



THE IMPACT OF THE PALAEOONTOLOGICAL TREATISES ON BIOLOGICAL AND EARTH SCIENCES

J. B. WATERHOUSE

DEPARTMENT OF GEOLOGY AND MINERALOGY, UNIVERSITY OF QUEENSLAND,
BRISBANE, AUSTRALIA

ABSTRACT

The palaeontological treatises, such as those edited by Y. A. Orlov, have provided the basis necessary for analysis of evolution, correlation, and aspects of continental drift and climatic change. In particular the Treatises have preceded palaeoecological studies which now demand radical reassessments of various geological assumptions. These include the need to completely revise the codes for stratigraphic nomenclature by incorporating a section on ecostratigraphy, which will then clarify and render biostratigraphy useful and realistic. Palaeoecology, provided that it is underpinned by proper systematic work as set out in the palaeontological treatises, also provides statistical data for calibrating the movement of continents and tectonic plates through the recognition of fossil biomes. It further reveals a pattern of drastic climatic changes, with major coolings every 30 million years, with rhythmic subcycles superimposed. These climatic oscillations caused episodic migration of life, and gave rise to short-lived episodes of rapid evolution, separated by long intervals of relative stability during which the tempo of evolution slowed down. On the other hand the superficial use of palaeontological treatises for information on correlation, time, environment, and geographic distribution is to be deplored, because the treatises do not provide such information with sufficient detail and are frequently inaccurate. The geological data must match the systematic data in accuracy before evolution and correlation and other geological aspects can be interpreted.

INTRODUCTION

At first sight, the palaeontological treatises have not had a far-reaching impact on other disciplines of the earth sciences. There have been several such invaluable treatises, including the French series that appeared just after the war (Piveteau, e.g. 1952), the great Russian series that markedly advanced classification of fossils, and was superbly illustrated with many line drawings (Orlov, e.g. 1960), and the American-British series that is still current, and provides the most useful and far-reaching summary of systematic knowledge (e.g. Moore, 1965). All have had a strong biological emphasis. It would be going too far to suggest that they have been revolutionary, but certainly they both demonstrate and have helped cause a remarkable explosion of knowledge on systematics. An outstanding example of this is offered by the study of Productid Brachiopoda by Muir-Wood and Cooper (1960), that preceded part of the Moore Treatise on Brachiopoda. In that work some 9 of the 19 families then recognised, and 68 of the 187 genera then recognised, were newly proposed.

Attempts have been made to relate this expanded systematic knowledge to other aspects of geology. Some authorities have drawn on the Treatise as a source for evolutionary studies (as reviewed by Kolata, 1975),

others as a source for demonstrating the stability of continents (e.g. Meyerhoff and Teichert, 1971), others as a source for examination of the great demise of life at the end of the Permian Period (e.g. Schopf, 1974), or even to demonstrate that no such demise occurred. Some of these analyses are particularly elegant. Yet none are acceptable. Detailed systematic biology can only be related to other aspects of geology, and some kind of successful correlation and even explanation propounded, when those aspects for which relationships are sought are examined in comparable detail. Boucot (1975) has made the same point. The treatises are not a source of information for *time*, or for correlation, or for ecology or geographic distribution, or even for species morphology and ranges. Their use of time subdivisions are often accurate only to about a period. As a result, the geologic information is out of scale, and out of phase with the systematic data, and can only yield distorted values. For instance, Schopf (1974) wished to analyse the cause of death of families in the Permian Period from data set out in the American-British Treatise series. Geographic distribution, correlation and timing are critical to such an analysis. Yet he used the Treatise as a source for distribution and timing, even though the Treatise time scale is not only incredibly crude, but not carefully applied

for the ranges of even families and genera through the text (e.g. Moore, 1965). Time, like other aspects of geology, was not the concern of the Treatise series.

But detailed systematic studies and summaries have played, and promise to play, a vital role in understanding of earth science and biology, once we abandon over-hasty analyses based solely on Treatise series. There is now a considerable overturning, if not revolution, in thinking on many aspects of geology—not only palaeontology—and much of this stems from, and is underpinned by the critical first step, provided by sound systematic study, as summarised in the palaeontological treatises edited by Orlov (1960) and Moore (1965).

1. PALAEOECOLOGY AND THE STRATIGRAPHIC CODE

In the following survey, I wish to comment on aspects of evolution, correlation, continental drift, world climate, and palaeoecology. All are mutually dependent, so that it scarcely is possible to touch on one aspect with bare adequacy without having laid the foundations from the other disciplines. But palaeoecology lies at the heart of many problems in evolution and correlation, and indeed earth history. The belated studies on this discipline have only now reached a reasonable rate of progress, triggered, as generally acknowledged, by the studies of fossil communities by Ziegler *et al.* (1968). Such studies on synecology and autecology must of course be based on systematics. Without sound identifications, ecologic analyses become inconsistent, and perhaps useless. It is therefore significant that the wave of palaeoecologic surveys has patently followed the appearance of the Treatise volumes on systematics.

Palaeoecology, as shown below, has far reaching implications for evolution of life, and indeed for earth history. Moreover it demands immediately and urgently a substantial development in our understanding of stratigraphy, as expressed by the International Code of Stratigraphic Nomenclature (Hedberg, 1972). The stratigraphic code is clearly based on ideas expressed by Hedberg in Schenk (1939), before the appearance of the great Treatises, and before the critical role of ecology was appreciated. The code has recognised three subdivisions in our understanding of stratigraphy in its broadest sense:—

- Lithostratigraphy
- Biostratigraphy
- Chronostratigraphy

The first category has occasioned little trouble, and has a hierarchy of nomenclature that can be verified in the field by other workers. The other two categories have occasioned proposal of alternative schemes. For biostratigraphy, and implicitly much of chronostratigraphy, the "International Code" has recognised a series of "biozones", all apparently of arbitrary nature, and of

roughly equal rank, with no hierarchy. Unlike the lithostratigraphic section, there is little immediate evidence that the zones need be other than arbitrary, because there is no obvious relationship to outcrops or collections. The fatal weakness in the scheme lies in the failure to recognise a separate section I call "Ecostratigraphy", that is, fossil communities, fossil associations, fossil biomes, which are based on actual presence of fossil species in outcrops. Ecostratigraphy is just as real, and natural, and verifiable as lithostratigraphy. Ecostratigraphy rather than biostratigraphy, provides the simple biologic counterpart to lithostratigraphy, and must be granted a key role in the stratigraphic code. There is a natural hierarchy, akin to the bed-member-formation-group hierarchy of lithostratigraphy, and this hierarchy proceeds as sub-community-community-province-biome, with the prefix fossil (Table 1). Subcommunities are based on spatially limited species, in clumps or clusters, and communities are based on prime species, estimated in terms of biomass, which can be established also on a proportional basis from hard parts in the fossil record. Often fossil communities depended on such parameters as lithotope, salinity, water depth. Provinces incorporate contemporaneous communities of one geographic area, and may often be characterised by genera. Distribution played a major role in their extent. Fossil biomes, like present-day biomes, incorporate fossil provinces of a major climatic regime, and were often characterised by families or even higher taxonomic ranks, in the way that upper Palaeozoic tropical biomes were characterised by Fusulinacea and compound Rugosa.

The recognition of Ecostratigraphy provides the key to understanding biostratigraphy. Biozones are based on species, even though the Code fails to discriminate species biozones from generic biozones. Species also characterise fossil communities, so that there is clearly some link between the two. But we cannot in practice directly match communities with biozones. If we did, we would have no need for one or other term. Moreover biozones have a substantial temporal implication, and also serve for mapping and correlation. If they were matched directly with fossil communities, we would find it extremely difficult to map the series of repeated and rapidly oscillating recurrent fossil communities outlined by Ziegler *et al.* (1968) in the Silurian of Wales, or by Waterhouse (1973b) in the Permian of New Zealand. Such fossil communities should be grouped into one biozone if it can be demonstrated by stratigraphic or fossil evidence that they were essentially contemporaneous, by sharing significant and short lived species. Whether the biozone is an acme zone, or a range zone, or assemblage zone often depends simply on whether the whole fauna, or one lineage has been studied. In the marine situation, the inshore and offshore shelf, and the continental

slope of one area and at one time would have been inhabited by a number of fossil communities, and these, by sharing certain forms, including plankton and nekton, can be correlated and assigned to one zone. Of course, it often happens that a biozone is represented in the fossil record by only one fossil community. But in such instances the sampling is substandard, and must be recognised as such. Perhaps such examples should be regarded solely as subzones, based on one community, and not necessarily attached to any zone. Essentially the biozone corresponds to a province. It can seldom be traced beyond finite geographic limits, and has to be correlated with contemporaneous biozones, that belonged to different biomes and provinces, by using different shared species.

In correlating such biozones, we could assign them to a superzone, which incorporates different biozones, from all contemporaneous provinces and biomes. Superzones correspond with a substage, which incorporates

Table 1

Summary of proposed unit-terms and hierarchies in stratigraphic classification

Litho-stratigraphic Category	Eco-stratigraphic Category (Fossil)	Bio-stratigraphic Category	Chrono-stratigraphic Category
			period
			series
			stage
	correlative biomes	superzone	substage
group			
	province	biozone	
formation			
member			
	community	subzone	
bed			
	subcommunity		

barren rock, and geological events and deposits of a particular segment of time, and these in turn are built into stages (Table 1). In this way, by recognising the natural and major section Ecostratigraphy, we can rationalise Biostratigraphy, and erect for it a hierarchy that has considerable reality.

2. PALAEOGEOGRAPHY

The recognition of the role of palaeoecology, which is based in part on systematic studies, also carries import-

ant implications for relating biology to continental drift. Leaving aside for the moment the effect on evolution and diversification as summarised through systematics, it has been established that sea-floor spreading may be calibrated through time by the effect on life, which is strongly affected by climate, which in turn depends on palaeolatitude. Fischer (1960) showed that diversity of life increased from poles to equator, and Waterhouse and Bonham-Carter (1975) showed that fossil biomes could be recognised as equatorial, temperate, and polar, and that the distribution of Permian biomes, as compared with present-day biomes, demonstrated continental displacement in various and complicated directions. In analysing Permian fossil biomes, Waterhouse and Bonham-Carter (1975) used a slightly emended Treatise classification (by Orlov and Moore) for the systematic analyses of Permian brachiopod families. But they avoided the facile trap of also using the Treatises as a data bank on geographic distribution and age. Instead these were analysed independently, from original literature and from extensive new studies, to provide geological detail of a standard comparable to that of the systematic detail in the Treatise series. Since fossil biomes were under enquiry, a prime analysis was based on Q-mode cluster analysis of the distribution and association of brachiopod families, brachiopods having been the predominant marine invertebrate fossil.

Three core groups were found to be readily separable. To enlarge the scope of the biomes, the association with other fossil groups, such as Fusulinacea and Rugosa was assessed by t-test and Chi-square. To interpret the geographic implication of the fossil biomes, the distribution was compared with distribution of glacial rocks (to be expected with polar biomes), and with oxygen-isotope temperature values and other criteria also dependent on climate and palaeolatitude. Finally, the Permian positions suggested by the Permian faunal biomes was found to compare well with palaeomagnetic evaluations (Vine, 1973), and in large measure, though not entirely, with evidence based on sea-floor spreading (Smith, *et al.*, 1973). At the heart of our work, lay the systematic studies by Orlov (1960) and Moore (1965).

3. CORRELATION

It has been mentioned that fossil communities episodically shifted in position, in keeping with changes in depth of water, and especially with the shift of bottom facies in the marine benthic world (Ziegler *et al.* 1968, Waterhouse, 1973b). Such shift appears to have had little perceptible effect on either species, or fossil communities, other than positional, for there was little morphologic change, and only slight change in composition of communities. But much larger biotic shifts also occurred, as became apparent through the biome analyses by

Waterhouse and Bonham-Carter (1975), and Waterhouse (1973b), in which some areas witnessed episodic changes in their type of province, and even type of biome throughout the Permian Period. These changes were too rapid and oscillatory to have been caused by rapid migration of continents. Instead, the faunal changes coincide with stratigraphic evidence for climatic change. This is to be expected. Climatic change would have induced considerable migration of life, and consequently a shift in position of biomes and provinces. It is these shifts, rapid geologically speaking, that provide sharp boundaries to a succession of zones through any geologic column. For instance, in subdividing columns, one is struck how, again and again, species, and often genera, and therefore many contemporaneous communities changed abruptly, and synchronously, not only over one region, but, within the limits of correlation, synchronously over the world. These changes were not induced by changes in substrate, or depth of water, for although these may have changed at some boundaries, at others they did not, as far as can be judged. Anyway it is obvious that a sandstone of one zone is likely to be intrinsically identical with that of a preceding or following zone: the sea-floor did not change except in terms of its biologic component, and in terms of small geographic shifts. Nor can we appeal except by special pleading, to biologically induced change, because, as discussed below, the fossil record shows long intervals of stability, with little biologic change. Something occurred that suddenly induced communities and species to change. And since these changes coincided with climatic change, it appears most likely that climatic change induced migration. Thus any sequence will record through its zones a series of climatically induced migrations into and out of the region.

In Fig. 1 a model is presented of fossil biomes fluctuating in position throughout the Permian Period. It is in part a conception, but has been modified by evidence for actual biome shifts, and by the presence of glacial rock at intervals (Waterhouse and Bonham-Carter, 1975). Clearly such climatic shifts would give rise to a sequence of different and perhaps repetitious zones in any one sequence, as is found in nature.

4. EVOLUTION

The wealth of systematic detail in the Treatise volumes must contain substantial information on evolution, as further summarised in Harland (1967). Some workers have tried to demonstrate evolution modes and tempo from computer analysis with premises of decline and initiation of new forms, and selection, (Kolata, 1975). But the analyses are not at specific level, despite claims to the contrary, and, together with the summaries in Harland (1967), lack any rigour over the all important factor of time and duration, and over other geologic

events, even to the simple parameters considered in ecological studies. And of course evolution must be studied from the actual record, not from computer simulated simplicities that ignore environmental parameters. What is clear is that, despite numerous and attractive appeals for the use of numerical systematics, and in particular to theorisations that Linnean classification is unsatisfactory, Linnean classification works. Intense study on morphology has not dissolved the boundaries between most genera—it has simply multiplied them. The great increase in number of genera and higher categories proposed for Productina by Muir-Wood and Cooper (1960) has not been subsequently deemed artificial, or anthropomorphic. It has spurred further work, with recognition of still more taxonomic subdivisions, as well as the acceptance of the entities proposed by Muir-Wood and Cooper (1960). In spite of the prevailing scientific philosophy in favour of gradual evolution, and alleged unreality of taxonomic subdivisions higher than species category, and in the face of the alleged truism that nature knows no boundaries, somehow the Linnean system with its emphasis on subdivision seems to work, and to stand the test of time.

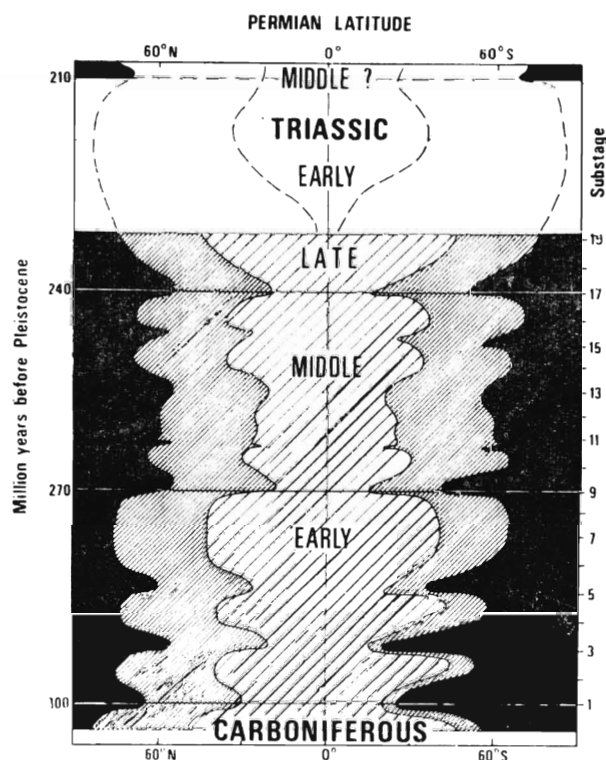


Fig. 1. Model of positional shift of biomes (marine) over earth throughout Permian Period, with north and south poles (N, S), and equator (0°). Time progresses upwards, substage by substage. Based as far as possible on fossil distributions, assessed by Q mode cluster analysis (Waterhouse and Bonham-Carter, 1975), with stratigraphic and climatic and radiometric data, summarised in part by Waterhouse (1976).

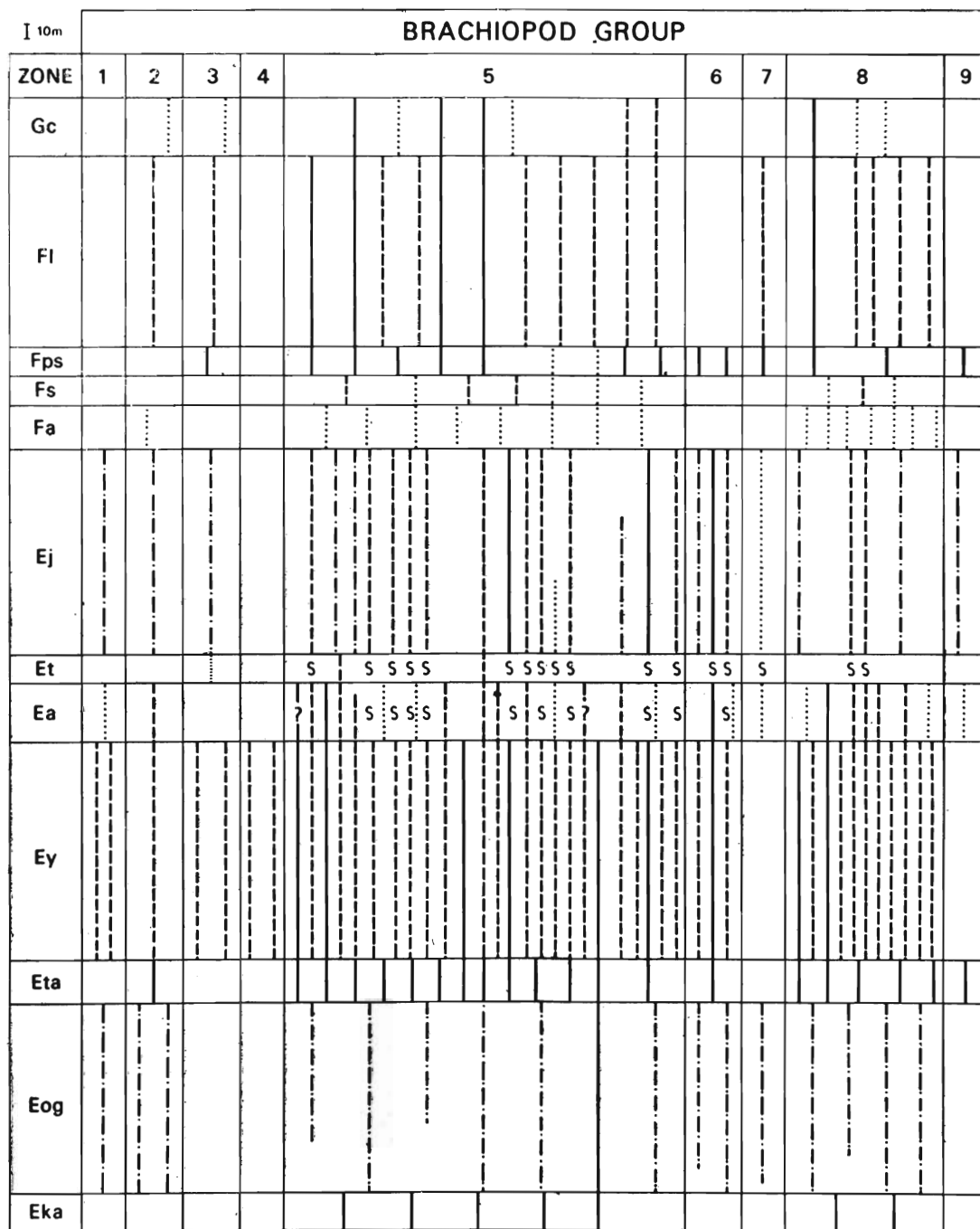


Fig. 2. Range chart of brachiopod species in Permian beds of the north Yukon Territory, Arctic Canada. Species that commence in a zone are assigned a distinct kind of line, and many are replaced from zone to zone though a few persist. The species are grouped as follows: 1. Inarticulate (zone Ea); Orthida; 2. Davidsoniacea; 3. Chonetidina; 4. Strophalosiacea; 5. Productacea 6. Rhynchonellida; 7. Atrypida; 8. Spiriferida 9. Terebratulida. Zones match the type stages and substages based also on biozones, of the Urals as follows:

GC—Lower Kazanian or Kalinovian; Fl—Nevolin; Fps—Filippovian; Fs—Krasnoufimian; Fa—Sarginian; Ej—Aktastinian; Et and Ea—Sterlitamkian; Ey—Tastubian; Eta—Kurmaian; Eok—Uskalikian; Eka—Surenan. The symbol S links species absent from an intervening zone. Thickness approximate, exaggerated for narrow zones.

To a number of workers, the basic pragmatic approach to systematics set out in the Treatise studies, is indeed based on reality. A growing school of thought suggests that evolution occurred not gradually, but episodically (Eldredge and Gould, 1972, and other papers). As Hayami and Ozawa (1975) point out, this is good accord with modern genetic theory, in which selection strongly in favour of one genotype may result in a very rapid change in morphology.

Our chart of Fig. 2 strongly suggests that the demise of some species, and the incoming of other species is to be coupled with the ecologic, and zonal and temporal model set out in Fig. 1. That is, the morphologic changes, and the outgoings and incomings of species, may have corresponded with climatic changes. By such a model, we may fuse all the component parts of palaeontology, systematics, ecology, correlation and evolution into one consistent and coherent whole. An abrupt climatic change must have elicited a strong response from stenothermal species. And these in turn must have played a role in trophism, and perhaps other aspects important to other biota, so that entire communities must have been affected, simultaneously within the limits of geologic time, across the world. In other words, severe climatic change broke down the homeostasis prevailing during the preceding regime, and induced considerable migration of at least stenothermal species. This affected reproduction, the food chain, and also must have affected geochemical conditions, and sometimes substrate, water sequence, involving ripple effects, with many secondary and tertiary consequences. It was during the crisis of climatic change and migration that species evolved, and communities changed. Stabilization of climate for a few hundred thousand or millions of years led to stabilization of new communities, consisting of new species, migrants, and static species, until the next climatic change. It is this theory that provides the best available explanation for evolution, and reconciles geologic and palaeontologic evidence with genetic evidence for short-lived, episodic, and rapid evolutionary change that affected a significant proportion of life from time to time.

DEATH OF FAMILIES

One new line of evidence in strong support of this thesis is provided by Q-mode cluster analysis of the brachiopod families that died during the Permian Period (Fig. 3). According to this analysis, the families that died out at the end of each substage, and start of the succeeding substage, show a strong correlation with two major factors. The first two substances of change appear to have critically affected families that inhabited temperate regions, and may have been related to the substantial withdrawal of shelf seas from these regions, or to some other cause. The remaining changes showed

strong correlation with climate, warm episodes causing loss of cold-water families, and cold episodes causing loss of warm-water stenothermal families. But during the final and climatic phase of the Permian Period, warm-water families suffered during a warm or perhaps very hot climatic episode, in strong support for the proposal by Meyerhoff (1973) and Waterhouse (1973a, 1974) that the world's climate was, at least briefly, so hot that equatorial life perished.

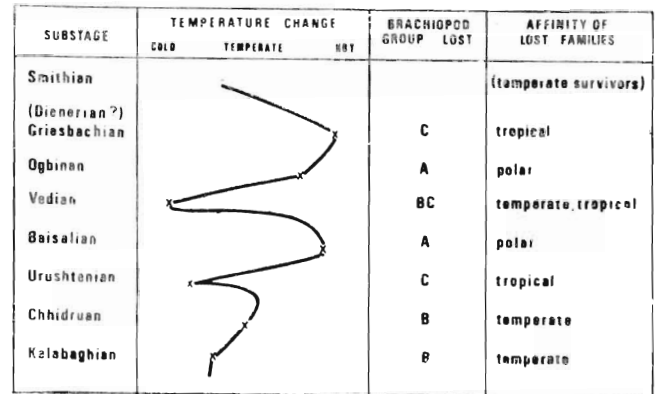


Fig. 3. Computer-based analysis of biome affinities of brachiopod families that died out at the start of successive substages (i.e. superzones as defined herein). The first losses may have reflected loss of shelf space in the northern hemisphere, and the remaining losses were controlled by climatic fluctuations.

THIRTY MILLION YEAR GLACIAL CYCLES

Finally, we note that the glacial record, and the temperature record based on oxygen-isotope values from calcium carbonate in shell-fish, may be plotted against preferred radiometric ages to strongly suggest a thirty million year major periodicity in climatic change (Fig. 4). Larger cycles are also present, at a spacing of perhaps 300 million years, and subcycles are also present. The overall spacing of climatic change provides support for episodic change to life, causing episodic migration and evolution, which affected both ecologic and morphologic expression of life.

SUMMARY

The great systematic treatises on biological systematics, edited by workers such as Orlov and Moore, have provided the necessary basis for advances in our understanding of palaeoecology, and correlation, movement of continents, and changes in climate. Palaeoecology, now underpinned by systematic study as summarised in the Treatises, must now assume its rightful place in our key to understanding and expressing stratigraphic concepts, with long overdue revision of the code of stratigraphic nomenclature. Through major analyses of ecologic associations through time and space, it becomes

clear that episodic geographic shifts of faunal and probably floral associations were the major factor in defining zonal sequences and had a strong correlation, possibly causal, with evolutionary advances, and extinction of families. These shifts were probably induced by changes in climate, which show a series of regular and major changes every 30 million years, with superimposed subcycles, and longer term changes.

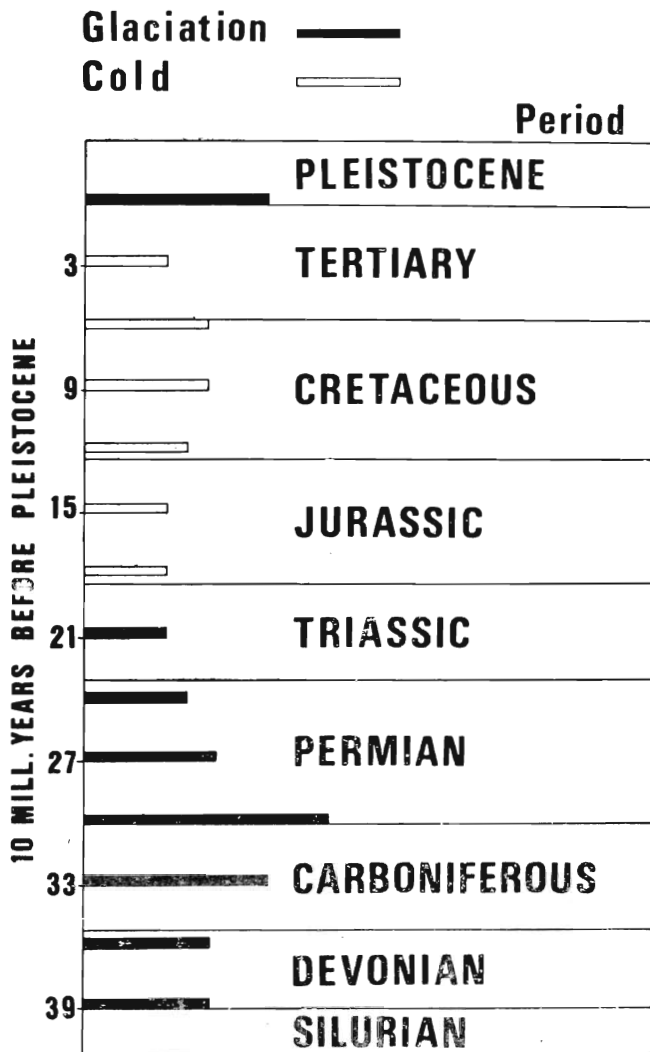


Fig. 4. Chart of Palaeozoic to Pleistocene major coolings or glaciations, summarizing radiometric evidence largely set out by Hulston and McCabe (1972, appendix 2), with some emendations to incorporate modern work, glacial episodes as in part discussed by Mahlzhahn (1957) and Waterhouse (1974), and oxygen-isotope low temperature values largely summarised by Bowen (1966).

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