancock, J.M. 1977. The historic development of concepts of biostratigraphic correlation. In: E.G. Kaufmann & J.E. Hazel (eds) *Concepts and methods of biostratigraphy*, pp. 3–22. Dowden, Hutchinson & Ross, Stroudsburg, Pa.
- Hedburg, H.D. 1954. Procedure and terminology in stratigraphic classification. *19th International Geological Congress, Algiers, 1952, Comptes Rendus* No. 13, 205–233.
- Holland, C.H. 1978. Stratigraphical classification and all that. *Lethaia* **11**, 85–90.
- Holland, C.H. 1983. Soviet and British stratigraphical classifications compared. *Journal of the Geological Society* **140**, 845–847.
- Holland, C.H. 1986. Does the golden spike still glitter? *Journal of the Geological Society* **143**, 3–21.
- Holland, C.H., Audley-Charles, M.D., Bassett, M.G., Cowie, J.W., Curry, D., Fitch, F.J., Hancock, J.M., House, M.R., Ingham, J.K., Kent, P.E., Morton, N., Ramsbottom, W.H.C., Rawson, P.F., Smith, D.B., Stubblefield, C.J., Torrens, H.S., Wallace, P. & Woodland, A.W. 1978. A guide to stratigraphical procedure. *Geological Society of London Special Report* **11**.
- Koren, T.N. 1984. Graptolite zones and standard stratigraphic scale of Silurian. *27th International Geological Congress Proceedings (Stratigraphy)* **1**, 47–76.

5.7 Zone Fossils

M. G. BASSETT

The practical application of biostratigraphy (Section 5.6) in correlating rock units carries with it the implication that the fossils used in any particular exercise have a time significance. In reality, the local time ranges of all fossils are likely to vary from section to section across the extent of their geographical distribution because of different evolutionary and ecological factors that controlled origins, rates and extent of distribution, and extinctions (Fig. 1). Thus the ranges of fossils across a given area may well be diachronous in detail, but nevertheless, by careful collecting from accurately logged sections, it is possible to plot out the limits of successive faunas and/or floras that are representative of successive intervals of time. Biostratigraphic units built up in this way remain the primary tools for dating and correlating Phanerozoic sedimentary rocks throughout the world.

The fundamental unit is the *biozone*, which is defined solely on the basis of its fossil content, without regard to either thickness or lithology. Fossils that characterize a particular biozone are termed *zone fossils*, or *index fossils*, and the names

of such taxa are then used for the name of the biozone itself; e.g. the *Monograptus ludensis* Biozone in the Silurian Period (based on a single index graptolite), the *Geminospora lemurata*–*Cymbosporites magnificus* Biozone in the Devonian Period (based on a combination of spore taxa), and the *Quenstedtoceras lamberti* Biozone in the Jurassic Period (based on an ammonite species). In general, the finer the taxonomic precision of the zonal index, the finer will be the degree of stratigraphic resolution in correlation, so that, for example, a biozone identified on the basis of a species will normally give a greater degree of accuracy than one based on genera or higher taxonomic groups.

Since different organisms evolve at different rates and are subject to different environmental constraints, their potential as biozonal indicators will also differ considerably. Ideally, for use in accurate and refined biostratigraphy, zone fossils should have a number of well defined characters: (1) a short vertical range resulting from rapid evolution; (2) a wide horizontal distribution, preferably intercontinental; (3) independence of facies control, as, for

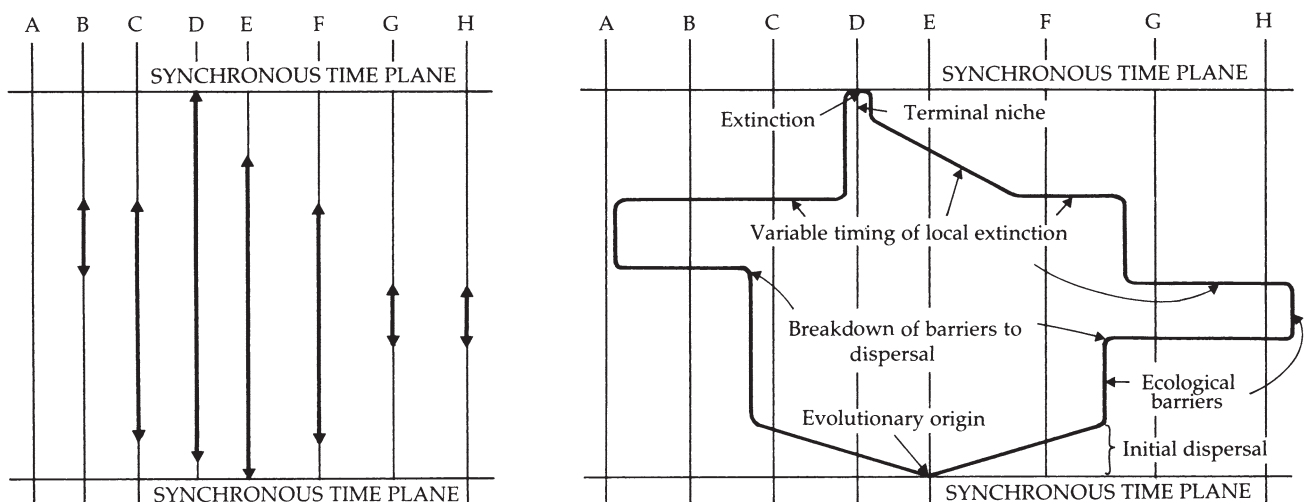


Fig. 1 Left, Hypothetical vertical ranges of a fossil species through eight measured stratigraphical sections A–H. Right, Geographical distribution of the same species illustrating some of the factors responsible for its stratigraphical expression. (After Taylor 1987.)

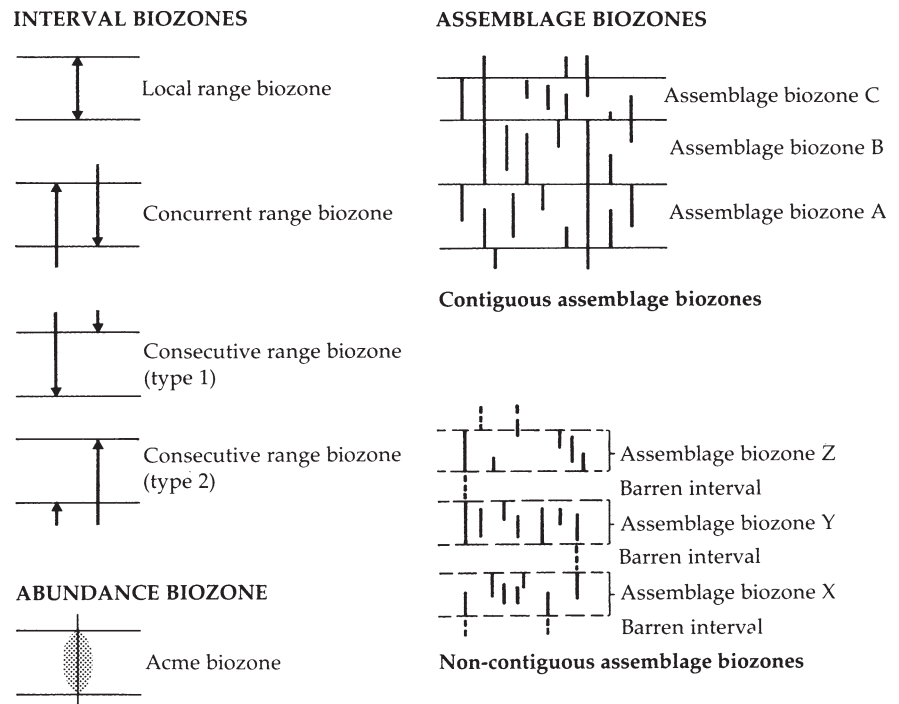


Fig. 2 Categories of biozones.
(After Taylor 1987.)

example, in wind-borne spores and in free-swimming as opposed to benthic organisms; (4) distinctive morphological characteristics to ensure accurate identification; and (5) a high preservation potential, as in animals with hard shells or skeletons. It is rare for all these conditions to be met fully, but good examples of fossil groups that satisfy most criteria are the graptolites, ammonites, conodonts, planktic foraminifera, and spores.

Fig. 2 illustrates some of the various categories of biozones that can be constructed using different data sets of vertical ranges of fossils (see, for example, Holland *et al.* 1978; North American Commission on Stratigraphic Nomenclature 1983; Taylor 1987). In the *local range biozone* the total known range of the zone fossil defines the limit of the unit. The co-occurrence of overlapping taxa is used to define *concurrent range biozones*, in contrast to the *consecutive range biozone* where one (or more) of the zone fossils ranges through an interval unaccompanied by taxa that overlap with it at other levels. An *acme biozone* relies for definition on the recognition of a maximum occurrence of a fossil that might otherwise range both higher and lower in the succession. In *assemblage biozones* the recognition of different taxa with varying vertical ranges forms the basis for definition, and in such cases the name of the biozone itself is generally based on one of the more common

members. It is clear that a zone fossil is not necessarily confined to the particular biozone that bears its name (Fig. 2).

The time-intervals represented by biozones, and thus their degree of accuracy in biostratigraphy, vary considerably throughout the geological column. Among the optimum levels of refinement currently available in Palaeozoic rocks are some graptolite biozones, which may give a resolution of correlation within one million years or less, whilst in the Mesozoic the time-span of some ammonite biozones and subzones may be as short as 200 000–250 000 years.

References

- Holland, C.H., Audley-Charles, M.D., Bassett, M.G., Cowie, J.W., Curry, D., Fitch, F.J., Hancock, J.M., House, M.R., Ingham, J.K., Kent, P.E., Morton, N., Ramsbottom, W.H.C., Rawson, P.F., Smith, D.B., Stubblefield, C.J., Torrens, H.S., Wallace, P. & Woodland, A.W. 1978. A guide to stratigraphical procedure. *Geological Society of London Special Report* 11.
- North American Commission on Stratigraphic Nomenclature 1983. North American Stratigraphic Code. *Bulletin of the American Association of Petroleum Geologists* 67, 841–875.
- Taylor, M.E. 1987. Biostratigraphy and paleobiogeography. In: Boardman, R.S., Cheetham, A.H. & Rowell, A.J. (eds) *Fossil invertebrates* pp. 52–66. Blackwell Scientific Publications, Oxford.

5.8 International Commission on Stratigraphy

M. G. BASSETT

The International Commission on Stratigraphy (ICS) is the largest scientific body within the International Union of Geological Sciences (IUGS). It is also the *only* organization concerned with the co-ordination of stratigraphy on a global scale. One of its major statutory objectives (Cowie *et al.* 1986) is the establishment of a standard, globally applicable stratigraphic scale, which it seeks to achieve through the co-ordinated contributions of a network of Subcommissions, Working Groups, and Committees. It also organizes a number of conferences each year, and the results of these conferences are usually published. The precise definition of stratigraphic boundaries and their accurate correlation is a prerequisite of this work, particularly between divisions of System, Series, and Stage rank, as a means of constructing an internationally agreed framework within which geological events can be plotted both laterally and successively through time. In Phanerozoic rocks, fossils provide the chief means of correlating the sub-divisions of geological time and the boundaries between them.

In practice, chronostratigraphic boundaries are defined at a unique point in a rock sequence at a specific locality, thus representing a unique instant in time and a standard against which other sequences can be correlated; this unequivocal method of definition is often called 'golden spike' stratigraphy (see Holland 1986; Section 5.6). Such a unique point defined within a rock section is now referred to as a Global Boundary Stratotype Section and Point (GSSP; Cowie *et al.* 1986), providing an immutable time signal within a globally standard stratigraphic scale, and the only place at that level in the scale where *by definition* time and rock coincide (Sections 5.6, 5.10.1).

The first inter-System boundary to be defined and agreed internationally in this way was between the Silurian and Devonian systems (Martinsson 1977); in this case, and after considerable discussion of possible levels and appropriate sections throughout the world by an international Working Group of the ICS, a point was selected in a succession at Klonk in Czechoslovakia which coincides with the first appearance in that section of the graptolite

Monograptus uniformis, taken to mark the base of the *uniformis* Biozone (Section 5.10.4); the strict definition of the GSSP is at a specific point within the rock sequence to mark the fixed point in time, and the base of the *uniformis* Biozone is not the defined level but is the datum used to correlate that point elsewhere. Similar subsequent decisions have been made for the Ordovician–Silurian (Section 5.10.3) and Pliocene–Pleistocene boundaries and for boundaries between Stage divisions within the Silurian and Devonian (Bassett 1985); fossils involved so far as a main basis for correlation include graptolites, conodonts, and ostracodes.

Within the ICS there are Subcommissions of international experts that monitor the latest specialized disciplines within each geological System, Working Groups to consider the formal definition of remaining inter-System boundaries, and Committees that carry out a variety of other standard-making stratigraphical work. This complex working organization has evolved in the long history of the ICS since its origins in 1878 (Martinsson & Bassett 1980; Cowie *et al.* 1986, p. 4). Most International Geological Congresses have had commissions and committees, with various names and with various durations, that have been concerned with international co-operation in stratigraphy, stratigraphic classification, and stratigraphic terminology. At the 11th Congress, Stockholm, 1910, a Commission on a Lexicon of Stratigraphy was created. This Commission functioned modestly through many subsequent Congresses. At the 19th Congress, Algiers, 1952, however, its name was changed to Commission on Stratigraphy and it was reorganized to include two Subcommissions: a Subcommission on the Lexicon of Stratigraphy and a Subcommission on Stratigraphic Nomenclature. Since that time the Commission on Stratigraphy has functioned continuously and many new Subcommissions have been added. In May 1965, the Commission applied formally for admission to the IUGS and was accepted as a commission of the IUGS. At that time the membership of the Commission was reduced drastically from 150–200 members to consist only of its officers and the presidents of its Subcommissions.

In its overall objective to clarify and co-ordinate principles of stratigraphic procedure, and to produce a unified nomenclature for a standard stratigraphic scale as a means of documenting global events unambiguously, the ICS also incorporates data from all other branches of stratigraphy, such as quantitative stratigraphy, magnetostratigraphy, chemostratigraphy, and geochronometry, to integrate with the biostratigraphic methods emphasized here and together they form the embracing discipline of *holostratigraphy*.

References

- Bassett, M.G. 1985. Towards a 'common language' in stratigraphy. *Episodes* **8**, 87–92.
- Cowie, J.W., Ziegler, W., Boucot, A.J., Bassett, M.G. & Remane, J. 1986. Guidelines and statutes of the International Commission on Stratigraphy (ICS). *Courier Forschungsinstitut Senckenberg* **83**, 1–14.
- Holland, C.H. 1986. Does the golden spike still glitter? *Journal of the Geological Society* **143**, 3–21.
- Martinsson, A. (ed.) 1977. *The Silurian–Devonian Boundary*. International Union of Geological Sciences, Series A, No. 5.
- Martinsson, A. & Bassett, M.G. 1980. International Commission on Stratigraphy. *Lethaia* **13**, 26.

5.9 International Geological Correlation Programme

J. W. COWIE

Introduction

In its life of over 15 years this joint programme of the International Union of Geological Sciences (IUGS), an independent non-governmental scientific body, and the United Nations Educational, Scientific and Cultural Organization (UNESCO) have sponsored a considerable body of geological research. This has been achieved in a number of ways (Skinner & Drake 1987):

1 Through the creation of a professional advisory secretariat with permanent headquarters in Paris and with, more recently, regional offices in various parts of the world to serve particularly remote (from Paris) and/or developing regions.

2 By means of grants to International Geological Correlation Programme (IGCP) projects whose scientific programmes and logistics have been reviewed and submitted through a Scientific Committee of volunteer, unpaid geologists from many parts of the world. (Finance comes to the IGCP from national government subscriptions on a codified basis.) These project grants are relatively small but are valuable 'pump-primers' or 'seed-money' serving as a validating and commendatory mechanism to attract other funds from national funding bodies, learned societies, geological surveys, commercial companies, and universities.

3 The individual IGCP projects are required, if they wish to continue to receive annual grants, to report

in good time each year to the IGCP Secretariat which briefs the Scientific Committee and the Board of IGCP for their respective annual meetings in February. At these meetings decisions are made regarding overall policy, guidance for projects (through their project leaders), and level of funding for the coming year.

The IGCP arose from a conference in Czechoslovakia in 1967 to meet the need for a more concerted international effort to solve some of the fundamental geological problems with which the IUGS is concerned. Through 1968 and 1969 the proposal moved forward. A final draft, completed in 1971, was adopted by the Council of the IUGS and the General Conference of UNESCO; this launched the IGCP as a co-operative venture, and its statutes were approved in 1972. In May 1973 the IGCP Board held its first session at the UNESCO headquarters in Paris with Sir Kingsley Dunham (U.K.) as Chairman. W.B. Harland (U.K.) had acted as Secretary of the IUGS Co-ordinating Panel during the formative period and F. Ronner was appointed as Secretary of the 1973 Board.

Aims and scope

The principal goal of the IGCP is to encourage international research on geological problems related to the identification and assessment of natural

resources and the improvement of man's environment. Continuing IGCP aims have been to stress the scientific achievements of the projects, improving man's environment, access to mineral resources, assistance in co-operation and communication between scientists from different regions, and the transfer of knowledge to developing countries. Assessments of the IGCP have been published by Reinemund & Watson (1983) and Skinner (1987).

The scientific scope of the IGCP has varied little since 1973; changes in emphasis have been subtle and have largely reflected changes in global geological policy and aims, with a slight shift, perhaps, from more academic, basic science to more applied, man-orientated aspects. Pure palaeobiology has not really been a part of the IGCP, but stratigraphy (including biostratigraphy) has played a significant role. The following projects are worthy of note in this context:

- 1 *Precambrian–Cambrian boundary* (Project 29).
- 2 *Ecostratigraphy* (Project 53).
- 3 *Biostratigraphic datum-planes of the Pacific Neogene* (Project 114).
- 4 *Upper Precambrian correlations* (Project 118).
- 5 *West African biostratigraphy and its correlations* (Project 145).
- 6 *Phosphorites of the Proterozoic–Cambrian* (Project 156).
- 7 *Early organic evolution and mineral and energy resources* (Project 157).
- 8 *Stratigraphic methods as applied to the Proterozoic record* (Project 179).
- 9 *Rare events in geology* (Project 199).
- 10 *Global biological events in Earth history* (Project 216).
- 11 *Floras of the Gondwanic continents* (Project 237).
- 12 *Stromatolites* (Project 261).

The range of topics with a palaeobiological emphasis is illustrated by those listed 10–12. New projects will probably be added by the IGCP, but there may be no new palaeobiological projects *per se* coming forward and this is a gap which palaeobiologists may wish to see filled — 12 out of 264 Projects in 15 years with only varying commitment may be considered too small a proportion of this international key programme.

Examples of palaeobiological projects

Project 261 on *Stromatolites* was started in 1987 with a meeting in Cardiff, U.K. Its full title is 'The biostratigraphical and environmental significance of stromatolites and other microbially derived

organosedimentary structures through space and time'. The aim is to understand microbial evolution and the factors affecting stromatolite morphogenesis, to establish their classification, biostratigraphic potential, and role in forming mineral and petroleum deposits. The approach is multidisciplinary.

Project 237 on *Floras of the Gondwanic continents* was started in 1986 and held a key meeting in São Paulo, Brazil at the 7th Gondwana Symposium in July 1988. The primary objective is to produce a general, up-to-date summary of the Upper Silurian to Lower Tertiary flora of the Gondwanic continents. An interesting aspect of IGCP work is the exploitation of training opportunities in developing countries via international co-operation of experienced scientists from many countries. In 1986 at the University of São Paulo a four-month training session was mounted in paleobotany and paleophytogeography. Further courses in 1987 and 1988 also involved African participants.

Project 216 on *Global biological events in Earth history* has, in its activities in 1986 and 1987, aroused very wide interest indeed and is probably the IGCP Project which holds the most interest for palaeobiologists in general. The project arose from a programme of the International Palaeontological Association (IPA) and is concerned with world-wide, traceable, exceptional changes ('events') within the biosphere. It aims at a better understanding of the dependence and interdependence of processes and extraordinary events in the biosphere, geosphere, and atmosphere. Global bioevents fall into several categories of pattern: innovation-events (especially important in the Precambrian and Early Phanerozoic), radiation events, spreading events, and extinction events (which may not be extremely short-term but may occur stepwise). Cyclic and acyclic processes are given special attention in their possible overlap. Probable causes are either cosmic (revolution of the Solar System within the Galaxy and impact of cosmic bodies; Section 2.12.2) or biological and abiotic (sea-level, oceanic physical and chemical composition, climate, oceanographic parameters; Section 2.12.1). Some causes may be catastrophic but resulting from combination with unstable or perturbed conditions. In 1988 an international meeting of Project 216 entitled 'Abrupt changes in the global biota' was held in Boulder, U.S.A. Already the Project's 15 or so pages of bibliography indicate the opportune and seminal aspect of this successful palaeobiological IGCP activity.

References

- Reinemund, J.A. & Watson, J.V. (eds) 1983. Science resources and developing nations: a review and a look into the future, 1978–1982. *Geological Correlation*, Paris, Special Issue, 1–166.
- Skinner, B.J. (ed.) 1987. Scientific achievements, International Geological Correlation Programme IGCP. *Geological Correlation*, Paris, Special Issue, 1–123.
- Skinner, B.J. & Drake, C.L. 1987. On the IGCP: an unclaimed success story. *Geotimes*, November, 11–13.

5.10 Global Boundary Stratotypes

5.10.1 Overview

J. W. COWIE

The most basic property of rocks which is utilized in stratigraphy is lithology; *lithostratigraphy* is concerned with the organization of rock strata into units based on their lithological character. Stratigraphy is also concerned with the organization of strata into two other types of units, however: (1) *biostratigraphy*, based on fossil content; and (2) *chronostratigraphy*, based on age relations. The latter, because of the nature of time, is the most abstract. Chronostratigraphic major boundaries have in recent decades been studied mainly by international working groups and projects (Lafitte *et al.* 1972; Harland 1973; Hedberg 1976; Bassett 1985). The different properties of rocks give rise to other branches of stratigraphy such as magnetostratigraphy, chemostratigraphy, stable isotope chemostratigraphy, and seismostratigraphy. This splitting of the subject into branches can lead to considerable complexity because the changes in a rock stratal succession based on one property may not coincide with those for another; different sets and types of units may be needed to assemble a unified time-scale. The newer term *holostratigraphy* covers the study of all aspects together and the general unity of stratigraphic studies should not be overlooked.

There is no consensus view of the principles and practice of stratigraphy. The position outlined here is that currently adopted by the International Commission on Stratigraphy of the International Union of Geological Sciences, which, in the true spirit of

science, will probably evolve or change radically in the next few decades.

The most reliable systems of stratigraphy deal with global processes which are universal, unidirectional in the sense of irreversible (time sequences can only be read one way) and non-recurrent, and non-repeatable. Included here, most significantly, is the evidence from biological evolution (sequential) and nuclear decay (metric). Biological evolution interacts through geological time with other factors, but is the main indicator of the direction of the arrow of time, of prime polarity. The evidence available so far shows that it cannot be stopped and reset. Nuclear decay also has polarity, but, unlike biological evolution, it can be stopped and reset; additionally, it has the great virtue of numeracy. Geochronometry has particular attraction for geoscientists working in unfossiliferous or sparsely fossiliferous rocks, but biostratigraphy gives the most useful and, at the present stage of research, generally the most accurate framework.

Those who work mainly with the earlier part of the Proterozoic Eon rocks and the Archaean Eon rocks find little help from the stratigraphic methods frequently used in the Phanerozoic Eon — in particular with respect to palaeobiology and biostratigraphy. In attempting to establish a global Precambrian chronostratigraphy current ideas favour a chronometric subdivision based upon intervals of 'geological convenience'. Such a chronometric approach does not rule out the possibility of separate thematic time-scales — biostratigraphic, magnetostratigraphic, chemostratigraphic. This applies especially to the later part of the Proterozoic where palaeobiological evidence is available. The Archaean–Proterozoic Boundary is placed at 2500

Ma. A tripartite subdivision of the Proterozoic in eras with boundaries at 1600 Ma and 900 Ma is widely recommended.

Today, stratigraphy is a subject in a dynamic phase of development, with diverse emphases on aspects like unique or recurrent cyclic events (event stratigraphy), such as ash falls, eustatic changes, glacial deposits, appearance or disappearance of a particular biota, and evidence of impacts of extra-terrestrial bodies. If these events can be shown to have global and isochronous effects, so that they are not merely parochial and diachronous masquerades, then they can be uniquely valuable in elucidating Earth history. Cyclicity is still being sought in the modern search for the 'pulse of the Earth'. Adjectives attached to stratigraphy proliferate, indicating renewed interest and involvement with stratigraphy as the keystone of the geological sciences — ecostratigraphy, seismic stratigraphy, chemostratigraphy, event stratigraphy, biostratigraphy, magnetostratigraphy, sequence stratigraphy, and others (Berry 1984).

International stratigraphy is much concerned with efforts to correlate standard global Series, Stages, and Systems, and a major part of this work has been to define boundaries between them (Fig. 1). Accurate communication without definition is impossible. A *Boundary Definition* utilizing a unique point in a rock sequence represents (if correctly selected), as nothing else in geology can, a unique instant of time; it defines unequivocally a standard against which other sequences can be correlated by the analysis of all available data. Biological/palaeontological species are subjective and the full range is unknown — because of incomplete research, or incompleteness of the geological record. This shortcoming can be overcome by using several independent groups of fossils to correlate faunal/floral assemblages (Glaessner 1984). It is salutary to recall that matters of *positive* science, which concern 'nature', require discovery, and apply some test of truth, should be distinguished from matters of *normative* science, which are regulated by man as part of his method of understanding nature and which apply tests of correctness and utility. The global stratigraphic scale (chronostratigraphy) is a norm which can be legitimately established by international agreement through an agreed voting procedure. It can be argued that choices in international stratigraphy should violate historical priority as little as possible, but this consideration can often be overridden by the higher priority of going for the best and making progress. Confusing historical



Fig. 1 The cover of a publication produced by the Subcommittee on Cretaceous Stratigraphy.

precedents may need to be set aside by an authoritative international decision (which is very likely to violate some established usage).

Historical geology depends on positional relationships of rock and mineral bodies and identification of the Earth's evolutionary trends. The importance of the boundary stratotype lies in its role as a future anchor to which all subsequent correlations can be tied, even if new palaeobiological or physical methods become available, because it is the only place where we actually know (by definition) that time and rock coincide within our classification.

A *Boundary Stratotype Point* defines, without doubt, an instant of geological time. A horizon will, at the *Global Stratotype Section and Point* (GSSP) locality, contain the Point, but the horizon may, traced laterally, be diachronous (cutting across time-planes) and may drift away from the instant of time defined by the point. The GSSP is the standard and is unique. The correctly selected GSSP gives an actual point in rock and is therefore not an abstract concept — all other methods can prove to be diachronic. It will be expected to remain fixed in spite of discoveries stratigraphically above and/or below. The main criterion is that any horizon and point selected must be capable of being correlated over

wide areas by any or all available methods. In a world which is not ideal, it is most unlikely that all selected stratotype points can meet all the ideal requirements; stratigraphy must therefore be a practical subject which responds to the needs of working geologists (Holland 1986).

GSSPs allow maximum flexibility with the use of multiple hypotheses to give minimum ambiguity and the greatest likelihood of stability. It is necessary to emphasize that each GSSP is the designated type of a stratigraphic boundary identified in published form and marked in the section as a specific point, constituting the standard for the definition and recognition of the stratigraphic boundary between two named global standard chronostratigraphic units. The type locality of a GSSP is the specific geographical locality in which the stratotype is situated.

Aspects to consider in the selection of a GSSP

Of great importance is the relationship of a stratotype section and point sequence to globally significant marker horizons in the immediate and accessible region, e.g. faunal or floral zone assemblages stratigraphically above or below the stratotype point, climatic markers such as tillites, and other factors assisting long-range (preferably global) correlation. Correlation must precede, accompany, and follow definition of a boundary. The choice of an appropriate boundary level for the point is only possible where a marker horizon has proved to be isochronous within the limits of precision attainable by stratigraphic methods. Auxiliary marker horizons as close as possible to the boundary level will give good approximate stratigraphic positioning where and when the primary marker is missing.

Other aspects to be considered include:

- 1 Continuity of sedimentation through the boundary interval — preferably a marine succession without major facies change. A continuous monofacial succession (or one with only rapidly alternating and repeating facies changes) will reduce possible errors resulting from stratigraphic gaps. It will also limit the occurrence of facies fossils and appearances and disappearances associated with environmental change rather than biological evolution of lineages.
- 2 Completeness of exposure: not in an isolated position but with a succession which can be followed easily — above and below the GSSP, and preferably laterally as well.
- 3 Adequate thickness of sediments.

4 Abundance and diversity of well preserved fossils: appearances and disappearances of single fossil species may be diachronous and therefore a bad guide for the location of a GSSP. Multispecies fossil zones (e.g. faunal assemblages) may be preferable. Taxa which are palaeoecologically tied to facies should be excluded from consideration (although all fossils are to some extent facies fossils). In order to minimize possible effects of environmental controls on different fossil groups, recognition of the boundary level should preferably be based on all available faunal and floral data.

The selection of appropriate fossils will vary greatly in different parts of the geological column. Ideally, selection of a point within an evolutionary lineage is desirable but recognition of such lineages can be subjective and not necessarily more accurate than the recognition of a particular assemblage zone. Such decisions must be left to the experts in each case. *Autochronology*, i.e. a single species taken out of a phylogenetic lineage (with its predecessor and successor known in detail) as the biological way of approaching a boundary free of ecological, facial, or sedimentary disturbing effect, may be a powerful tool when available.

5 Favourable facies for the development of widespread, reliable, and time-significant correlation horizons: this requires that the GSSP should not be in or close to conglomerates, breccias, olistostromes, turbidites, or remanié deposits. This should, as far as possible, eliminate variation of chronostratigraphic or chronometric age within the stratotype section near the stratotype point. Even if, for example, fossils in derived blocks and surrounding matrix appear to be of the same species and age, the danger exists that new techniques or new finds (palaeobiological or physical, such as magnetostratigraphy) might discriminate between the blocks and matrix, introducing an unacceptable imprecision.

6 Freedom from structural complication, metamorphism, or other alteration: currently the question of exotic accreted terrains is pressing, but the problem of the relationship between present and past position may not adversely affect global stratigraphy.

7 Freedom from unconformities: an *obvious* boundary should be suspect. Either it is too obvious because there is a marked change in lithology or because there is a marked change in fauna or flora. In either instance the change may imply a time-break, and consequently an unsuitable horizon at which to fix any time definition; no disconformities, unconformities, cryptic paraconformities, or time-

breaks in sedimentation any longer than a brief diastem can be tolerated close to a GSSP.

8 Amenability to magnetostratigraphy and geochronometry: these factors are probably the most important for future work and some would argue that no GSSP should be accepted without one or both.

Boundary stratotype procedure

One of the main aims of the *Boundary stratotype procedure* is to attain a common language of stratigraphy that will serve geologists world-wide and avoid petty argument and unproductive controversy. Development of a standard global stratigraphic scale which is stable for a considerable period of time is the objective. Testing can then proceed. If new developments demand revision, this can be considered in exceptional circumstances such as: (1) permanent destruction or inaccessibility of an established stratotype; or (2) violation of accepted stratigraphic principles.

In the overwhelming majority of cases in the Phanerozoic Eon, correlation must precede the definition of a boundary. Unless preliminary choices are made, however, progress may be slow as the process of testing a candidate or the competition between candidates may be the stimulus required for improvement of needed correlation techniques and of the correlation itself. Correlation must precede the selection of boundary stratotype candidates to a considerable extent, but in practice the procedure may be complex. The finding of the best stratigraphic level and best geographical site may have to proceed in tandem for a time. Correlation to a satisfactory degree is necessary but improvements in correlation should continue after a boundary stratotype has been selected. In the Phanerozoic Eon, where the prime polarity factor is biological evolution, boundaries will normally be guided in their definition by chronostratigraphy (led by biostratigraphy), but in the Proterozoic and Archean Eons guidance will be chronometric at the present stage of research. Chronostratigraphy can be expected to be used increasingly for boundaries late within the Precambrian successions.

It would be unwise (or impossible) to specify which criteria are essential and which are desirable up and down the geological time-scale, because of the multiplicity of criteria involved, and the variation in circumstances. Only a brief preliminary checklist can be suggested:

1 Explicit motivation for the preference.

2 Correlation on a global scale.

3 Completeness of exposure.

4 Adequate thickness of sediments.

5 Abundance and diversity of well preserved fossils.

6 Favourable facies for widespread correlation.

7 Freedom from structural complication and metamorphism.

8 Amenability to magnetostratigraphy and geochronometry.

Accessibility and conservation. These two topics are contrasting but complementary factors. Recent experience has shown that if access to an important outcrop is too easy and unrestricted then excessive collecting (even vandalism and plunder) may destroy the outcrop. Conservation and some restriction is therefore necessary in developed regions. Conservation in more remote regions may be easier but this depends on regional geological activity by outsiders.

A problem for access/conservation may be weathering, e.g. heavy rainfall can form rapid mud flows from a marly sequence, frost can form screes which soon cover an outcrop, and outcrops on sea coasts may be particularly subject to rapid erosion.

There must be no insuperable physical and/or political obstacles to access by geologists of any nation, and access should preferably be afforded without great expense and ideally without much bureaucracy. At the International Geological Congress in Moscow (1984) it was agreed that a reasonable amount of collecting must be possible at a stratotype section. Although it is difficult for any group of geologists to commit any nation or organization to guarantee access and conservation for the indefinite future, total accessibility must assume considerable importance. If a GSSP were found to be inaccessible in the future, this would be a very powerful argument for a reassessment of the geographical location.

There is a metamorphosis once a GSSP has been ratified by the International Union of Geological Sciences:

1 Beforehand, all methods of correlation are enlisted to define a globally valid GSSP and to distinguish between what belongs to System X and what belongs to System Y.

2 After the decision the GSSP can be used to indicate without ambiguity what constitutes earliest System X and latest System Y. Correlation has in any case to precede the definition of a GSSP. Possibilities of correlation should be tested simul-

taneously, of course, at different levels close to the boundary.

There is no conflict between the global boundary stratotype concept and global, isochronous, event stratigraphy. The combination of global environmental change and major biotic changes (which may be caused by biological evolution) brings together lithostratigraphy and biostratigraphy to provide event stratigraphy. Stratotypes bring stability by an agreed point in rock representing a unique instant of time. The ultimate reference is to rock and not to abstractions.

In this work during the past decade or two, much inspiration and guidance has been derived by the international geological community from the brilliantly-expressed published results of the Silurian–Devonian Boundary Committee which have the great virtue of being based on practical experience in actually defining a GSSP (McLaren 1977; see also Section 5.10.4).

References

- Bassett, M.G. 1985. Towards a 'common language' in stratigraphy. *Episodes* **8**, 87–92.
- Berry, W.B.N. 1984. The Cretaceous–Tertiary boundary — the ideal geologic time scale boundary? *Newsletter on Stratigraphy* **13**, 143–155.
- Glaessner, M.F. 1984. *The dawn of animal life*. Cambridge University Press, Cambridge.
- Harland, W.B. 1973. Stratigraphic classification, terminology and usage. Essay review. *Geological Magazine* **110**, 567–574.
- Hedberg, H.D. (ed.) 1976. *International stratigraphic guide*. Wiley Interscience, New York.
- Holland, C.H. 1986. Does the golden spike still glitter? *Journal of the Geological Society* **143**, 3–21.
- Lafitte, R., Harland, W.B., Erben, H.K., Blow, W.H., Haas, W., Hughes, N.F., Ramsbottom, W.H.C., Rat, P., Tintaut, H. & Ziegler, W. 1972. Some international agreement on essentials of stratigraphy. *Geological Magazine* **109**, 1–15.
- McLaren, D.J. 1977. The Silurian–Devonian Boundary Committee. A final report, pp. 1–34. In: A. Martinsson (ed.) *The Silurian–Devonian Boundary*. International Union of Geological Sciences, Series A, No. 5. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

5.10.2 Precambrian–Cambrian

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Historical background

The base of the Cambrian System, which is perhaps better termed the 'Precambrian–Cambrian Boundary' to emphasize the role of Precambrian studies as well as Cambrian research, is proving a difficult major geological horizon for which to establish a global standard. Interest was somewhat muted in the nineteenth century when so many enthralling problems concerning the younger parts of the geological column engaged attention. The relatively abrupt appearance of skeletalized fossils near the base of the Cambrian system is perhaps the greatest palaeobiological enigma, and this did not escape the attention of early geologists. It was not until the twentieth century, however, that much progress was made, as a consequence of the acceleration in exploration of the Earth's surface and the examination of sedimentary successions spanning the Precambrian–Cambrian transition (equivalent in age for most geologists to the Proterozoic Eon–Phanerozoic Eon transition).

In 1835 A. Sedgwick named the 'Cambrian Series' but his Lower Cambrian succession was largely without a fossil basis and would now be considered to include some Precambrian rocks as well. From the time of Cuvier in the eighteen-thirties it was assumed that natural breaks divided rocks in a world-wide pattern and that the 'Cambrian' rested unconformably on 'Archaean and Precambrian basement series'. Thus the base of the Cambrian was stratigraphically coincident with the unconformity first seen below the 'Cambrian' transgression. Vestiges of these ideas still persist and may yet be rejuvenated in event stratigraphy. Even as late as the nineteen-forties it was a tradition to regard, in the absence of other evidence, rocks without fossils at this level as Cambrian in age. Three decades ago workers equated the first horizon with trilobites ('Olenellus Zone') with the base of the Cambrian. The Archaean and Proterozoic Eons were grouped into rock units limited by unconformities that were thought to have a world-wide validity and occurrence. In recent decades, more and more successions have been described with apparently continuous sequences ranging from fossiliferous Cambrian rocks down into unfossiliferous strata of

a lithological facies which could be expected to yield fossils but do not. A 'Symposium on the Cambrian System and its Base' at the 1956 International Geological Congress in Mexico was followed by a conference in Paris on the Precambrian–Cambrian Boundary in 1957. Further discussion took place in Copenhagen at the International Geological Congress in 1960. Research by Soviet geologists published in the nineteen-sixties was responsible largely for the establishment in 1972 (through stimulus from V.V. Menner, W.B. Harland, M.F. Glaessner, C.J. Stubblefield, and J.W. Cowie) of the Working Group on the Precambrian–Cambrian Boundary by the IUGS's International Commission on Stratigraphy (ICS) (Section 5.8).

Precambrian–Cambrian Boundary Working Group

At the first meeting in Yakutia, eastern Siberia, U.S.S.R., it was agreed that the Working Group should seek international agreement on the definition of the Precambrian–Cambrian Boundary in litho-, bio-, and chronostratigraphic terms based on a point in a standard rock sequence (Global Stratotype Section and Point — GSSP; Section 5.10.1) coupled with elucidation of the significant palaeobiological transitions occurring at, or about, this stage in the Earth's history. Selection of the GSSP would be based on biostratigraphy but all possible methods of correlation should be enlisted (Cowie 1985).

Up to 100 members from 20 countries have been involved in the Working Group, all recruited as individuals with relevant expertise, and at present there are 24 Voting Members. All serve as individual scientists and not as delegates of any nation or institution. From 1974 to 1988 the Working Group also functioned as IGCP Project 29: 'Precambrian–Cambrian Boundary'.

From 1972 to 1987, a series of meetings was organized to examine and discuss Precambrian–Cambrian Boundary sections. Plenary sessions and workshops were held in Montreal, Canada (1972), Paris, France (1974), Moscow, U.S.S.R. (1975), Leningrad, U.S.S.R. (1976), Sydney, Australia (1976), Beijing, China (1978), Paris, France (1980), Golden, Colorado, U.S.A. (1981), Kunming, China (1982), Bristol, U.K. (1983), Moscow, U.S.S.R. (1984), Uppsala, Sweden (1986), St. John's Newfoundland Canada (1987), and south China (1987).

Field meetings were also held, involving both examination of sections and discussions leading to

subsequent research with local geologists. The following areas were visited: east Siberia, U.S.S.R. (1973 and 1981), Normandy and Brittany, France (1974), Ural Mts., U.S.S.R. (1975), Georgia, U.S.S.R. (1975), Anti Atlas Mountains of Morocco (1975 and 1976), Flinders Ranges in South Australia (1976), Iberian Peninsula of Spain and Portugal (1976), central and south China (1978 and 1982), eastern Newfoundland, Canada (1979), Mackenzie Mountains, Canada (1979), Nevada–California, U.S.A. (1981), Wales and England (1983), south Sweden (1986), Newfoundland (1987), and south China (1987) (Fig. 1).

The Precambrian–Cambrian transition is not signalled only by the skeletalization of fossil hard parts but is part of a major physical-chemical-biological changeover (possibly an 'explosion') shown also by the following (and other) changes and signals:

- 1 Decrease in dolomite accumulation.
- 2 Sharp drop in stromatolite formation and change of morphology.
- 3 First widespread appearance of red biogenic limestones.
- 4 Global accumulation of large phosphorite deposits (especially in the U.S.S.R., People's Republic of Mongolia, and China, but also elsewhere).
- 5 Considerable changes in the morphology and biological 'programming' of trace fossils.

At the 1983 Bristol meeting, candidates for the Global Stratotype Section and Point were discussed in some detail, and three were selected for further consideration: Ulakhan-Sulugur on the Aldan River in east Siberia, U.S.S.R.; on the Burin Peninsula, of eastern Newfoundland, Canada; and at Meishucun in Yunnan Province, southern China. At that time it was decided that the boundary stratotype should be placed as close as practicable to the lowest known appearance of diverse shelly fossils with a good potential for correlation (Luo Huilin *et al.* 1984; Rozanov 1984; Narbonne 1987).

These three candidates remain as prime choices in 1989 but new areas may well present important stratotype candidates in the future. They include the Olenek uplift region of northern Siberia (near the Anabar massif) and the Elburz mountains of Iran; the latter, in particular, has rich fossiliferous strata near the putative boundary and the former has great potential for correlation globally.

In 1987 a new GSSP candidate was presented by the Canadian and U.S. members of the Working Group at a slightly different level to the former Newfoundland candidate and guided by trace fossils as well as body fossils. It was claimed that



Fig. 1 Current geography of some important Precambrian–Cambrian boundary sections (circled) and Precambrian cratons (stippled). 1, North Wales, Shropshire and Nuneaton, England. 2, Bornholm and southern Sweden. 3, Northern Poland. 4, Troms, Norway, and Finnmark. 5, Onega Peninsula. 6, Sukharika river, Igarka region. 7–10, Anabar region: 7, Eriechka river; 8, Kotui river; 9, Fomitch and Rassokha rivers; 10, Kotuikan river. 11, Olenek uplift. 12, Chekurovka, lower reaches of Lena river. 13, middle reaches of Lena river. 14, Aldan river. 15, Kuznetask Alatau and northeastern Sayan. 16, Karatau, southern Kazakhstan. 17, Salt Range and Hazara district, Pakistan. 18, Mussoorie, Lesser Himalaya of India. 19, Meishucun, near Kunming, eastern Yunnan. 20, Maidiping, near Emei, southwestern Sichuan. 21, Northwestern Guizhou. 22, Southwestern Shaanxi. 23, Eastern Yangtze gorges, western Hubei. 24, Western Xinjiang. 25, Salanygol, Mongolian People's Republic. 26, Ediacara, Flinders Range, South Australia. 27, Mount Lofty and Yorke Peninsula, South Australia. 28, Amadeus and Georgina Basins, Northern Territory. 29, Nama Group, Namibia. 30, Anti Atlas and High Atlas, Morocco. 31, Sierra Morena and Montes de Toledo, Spain. 32, Cantabria and Asturia, northern Spain. 33, Montagne Noire, Hérault, France. 34, Brioverian of Normandy and Brittany, France. 35, Fortune Bay, Burin, Bonavista, and Avalon Peninsulas, southeastern Newfoundland. 36, St John, New Brunswick. 37, Nahant and North Attleborough, Massachusetts. 38, Carborca, Sonora, Mexico. 39, Mount Dunfee, Nevada and White Inyo Mountains, northwestern California. 40, Mackenzie, Selwyn, and Wernecke Mountains of Yukon and Northwest Territories, northwestern Canada. 41, Corumba Group, State of Matto Grosso, Brazil. 42, Elburz Mountains, northern Iran. Localities 5–16 are in the U.S.S.R. and 19–24 are in the People's Republic of China. (After Brasier *in* Cowie & Brasier 1989.)

although the Precambrian–Cambrian boundary marks a fundamental change in Earth history with the first development of abundant skeletal and bioturbating organisms, and there is general agreement with the principle of placing the boundary '... as close as practical to the first appearance of abundant shelly fossils ...', marked provincialism of the earliest skeletal fossils and their virtual restriction to carbonate facies have hampered global correlation in the boundary interval. Trace fossils are especially common in siliciclastic facies, in which shelly fossils typically are rare and poorly preserved. Correlation in siliciclastic facies is critical, as these deposits comprise nearly 70% of exposed rocks in the bound-

ary interval. Crimes (*in* Cowie & Brasier 1989) has outlined three globally-correlatable trace fossil zones that occur below the lowest trilobites.

Future research

It is clear that much research remains to be done on the palaeobiology of the Precambrian–Cambrian (Proterozoic–Phanerozoic) transition. Future work should include:

- 1 Integration of a global table of correlation by further documentation of stratotype sections using all available techniques.
- 2 Calibration of trace fossil data with the earliest

skeletalized body fossils, particularly in Asia, with revision and updating of range charts. These tables also should incorporate First Appearance Datum (FAD) and Last Occurrence Datum (LOD) of the main skeletal fossils, ichnofossils, and acritarchs, and evidence from sea-level curves, geochemistry (including stable isotopes), and magnetostratigraphy.

3 While not departing greatly from previous criteria regarding the stratigraphic level chosen for the Global Stratotype Section and Point, it seems agreed: (i) the level should be traceable into carbonate platform successions in Asia through the early skeletal fossil sequence and/or by chemostratigraphy, magnetostratigraphy, or sequence–event stratigraphy; (ii) the level should also be traceable into clastic platform successions linking with the trace fossil sequence and/or chemostratigraphy, magnetostratigraphy, or sequence–event stratigraphy; and (iii) tracing of the level into deeper sedimentary basins could be achieved through chemostratigraphy, magnetostratigraphy, and sequence–event stratigraphy.

References

- Cowie, J.W. 1985. Continuing work on the Precambrian–Cambrian Boundary. *Episodes* 8, 93–97.
- Cowie, J.W. & Brasier, M.D. (eds) 1989. *The Precambrian–Cambrian Boundary*. Oxford University Press, Oxford.
- Luo Huilin, Jiang Zhiwen, Wu Xiche, Song Xueliang & Ouyang Lin 1984. *Sinian–Cambrian Boundary strata section at Meishucun, Jinning, Yunnan, China*. People's Publishing House, Yunnan.
- Narbonne, G.M. 1987. Trace fossils, small shelly fossils and the Precambrian–Cambrian Boundary. *Episodes* 10, 339–340.
- Rozanov, A. Yu 1984. The Precambrian–Cambrian Boundary in Siberia. *Episodes* 7, 20–24.

5.10.3 Ordovician–Silurian

C. R. BARNES & S. H. WILLIAMS

Historical background

The Ordovician System was introduced by C. Lapworth in 1879, in a successful attempt to solve the mid-nineteenth century acrimonious debate begun by A. Sedgwick and R. Murchison. Lapworth

established a stratigraphy both in southern Scotland and in Wales, primarily by employing graptolites to develop biostratigraphic subdivision and correlation (Fig. 1).

It was soon recognized that both upper and lower boundaries of the system were marked by widespread breaks in sedimentation. The global regression during the Late Ordovician is now thought to be related to a glaciation in the Southern Hemisphere; evidence was first documented in Northern Africa, but periglacial deposits have since been found in South Africa, South America, Spain, and possibly northwest France (Rong *in* Bruton 1984). Brenchley and Newall (*in* Bruton 1984) estimated that the glaciation extended northwards to 40°S, with a high sea-level stand during the Rawtheyan Stage, global regression in the Early Hirnantian Stage (*Paraorthograptus pacificus*/*Climacograptus? extraordinarius* Zone), then dramatic eustatic rise during the *Glyptograptus persculptus* Zone.

Evidence for such eustatic change is seen in many areas, where late Ordovician regressive sequences are commonly followed by a hiatus equivalent to the *C? extraordinarius* Zone or longer, then by sudden onset of black shale sedimentation during the *G. persculptus* Zone or *Parakidograptus acuminatus* Zone. A distinctive shelly fossil assemblage termed the *Hirnantia* fauna is found within many of these late Ordovician marine deposits. It is diachronous, probably ranging in age from the *Dicellograptus anceps* Zone (*D. complexus* Subzone) to the *G. persculptus* Zone, and has been considered to represent a cold water fauna related to the late Ordovician glaciation. Such conclusions have, however, been questioned (Rong *in* Bruton 1984). In addition to the eustatic changes, a major palaeobiological event occurred during the Late Ordovician; this is one of the four largest mass extinctions during the Phanerozoic (Section 2.13.2).

Ordovician–Silurian Boundary Working Group

In 1976, the Ordovician–Silurian Boundary Working Group of the IUGS Commission on Stratigraphy (Section 5.8) was created to formally define the stratigraphic level and boundary stratotype location for the base of the Silurian System. Over the subsequent eight years it received over 50 reports from geologists around the world and organized major field excursions. The criteria which ideally should

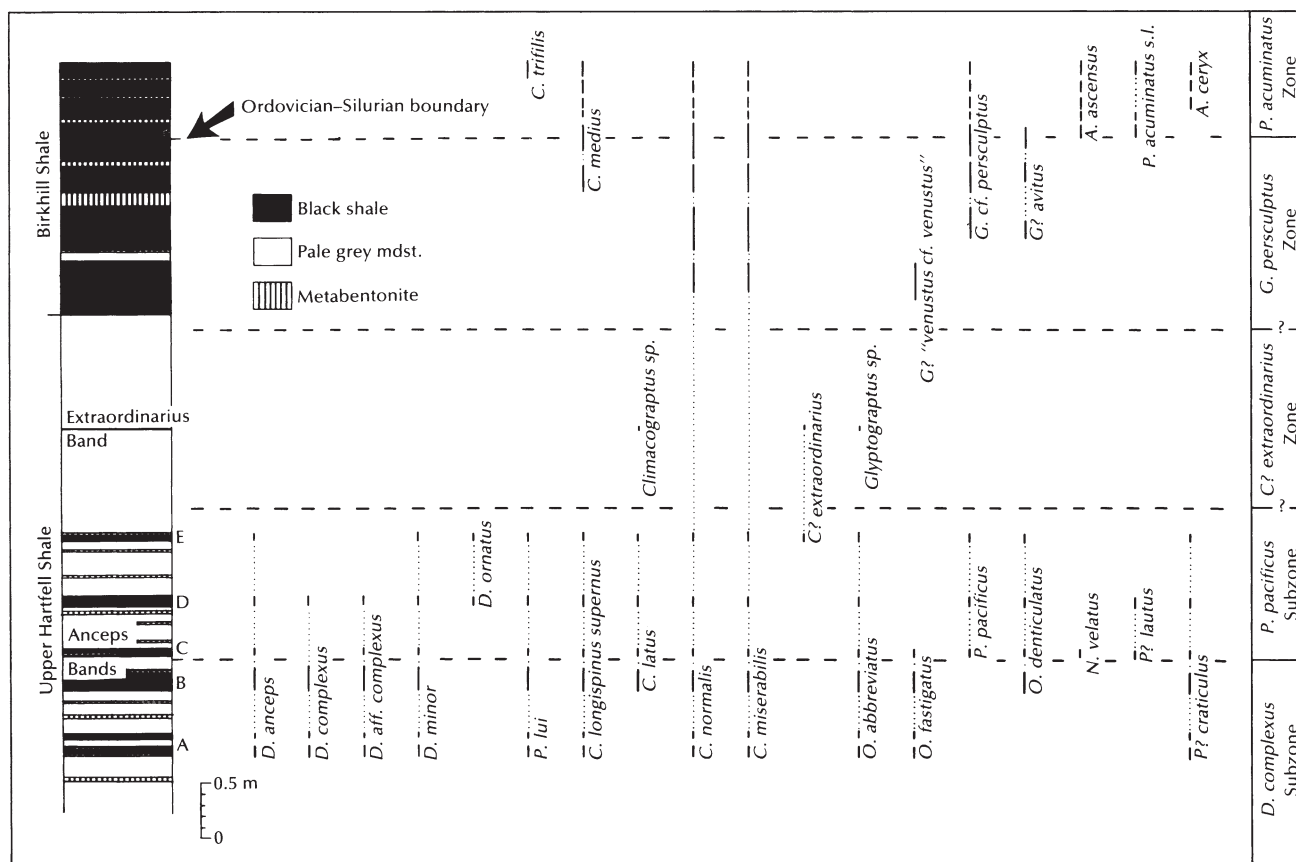


Fig. 1 Stratigraphy and graptolite ranges of the Late Ordovician and Early Silurian in the Linn Branch, Dob's Linn, near Moffat, Southern Uplands, Scotland.

be met by boundary stratotypes are set out in Section 5.10.1. The task of the Working Group proved unexpectedly difficult as sections became subjected to intense research. In most localities thought to approach the ideal criteria, one or more stratigraphic breaks occurred (e.g. disconformity, barren interval, or regional regression) and they were therefore deemed inadequate for stratotype status. The recognition that a low sea-level stand near the boundary exposed many regions of earlier deposition forced the Working Group to focus on sections representing marginal basins (e.g. Anticosti Island, eastern Canada) or deep oceanic settings (e.g. Dob's Linn, southern Scotland). These were contrasting sections in many of their attributes, and neither provided a perfect candidate for the boundary stratotype.

Anticosti Island in the Gulf of St. Lawrence, Quebec, preserves a 1500 m stratigraphic section of late Ordovician–early Silurian age. Limestones and minor shales predominate and represent deposition within a low latitude marginal basin.

The strata are accessible, well exposed, scarcely deformed or thermally altered, and yield prolific, well preserved fossils (Barnes 1988). Graptolites are rare, but biostratigraphic control is possible with several other fossil groups, of which conodonts are the best studied. McCracken & Barnes (1981) proposed a system boundary 0.9 m above the base of member 7 of the Ellis Bay Formation at Baie Ellis, based on the first appearance of *Ozarkodina oldhamensis*. The section possesses most of the characteristics required for a stratotype, but lacks sufficient graptolites to provide good correlation into oceanic facies.

Dob's Linn lies within the Southern Uplands of Scotland, northeast of Moffat. The Moffat Shale Group comprises over 100 m of black, grey and siliceous shale and is divided into four formations ranging from the *Nemagraptus gracilis* Zone (Llandeilo) to the *Rastrites maximus* Zone (Llandovery). With the exception of the Upper Hartfell Shale Formation, most of the Moffat Shale is continuously graptolitic and has been renowned for its

rich, diverse fauna since Lapworth published his landmark study in 1878. Other fossil groups are, however, mainly absent, with the exception of rare deep-water trilobites, brachiopods, and conodonts.

The late Ordovician and early Silurian succession at Dob's Linn has recently been subjected to critical, systematic study (see Williams 1988). Although most of the Upper Hartfell Shale is composed of grey, non-graptolitic mudstones, occasional graptolitic black shale bands occur. Of particular importance to the Ordovician–Silurian boundary are the *Anceps* Bands and *Extraordinarius* Band (Fig. 1). The *Anceps* Bands yield a rich, diverse fauna; in contrast, the following *Extraordinarius* Band contains only three graptolite taxa, as does the lowest part of the Birkhill Shale belonging to the *G. persculptus* Zone. During this and the succeeding *P. acuminatus* Zone, new taxa appear to give a more diverse, typically Silurian assemblage. The Ordovician–Silurian boundary was historically considered to lie at the boundary between the Upper Hartfell and Birkhill Shale; the Working Group, however, considered this to be an unsuitable horizon at which to place the boundary, owing to unfossiliferous strata and the lack of major faunal change. The boundary was consequently defined at the base of the *P. acuminatus* Zone, 1.6 m above the base of the Birkhill Shale. It is recognized by the first occurrence of *Akidograptus ascensus* and *P. acuminatus*, an event which may be accurately correlated in many sections throughout the world.

The final recommendation of the Working Group, with Dob's Linn as stratotype, was approved by the IUGS in 1984. Some concerns about the decision were expressed by Lesperance *et al.* (1987).

References

- Barnes, C.R. 1988. Stratigraphy and palaeontology of the Ordovician–Silurian boundary interval, Anticosti Island, Quebec, Canada. *Bulletin of the British Museum (Natural History)* Geology Series **43**, 195–219.
- Bruton, D.L. (ed.) 1984. *Aspects of the Ordovician System*. Paleontological Contributions from the University of Oslo, No. 295. Universitetsforlaget, Oslo.
- Lapworth, C. 1878. The Moffat Series. *Quarterly Journal of the Geological Society of London* **34**, 240–346.
- Lapworth, C. 1879. On the tripartite classification of the Lower Palaeozoic rocks. *Geological Magazine* (Decade 2) **6**, 1–15.
- Lesperance, P.J., Barnes, C.R., Berry, W.B.N., Boucot, A.J. & Mu Enzhi. 1987. The Ordovician–Silurian boundary stratotype: consequences of its approval by IUGS. *Lethaia* **20**, 217–222.
- McCracken, A.D. & Barnes, C.R. 1981. Conodont biostratigraphy and paleoecology of the Ellis Bay Formation, Anticosti Island, Quebec, with special reference to late Ordovician–early Silurian chronostratigraphy and the systemic boundary. *Bulletin of the Geological Survey of Canada* **329**, 51–134.
- Williams, S.H. 1988. Dob's Linn, the Ordovician–Silurian boundary stratotype. *Bulletin of the British Museum (Natural History)* Geology Series **43**, 17–30.

5.10.4 Silurian–Devonian

C. H. HOLLAND

The standardization of the Silurian–Devonian boundary can be taken as a case history in international stratigraphic procedure. As the first such boundary to be agreed in modern fashion, some have regarded it as a kind of model. Others see the period of more than 12 years involved in settling the matter as being something of a warning. The main problem, causing this long gestation, was that of the 'lost series' (now referred to as the Přídolí) — a series lost in previous erroneous correlations.

Historical background

In 1834 R. Murchison showed the Tilestones of south Wales to be the basal part of the Old Red Sandstone. Later he moved the basal boundary to the top of the Tilestones, perhaps because by then he regarded their lower part as corresponding to the Downton Castle Sandstone of Shropshire, which he had previously taken as the top of his Upper Ludlow Rock. There is no available section crossing from the marine Devonian rocks in their type area of Devon into the Silurian System in its type area in the Welsh borderland. The different positions of the boundary accepted by various subsequent authors through the years have been documented by White (1950).

White chose the base of the Ludlow Bone Bed as the base of the Old Red Sandstone, making for the sake of practicality the 'slight adjustment' necessary beyond the boundary originally designated by Murchison. Later workers in the Welsh borderland were grateful for the stability thus achieved. In their revision of the Ludlow Series in its type area,

Holland *et al.* (1963) designated a standard section for the base of the Ludlow Bone Bed at 'Ludford corner' in the town of Ludlow, Shropshire. In the meantime, Martinsson was achieving success in the use of ostracodes to correlate the Welsh borderland succession into the Baltic region and beyond, and Boucot was beginning to recognize the presence in such areas as Podolia (Ukraine, U.S.S.R.) of a brachiopod fauna which appeared to fall between that of the Ludlow Series and that of the Gedinian in Belgium.

Committee on the Silurian-Devonian Boundary

In Central Europe, however, research workers, building upon the monumental work of Barrande, were becoming increasingly disillusioned with a Silurian-Devonian boundary that they found considerably difficult to use in correlation. They needed a succession in fully marine facies. At a meeting in Prague in 1958 Czech stages were formalized, but much more was achieved at the epic Bonn-Brussels meeting of 1960 organized by H.K. Erben. There was one particular discussion (at the back of a coach) during this meeting when everything became clear. Suddenly there was the realization that the graptolites did not disappear in some mystical way at the end of Silurian time but continued into the Devonian. After the meeting, correlation tables were

rapidly changed, much new work was initiated, and the Committee on the Silurian-Devonian Boundary began its 12 years of work. Because of the previously erroneous correlation, the choice of a horizon for the boundary had to come first and it was inevitable that this would involve a measure of compromise (Fig. 1A). A level at the base of the *Monograptus uniformis* Biozone was first suggested by Holland (1965) and received early support in a paper by Czech colleagues. This horizon was eventually accepted by the Committee. At this time, the Committee also developed a set of criteria which it judged to be important in the subsequent selection of a location for the boundary stratotype. These included level of faunal and floral development, stratigraphic considerations, structural situation, facies diversity, geographical accessibility, and the possibility of conservation of the section. After many submissions had been received and members of the Committee had undertaken a variety of field visits, a short-list of four candidates emerged for the boundary stratotype: Morocco; Nevada, U.S.A.; Podolia, Ukraine, U.S.S.R.; and Bohemia, Czechoslovakia.

In the desert country on the edge of the Sahara in southwest Morocco, the Silurian-Devonian Boundary can be located near the small oasis of Ain Deliouine. It is difficult of access, but the factor most weighing against this section was the serious effect of desert weathering upon the graptolites

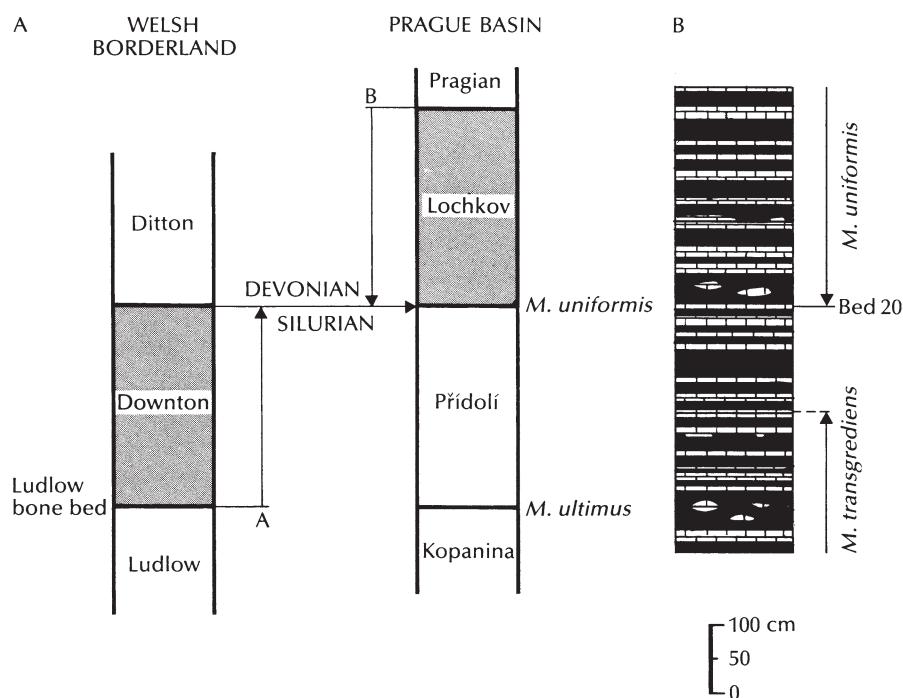


Fig. 1 A, The compromise involved in establishing international agreement on the placing of the Silurian-Devonian Boundary. (After Holland 1986.) B, Boundary stratotype for the base of the Devonian System at Klonk, Prague Basin, Czechoslovakia. (After Chlupáč *et al.* 1972.)

close to the boundary. In Nevada, the basin and range country provides good Silurian–Devonian sections. In spite of the tectonic isolation of the ranges, individual sections (such as those in the Roberts Mountains) are clear. It is important, however, that decisions on stratigraphic standardization should be achieved with reasonable expedition, and work in Nevada was insufficiently advanced. Podolia in the Ukraine is a magnificent area for Silurian–Devonian geology, with highly fossiliferous strata exposed in structurally simple sections along kilometre after kilometre of the Dnestr River and its tributaries. Unfortunately, no graptolites had been found in the beds immediately below the chosen horizon and there were also some problems of access. So Barrande's classic area in the Prague basin (Barrandian area) was chosen for the stratotype (Chlupáč *et al.* 1972), backed by extensive collections in the National Museum, Prague. The section at Klonk (Fig. 1B) was preferred to the structurally more complex alternative at Karlstejn; the 'golden spike' was placed at the point where *Monograptus uniformis* first appears within 'Bed 20'.

This final decision was ratified at the International Geological Congress in Montreal in 1972, when the Committee on the Silurian–Devonian Boundary

reported through the Chairman, D. J. McLaren, to its parent body, the International Commission on Stratigraphy (Section 5.8), and thence to the International Union of Geological Sciences (Martinsson 1977). Since then the choice of horizon has proved significant, allowing for sensible correlation tables in which the Přídolí Series plays its part as the fourth series of the Silurian System.

References

- Chlupáč, I., Jaeger, H. & Zikmundova, J. 1972. The Silurian–Devonian Boundary in the Barrandian. *Bulletin of Canadian Petroleum Geology* **20**, 104–174.
- Holland, C.H. 1965. The Siluro–Devonian Boundary. *Geological Magazine* **102**, 213–221.
- Holland, C.H. 1986. Does the golden spike still glitter? *Journal of the Geological Society* **143**, 3–21.
- Holland, C.H., Lawson, J.D. & Walmsley, V.G. 1963. The Silurian rocks of the Ludlow district, Shropshire. *Bulletin of the British Museum (Natural History) Geology Series* **8**, 93–171.
- Martinsson, A. (ed.) 1977. *The Silurian–Devonian Boundary*. International Union of Geological Sciences, Series A, No. 5. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- White, E.I. 1950. The vertebrate faunas of the Lower Old Red Sandstone of the Welsh borders. *Bulletin of the British Museum (Natural History) Geology Series* **1**, 49–67.

5.11 Fossils and Tectonics

R. A. FORTEY & L. R. M. COCKS

Introduction

The history of palaeontology has been closely connected with contemporary developments in other branches of the earth sciences. Until 30 years ago the subdisciplines of geology were less clearly separated than they are now, and the all-round geologist might routinely use fossils as part of his armoury of field data in unscrambling the problems of a structurally complex area. Fossils had an immediate part to play in resolving tectonic problems, and the structural geologist would use them at an early stage in the generation of his hypotheses; conversely, many invertebrate palaeontologists would not feel abashed at concocting

structural hypotheses of their own. In the U.K. this was particularly true of Lower Palaeozoic studies, and it would not be overstating the case to say that palaeontology made as much of a contribution to working out the structure of Wales as any other geological discipline. In the nineteenth century the great works of Murchison and Sedgwick carried their palaeontological notes and appendices (e.g. Murchison 1839), and it is obvious that these authors used the fossils as guides and friends to find their way through these 'interminable greywackes'.

Nowadays there are few great generalists of this kind — the sheer proliferation of techniques and knowledge has made it impossible. As a consequence, tectonics, geochemistry, and sedimentology

have separated as independent disciplines, and theories of structural intent may come from any one of them. Palaeontology is too often neglected entirely — but this is to miss evidence of practical usefulness. Conversely, the number of palaeontologists with an eye for structural problems has also diminished, partly because of the growth in the palaeobiological side of the subject, and partly because of the increasing specialization which is characteristic of all science.

Fossils do, however, still have an important part to play in the testing of tectonic theories in parts of the world where metamorphism has not destroyed the evidence entirely — and even in global problems. Perhaps the best way to regard fossils in a tectonic context, and the role of palaeontology as a separate discipline, is as a critical test of theories generated from any of the other geological sub-disciplines; conversely, theories derived from palaeontological evidence must themselves pass muster with the tectonicist, the geochemist, or the sedimentologist. No matter how a theory is originally derived, it becomes plausible only when supported by different lines of evidence from several disciplines. The unique contribution of palaeontological evidence is that it does not depend directly or covertly on other sources of evidence; circular arguments are always hard to avoid in geology, and fossils can cast a hard factual light on tectonic speculation.

Classical uses of fossils in tectonic problems

The most basic use of fossils, especially invertebrates, is in the dating of rocks. In spite of the tremendous advances in radiometric geochronology there is no substitute for a reliable palaeontological age, because, unlike radiometric 'clocks', fossils cannot be 'reset' by later events (see also Section 5.10.1). Limitations are only set by the recognition of the fossils themselves — but occasionally these can be powerful limitations if the rocks that contain them have been heavily cleaved, distorted, or metamorphosed. Even so, it is surprising how much punishment fossils can endure before they are completely obliterated. For example, in the Appalachians Silurian brachiopods have survived sillimanite grade metamorphism to date a huge tract of otherwise barren metamorphics (Boucot & Thompson 1963); in the Alps belemnites are still recognizable after enduring extreme tectonization. Generally, fossils in shales are severely affected before those in limestones or sandstones. Even such

distortions have their uses, if the original dimensions of the fossil are known, because they can provide a measure of extension or compression and thereby permit the calculation of the strain ellipsoid affecting the enclosing rocks.

The classical uses of palaeontological dates in tectonics can be summarized in three categories:

1 *The dating of phases of movement or igneous/metamorphic activity from unconformities.* An unconformity between two sedimentary formations can provide a close control on the age of movement, which is after the youngest fauna or flora found below the unconformity and prior to the oldest fauna found above it. This can provide a very precise control, as in the famous Bala unconformity in the Ordovician of north Wales where there is a gap between the Middle Caradoc and the Middle Ashgill. Dates for phases of intrusion or metamorphism are only 'older than' the age of the earliest overlying sediment and need supplementary evidence from radiometric dating.

2 *The determination of facing direction or 'way up' in folded areas.* In geologically complex country the younging direction of beds is frequently obscure, especially where the rocks are monotonous in lithology. Fossils often provide the only means of unscrambling such successions. The classic example is C. Lapworth's interpretation of the Southern Uplands of Scotland, which ran in tandem with the same author's identification of the sequence of graptolite faunas. Lapworth made sense of a hitherto uninterpretable stretch of country, comprising apparently endless shales. It is only recently that Lapworth's structural interpretation has been revised; even now, his palaeontological evidence stands almost intact.

3 *Dating volcanic activity.* Submarine or subaerial volcanics are often interbedded with fossiliferous rocks, and have long been dated thereby. Volcanics play an important part in the history of active continental margins. More recent work on the geochemistry of such rocks is able to identify the palaeogeographical setting precisely (such as whether they are island arc or back arc volcanics). With fossils to provide the chronology, the tectonic and volcanic history can now be detailed more informatively than in the days before plate tectonic modelling. Such an approach has profoundly altered our understanding of marginal basins, such as the Caledonian Welsh basin (Kokelaar & Howells 1984). A few kinds of fossils — graptolites and radiolaria especially — can even be found in the sediments

associated with ocean-floor basalts. These provide the only non-radiometric evidence for the date of eruption of ocean-floor magma, and for the subsequent obduction of volcanics.

Such applications rely on fossils as tools for dating rocks, without necessary regard to the palaeobiology, palaeoecology, or distribution of the organisms concerned. Although such uses have a long tradition, they are as appropriate today as they ever were. For those with the patience to search tectonized areas new faunas still turn up; and when they do, the implications can be important. For example, unpromising-looking limestones in the Highland Border Complex of Scotland have recently yielded Ordovician silicified faunas (Curry *et al.* 1984) which not only rule out at least one previous tectonic interpretation, but also suggest the presence of former Ordovician basins in the area now occupied by the Midland Valley. Other recent applications of fossils in tectonics draw on the whole range of properties of fossil assemblages as well as their capacity to date rocks. These are considered next.

Nappe tectonics

Nappes are the characteristic feature of the Alpine style of deformation, in which great, dislocated folds are translated horizontally — in some cases many kilometres from their original 'root zone'. Nappe may pile on nappe, often with the highest nappe being the one that has travelled furthest. Such scrambled geology often resists interpretation. Fossils can contribute in several ways to unravelling these complexities: (1) they can date each nappe 'package', which often has a discrete stratigraphy when compared with its neighbours; and (2) the kind of facies and faunal assemblages can often contribute to locating the site from which the nappe has travelled, or help towards the reconstruction of the original palaeogeography. It is only unfortunate that nappe country is often also metamorphosed, removing fossil evidence. Even so interpretation can proceed on occasion by extrapolation from adjacent, less metamorphosed areas.

The interpretation of the Swedish Caledonides in terms of nappe tectonics is a relatively recent innovation; faunal evidence is sporadic, but has made a vital contribution to unravelling the complex tectonics in the upper allochthon of the Trondheim region (Gee & Roberts 1983). In a generally analogous way the somewhat monotonous tract of domi-

nantly clastic Upper Palaeozoic rocks of southwest England is now being reinterpreted as a nappe complex. Fossils (especially conodonts and goniatites where these occur) supply valuable fixed points in this shifting stratigraphy. In the continuation of the Alpine belt eastwards into the complex regions of Timor, where arcs have appeared, disappeared, and collided, the microfossil stratigraphy (especially using foraminifera) has proved the key to unlocking the late Tertiary structural history (e.g. Audley-Charles 1986). In such areas the structural geologist and the palaeontologist work closely together, to their mutual benefit.

Palaeobiogeography and tectonics

Fossil taxa, unless they are unique examples, have a spatial distribution which can be used to construct palaeobiogeographical maps. For post-Palaeozoic distributions these maps can be tested against continental reconstructions derived from geophysical data, but nowadays the fossils themselves are not often used as the basis of reconstructing past geography, although they were very much part of the argument about Pangaea in the twenties and thirties (see also Section 6.5.2). In the earlier Palaeozoic, however, geophysical data are sparse and ambiguous, and the continental configurations were different both from Pangaea and from the present; here fossil distributions can still contribute to hypotheses about the disposition of ancient continents. Such continents were, of course, separated by oceans as they are today — but oceans that have long since vanished. The proof of their former existence is tectonic, in that the disappearance of an ocean by subduction leaves a unmistakable tectonic imprint. But former oceans also influenced palaeobiogeography. Oceanic separation tends to induce endemism in the seas surrounding separated continents — especially among shallow-water organisms — and particularly if oceanic separation is accompanied by latitudinal separation and hence a climatic barrier. The former existence of such an ocean can then be recognized by the close apposition today of two large areas with their own endemic shallow-water faunas. Between such areas there should be a 'mobile belt' with its own faunal peculiarities, as we describe below. These palaeobiogeographical differences should not be attributable to some other physical factors, such as salinity or substrate.

Once the possibility of the existence of a former ocean is identified using fossils, the tectonicist and geochemist may search for the other signatures that

a vanished ocean leaves in the folded rocks. One example concerns the Ordovician history of the British Isles. It has long been recognized that the early Ordovician rocks of northwest Scotland were very different from those of Wales and the Lake District, and contained different faunas. Recent plate tectonic interpretations explained such differences by postulating the existence of a former ocean — a 'proto-Atlantic' or Iapetus. The destruction of this ocean at the end of the Lower Palaeozoic resulted in the Caledonian mountain belt, which extends both southwards into the Appalachians and northwards all along the western coast of Scandinavia. Northwest Scotland (indeed Scotland as far south as the Southern Uplands) belonged to the North American side of Iapetus, which explained both the faunal differences and the tectonics. The continent at the other side of the ocean was regarded as comprising the Anglo-Welsh area (together with the rest of Southern Europe) as well as Baltica. However, faunal studies showed great differences between the shallow-water trilobite and brachiopod faunas of Southern Europe, including England and Wales, and those of the Baltic platform. These areas approach one another closely today, and it is not possible to explain away these differences simply as a geographical cline. Cocks & Fortey (1982) showed that the differences in the Early Ordovician were consistent with climatic separation: Laurentia (and Scotland) was tropical; Baltica was probably at temperate latitudes; while the Anglo-Welsh area was likely to have been at high palaeolatitudes as part of an Ordovician Gondwana (Fig. 1). An oceanic tract, called Tornquist's Sea, was considered to have separated Baltica from the Anglo-Welsh area. Since this ocean subsequently closed, the region of closure should have the appropriate tectonic style.

Geological investigations being carried out at the moment seem to confirm the idea of a vanished Tornquist's Sea. This is a case where a knowledge of fossils has led directly to new tectonic interpretations. Such methods do depend on the actualistic assumption that climatic zones controlled the distribution of fossil taxa in the same way as they control the distribution of the living biota. The fact that other, independent geological evidence seems to confirm the conclusions drawn from fossils vindicates these methodological assumptions.

Biofacies and tectonics

Recent marine environments are diverse and provide different habitats for animals and plants ac-

cording to such factors as substrate type, water depth, temperature, oxygen saturation, and so on. Communities of benthic organisms tend to 'club together' in appropriate environments, even though many such communities intergrade in complex ways. There is no reason to suppose that fossil faunas were any different, although identification of fossil 'communities' is hampered by the partiality of the fossil record. None the less it is common to find constant associations of fossil taxa (usually genera) associated with particular palaeoenvironments. Sometimes these generic associations persist for tens of millions of years. Many different terms have been applied to describe such associations — communities, community types, constant generic associations (CGAs), for example — but the one in commonest currency is *biofacies*, the palaeobiological equivalent of the sedimentary lithofacies (Sections 4.17, 4.18).

Biofacies can be important aids in tectonic problems. Some of the more important biofacies are related to the depth-temperature profile running from shallow-water epicontinental to deep-water oceanic. As we have seen, the shallow-water faunas may lead us to conclusions about palaeoclimatic distribution of faunas — and hence to conclusions about the presence of ancient oceans. In a complementary way, the more exterior, ocean-facing biofacies may afford a method of charting the edges of former oceans, or at least deep marginal basins. Such marginal biofacies should be found along putative sites of former subduction. However, the deeper biofacies do *not* provide a ready method of saying which side of an ocean a fauna occurred, because one of the properties of exterior biofacies is that they are less tied to one particular continent — some genera may, indeed, be pandemic. An example from the Ordovician, contemporaneous with Iapetus (above), is the distribution of the graptolite *isograptid biofacies*. Even at the same time as the epicontinental faunas were divided into separate endemic faunas, corresponding with the distribution of continents and climatic belts, the isograptid biofacies is found worldwide, but its distribution corresponds very closely with the margins of the proposed continents (Fig. 2). This means that the discovery and mapping of sites containing the isograptid faunas can contribute to the understanding of global tectonics: since such a biofacies can be readily identified, even from small fragments (Fortey & Cocks 1986), it can afford valuable clues to the former existence of deep basins in advance of detailed geological mapping.

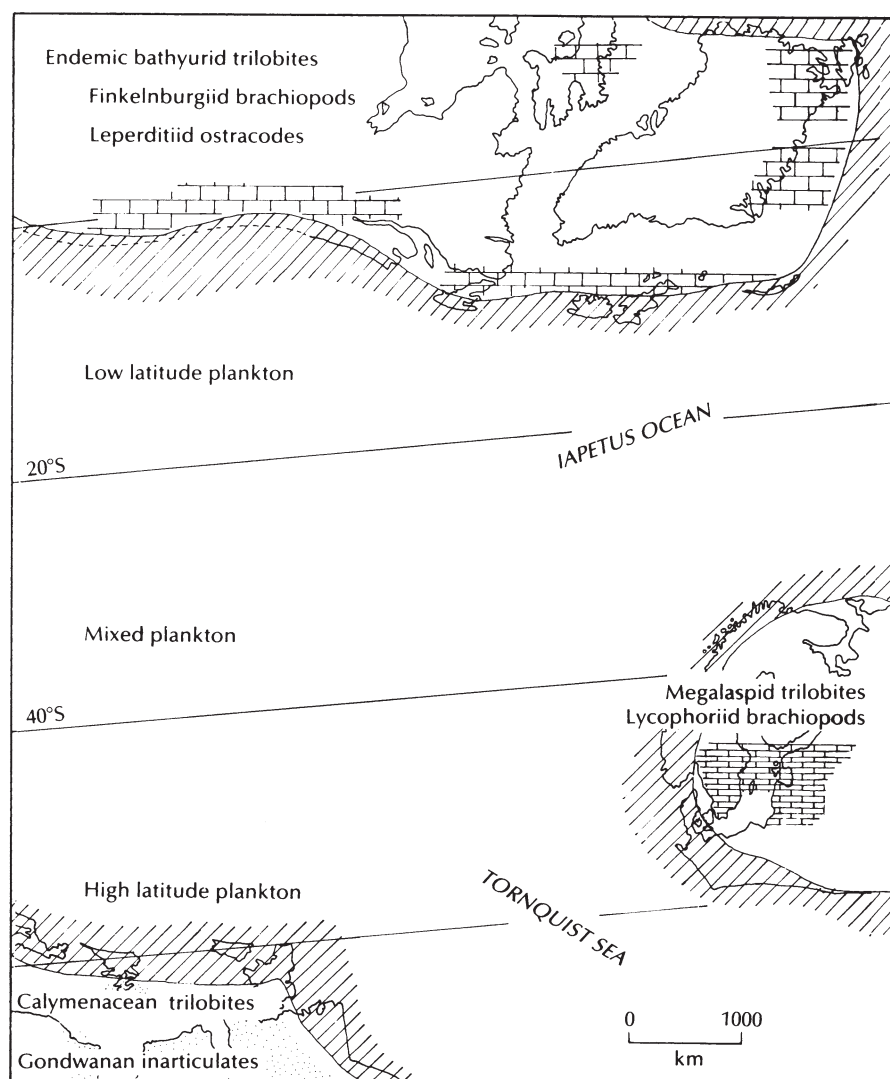


Fig. 1 Lower Ordovician (Arenig–Llanvirn) reconstruction of the North Atlantic area showing the use of endemic shallow-water faunas, temperature-dependent plankton, and lithological facies to infer the presence of former oceanic areas. Large blocks = tropical limestones; small blocks = temperate limestones; stippling = Grès armoricain and associated lithofacies; cross-hatching = marginal bio- and lithofacies belts at the edge of the former continents. Some of the characteristic endemic faunas are listed. (From Fortey & Cocks 1988.)

Where continents converge during phases of subduction, the normal sequence of biofacies may become tectonically reshuffled. This may allow some estimate of the horizontal and vertical displacement involved during earth movements. In the Cambrian–Ordovician Cow Head Group of western Newfoundland (James & Stevens 1986), autochthonous shales accumulated off the edge of the North American shelf, and were augmented by gravity slides of boulders derived from shallower biofacies. Fossils from these boulders show that the gravity slides included samples from deep shelf environments, originally at several hundred metres water depth, as well as typical shelf limestones. Subsequently, the whole Cow Head Group has been thrust onto the platform — moving deep-water biofacies onto shallow-water biofacies in the process.

Independent proof for suspect terranes

Suspect terranes are pieces of crust of less than continental size, the original position of which is in dispute; some have become detached and displaced, even for many hundreds of kilometres. It is obvious, from such major tectonic movements as the San Andreas Fault in western North America today, that relative displacement of terranes can occur quite quickly. However, in analysing fossil distributions which can indicate such terrane movement in the past, it is essential to be sure that the correct comparisons are made between relevant fossils of the same age and biofacies. It is much easier to differentiate movements north–south across latitudes by palaeontological methods, since temperature plays such an important role in controlling the distribution of many fossils, than east–west across

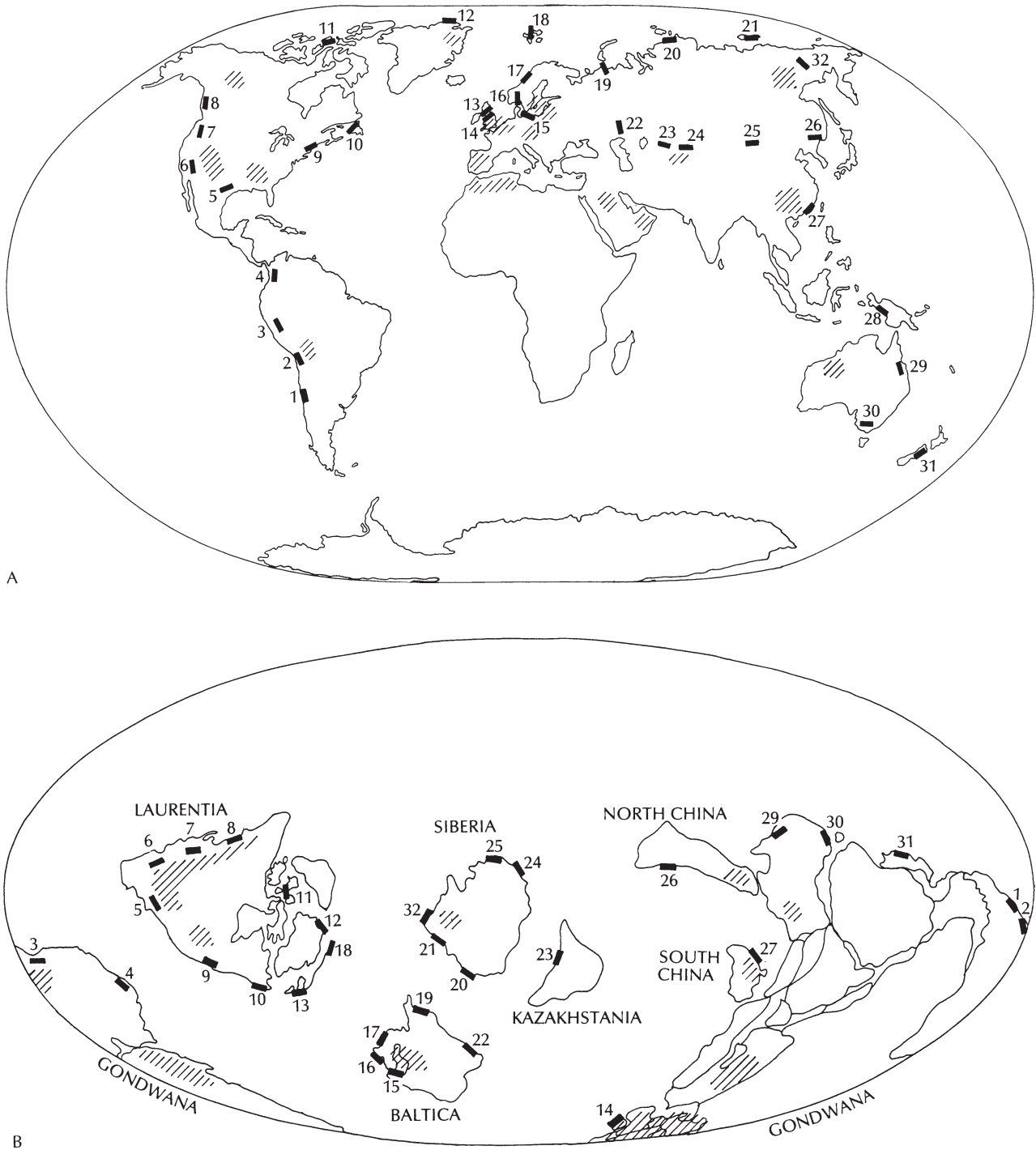


Fig. 2 A, Distribution of Arenig–Llanvirn isograptid graptolite faunas (black rectangles) and shallow-water non-isograptid faunas (cross-hatching) on a modern geographical map. B, The same data plotted on a palaeogeographical reconstruction (originally compiled from palaeomagnetic data but modified by biostratigraphic information) to show how the isograptid biofacies plots out at former continent edges. (From Fortey & Cocks 1986.)

longitudes, where significant terrane movement can occur without appreciable change in the faunas. For example, an analysis of fusuline foraminifera of Permian age along the western North America belt

reveals that verbeekid fusulines, which are characteristic of the Eurasian Tethys, are confined to a fault-bounded area, the Cache Creek Terrane of British Columbia; in contrast, the surrounding areas

have fusulines of non-Tethyan, North American cratonic aspect (Monger & Ross 1971). Such work has led to the recognition of nine separate allochthonous terranes along the Pacific seaboard, some of which appear to have been as far away as Japan in Permian times (Fig. 3). Some longitudinal displacements may be detected when discrete faunal provinces that were originally separated, perhaps by a major oceanic barrier, subsequently become juxtaposed after terrane movement; but this can be recognized only when differing faunas are displaced towards one another, as opposed to tracking the east-west path of a terrane diverging away from its parent palaeocontinent.

Tectonic uses of sea-level curves

By assessing the distribution of benthic fossils in a basin at a single geological period, shallow- to deep-water assemblages may be recognized, with diversity (number of different species) increasing away from the shore. From these distributions a qualitative assessment of water depth (at least from shore-face, shallow shelf, mid-shelf, deep shelf, to oceanic assemblages) may be made (see also Section 4.19.5). By plotting and comparing these relative palaeodepths from one area over a succession of geological ages, a graph may be drawn up of changing depths with time, known as a *sea-level curve*. Whilst such curves are relatively objective, their interpretation requires more thought, since the change of sea-level at one place can be caused either by the rise and fall of the sea itself (eustatic changes), or by the rise and fall of the ocean floor (tectonic changes), or by a combination of the two. However, if the migration of biofacies indicating a transgression or regression is paralleled at exactly the same time in several tectonically independent palaeocontinents, then it is fairly certain that the sea-level changes were eustatic (Fig. 4). For example, sea-level changes appear to have been at their highest during the Cretaceous (Cenomanian) and Ordovician (Caradoc), which explains the wide-spread transgressive sequences recorded from those times, and at their lowest during such events as the late Ordovician and late Permian glacial intervals, when substantial amounts of water must have been locked up as polar ice.

When sea-level curves are anomalous and move in different ways in different places, then tectonic control is indicated. Fig. 5 shows an analysis of sea-level curves for Wales during an extended interval of nearly 70 Ma in the Ordovician and Early Silurian,

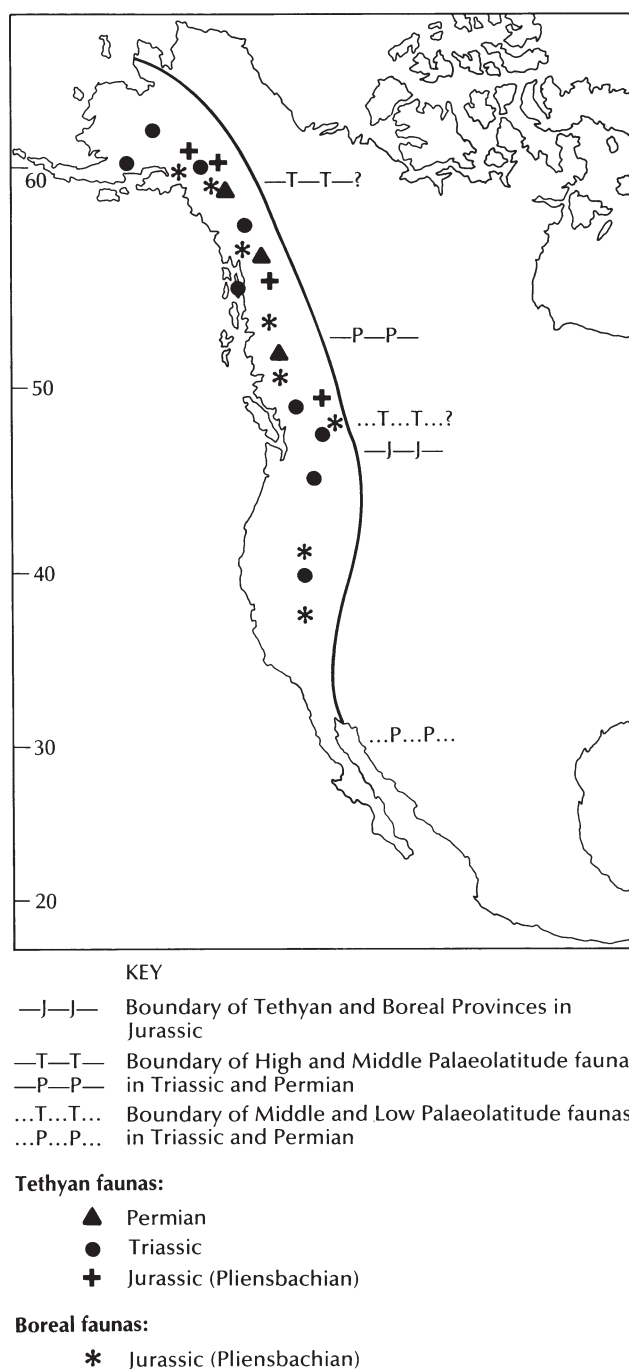


Fig. 3 Displaced terranes of the North American Cordillera with latitudinally displaced Permian, Triassic, and Jurassic faunas, showing how displacement of faunas reveals the sense of movement. (From Hallam 1986.)

as compared with the global eustatic sea-level curve (Fortey & Cocks 1986). The separate curves for north Wales and south Wales parallel the global curve for much of the period, but in the Late Arenig, Llandeilo, and Late Caradoc the north Welsh curve is much displaced from the global curve and displacement occurs in the south Wales curve at the

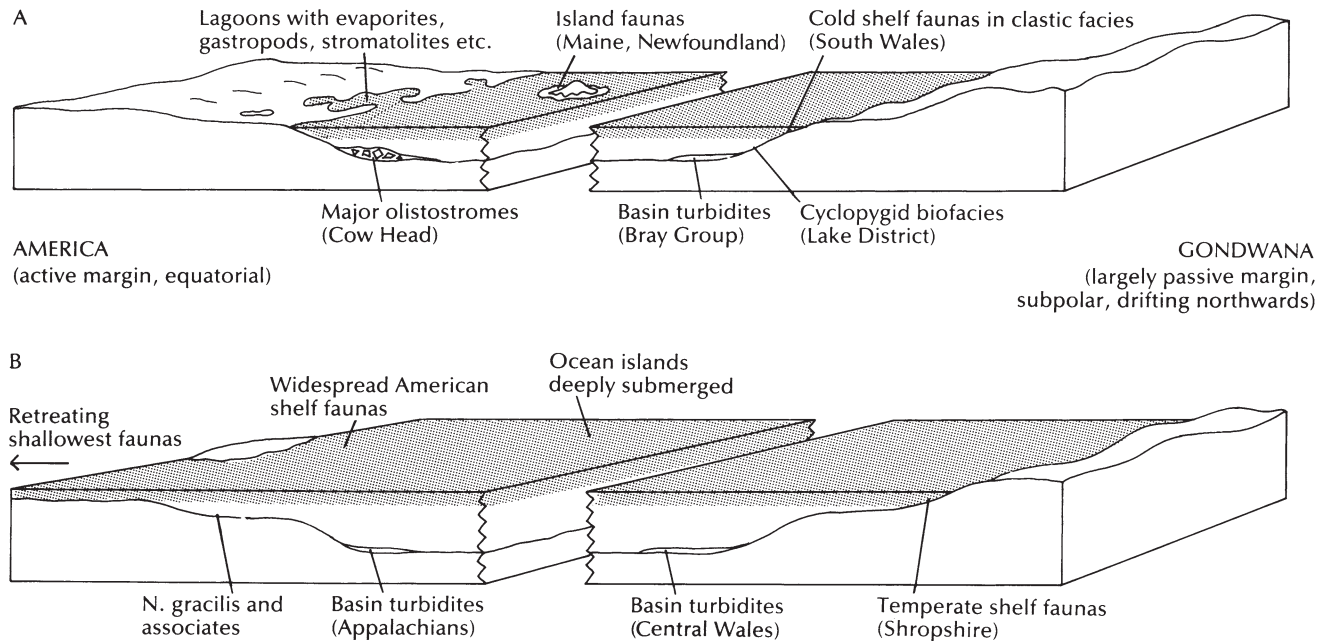


Fig. 4 Contemporary facies on opposite sides of the Iapetus Ocean. A, in regressive early Ordovician (Llanvirn) times. B, in transgressive middle Ordovician (Caradoc) times. (From Fortey & Cocks 1988.)

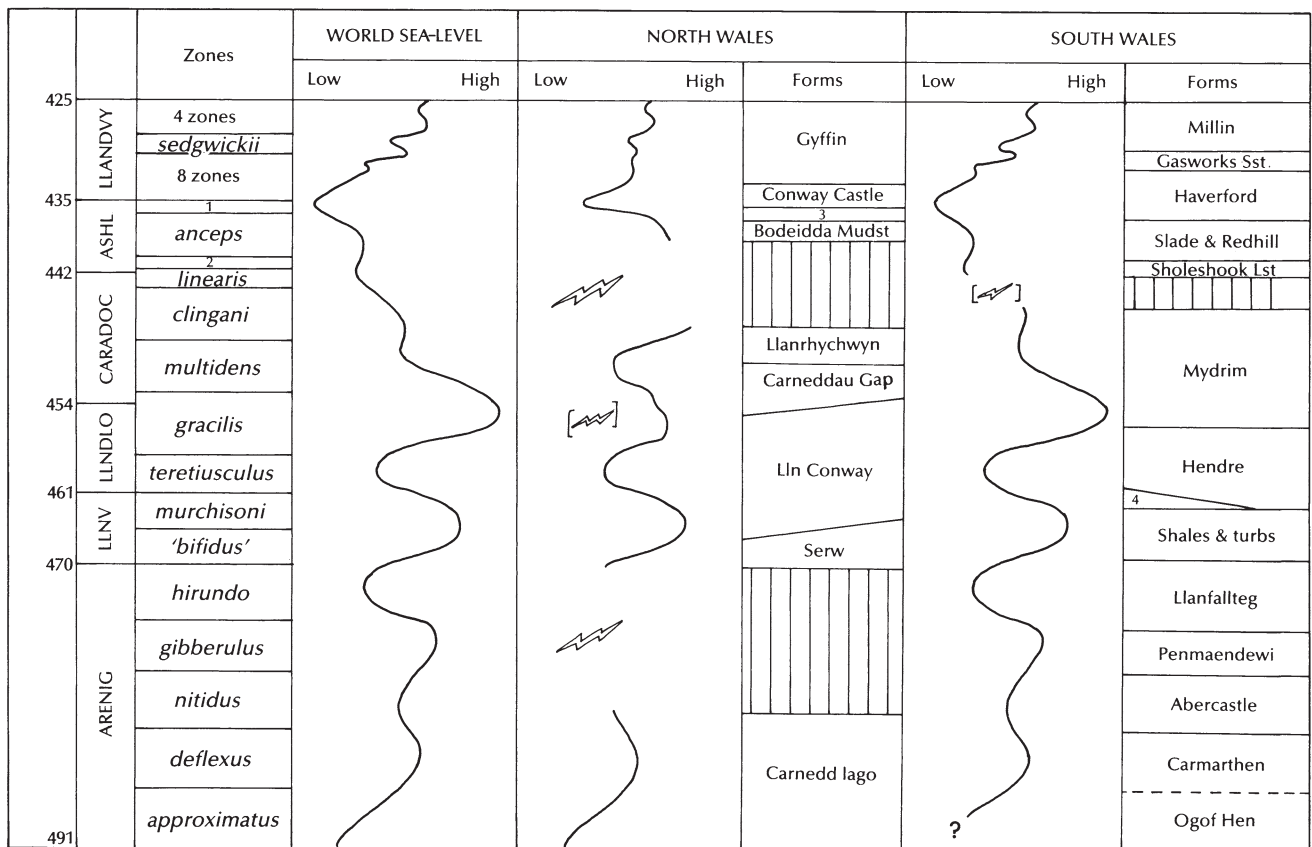


Fig. 5 Sea-level curves recording onlap and offlap of sediments for the Ordovician and Lower Silurian, comparing the global eustatic curve (left) with two local curves from north and south Wales (including the stratigraphical sequences from which they were derived). Note how the local eustatic curves follow the global curve except when they are modified by nearby tectonic activity. (From Fortey & Cocks 1986.)

same (late Caradoc) time. These discrepancies reveal not only periods of contemporary tectonic unrest, but how far-reaching any particular tectonic disturbance was. It is interesting to note, for example, that the sea-level curve is affected by the late Llandeilo volcanicity in north Wales, which includes the volcanic outpourings of what are today Snowdon and other mountains, whilst the contemporary curve for south Wales, only 120 km to the southwest, appears to have been closer to the global curve. This indicates that, assuming an Ordovician geographical separation of the two areas similar to that seen today (which seems likely), the volcanic tectonicity in north Wales was relatively restricted in area.

References

- Audley-Charles, M.G. 1986. Rates of Neogene and Quaternary tectonic movements in the Southern Banda Arc based on micropalaeontology. *Journal of the Geological Society* **143**, 161–175.
- Boucot, A.J. & Thompson, J.B. 1963. Metamorphosed Silurian brachiopods from New Hampshire. *Bulletin of the Geological Society of America* **74**, 1313–1334.
- Cocks, L.R.M. & Fortey, R.A. 1982. Faunal evidence for oceanic separations in the Palaeozoic of Britain. *Journal of the Geological Society* **139**, 465–478.
- Curry, G.B., Bluck, B.J., Burton, C.J., Ingham, J.K., Siveter, D.J. & Williams, A. 1984. Age, evolution and tectonic history of the Highland Border Complex, Scotland. *Transactions of the Royal Society of Edinburgh (Earth Sciences)* **75**, 113–133.
- Fortey, R.A. & Cocks, L.R.M. 1986. Marginal faunal belts and their structural implications, with examples from the Lower Palaeozoic. *Journal of the Geological Society* **143**, 151–160.
- Fortey, R.A. & Cocks, L.R.M. 1988. *Arenig to Llandovery faunal distributions in the Caledonides of the North Atlantic Region*. Special Publication of the Geological Society No. 36.
- Gee, D.G. & Roberts, D. 1983. Timing of deformation in the Scandinavian Caledonides. In: P.E. Schenk (ed.) *Regional trends in the geology of the Appalachian–Caledonian–Hercynian–Mauritanide–Orogen*, pp. 279–292. Reidel, Dordrecht.
- Hallam, A. 1986. Evidence of displaced terranes from Permian to Jurassic faunas around the Pacific margins. *Journal of the Geological Society* **143**, 209–216.
- James, N.P. & Stevens, R.K. 1986. Stratigraphy and correlation of the Cambro-Ordovician Cow Head Group, Western Newfoundland. *Bulletin of the Geological Survey of Canada* **366**, 1–143.
- Kokelaar, B.P. & Howells, M.F. (eds) 1984. *Marginal basin geology*. Special Publication of the Geological Society No. 16.
- Monger, J.W.H. & Ross, C.A. 1971. Distribution of fusulinaceans in the western Canadian Cordillera. *Canadian Journal of Earth Sciences* **8**, 259–278.
- Murchison, R.I. 1839. *The Silurian System*. John Murray, London.