

MODERN PALEONTOLOGY: USING BIOSTRATIGRAPHY TO THE UTMOST

Arthur J. BOUCOT

Department of Zoology, Oregon State University
Corvallis, Oregon 97331-2914, U.S.A.

ABSTRACT

Emphasized here is the presence of two "types" of biostratigraphy. The first, associated with Alcide d'Orbigny who was its discoverer, consists of the relatively small number of marked changes in the overall marine, benthic, chiefly level-bottom biota. These are the boundaries between d'Orbigny's *étages* and *sous-étages*, which I have recently termed Ecologic-Evolutionary Units and Subunits. The second, associated with Albert Opper who was their discoverer, are the within *étage* or Ecologic-Evolutionary Unit changes of a more gradual type. The gradual changes consist of the within community, species-to-species, changes shown by each genus belonging to each community. By paying more attention to the character of the changes occurring within each community, genus-by-genus, and then overlapping the subsequent Opperian zonation possible with that taken from adjacent, interfingering communities, we may achieve a higher level of reliable, more precise biostratigraphy than by merely using miscellaneous taxa from varied communities. This approach requires that an ecostratigraphic sampling program be employed, i.e., tracking specific communities, through evolutionary time (within each ecologic-evolutionary unit), from section to section (because few sections represent the same community, i.e., environment, for a geologically lengthy time interval). This approach maximizes the phyletic evolutionary content of the fossil record, the Opperian, while also taking advantage of extinction, adaptive radiation and dispersal, the d'Orbignyan.

Key Words: Biostratigraphy, Correlation precision, Gradual biostratigraphy (Opperian), Abrupt biostratigraphy (d'Orbignyan), Quantum evolution, Biogeography, Extinction, Adaptive radiation

RESUMEN

Se hace énfasis en la presencia de dos "tipos" de bioestratigrafía. El primero, asociado con Alcide d'Orbigny, que fue su descubridor, consiste en el relativamente reducido número de cambios importantes en el conjunto marino bentónico, principalmente los del fondo. En este caso tenemos la delimitación entre los *étages* y los *sous-étages* de d'Orbigny, que recientemente he denominado Unidades y Subunidades Ecológico-Evolutivas, respectivamente. El segundo, asociado con Albert Opper que fue su descubridor, son los cambios, de un tipo más gradual, dentro de los *étages* o Unidades Ecológico-Evolutivas. Dichos cambios son intracomunitarios o intraespecíficos, como los que se muestran en cada género perteneciente a una comunidad. Si prestamos más atención al carácter de los cambios intracomunitarios, género por género, y sobreimponemos entonces la posible zonación opperiana subsecuente con los datos de otras adyacentes, con las que tengan cambios laterales, podemos conseguir un mayor grado de fiabilidad, una más precisa bioestratigrafía, que si usamos meramente diversos taxones de varias comunidades. Este ensayo requiere que se emplee una técnica de muestreo ecoestratigráfico, es decir un seguimiento de comunidades específicas a lo largo del tiempo (en cada unidad ecológico-evolutiva), de sección a sección (ya que pocas secciones representan la misma comunidad p. ej.: un ambiente, para un período de tiempo geológicamente prolongado). Este método destaca el contenido evolutivo filético (sentido opperiano) del registro fósil, mientras que también saca provecho de la extinción, radiación adaptativa y dispersión (sentido d'Orbigniano).

Palabras clave: Bioestratigrafía, Correlación de precisión, Bioestratigrafía gradual (opperiana), Bioestratigrafía de eventos (d'orbigniana), Evolución cuántica, Biogeografía, Extinción, Radiación adaptativa.

INTRODUCTION

The paleontologist has done more with morphology, taxonomy and biostratigraphy during the past two centuries than with anything else. Since 1859 the data of morphology and taxonomy have provided much of the basic evidence from which many of our phylogenetic and evolutionary concepts (such things as Cope's Rule) have been based. Without this morphologic *cum* taxonomic data many as-

pects of our current understanding of the evolutionary process would have been impoverished; it is hard to conceive of a modern understanding of evolution from which ALL the data of morphology and taxonomy derived from the fossil record has been removed. What would we do without the evolutionary services of *Archaeopteryx*, to mention just one mainstay of our thinking! Biostratigraphy, however, although of monumental service to the geologist for the dating and correlation of fossiliferous beds on

local, regional and global scales has never appeared to have attracted very much concern or interest from the evolutionist. It seems to me that this has been a great oversight, one which needs to be rectified as soon as possible.

When referring to the significance of biostratigraphies for evolutionary purposes I am thinking here of what one may refer to as abrupt and gradual biostratigraphic changes. Abrupt biostratigraphic changes, as contrasted with the gradual type, signify such things as extinction, adaptive radiation, dispersal, rapid climatic gradient alterations, geographic alterations, and the like. Gradual biostratigraphic changes reflect non-adaptive radiation, within community group, phyletic evolution of the type I described in 1978.

William Smith, the founding Father of stratigraphy, made it clear by the end of the Eighteenth Century, that there is a unique sequence of beds, based on a combination of physical and biological criteria (fossil content) in at least one region (much of England in his case). Smith's monumental conclusion was then extended from England to cover much of Continental Europe. However, because each bed or sequence of very similar beds, can be viewed as representing a unique packet one is faced with the problem of deciding whether said packet represents purely local, possibly regional, or even global uniqueness. This is basically a sampling problem. The reasons for the existence of this sampling problem are complex. Heavily involved in local and regional biostratigraphies are purely local and regional environmental changes, many of which do not have a global extent. Fernández López (1986, 1987) has effectively considered the modern aspects of biostratigraphy, effectively relating them to the classic problems of dating and correlating fossiliferous strata.

ABRUPT VERSUS GRADUAL BIOSTRATIGRAPHY

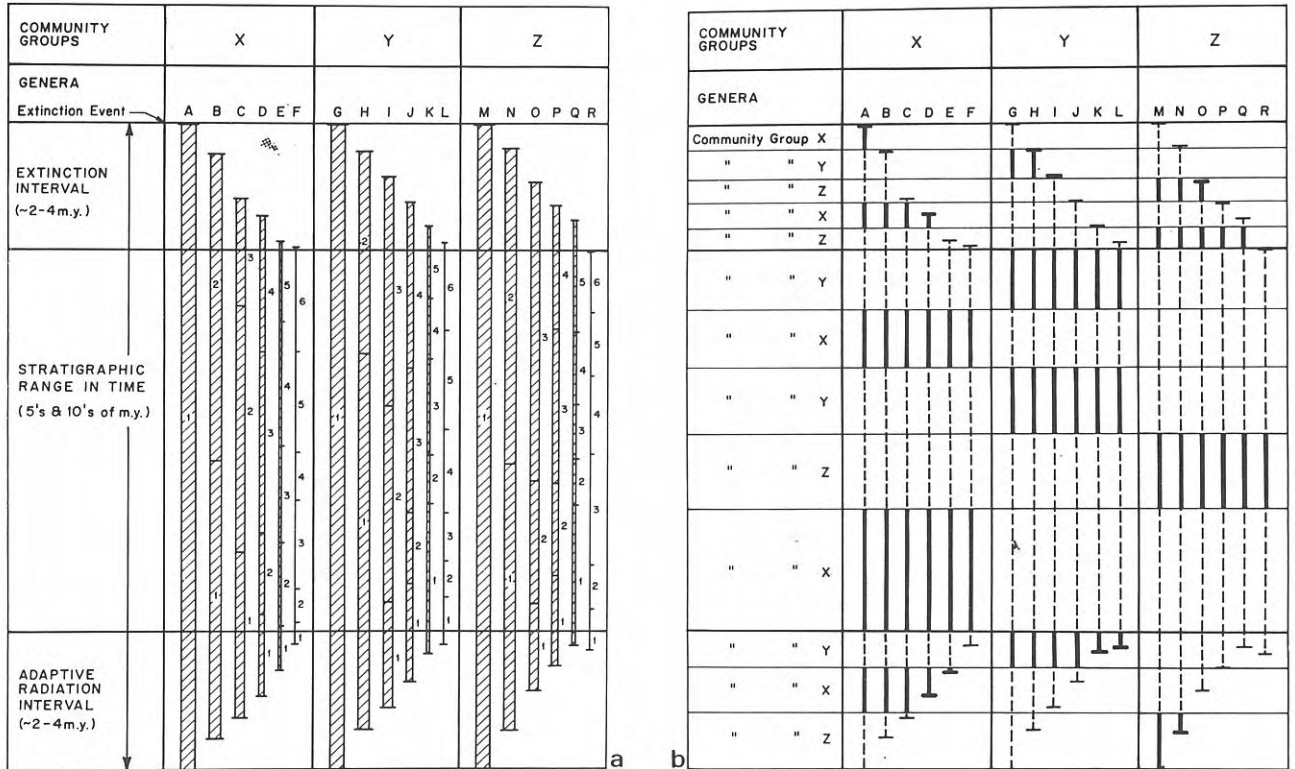
Abrupt Biostratigraphic Boundaries

Since d'Orbigny's monumental publications (1849-52), which made him the Father of biostratigraphy, there has been little doubt about what constitutes globally abrupt biostratigraphic changes. The abrupt biostratigraphic changes are what I designated (1983; 1987; in press, a) as Ecologic-Evolutionary Unit boundaries. I suggested the term Ecologic-Evolutionary Unit, in preference to d'Orbigny's term *Étage* because of the many other uses to which the term stage has been put by earth scientists, and also to emphasize that d'Orbigny's basic units do have fundamental evolutionary significance that take place between ecologic constraints. There is still little agreement about the cause or causes of extinctions, but it is clear that many of the ecologic-evolutionary unit boundaries mark the terminal, community collapse phase (McLaren's biomass) of major extinctions. Far less attention has been given, however, to the geologically immediately subsequent adaptive radiation part of many of these same boundaries. Nobody

has tried to provide an alluring extra-terrestrial explanation for the adaptive radiations. I have emphasized (in press, b) the still biologically mysterious character of these major adaptive radiations. Specifically, what microevolutionary mechanism should be used to explain why so many taxonomically unrelated, major groups existing side-by-side within the same communities should adaptively radiate at about the same time? I have no suggestion other than to appeal to the population biologist for help. It is clear that the major adaptive radiations of the Phanerozoic correlate poorly with geologic phenomena such as changing global climatic gradients, changing paleogeography (including regressions and transgressions of epicontinental seas), changing levels of mountain building, changing levels of vulcanism, and the like (Boucot, 1983, Fig. 3) nor do they correlate very well with changing levels of provincialism in the biogeographic sense.

Let us admit our present failure to explain these geologically abrupt adaptive radiations. Before abandoning the problem to the biologist we still have much work to do. I have (in press, c) emphasized how little real stratigraphic detail we have concerning specific adaptive radiations. For too long we have been satisfied to merely plot stratigraphic ranges involved in adaptive radiations without any concern for the nature of the individual taxa involved. What do I mean by this statement? I am specifically concerned that we have not carefully collected, cm.-by-cm., the information *within individual communities* that would tell us which specific taxa appear first during a specific adaptive radiation. We need to find out whether the first taxa to appear during an adaptive radiation, within a specific community type, are the eurytopes or the stenotopes, the provincials or the cosmopolitans. I would assess eurytopy versus stenotopy here by finding out how many individual communities the individual taxa occur in, as well as the environmental breadth of those communities—rough water versus quiet water, nearshore versus far offshore, and the like. Provincialism versus cosmopolitanism, which correlates positively with stenotopy versus eurytopy, can be evaluated by finding out about geographic distribution relative to the biogeographic units appropriate to each time interval. We need to learn whether the order of taxonomic appearance during an adaptive radiation is a largely random phenomenon relative to these factors, or whether there is a definite pattern involved. The same evaluation should be made (in press, c) for order of extinction. We need to determine whether it is the more fragile, more stenotopic, more provincial taxa, within a specific community, that become extinct earlier and adaptively radiate later. This information might be useful to the population biologist trying to devise a reasonable microevolutionary explanation for us.

Figure 1 (from Boucot, in press, c) diagrammatically indicates the possibility that the more stenotopic, more provincial, less numerically abundant taxa in each community are those which appear last during an adaptive radiation interval and disappear



Figures 1a, b. Fig. 1a is intended to show the predicted, average abundance relations expected to occur within three communities (X, Y, Z) during a typical Ecological-Evolutionary Unit. Fig. 1b is intended to illustrate the stratigraphic range effects obtained from the interbedding of more than one environment within any stratigraphic section. Fig. 1a represents the "true" stratigraphic ranges, for genera (A through R, distributed in communities X, Y and Z, with the species of each genus being indicated by arabic numerals) for which there has been NO environmental change in the three stratigraphic sections (one each, for communities X, Y and Z). Line widths in Fig. 1a are proportional to the numerical abundance of each genus.

Fig. 1b diagrams what might be expected during the same Ecological-Evolutionary Unit from the fossil record of communities X, Y and Z, IF they occurred in an interbedded manner within a SINGLE stratigraphic section (rather than the three, separate sections indicated on Fig. 1a). Note the following: The "known" stratigraphic ranges (as contrasted with the "true") of many taxa, and predominantly the less abundant genera, will be far less than their "true" ranges owing to the vagaries of environmental controls over occurrence and non-occurrence of particular taxa in particular environments. In most instances it is the less abundant, more rapidly evolving genera that have the artefactually shortest recorded stratigraphic ranges. The dashed lines on Fig. 1b indicate the "true" ranges, and the solid lines the actually observed ranges.

The moral of these two figures is that in order to obtain more reliable "true" stratigraphic ranges, particularly for the less abundant genera, one must sample sections where the particular community containing the desirable genera occurs at the very beginning of an adaptive radiation and at the very end of an extinction interval. To do otherwise commonly ensures that the "known" stratigraphic range will be less than the "true" range, as well as providing an artefactual step-wise pattern of both adaptive radiation and extinction.

first during an extinction interval. These are the taxa, genera and subgenera, whose species are phyletically evolving most rapidly (Fig. 1a). However, until far more cm-by-cm work has been done during both adaptive radiation and extinction intervals, we will be uncertain about the prevalence of this pattern. Figure 1b also emphasizes that environmental changes within stratigraphic sections have a profound effect on the "known" stratigraphic ranges of taxa, with the numerically rare genera and their species being far less well sampled than is the case with the numerically abundant genera. Note too that such sampling problems can artefactually gene-

rate a step-like pattern of both appearances during adaptive radiations and disappearances during extinctions.

Abrupt Biostratigraphic Subunits

In most of the discussion (1983; 1987; in press, a) I have dwelt on the major ecologic-evolutionary units. I have mentioned in a few cases something about the globally significant, recognizable ecologic-evolutionary subunits. I am thinking here of such things as the basal Tommotian part of the Lower Cambrian, the Silurian-Devonian boundary (within

the major, later Llandovery-Frasnian ecologic-evolutionary unit), as well as the later Eifelian Kačak Event horizon, the later Givetian Taghanic Event horizon, and the Mississippian-Pennsylvanian boundary event within the Permo-Carboniferous ecologic-evolutionary unit, as well as the appropriately well delineated post-Paleozoic ecologic-evolutionary subunits recognized within the Jurassic-Cretaceous and the Cenozoic. These subunits are well known to the practising biostratigrapher, and are heavily relied on for long range correlations; we would be in difficulty for long range correlations if we only had the abrupt biostratigraphic boundaries of the major ecologic-evolutionary units.

Gradual Biostratigraphic Boundaries

If one could only correlate long range by means of abrupt biostratigraphic unit and subunit boundaries, i.e., ecologic-evolutionary unit and subunit boundaries, there would be geologically lengthy time intervals for which reliable, precise biostratigraphic correlation would be impossible. The solution to reliable, global, biostratigraphic subdivision and correlation within the major ecologic-evolutionary units and subunits, d'Orbigny's étage and sous-étage, was devised by Oppel (1856-58; see Berry, 1987, for a concise discussion) shortly after d'Orbigny's work had been published. Oppel took advantage of the fact that there is a strongly reliable statistical tendency for the time-stratigraphic ranges of individual taxa, commonly species and more finely split genera, to remain roughly constant, although overlapping. Oppel's method works to a large extent because it is controlled, under favorable conditions, by evolutionary changes. What is involved here is that for well sampled species and genera, whose known stratigraphic ranges are approximately equal to their true, evolutionary ranges, an overlapping of time ranges of taxa will provide a reliable means of refined biostratigraphic correlation. This is the case because the phyletic evolutionary change from one species of a genus to another seldom coincides in time with similar changes affecting unrelated genera. However, when too many taxa are employed whose known ranges are poor approximations of their true ranges the method will be of far lower reliability and precision. It is crucial (see Boucot, in press, c, for explanation) when trying to maximise the utility, reliability and precision of the Oppelian method that one study the taxa through time present in individual communities, rather than an assortment of miscellaneous taxa derived from varied communities taken from varying environments. Oppelian correlation within specific community types (= my term community group) is one of the pillars on which the ecostatigraphic method is based, the other being concern for biogeographic distinctions that affect global correlations.

Within Community, Gradual Change

Figure 2 diagrammatically models the general pattern of phyletic evolution expected within a single community taken from a typical Ecological-

Evolutionary Unit (Boucot, 1978). Line widths for each genus (capital letters A through I) are proportional to the numerical abundance of specimens. The arabic numerals represent the species of each lettered genus. Note the strongly inverse correlation between the numerical abundance (line width) of each genus and its rate of phyletic evolution (vertical spacing of the arabic numerals). This is, of course, merely a reflection of biostratigraphic experience for the past century and more that rare genera and their species commonly provide a more reliable guide to precise stratigraphic correlations than is the case with the stratigraphically long ranging abundant genera and their commonly long ranging species.

The implications of community evolution, as diagrammed in Fig. 2, for the Oppelian scheme of biostratigraphy are many. Precision in correlation will be best achieved by employing the overlapping time ranges of rapidly evolving lineages. Greatest reliability will be achieved when as many as possible of these lineages occur together within the same, evolving community group (an evolutionary, time sequence of communities, such as are shown in Fig. 2). Greater precision can be achieved when the rapidly evolving species from two adjoining community groups are overlapped in the Oppelian manner. Even greater precision can be achieved if three adjoining community groups are employed, as well as adding similar data from evolving planktonic community groups. Long ranging species, commonly belonging to abundant, cosmopolitan genera, will be of little use for correlation purposes, and should be omitted from the analysis. It is amusing to note here in passing that the community names of the ecologist are taken from the abundant genera and species, those which are slowly evolving. I suggest that these are more appropriate as community group names, whereas it is the rare genera and their rapidly evolving species that should be used to name the time sequence of evolving communities within each community group.

QUANTUM EVOLUTION AND PHYLETIC EVOLUTION

Simpson (1944, 1953) coined the term quantum evolution as an explanation for the microevolutionary processes he concluded to take place during adaptive radiations, processes for which we almost invariably lack a generic and specific level fossil record between families and higher taxa, and following which phyletic evolution sets in for geologically lengthy intervals. Schindewolf (1950) made essentially the same distinction with his terms *typogenesis* and *typostasis*, while Krasilov (1969) employed the terms *kogerentim* and *nekogerentim*, and I (1978) used the terms *metacladogenesis* and *diaccladogenesis*. It is interesting to realize that each worker apparently recognized the distinctions in an independent manner.

GLOBAL, REGIONAL AND LOCAL BIOSTRATIGRAPHIC CHANGES

From well back in the past century biostrati-

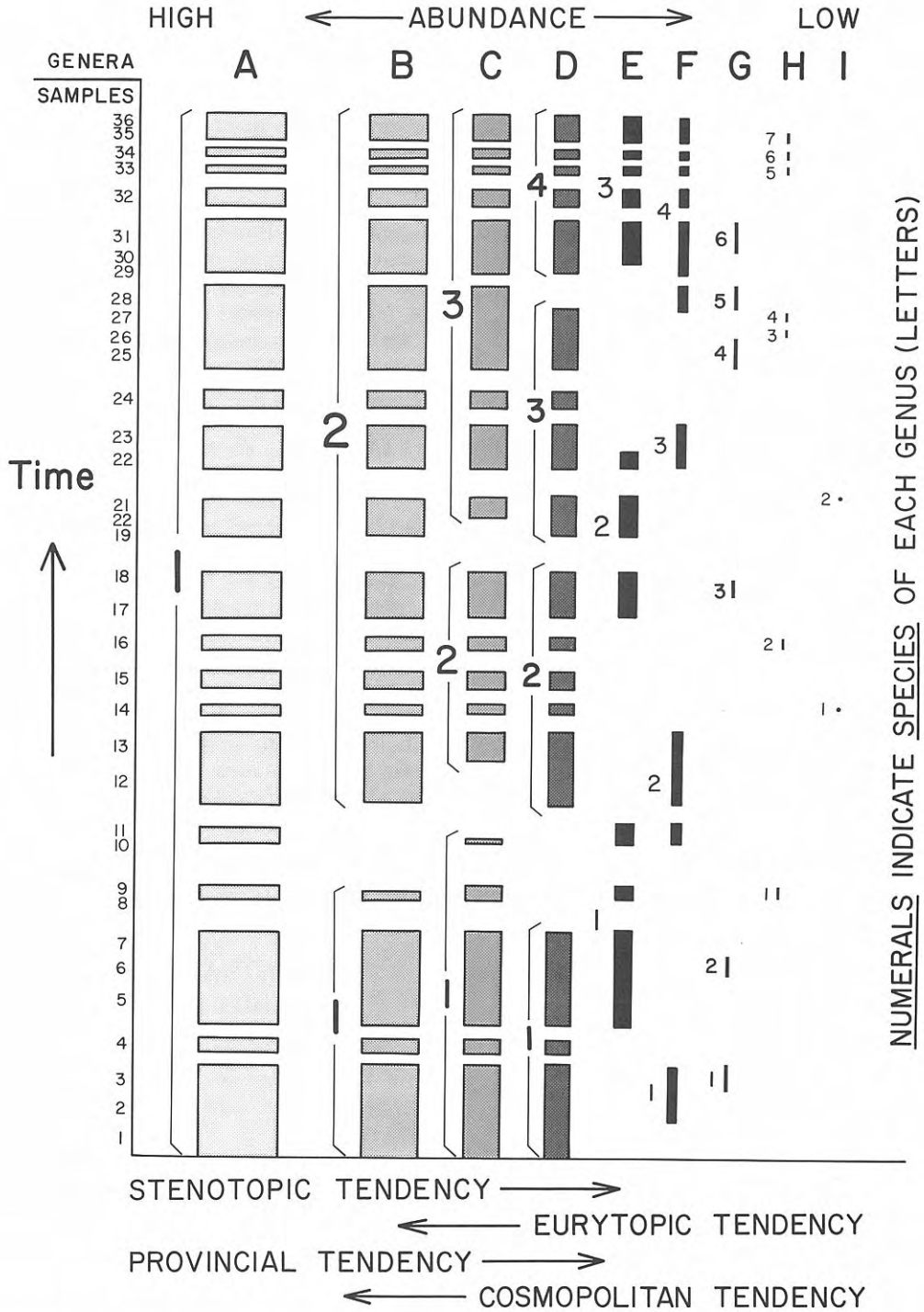


Figure 2. Diagram showing the characteristics of an evolving community group (numerals on the left hand column represent samples —note the numerous unsampled intervals— unsampled due to lack of exposure or other reasons; the capital letters represent unrelated genera belonging to the community group; the arabic numerals represent the phyletically evolving species of each genus). Line widths in each column are proportional to abundance—note that the species of each genus tend to maintain similar abundance levels, i.e., the species of rare genera tend to remain rare, and vice-versa. The patterning is for artistic effect only. Note that the species of the rare genera are the most rapidly evolving and vice-versa. In the naming of communities one would find the species of the less abundant genera most useful, i.e., those undergoing the higher levels of evolutionary change, whereas in the naming of the Community Group the naming would tend to employ the more abundant, slowly evolving genera. The exact number of communities named will be a function of sampling adequacy —the better the sampling the more likely that rare genera and their species will turn up that will make possible the naming of more communities. Note too, that the rare genera and their species tend to be more stenotopic (occur in only one community group and in a more limited environment in terms of substrate and distance occupied on the shoreline to shelf margin transect) and occur in a more biogeographically endemic condition. (from Boucot, 1983).

graphers have understood that some abrupt biostratigraphic changes are global in extent, some regional, and others merely local. Discussed above are the abrupt global biostratigraphic changes commonly involving globally extensive extinctions and adaptive radiations. What about the regional and local changes? We are also well aware that some regionally constrained biostratigraphic changes signify marked extinctions followed by adaptive radiations. In this category one thinks immediately of the major changes, both increase and decrease, in the earth's climatic gradient. In all of the cases that have been carefully studied it is found that a major change in global climatic gradient affects high latitude biotas markedly, whereas this is not always the case at lower latitudes. Stanley and Campbell (1981) have made a good case for the heightened climatic gradient of the Plio-Pleistocene being responsible in large part for the extinction of much of the continental shelf benthos in the North Atlantic and adjoining Arctic Ocean, whereas the Pacific Ocean was unaffected, presumably because of the absence of any good connection to the cold water Arctic Ocean source during this time interval. We are also well aware that the Southern Ocean's generation in the Paleogene was also accompanied by an extinction of the temperate biota, followed shortly by the adaptive radiation which gave rise to the Antarctic cold water biota (Zinsmeister, 1982, submitted; Zinsmeister and Feldmann, 1984). Going back into the Paleozoic it is similarly easy to recognize the Pennsylvanian generation of a Gondwana Realm cold water benthos coincident with the initiation of sealevel glaciation, and the extinction of that biota with the consequent mid-Permian lowering of the global climatic gradient. I have (1988) indicated the probability that a mid-Devonian lowering of the global climatic gradient can be held responsible for the extinction of the cool climate, high latitude Malvinokaffric Realm benthos of the Period. Kauffman (1987) has also indicated that the tropical regions of the latest Cretaceous were far more affected by the end Cretaceous extinction event than was the case at more temperate latitudes. In any event it is clear that there are significant, even major *regional* extinctions and adaptive radiations that are not coincident in time with similar magnitude, *globally* extensive extinctions and adaptive radiations.

This makes sense when one realizes that polar regions, in which organisms must be adapted to a high level of light and temperature seasonality as contrasted with lower latitudes, whether occupied by a temperate or cold climate biota, will always be more sensitive to major changes in the global climatic gradient, up or down, than will lower latitude biotas.

Turning to the purely local level we have far more trouble recognizing extinction and adaptive radiation events restricted to any one locale. Most of this problem is undoubtedly a sampling problem. Virtually every local stratigraphic section is replete with local disappearances and appearances. Most of these appearances and disappearances, when viewed

against the regional and global stratigraphic ranges of the taxa involved, are seen to merely reflect local changes in environment that exclude or permit the existence of particular taxa. Still, when one turns to the taxa known to be endemic to a particular locale there is still the possibility that truly local extinctions and adaptive radiations might be involved. Because of the far greater rarity as individuals of most endemic taxa (Boucot, 1975; in press, b) there is, however, far more difficulty in recognizing purely local extinctions and adaptive radiations. Turning to the Neogene, where our biostratigraphic resolution is far better in many instances, one can think of some of the Paratethyan area extinctions and adaptive radiations as being very local events, or at least involving a small region (Steininger et al., 1988).

Considering all of the above it is reasonable to conclude that there is a virtually complete spectrum of extinctions and adaptive radiations recorded in the global, regional and local biostratigraphies. But, with the reservation that many of the purely local biostratigraphies will be dominated by local environmental changes that definitely do not represent extinctions or adaptive radiations in the true, global or regional sense. Still, there are bound to have been a large number of very local extinctions and adaptive radiations; just think for a moment of the modern situation with its virtually pinpoint cave biotas, lava tube biotas, isolated mountain top biotas, isolated nearshore and oceanic island biotas, hot spring biotas, isolated desert spring and stream biotas, and the like—all of them easily subject to both extinction and adaptive radiation

BIOSTRATIGRAPHY AND BIOGEOGRAPHY

The correlations between Ecologic-Evolutionary Unit boundaries, i.e., most of the abrupt biostratigraphic changes, and biogeography are poor (Boucot, 1983, Fig. 3). The introduction of barriers to reproductive communication, which gives rise to biogeographic changes in the first place, are first manifest at the specific level, then the generic level, and finally the familial IF the reproductive isolation involves enough environmental changes (Quantum Evolution type families) or if it persists long enough (non-Quantum Evolution generated families; see Boucot and Wilson, in prep., for an account).

The biostratigraphic effects of provincialism are to produce a number of individual, provincial biostratigraphies, between which correlation is less reliable than within the provincial unit. The only evolutionary effect observed here is that phyletic, within community, rates of evolution tend to be more rapid at the species level because of the overall smaller size of the populations involved, when contrasted with similar community types existing under more cosmopolitan conditions.

THE BIOSTRATIGRAPHIC RECOGNITION OF BOTH EXTINCTION AND ADAPTIVE RADIATION HORIZONS

Despite all of the concern during the past few decades with extinctions and their causes it remains true that the so-called statistical approach to their recognition has done little more than achieve the level already attained by biostratigraphers towards the end of the past century, i.e., the ability to recognize the major events and a few of the second order items (see Boucot, 1987, for discussion). The more accurate way in which to detect these key horizons, not only the first order items but also those of lower rank, is to pay careful attention to the abrupt biostratigraphic boundaries of all ranks, globally recognized and regionally recognized, and to then carefully investigate each one. Standard biostratigraphy has far more precision for this purpose than the so-called statistical approach because the biostratigrapher is always concerned with *both* known stratigraphic ranges of taxa and with changes in abundance (this last concern was first shown by d'Orbigny!). Significant changes in abundance of individual taxa have fully as much meaning as do stratigraphic ranges for these purposes. For example, biostratigraphers are well aware that the discovery of "living fossils" such as *Latimeria*, *Sphenodon* and *Neopilina* in very small population, geographically restricted occurrences today, does not detract from the fact that insofar as the fossil record is concerned they became extinct at the end of the Cretaceous for the first two and the end of the Middle Devonian for the third, i.e., major changes in the abundance of a taxon are fully as important for biostratigraphic purposes as are their absolute ranges.

Coming back to the Introduction, and William Smith, we need to emphasize that the rock record is replete with abrupt changes in fossil content, both taxic and relative abundances. In order to recognize global events we achieve highest capability when employing significant, easily recognizable changes in overall biota—from within the same basic environment, such as the level bottom, the reef complex of communities, the riverine, the lotic, and so forth—that are global in extent. I am using the term "global" with the reservation that one remains within the same major latitudinal belt, i.e., it would be misleading to compare the distinctive higher latitude biotas for any time interval with those occurring in contemporary lower latitudes. In other words, greatest precision in recognizing major, globally distributed biotic changes is had when one pays careful attention to community changes that involve not just taxic ranges but also abundance changes. These are the vertical biofacies changes that have caught the attention of the biostratigrapher since the first half of the past century, once there was enough accumulated data from a more than regional sample. This is the data that enabled John Phillips (1840) to insist on such things as Palaeozoic, Mesozoic and Cenozoic, following which d'Orbigny made his classical subdivisions.

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