PLATES AND PROVINCIALITY, A THEORETICAL HISTORY OF ENVIRONMENTAL DISCONTINUITIES

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ABSTRACT. Global tectonics furnishes a basis for understanding the historical sequence of major environmental changes. The number of provinces has varied according to the degree of continental fragmentation and separation and to the latitudinal thermal gradients, while the quality of the ecosystems within provinces has varied with latitude and with continentality. The history of these factors as implied by continental reconstructions suggests that there have been two major biogeographic systems, one (chiefly Palaeozoic) founded on the polar position of the large continent of Gondwana and characterized by low latitudinal thermal gradients and low provinciality, and one (Late Mesozoic and Cenozoic) founded upon dispersed Gondwana and Laurasian continents, high latitudinal thermal gradients, and high provinciality. Probably, each system grew from the fragmentation of a supercontinent.

THE discipline of biogeography has been approached from two distinctive directions (Simpson 1953). The first and more traditional approach has been to identify and describe the biotic composition of different regions, and to account for the patterns of distribution of biotic elements among the regions in terms of their place of origin, their migratory abilities, and the nature of the available dispersal routes and barriers. The second approach is to study the ecological parameters of biotas in different regions with interest not only in the adaptations that fit individuals for survival in the environments that they occupy, but (especially in recent years) in the adaptations that underlie the characteristic economies of their populations and communities, those adaptations to the temporal and spatial environmental patterns that have been referred to as 'adaptive strategies' (Levins 1968). Trends, gradients, and other patterns in provincial ecology among various regions may then be identified and, hopefully, interpreted.

Palaeobiogeography has chiefly taken the first approach. It has been more closely allied to its neontological counterpart than are many palaeontological disciplines, since a historical perspective is obligatory in interpreting distribution patterns that result from past events, and the biogeography of fossil and of living organisms are both of great concern to palaeontologists and neontologists alike. This mutual concern is not so evident in studies of the second sort, studies of provincial ecology, for while the faunal composition depends in great measure on historical factors, the ecological structure and function at any time is presumably regulated chiefly by the ambient environment. The power of abstraction and generality that is provided by an ecological approach partly results in a glossing over of the historical bases of the biota. However, both approaches illuminate different aspects of what is clearly the same subject, and what is most desirable is a combination that would permit a judicious assessment of the relative significance of the historical and ecological factors that underlie any given biogeographic configuration. Biogeographical barriers around a province determine the ability of a given taxon to disperse into

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that province, and the ecological state of the province determines which taxa can succeed as colonizers. The composition of the provincial biota must therefore depend to an extent upon the differential fitness or differential adaptive potential of available taxa to the environmental regime of the province, while the ecological effects of the particular taxa that do occupy a province must play a role in determining provincial structure and ecosystem functions therein.

The recent development of the theory of global tectonics provides an unprecedented opportunity to develop a unified discipline of palaeobiogeography (Sylvester-Bradley 1971). It is obvious that the changing patterns of continents, of deep-sea floor, and of island arcs that result from plate tectonic processes will provide a model for the reconstruction of changing opportunities for biotic migrations. Furthermore, many important parameters of the environmental regime, especially climatic factors, are related to continental geography. Plate tectonics provides for the first time a basis in theory for reconstruction of the historical sequence of change of major features of past environmental regimes, and does so independently of biotic evidence. Therefore it is now possible that both the historical and ecological aspects of palaeobiogeography may be united in a common theoretical structure, for which ecological and evolutionary theory provide the building blocks and global tectonics the framework. While this article does not attempt any such grand synthesis, its purpose is to indicate some of the general relations that may lead to such a union eventually.

MARINE PROVINCES AS BIOGEOGRAPHIC ENTITIES

Biotic provinces are regions inhabited by characteristic association of organisms, bounded by barriers that prevent the spread of the characterizing taxa into other regions and that also prevent the immigration of many foreign species. The barriers, which are commonly climatic or topographic, are environmental discontinuities.

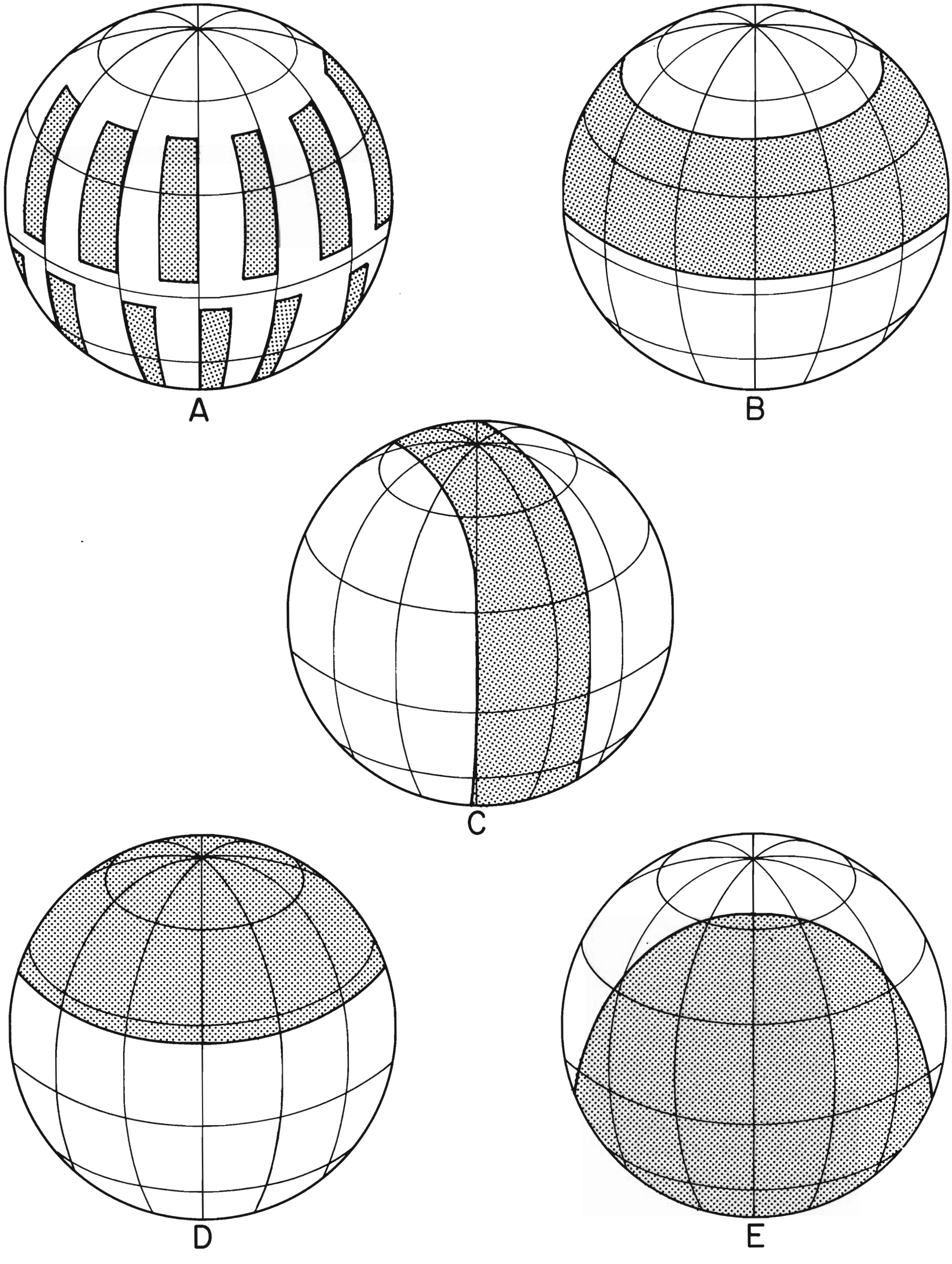
For the marine benthos of the continental shelves, important provincial barriers are formed by topographic features such as land and deep-sea floor. Since differential continental movements are controlled by lithosphere plate motions, and as deep-sea floor is created, transported, and consumed by plate tectonic processes, such barriers are under considerable tectonic control. These effects are clearly demonstrated in the recent pattern of shallow marine provinciality (Valentine 1971). Abyssal ocean floor, generated at ocean ridges, forms effective barriers: in the east Pacific, where the East Pacific Rise has generated the abyssal East Pacific Barrier of Ekman (1953); in the Atlantic, the abyssal floor generated by the mid-Atlantic ridge forms a barrier and separates distinctive eastern and western Atlantic provinces; and around Antarctica there is an encircling east–west ridge and a large endemic element. At present most of the ridge systems trend north–south rather than east–west, and a north–south trend of coastlines and shelves is dominant. East–west dispersal is therefore particularly difficult owing to this dominant trend of the principal topographic barriers, the effectiveness of which is increased by the relatively emergent condition of the continents and consequent lack of important epicontinental seaways. In contrast to the ridges, the chains of island arcs along subduction zones, which must be fairly continuous since they follow an entire plate margin, form super-highways of dispersal.

For marine organisms of the continental shelves, climatic changes can be effective ecological barriers and commonly form provincial boundaries. The climates change most frequently where hydrographic regimes change along north–south trending coasts. Large changes are localized at points, headlands, embayments, and other such features because they help to control current patterns and to determine the boundaries of water types, the location of upwellings, and other hydrographic factors over the shelves. Marine poikilotherms are very sensitive to temperature changes, owing at base to the temperature-dependence of metabolic activity rates (Hutchins 1947, Kinne 1963). Therefore many species find abrupt hydroclimatic changes limiting chiefly because of the temperature although other factors may play a role, and the faunal composition changes more greatly across the climatic contrast than along an average shelf segment. The empirical relations between climate and marine provinciality were established by the mid-nineteenth century (e.g. Dana 1853*a*, *b*); recent discussions of this relation are by Hall (1964), Valentine (1966, 1971), and Hazel (1970).

The climatic patterns on continental shelves should be heavily dependent upon the geography of continents. Although it is not yet possible to predict confidently the climatic pattern resulting from different continental configurations from first principles, it is nevertheless possible to venture a few general interpretations of geographic-climatic models. As usual in such exercises, the easiest cases are extremes; several possibilities are depicted in text-fig. 1.

If all the earth's continents were fragmented into small blocks and spaced around the globe, their shelves would be warm in low latitudes and cool in high. If the continents were assembled into a band encircling the world in low and intermediate latitudes of one hemisphere (text-fig. 1B), the band could stretch from 10° to about 51° 30′, and would completely isolate a polar ocean. The equatorward shore of the ring continent would be warm and mild while the poleward shore would be quite cold, since radiation of heat to space exceeds input at those high latitudes and latitudinal heat transport would be restricted essentially to the atmosphere. If the continental ring was oriented in a north–south direction (text-fig. 1C) dividing the world ocean into east–west hemispheres, a latitudinal thermal gradient would be expected along the shelves. Even in high latitudes, however, relatively warm waters should be found, since there are no topographic barriers to poleward heat transfer. East coasts should be warmer, since currents along the western ocean margins (western boundary currents) would originate in low latitudes, while currents along eastern ocean margins (eastern boundary currents) originate in higher latitudes. Furthermore, upwelling is more intense along west coasts, and this would introduce relatively cool water to the shallow shelves (see Stommel 1948, for an explanation of the asymmetry of eastern and western boundary currents). At very high latitudes it is probable that a cyclonic gyre would be present, carrying cool waters.

If all the continental material was assembled into a supercontinent of generally circular outline and centred on a pole (text-fig. 1D), then the shore would lie in rather low latitude (about 24° 30′) and the shelf would be generally warm and have a very similar hydroclimate all around. If, however, this supercontinent were centred on the equator (text-fig. 1E), it would extend well into high latitudes in both hemispheres (to about 65° 30′); the poleward-facing coasts would be cool, and there



TEXT-FIG. 1. Some geometrically 'clean' models of hypothetical continental patterns; the continents, stippled, have the same emergent area as those at present.

would be a climatic gradient proceeding both north and south from the equator along both east and west coasts. The differences in the sources of eastern and western boundary currents and in upwelling would cause east coasts to be warmer, latitude for latitude, than west coasts at low and intermediate latitudes. At high latitudes it is likely that cool westward-drifting waters would bathe the shelves.

It is possible to theorize about the provincial structure of the marine shelves in our various model worlds from principles and analogies based on the present marine provinces. In text-fig. 1A, each continental mass would have a somewhat endemic biota, unless there were extensive chains of islands in the intercontinental oceanic seaways. The chances of islands being present are probably less if the masses fragmented from an original supercontinent so that a ridge lay between each of them. If any of the continents were converging, the intermediate seaway might contain island arcs associated with the subduction zone, or might be more likely to contain 'mid-plate' volcanic chains (such as the Hawaiian chain), which seem to occur away from ridges, though this relation is at present merely an empirical observation. At any rate, each continent might support only a single provincial biota. However, each would probably be provincially distinct, so that total provinciality would be high; there are 24 continents in this model.

Provinciality associated with the ring continent in text-fig. 1B is simple; two provinces would be present, one encircling the equatorward coast and the other the poleward coast. However, the ring continent of text-fig. 2C is more complicated. As the oceans stretch close to the poles it is probable that latitudinal provinces would exist, in which case there would have to be at least four equatorward provinces and four poleward ones for a total of eight. If the thermal gradient were sufficiently high so that intermediate-latitude provinces appear between equatorial and high-latitude regions, then there would be an intermediate province on each side of each ocean in each hemisphere, doubling the total number of provinces to 16.

Only a single shelf province would be present around the continent of text-fig. 1D; the shoreline is at a constant latitude and topographic barriers cannot exist around a supercontinent (providing that it is not a ring continent). But in text-fig. 1E the supercontinent might well support several provinces, based on the differences in hydrographic and thermal regimes on east and west coasts, and on the probability of a sufficient latitudinal thermal gradient to support high-latitude provinces. Even if the thermal gradient were so low as to permit most poikilotherms to range to the poleward extremes of the continent, the climatic differences between the east and west coasts might be great enough to permit a degree of endemism that would mark them off as being provincially distinct. Of course if the poleward coasts were sufficiently cool to support many endemic cryophiles, then at least four provinces would appear.

From considering these models, and from the 'actualistic' model of the present oceans, a few very broad generalities are possible, even though the artificial models are geometrically 'clean' and thus unreal, and although the hydrographic and climatic patterns that would be associated with even these 'clean' models are not completely certain. A further difficulty is the neglect of continental relief, which may play a significant role in the climatic picture.

At any rate, high provinciality is found when the continents are very fragmented to provide many topographic barriers, and when the continents stretch out over much latitude and thermal gradients are high, to create many climatic barriers (text-fig. 1A). Lowest provinciality is associated with a supercontinent (text-fig. 1D). In general, east–west topographic barriers should be more effective than north–south ones of equal width and character, for the topographic discontinuity will be supplemented by a climatic discontinuity. Successful dispersion across the topographic barrier would tend to lead more often to successful colonization when the donor and receptor provinces are climatically similar, as across north–south barriers.

For north-west trending coasts, east-facing shores will ordinarily be warmer, latitude for latitude, than west-facing ones, owing to the motion of major oceanic gyres. Equatorward-facing coasts will ordinarily be much warmer than poleward-facing ones, even at the same latitude; the continental mass protects the shore from cold water if it lies to poleward and from warm water if it lies to equatorward. For all of these generalities, exceptions may occur owing to special circumstances, which arise frequently in a world that is geometrically irregular and complex. An important example is the warming of north-western Europe by the Gulf Stream System.

MARINE PROVINCES AS ECOLOGICAL ENTITIES

Judging from the present biosphere, the structures of marine ecosystems are sensitive to differences in the environmental regimes of different provinces. This is especially noticeable in the numbers of species present (called the species diversity here) and in the modal feeding and habitat adaptations, which affect the structure of the trophic web. As these differences are reviewed elsewhere and are known through the contributions of an unusually large number of investigators, they will only be briefly sketched here with documentation based on secondary sources with good bibliographies; see especially McArthur and Wilson 1967, and Margalef 1968. These interpretations are of course only hypotheses, which taken together form a preliminary model of ecosystem regulation.

Provinces in present high latitudes contain a high proportion of species that have high reproductive potentials, broad habitat tolerances, and generalized food requirements; they are commonly omnivores or, in the sea, detritus feeders, which certainly have a generalized food source. These adaptations seem geared towards existence in an environment wherein primary productivity and therefore most trophic resources fluctuate seasonally and where mortality can be very high during inclement periods. The population must be flexible and opportunistic, expanding rapidly over broad regions during favourable periods and maximizing its chances for survival during inclement periods.

Marine animal communities in high latitudes, being composed chiefly of species with these adaptive traits, have a characteristic structure. They are of low diversity, for only relatively few populations with such high energy demands can be supported on a given resource base. They range through a variety of habitats and during favourable periods tend to be rather similar over a broad region, though they may often change in composition through time as now one, now another population becomes abundant. And they have few trophic levels, with diversity concentrated on the lower ones.

Marine animal provinces in high latitudes, being composed of these sorts of communities, are also of low diversity. They also contain a relatively high percentage of taxa that are infaunal detritus feeders and omnivorous predator-scavengers. If all marine provinces were in high latitudes, or if they all had resource regimes similar to those in present high latitudes, then the entire marine biota would contain high proportions of taxa with flexible adaptive strategies, and total marine diversity would be low.

In more stable environments, such as in the tropics, large population sizes are not so important to survival, as primary productivity is relatively steady and trophic resources will be rather stable. Specialization in food items is possible and indeed assures an efficient predator of a relatively private food supply; habitat specialization assures a population of a place to live. The specialized tropical forms can often feed broadly when opportunities arise, but presumably can subsist on a narrow resource base when necessary. In communities of such species, diversity may be high, as large numbers of specialized forms with low resource requirements can share a given energy base and a given range of habitats. Trophic energy flows along chains of predator-prey specialists or through local habitats, each of which may be occupied by a distinctive cluster of specialists. These diverse communities are spatially heterogeneous but do not vary much through time. Marine provincial regions in low latitudes, then, are of high diversity and contain numerous community associations. If all marine provinces were in low latitudes and/or had stable resource regimes, then clearly the marine biota would be diverse and would contain high proportions of trophic and habitat specialists.

Within each marine province, then, each community should display a characteristic structure that derives from the frequencies of various adaptive strategies among its component populations which are based in turn upon the resource regimes (and on other factors such as spatial heterogeneity). If there were an even gradient in productivity from equator to pole there should be an even gradient in community structures. However, the latitudinal changes in hydroclimate that cause provincial boundaries appear also to create discontinuities in the gradients of productivity, and therefore communities in analogous habitats but in latitudinally distinctive provinces have rather different structures. Part of the change in faunal composition between such provinces should be due, not only to replacements by ecological equivalents, but to the accommodation of the change in frequency of feeding types that is required in the different trophic webs. Although detailed comparative data on trophic structures are not available for separate provinces, distinct differences are recorded in the trophic compositions of certain higher taxa between provinces. For example, along north-western America, the gastropod fauna has the highest proportions of carnivores, in the tropics and in the Arctic. In the tropics they are relatively specialized predators for the most part, but in the Arctic they are mostly generalized predator-scavengers. Herbivores are proportionately most abundant in temperate water, especially cool-temperate water where macroscopic algae particularly flourish. Among the bivalves, detritus feeders are most common in the Arctic. Thorson (1962) has documented somewhat similar trends in feeding types along western Europe from Gibraltar to Murmansk. And Arnaud (1970) has shown that within several higher taxa, scavengers are more common around Antarctica than in lower latitudes.

If we examine provinces within the same climatic zone but on opposite sides of oceans or of continents, differences in ecosystem structures, including diversity, appear to be present within similar habitats. Sanders (1969) suggests that these diversity differences are owing to continentality; the shelf waters along the smaller oceans are more affected by the perturbations of climate that are associated with the continents, while larger oceans have an ameliorating effect on climate so that bordering shelf waters are more 'maritime'. Longitudinal diversity trends on the world's shelves do indeed agree with this pattern (Valentine 1971). In the tropics, highest diversities occur in provinces that are chiefly developed on island chains or along the shelves of small continents in large oceans (Indo-Pacific), and least diversities on the shelves of large continents facing small oceans (Atlantic); this trend can be traced at other latitudes as well. Since productivity should be most unstable in waters of highest continental influence, owing primarily to seasonality of nutrient supply, this diversity pattern can be interpreted as owing to the same basic cause, adaptation to different trophic resource stabilities, as the latitudinal diversity gradients. If this is correct, the trophic structure of ecosystems in longitudinally separated provinces should vary in concert with the diversity. Data are sparse but suggest that this is the case.

It is a commonplace that many taxa have relatively restricted trophic requirements. Protobranch bivalves, for example, are chiefly infaunal deposit feeders. It is not surprising then that these forms are most important in benthic communities of high latitudes, where deposit feeding is a favoured strategy. They are also important in the deep-sea, where primary production is entirely lacking. The general correspondence that appears likely between feeding types and environmental regimes, not only on the shelves but in other biomes as well, suggests caution in interpreting many taxonomic patterns historically. That is, the protobranches probably originated neither in the deep-sea nor in the Arctic, but are successful in these regions because they possess functions that are particularly suitable therein. In general, to the extent that a given taxon contains many species of a particular trophic strategy, that taxon should be related to the environmental regime that characterizes the province. It follows that as the planetary environmental regime changes owing chiefly to continental motions and their climatic consequences, the relative opportunities for taxa with different adaptive strategies wax and wane, creating periods of dominance or decline.

Based upon this model of the primary regulation of ecosystem structure by trophic resource regime, it is possible to predict the general ecological character of the benthic ecosystems within the provinces inferred for text-fig. 1. It is assumed that spatial heterogeneity and other possible diversity regulators are essentially the same from province to province. In text-fig. 1A, the average ecosystem is of high diversity in low latitudes and low diversity in high latitudes. In text-fig. 1B, communities in the equatorial province would not be so diverse as those in equatorial regions of text-fig. 1A, for continentality is higher; and in the poleward province, diversity would be very low, since solar seasonality and continentality are both high. In text-fig. 1C, a latitudinal gradient in diversity should occur, with the more rapid changes at discontinuities in the hydrographic regime. Diversity should be slightly more than in text-fig. 1B in low latitudes and considerably more in high latitudes. In text-fig. 1D, diversity should be extremely low despite the relatively low latitude of the coastline owing to the extreme continentality, while in text-fig. 1E, diversity would be relatively low in low latitudes and even lower in high latitudes where seasonality of solar radiation would enhance the instability owing to continentality.

Thus in summary the models in text-fig. 1 rank in the following order, from most diverse to least: 1A (high provinciality and high intraprovincial diversity); 1C (intermediate provinciality and intermediate intraprovincial diversity); 1E (intermediate provinciality but low intraprovincial diversity); 1B (low provinciality and low intraprovinciality diversity); and 1D (lowest provinciality and low intraprovincial diversity). In all these cases, the quality of the ecosystem structures should correlate with the intraprovincial diversities; in low-diversity situations detritus feeders, scavengers, and omnivorous generalists, together with suspension feeders that are gregarious, of generalized habitat requirements, and that feed near the bottoms, would all be particularly favoured; in high-diversity situations, trophic and habitat specialists would be favoured.

The continents have been treated as if they were totally emergent, while the addition of epicontinental seas would clearly change these cases. Seaways across a continent could provide dispersal routes between provinces for shelf organisms. Shelves covered by broad arms of the sea would have different environmental regimes from oceanic coastal shelves, producing large endemic elements in many epicontinental seas to give rise to additional provinces (see Johnson 1971; Hallam 1972). Furthermore, although they themselves may be more variable than the ocean-facing shelves, they will tend to enhance environmental stability in general and to reduce the effects of continentality. If a supercontinent such as depicted in text-fig. 1D were broadly inundated by epicontinental seas, diversity should rise significantly, owing both to the rise of endemics on the continental platform and to the amelioration of environmental fluctuations along the oceanic shelf, leading to higher trophic stability and higher intraprovincial diversity.

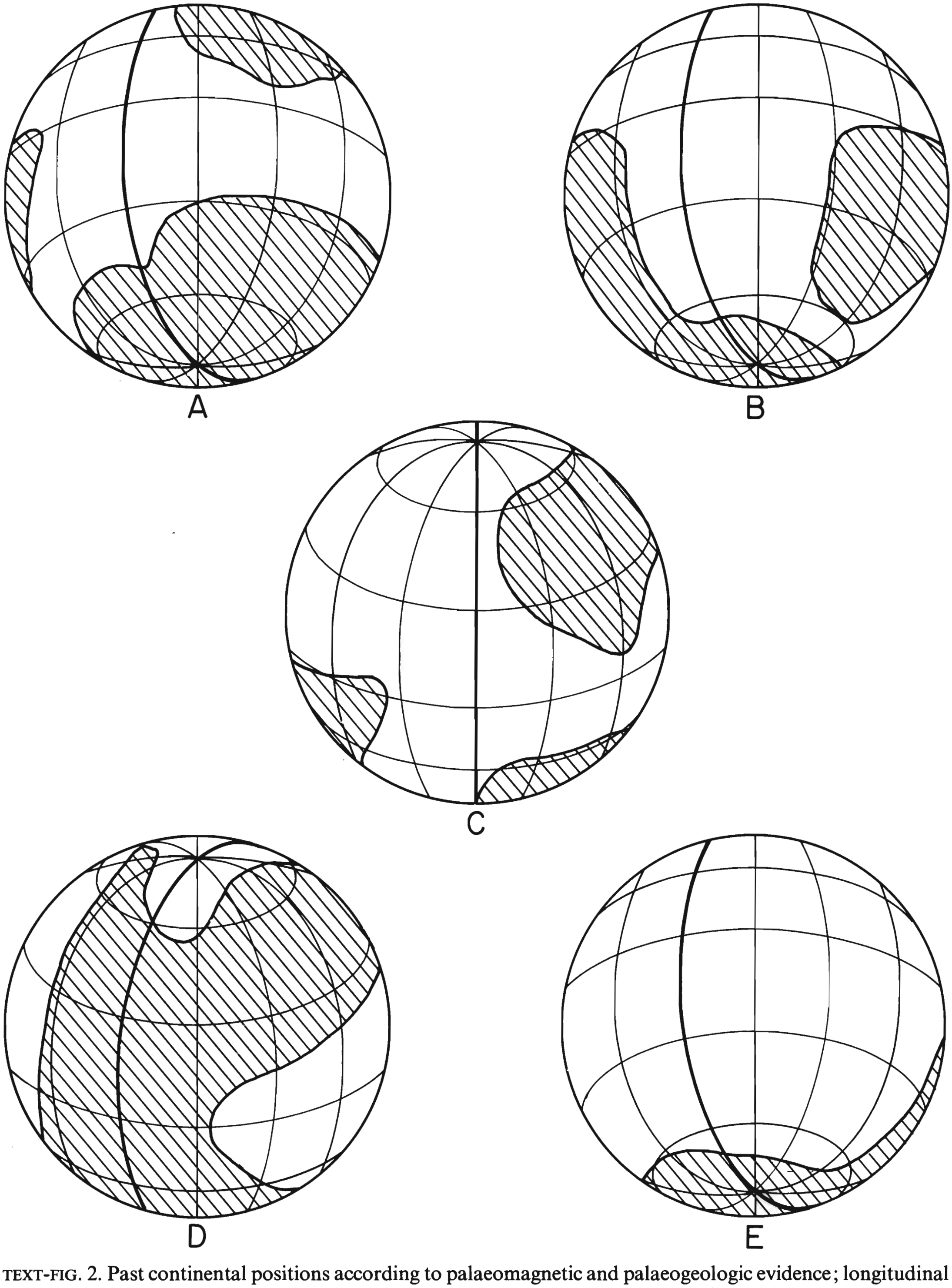
APPLICATIONS TO PHANEROZOIC CONTINENTAL PATTERNS

Although none of the continental patterns that have been suggested for the Phanerozoic approximate any of the geometrically clean models closely, they nevertheless share certain features with different models at different times. Using the models and the present oceanic configuration as partial analogues or at least as heuristic devices, a general reconstruction of the major trends in Phanerozoic biogeography is possible.

The Phanerozoic (and late Pre-Cambrian) continental patterns are assumed to have had the following history (Valentine and Moores 1971, 1972; Smith *et al.* this volume). Sometime in late Pre-Cambrian (perhaps around 700 m.y.b.p.) the continents were assembled into a geographically compact mass, perhaps into a single supercontinent. Near the beginning of the Phanerozoic this mass fragmented into four distinctive continents, approximating Gondwana, Asia, Europe, and North America (although the last three do not quite correspond to their present constitutions). Then Europe and North America were sutured during the Caledonian and associated orogenies to reduce the number of major continents to three. The Euramerican continent then sutured on to Gondwana during the Hercynian orogeny, reducing the major continents to two, and finally with the suturing of Asia along the Urals the familiar supercontinent of Pangaea was created. It seems likely that the Gondwana continent included a pole throughout the Palaeozoic. Perhaps during its early history and certainly during its latest Palaeozoic history, the landmass containing Gondwana stretched across the equator and into the opposite polar hemisphere (text-fig. 2B, 2D). This configuration, creating an east-west barrier to currents, is believed to have had fundamental biogeographic consequences.

Late Pre-Cambrian provinciality is inferred to have been low, partly because a supercontinent lacks topographic barriers, and partly because the inferred configuration is one that supports only a low climatic zonation. The western boundary currents that originate from a westward flowing equatorial current and that then run poleward along the eastern continental shelf begin as warm currents, having drifted in low latitudes across an ocean far broader than any present today. As southern Gondwana was not crossed by an east-west epicontinental seaway north of the pole (see maps, this volume) there was no circumpolar drift such as now encircles Antarctica; it is precluded by the continental barrier. At least part of the western boundary current must have turned eastward around the poleward part of the continent (see text-fig. 2B) and then northward as an eastern boundary current along the western continental shelf. Thus even the highest-latitude shelves would receive a steady supply of relatively warm water, a sort of Gulf Stream effect. The western shelf waters would presumably be cooler than the east, owing to the sojourn of a part of them in high latitudes and to upwelling. It is conceivable that only two ocean shelf provinces would be developed around this continent, an eastern and a western one, with a large number of lineages appearing in both. What little is known about the biogeography of the late Pre-Cambrian Ediacaran biota (Glaessner 1971) is consistent with this possibility, for its elements appear to be unusually widespread, considering the fragmentary nature of the record. Indeed, Gondwana provinciality should have been low throughout the Palaeozoic, with some differences between the Tethyan and Pacific shelves and, perhaps, a southern province at times.

The Laurasian continents seem also to have each supported only limited provinciality along their oceanic margins during the Palaeozoic, although when epicontinental seaways were widespread epicontinental provinces sometimes developed, and when epicontinental barriers appeared these provinces were multiplied (Johnson 1971). Text-fig. 2A-C depict the approximate dispersion pattern of the continents during the early Devonian, after the reconstruction of Smith *et al.* (this volume). With the North pole relatively free of continental influence and the southern Gondwana shores bathed by relatively warm water, latitudinal zonation should have been low. Laurasian provinciality would be chiefly a matter of the geography of epicontinental seaways and of deep-sea barriers. As the reconstructed longitudinal positions of the continents are largely arbitrary, the oceanic intervals between them, as depicted in text-fig. 2A-C, may have been much narrower and can be greatly reduced by longitudinal repositioning (see Cocks and McKerrow, this volume). By the Late Permian, topographic barriers had essentially disappeared and provinciality was evidently based on the Tethyan, Pacific, and Boreal regions, a hemispherically asymmetric arrangement growing out of the geography of the emergent Pangaea.



TEXT-FIG. 2. Past continental positions according to palaeomagnetic and palaeogeologic evidence; longitudinal positioning is arbitrary. A–C, Early Devonian positions, with an arbitrary longitudinal great circle (heavy line) for reference; D–E, Permian–Triassic, with a longitudinal reference circle. Continental positions are after Smith *et al.* (this volume).

If the quality of the provincial biotas can be related to the adaptive strategies implied by their environmental regimes, then the late Pre-Cambrian faunas should have been of low diversity and have been composed chiefly of detritus feeders and other trophic generalists, and a large proportion of the benthos should have been infaunal. An extensive infaunal element probably did not exist much earlier than this, as suggested by the general lack of trace fossils and of bioturbation. It is in fact reasonable to associate the rise of burrowing metazoans (at least of burrowing coelomates) with the concentration of continents during the late Pre-Cambrian. The coelom itself was primitively an adaptation for burrowing (Clark 1964) and was probably evolved at this time, giving rise to a number of coelomic architectures that varied chiefly in the plan of partitioning of the coelom and that were each adaptive to a major mode of life (Clark 1964; Valentine and Moores 1972).

With the separation of the Laurasian continents from the late Pre-Cambrian landmass, diversity should have risen within ecosystems owing to amelioration of continentality, and specialized lineages should have developed as elaborate trophic structures became permissible. The appearance of many epifaunal coelomates and the consequent development of skeletons, presumably as an aid in epifaunal locomotion and as an adaptation for sessile feeding (Clark 1964; Fox, pers. comm.), is marked in the record as the Pre-Cambrian–Cambrian boundary. By the Mid-Palaeozoic, large numbers of habitat and trophic specialists occupied the epibenthic environment.

It would be expected that species diversity should decline in the Late Palaeozoic as continentality increased, and perhaps it did. However, the continental configuration appears to have been unusually favourable for preserving high diversity, all things considered. This is owing to the extensive development of east–west trending coasts facing equatorward along Tethys. Especially there, chiefly along the oceanic margin and backed by epicontinental seas, reefs, and other communities of some complexity persisted even as continentality rose. Finally the regressions of Late Permian stranded the major reef structures with widespread extinction of their specialized lineages in addition to the more specialized elements in non-reef communities, returning the ecosystems to a structural state reminiscent of present high-latitude communities and perhaps very similar to that of the late Pre-Cambrian.

The Mesozoic Era opened with very low provinciality, perhaps with only a single shelf province of flexible, cosmopolitan animals around Pangaea; the more specialized endemic forms had become extinct. It seems likely, however, that some more specialized lineages could have found refuge on island arcs or on mid-plate volcanic chains that lay beyond the influence of the supercontinent. Batten (1971) has described gastropod lineages that disappear from the record in the Permian to reappear only in the Upper Triassic, and which could have weathered the Permian–Triassic crisis aboard oceanic islands. With the progressive breakup of Pangaea, including the spectacular fragmentation of Gondwana, both provinciality and average intra-provincial diversity rose. A key event during the Mesozoic or Cenozoic occurred when a circumpolar current became established south of South America and Africa, encircling Antarctica–Australia. This must have led to a sharp increase in the latitudinal thermal gradient, creating a barrier to the transport of heat to the shores of the polar continent. At the same time the waters at the opposite pole became increasingly isolated as the Laurasian continents moved into higher northern latitudes, and the basis for rather symmetrical and rather steep thermal gradients in both hemispheres was established.

The modernization of the structure of benthic communities appears to have been particularly accelerated during the Mid-Cretaceous, perhaps owing in part to increasing stabilization of productivity associated with Euramerican fragmentation and with widespread epicontinental transgressions. The Mesozoic–Cenozoic boundary, although influenced by a regression that may have contributed to the biotic turnover then, does not appear to have marked a distinctive change in ecosystem structures nor a decline in diversity of any duration.

Thus there appears to have been two great systems of marine shelf biotas during the Phanerozoic, essentially the Palaeozoic and the post-Mid-Cretaceous, preceded and separated by periods of transition. The first system grew from a foundation in the late Pre-Cambrian, when the basic architectures of coelomate ground-plans was probably evolved, and was elaborated with the appearance of skeletons and of many living phyla during the Cambrian; these events established the higher taxonomic composition of the Palaeozoic metazoans. The biogeography of this system was anchored upon a large polar continent, which while probably causing more widespread continentality than is present today nevertheless created a mild thermal pattern of relatively low provinciality. The Cenozoic is in sharp contrast; it is founded in a sense upon the Permian–Triassic supercontinent with a taxonomic composition largely owing to the interplay of Palaeozoic survivors with Mesozoic opportunities. Provinciality tended to be high and the variety of environmental regimes increased, owing to the north–south pattern of continental dispersion and to the cooling poleward shelves. Therefore living communities display a range of structure, and their component populations a range of adaptive strategies, that greatly adds to the pleasures of living in a richly diverse biosphere.

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