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A Paleozoic Pangaea

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During the past 15 years the revolution precipitated by plate tectonics has profoundly affected the earth sciences as well as those aspects of the life sciences that deal with the distribution of biota. This revolution has resulted in a new set of ground rules for biologists and geologists that depend on the acceptance and consequences of a mobile earth rather than one remarkable for the long-term stability of its major landmasses.

profound shift in geologic thought, we should be careful that we do not accept uncritically new paleogeographies that may later be perceived to be in error.

Most geologists agree that plate tectonics and sea-floor spreading have been important processes during the Mesozoic and Cenozoic. The generally accepted picture is that the present continents were sutured together into a supercontinent, Pangaea, during the Permian and

Summary. Paleozoic paleogeographies should be consistent with all available, reliable data. However, comparison of three different Devonian paleogeographies that are based largely or wholly on the data of remanent magnetism show them to be inconsistent in many regards. When these three paleogeographies are provided with possible ocean surface current circulation patterns, and have added to them lithofacies and biogeographic data, they also are shown to be inconsistent with such data. A pangaeic reconstruction positioned in the Southern Hemisphere permits the lithofacies and biogeographical data to be reconciled in a plausible manner.

There is now limited dissent about the reality of plate tectonics, sea-floor spreading, and continental drift—a totally different climate from that which frustrated Alfred Wegener and his sympathizers. The Wegenerian concept of continental drift was almost totally rejected by most Northern Hemisphere geologists and geophysicists during the first half of this century, followed by an almost indecent about-face during the late 1960's (*1*). Only when the geophysical and geological data from the oceans became overwhelmingly compelling were geophysicists forced to abandon the thinking of well over a century. Geologists were unwilling to take the conclusions of their Southern Hemisphere colleagues seriously until the geophysicists capitulated. As we approach the end of the century that has witnessed such a

the earlier parts of the Triassic. Beginning in the later Triassic and Jurassic, Pangaea began to break up more or less along a fracture zone represented by the present Mid-Atlantic Ridge. This breakup finally became complete sometime during the Early Cretaceous. Since that time, the circum-Atlantic continents have been drifting away from each other. Australia, New Zealand, and New Guinea (one block geologically speaking), peninsular India, and Antarctica are thought to have had more complex paths, and there is considerable debate over the movement of Madagascar since the mid-Mesozoic. The complexities of the Caribbean and Gulf of Mexico region and the Mediterranean region (both in the broad sense) are subjects of great contention. But the big picture enjoys general agreement.

Serious disagreements on a global scale arise about interpretations before the Permian. There is no big picture to which most investigators adhere—no pre-Permian, period by period Paleozoic series of paleogeographies that has proved acceptable to most specialists. Rather, a number of possible reconstructions have been proposed, and some have gained a measure of uncritical acceptance in the geologic and paleontologic communities.

Why is there a Paleozoic problem? Most students of earth history assume that currently operative processes also operated during the Paleozoic. Plate tectonic and sea-floor spreading processes, however, are not accepted by some before the Mesozoic. In the earth sciences, data become less abundant, and commonly less reliable, as one moves back in time, but this alone is inadequate to explain the dichotomy of opinion about Paleozoic and post-Paleozoic paleogeographies. Van Andel (*2*) points out that this anomaly stems in large part from the presence of reliable marine geologic and geophysical data for the Cenozoic and Mesozoic, and the absence of such data before the Mesozoic. The data of continental geology and geophysics are potentially available for reconstruction of paleogeographies before the Permian, although the geophysical data seem adequate now only to extrapolate back through the Triassic and Permian. In the absence of such data before the Mesozoic, there are fewer constraints of the type imposed on post-Mesozoic paleogeographic reconstructions. Although both biogeographic and lithofacies data do provide constraints (*3*), they are often ignored. The pre-Permian paleogeographic problem stems then from the fact that different specialists have entered the fray using different weapons.

Most pre-Permian paleogeographies are based largely or entirely on interpretations of paleomagnetic evidence with limited or no effective use of paleontologic and other types of geologic evidence. The Smith, Briden, and Drewry

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maps (*4*) and the Smith, Hurley, and Briden maps (*5*) are examples of geographic reconstructions that depend on paleomagnetic evidence. Engel and Kelm (*6*) use geochemical data but apply their information only to the Precambrian.

Many paleontologists concerned with marine invertebrates have used the paleomagnetic maps, modifying them in varied, often minor, ways according to the dictates of the fossil data; some have made modifications according to lithofacies data (*6a*). Others plot their data on a fixed, modern base map. Still others adopt an almost kaleidoscopic viewpoint, moving fragments of the modern continents about according to their biogeographic affinities at any one time. Because paleontologists often have interests restricted to relatively small Paleozoic time spans, and to one particular group of organisms, it is hardly surprising that their paleogeographic conclusions are often at variance with each other (*7–9*). Paleozoic paleogeography is clearly in a state of flux.

We have constructed pre-Mesozoic paleogeographies (*3*) that are based largely on varied biogeographic, climatic, and gross sedimentary rock data, assuming that prior to the Permian, when oceanic geological and geophysical evidence is lacking, the most satisfactory paleogeographies will be obtained by considering and integrating as many varied, unrelated classes of data as possible. To ignore entire classes of geologic and biologic information leads to unreasonable geographic concepts and internally inconsistent reconstructions.

In this article we will (i) review some of the classes of information that have been largely avoided by others in making pre-Mesozoic paleogeographies, showing how this information is basically violated by some Paleozoic reconstructions and (ii) further consider an alternative pangaeic reconstruction which we have previously proposed (*3*) and which reconciles varied biogeographic and other types of data. Although we have avoided paleomagnetic data as less reliable in the Paleozoic (*10*) than other data, we believe that a pre-Permian Pangaea best reconciles the varied independent classes of other data that must be considered in paleogeographic reconstructions.

In proposing a pangaeic reconstruction, we do not intend to suggest that it is the only alternative that might reconcile all these varied classes of data. Nor do we intend to suggest that it is necessarily the definitive solution to the Paleozoic paleogeographic problem. Rather, we propose the Pangaea as a basis for keeping open the dialogue with regard to the possibilities for pre-Mesozoic reconstructions and to show that there are alternatives that are supported by many classes of geologic and biologic data.

Are Paleozoic Paleogeographies a General Problem?

Why should nongeologists concern themselves with whether or not there are acceptable period-by-period paleogeographies for the Paleozoic? For the biologist (*11*) concerned with evolutionary processes it is important to learn what constraints may be placed on varied evolutionary hypothesis by biogeographic history. For example, at what biogeographic level, or levels, is allopatric speciation an important process? During the evolution of animal and plant communities, defined as time-recurrent associations of organisms, how unchanging are the basic taxonomic contents of those communities? Do taxa have the capability of commonly moving from one biogeographic unit into another with any frequency?

The correlations in the Mesozoic and Cenozoic between plate tectonic features and raw material deposit occurrences of varied kinds—from base metals to sedimentary phosphate and petroleum—should be tested against varied pre-Permian paleogeographies as a means of discovering similar, older deposits.

Reconstructing Pre-Permian Geography

Many classes of information are necessary to reconstruct Paleozoic paleogeographies. It cannot be assumed that the major post-Paleozoic landmasses maintained their integrity during the Paleozoic, any more than it can be assumed that they maintained similar positions relative to each other or to the earth's axis of rotation.

In the Paleozoic, reliable data are lacking about the presence of oceanic, truly abyssal deposits, as contrasted with continental slope, bathyal, and truly continental sedimentary deposits. Their absence is thought to relate to sea-floor spreading in that marginal oceanic deposits are commonly moved beneath other crustal materials, including continental crust, and there made unrecognizable by metamorphism and remobilization. Most geologists assume, however, that oceanic regions, with abyssal deposits, were widespread during the Paleozoic, despite the absence of positive evidence from the rocks preserved for study.

The Paleozoic platforms form a number of pieces with which to begin the Paleozoic geographies. Platforms are defined as those parts of a continent, or other major landmasses, that have an older, Precambrian crystalline basement overlain by later Precambrian and younger sedimentary rocks. Peripheral to platforms one may find "geosynclinal" deposits. These represent somewhat deeper water, upper bathyal and deeper shelf, marginal environments similar to those of modern continental margins as well as some active island belts well removed from present continents. The positions relative to the presently associated platforms of many of the pre-Mesozoic geosynclines need to be examined carefully. Their positions after the Paleozoic need not accord with those before that era. The question is how to devise a way of relating these varied pieces both to each other in time and space and to their overall position on the earth—their latitude and longitude through time.

The data of remanent magnetism at best provide information only about past inclination from the equator. They give no information about latitude north or south and no inkling of longitude. There is general agreement that the evidence of remanent magnetism should be used whenever possible, but there is wide disagreement as to what constitutes adequate evidence (*12*).

It is important in working out Paleozoic geography to establish and effectively use as many climate-correlated criteria as possible, because the distribution of these, time interval by time interval, will provide rough clues about latitude with which to independently check the information provided by remanent magnetism. It should be kept in mind, however, that climatic features of the Quaternary, as well as of the Mesozoic and Tertiary, depart substantially from pure association with latitude in many places and may by analogy do so in the Paleozoic. Establishing reliable longitudinal positions through time will be more difficult.

Paleobiogeographic criteria provide information about which regions, terrestrial and marine, maintained reproductive communication because of similarities of their biotas. For the marine environment, and in particular the shallow seas that covered large parts of the Paleozoic platforms and marginal shelf environments, reproductive communication most commonly depends on surface current circulation patterns. Shallow-water currents provide an essential means for the dispersal of organisms and their reproductive propagules because the behavior of water currents on a rotating sphere like the earth can be diverted in many ways by a variety of landmasses and marine features. For the continental environment, similarities of biotas commonly imply migration routes available to both plant and animal populations.

Climatic criteria. Geologists and paleontologists use varied criteria to recognize indications of past temperature and humidity, including alternating humid and dry conditions (conditions of seasonal moisture). Only climatically uniform time intervals are useful as a basis for deductions about latitude—seldom intervals as long as the Paleozoic periods, which were rarely climatically uniform from beginning to end (*13*).

1) Temperature. Evaluation of past temperatures and temperature gradients depends chiefly on qualitative physical and biological indicators of warm to hot and cool to cold environments (*14*). For example, a variety of sediments and soils are known to form today under warm and cool climates. Their lithified equivalents in the geologic record are assumed to carry the same temperature connotations. (i) Warm temperatures: biogenic calcium carbonate sedimentation is most characteristic today of shallow-water, warm temperate, subtropical and tropical regions. Carbonate sediments are uncommon in cooler waters because of dissolution, except in regions of very high production. Thus, warm temperatures of the past are recognized by the presence of abundant marine limestone, calcareous shale, and dolomite. Warm temperatures are also commonly recognized by the presence of abundant ferric iron minerals in sedimentary rocks, which give red, orange, and yellow colors to marine and nonmarine rocks. Sedimentary iron and manganese deposits, laterites, and the products of lateritic weathering such as nonmarine bauxite are also warm temperature indicators in the stratigraphic record. We have compiled the distribution of some of these items for the Paleozoic (*3*). Warm climate criteria also include carbonate reefs constructed by marine plants and animals, high taxic diversity at species to class levels, communities with many species, and a large number of ecologic complexes in addition to reefs (thickets and forests of one kind or another in the marine environment). Marine evaporites are characteristic of warm regions where water circulation with the oceanic reservoir was restricted, and where freshwater input was lower than rate of evaporation. (ii) Cool to cold temperatures: in regions characterized by cool to cold temperatures, past and present, it is common to find abundant, unweathered silicate minerals, in addition to quartz, in clastic sedimentary rocks. Glacial deposits, nonmarine and marine, as well as other physical evidences of continental glaciation are excellent indicators of cool to cold climate. There is little (*15*) preserved evidence of high elevation, montane glaciation in the pre-Pleistocene record because of the erosional destruction of high elevation regions; we have, for example, abundant mountain roots but no "fossil" mountains. Evidence of Paleozoic and earlier glaciation is limited in the geologic record. There are a few Precambrian interludes, a brief interval near the end of the Ordovician and the beginning of the Silurian, an interval in the Late Carboniferous and Early Permian, and regionally restricted glaciation during the later Permian.

2) Humidity. There are a number of features that provide the geologist with some measure of humidity. Coal deposits, for example, indicate high humidity as well as the presence of environmental conditions favorable for the preservation of plant material (*3*). Because swamp vegetation leading to coal and high humidity may occur in both low and high latitude regions—that is, tropical swamps to northern or southern muskegs—coals in themselves are not an index to tropical or subtropical conditions, although some coals have formed in warm swamps.

Low levels of humidity correlate with the presence of evaporite deposits. Seawater evaporites form commonly in areas having restricted circulation with the sea where conditions for preservation of the precipitated salts are favorable. Such conditions are normally found only in low latitude desert belts, although there may be significant latitudinal perturbations of this environment due to orographic and other features. Nonmarine evaporites, formed in landlocked basins, are almost absent before the Cenozoic but, when present, may merely indicate local areas of aridity. Nonmarine evaporites in the Cenozoic tend to occur chiefly in desert belts at low latitudes, but high latitude nonmarine evaporites are known today—even in Antarctica. There are few nonmarine Paleozoic evaporites but many of marine origin.

Seasonal areas of aridity in warm regions are indicated by the presence of the class of soils called calcretes, in which calcium carbonate nodules and layers form within the soil profile. In general, calcretes form at higher latitude than the desert regions in which gypcretes and silcretes tend to form and where marine evaporites are expected. Arid regions are also indicated by the presence of ancient eolian dune deposits of the type present in part of the Permian in the western United States.

Plant morphologic structures may provide clues to differing levels of humidity. Tree rings, for example, may correlate with seasonal levels of humidity, as well as temperature, and other variables (*3*). Swamp vegetation commonly has certain morphological characters indicative of its environment.

3) Seasonality. Seasonality for geologic purposes may be divided into wet-dry and cold-warm since there has been little effort to recognize seasonal changes in wind direction or other types of seasonality within the geologic record. Botanical features, such as tree rings, may indicate seasonality of different types (the lack of tree rings can be taken to indicate a low level of seasonality). Calcretes are indicative of wet-dry seasonality in fairly dry regions with warm average temperatures. Finely laminated sedimentary rocks may also provide an index of seasonality; there may be varved sediments of glaciated regions or laminated sediments present in some evaporite basins, where the laminae might reflect changes in water supply, not all of which need be purely seasonal.

Paleobiogeography

Paleobiogeography is the study of the distribution of organisms in time and space. It should be recognized that the flora and fauna of the past and the present are not distributed in a random manner and that the global flora and fauna never have been uniformly and homogeneously distributed (*16*). First-order biogeographic controls are north-south correlated temperature, light, and other physical variables related to seasonality and latitude; organisms with different tolerances to these variables are latitudinally organized. Second-order distribution patterns are longitudinally distinct groupings of organisms that are reproductively isolated by physical barriers such as ocean currents, watermasses with different properties, land barriers, salinity barriers, and many others. Distance itself may be a reproductively isolating factor for organisms whose propagules have limited viability and low dispersal potential.

Similar associations of organisms at present and in the past indicate biogeographic continuity. When the paleontologist finds similar biotas, particularly at the generic level or lower, in what are now remote parts of the world, some thought must be given to how they were formerly kept in reproductive communication.

Longitudinal criteria. Paleozoic longitudinal positions can be worked out from the well-established Pangaea of the Permian and earlier parts of the Triassic. One feature commonly employed in assembling the Permian-Triassic Pangaea is the fit between adjacent continents on the margins of the North and South Atlantic oceans. The Atlantic margins of Africa and South America fit together although there is concern about what depth or position out on the continental shelf or slope provides the most realistic fit. The fit between North America and Europe is less convincing. It involves the thorny problem of how to cope with the Caribbean and Central America, for which there is inadequate room, as well as the shuffling about of some Mediterranean pieces and the Iberian Peninsula (*17*).

Geologists generally agree about what constitutes evidence for plate sutures—the suturing together of portions of the crust. These features include a variety of geological phenomena that may, for brevity, be lumped together as certain tectonic lineaments and ophiolite zones. But, there is disagreement whether plate sutures indicate that the pieces of crust on either side of the suture were remote from each other prior to suturing, or might in some cases have been close (*3, 18*). Each individual case of suturing must be decided on its own merits. After the Paleozoic there is good evidence from marine geology and geophysics for long distance plate movements before some suturing events. But direct evidence for long distance plate movement in the Paleozoic is lacking, and it cannot be assumed that Paleozoic sutures represent the junction of plates that were formerly far apart.

For the Permian and later periods, reliable paleomagnetic evidence, consistent with independent data, provide a firm basis for estimating some important plate movement parameters. But, before the Permian, the inconsistency of paleogeographic interpretations, based on paleomagnetic data, with other independent classes of data such as historical biogeography, leads us to conclude that the available paleomagnetic data alone are inadequate for reconstructing reliable paleogeographies. When more reliable pre-Permian paleomagnetic data become available, they will go far toward solving many questions that cannot now be addressed satisfactorily.

On this Permian Pangaea are superimposed the available climatic criteria useful for establishing latitude and Permian biogeographic data. The biogeographic relations of marine organisms, considered within the context of Permian land-sea relations, are used to arrive at rational current circulation patterns (*3*). One next works back systematically in time toward the Cambrian, using climatic and biogeographic data available for each time interval.

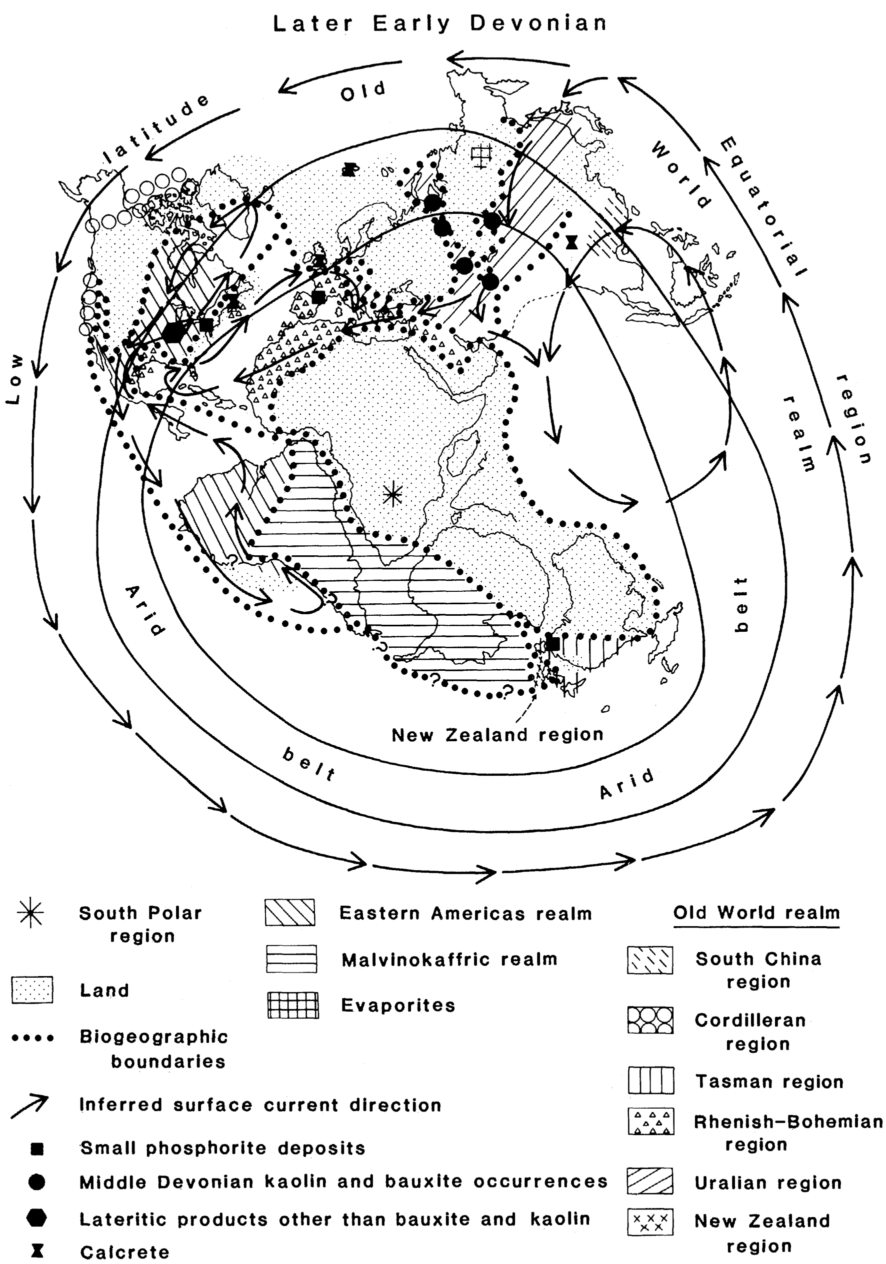


Fig. 1. Later Early Devonian (Emsian) paleogeography and biogeography [modified from (*3*)]. The South China region has been added (*30*). The map shows Early Devonian landmasses, and oceanic surface currents inferred from this landmass placement; the South Polar region; a low-latitude equatorial region; a low to mid-latitude arid belt; varied lithologic deposits; and the major marine, shallow-water biogeographic units recognized for the Devonian.

Proposed Paleozoic Paleogeographies

A variety of period-by-period paleogeographies, all different, have been proposed for the Paleozoic. Prominent among these are the reconstructions of (i) Smith, Briden, and Drewry (*4*) and Smith, Hurley, and Briden (*5*), (ii) Scotese *et al.* (*19*) and Bambach *et al.* (*20*), (iii) Morel and Irving (*12*), and (iv) Boucot and Gray (*3*). Smith and his coworkers and Morel and Irving use paleomagnetic evidence exclusively; Scotese *et al.* and Bambach *et al.* give it first priority, following paleomagnetic rather than other data when apparent conflicts arise. The fact that all these remanent magnetism-based reconstructions rely basically on the same data, and yet are significantly different from one another, indicates that the raw data have been weighted differently. In other words, the paleomagnetic data provide fewer constraints on interpretation than might at first be supposed. These reconstructions also make use of varied tectonic lineaments, such as mountain belts and ophiolite belts, to suggest which previously separated regions were brought together by plate tectonic processes, under the assumption that such features indicate major separation of the sutured terranes.

Boucot and Gray (*3*), who rely primarily on biogeographic and geologic evidence of climate for their reconstructions, conclude that not all tectonic features need represent suturing of far removed pieces of crust. Joining of the Paleozoic platforms and adjoining nonplatform terranes as a major pangaeic body, of the type inferred by Engel and Kelm (*6*) for the late Precambrian, best fits the varied information (*3*). Boucot and Gray center their inferred Paleozoic Pangaea on the South Pole during the Cambrian and move it as a unit to a position between the North and South poles by the Permian.

All these reconstructions agree on some points while disagreeing about others. The Gondwana regions (South America, Africa plus Arabia, Antarctica, Australia in the larger sense including New Zealand, New Guinea, the intervening seas, and part of Timor, and peninsular India) are commonly joined together in all reconstructions and placed in the Southern Hemisphere. The chief disagreements, particularly with regard to the reconstruction of Boucot and Gray (*3*), centers about (i) the treatment of North America and Eurasia, (ii) whether southern Europe should also be joined with Gondwana, and (iii) the treatment of Asia as a block or as a number of discrete entities.

Boucot and Gray (*3*) place Eurasia and North America largely in the Southern Hemisphere during the lower Paleozoic. The other reconstructions place them well within the Northern Hemisphere. Although the evidence is consistent with a Northern Hemisphere placement in the Late Carboniferous and Permian, the geophysical, geological, and biologic evidence is permissive of a Southern Hemisphere placement in the lower Paleozoic; this is also more consistent with the available Cambrian-Devonian biogeographic and lithofacies evidence.

With regard to Asia, the reconstructions based primarily on paleomagnetic data do not account for the geological evidence indicating the presence of several parallel lithofacies belts extending from the Uralian–Novaya Zemlya region south through central Asia and then east into western Heilongjiang (*21*). Lithofacies belts are regions underlain by characteristic suites of sedimentary and volcanic rocks. A lithofacies belt may consist, for example, largely of limestone, calcareous shale and dolomite, or it may consist largely of noncarbonate terrigenous rocks and varied volcanic rocks. These parallel lithofacies belts make a fragmented Paleozoic Asia unlikely (*21*).

With regard to the treatment of southern Europe, the pre-Carboniferous lithostratigraphy, lithofacies relations, biostratigraphic, and biogeographic relations of Europe, North Africa, and the Near East are so intimate as to preclude any serious possibility for their having been far removed from each other, as has been shown especially for the Silurian (*22*). The reconstructions of Smith and his co-workers (*4, 5*), Scotese *et al.* (*19*) and Bambach *et al.* (*20*), and Morel and Irving (*12*) disregard the significance of the stratigraphic geology of these regions, and the remarkably low probability that regions with such similar, intergrading stratigraphies would have developed them simultaneously while remote from each other. Europe, Africa, and the Near East represent one huge platform during the Cambrian-Devonian interval. There is no evidence for a Mediterranean Sea at this time. The modern Mediterranean Sea, considered in terms of its bounding Paleozoic strata, is merely a larger, more complex Red Sea rift separating continental platform blocks that previously were a single block. To those

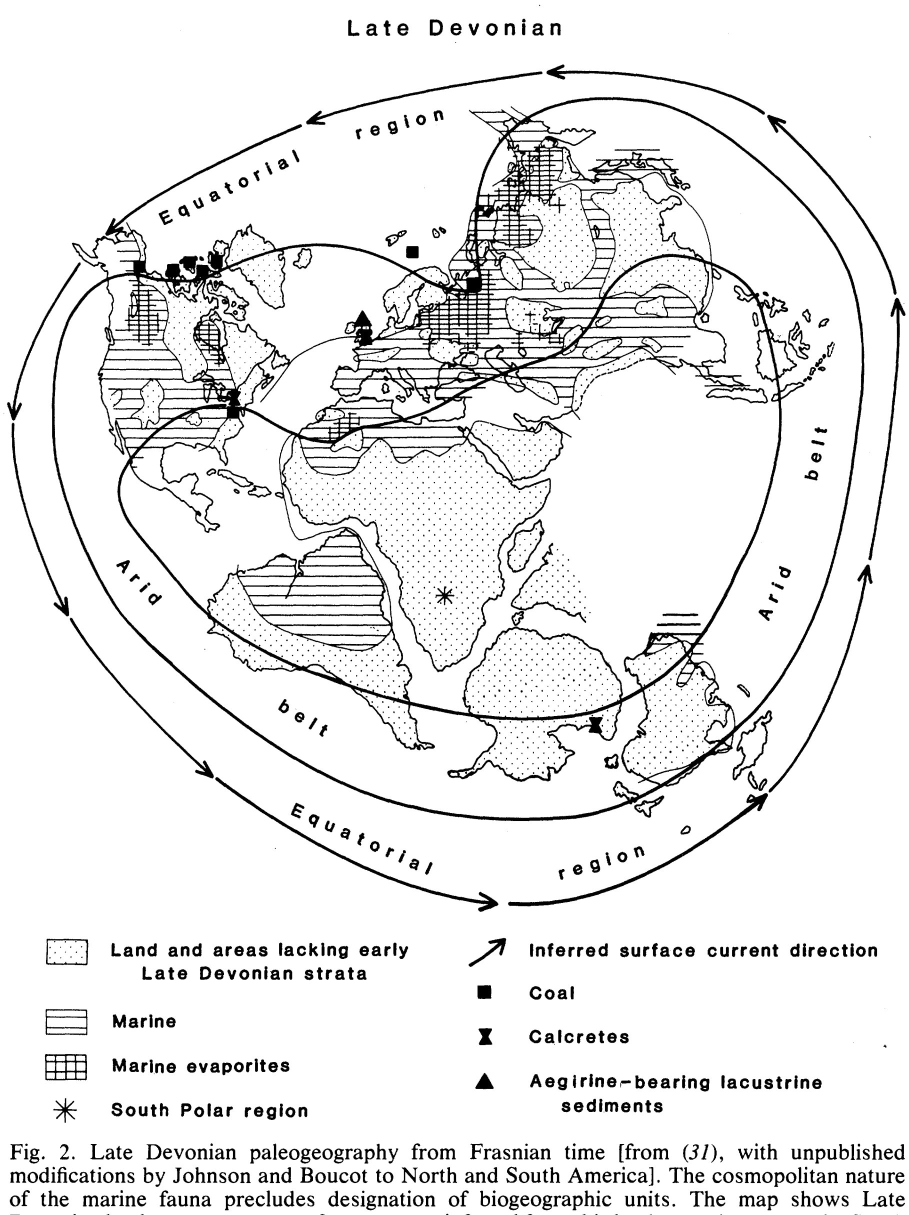


Fig. 2. Late Devonian paleogeography from Frasnian time [from (*31*), with unpublished modifications by Johnson and Boucot to North and South America]. The cosmopolitan nature of the marine fauna precludes designation of biogeographic units. The map shows Late Devonian landmasses, ocean surface currents inferred from this landmass placement, the South Polar region, varied lithologic deposits, a low-latitude equatorial region, and a mid-latitude arid region.

unfamiliar with European geology, it is necessary to point out that the late Paleozoic Hercynian fold belts and their associated late Paleozoic geosynclinal strata are superimposed on this huge Cambrian-Devonian platform. The Hercynian fold belts should not be viewed as suture zones welding together platform blocks that were a great distance apart prior to the Hercynian interval. Fold belts and geosynclinal cum continental margin environments occur in some instances on, rather than merely bordering, former platforms. The Rocky Mountain geosyncline of the Cretaceous is an example.

Devonian Example

Using several of the proposed Devonian paleogeographies (*5, 12, 20*) as examples of the diversity of pre-Permian reconstructions, we can show why we find them unacceptable in terms of the available geologic and biologic evidence. The Devonian is sufficiently remote in time from the paleogeographically well-known Permian to make it of interest. In addition, many data are available for the Devonian, and the Early Devonian is a time of high biogeographic and climatic differentiation, whereas the Late Devonian was characterized by both low climatic gradient and a very low level of biogeographic differentiation—that is, by a cosmopolitan fauna. A discussion of the Devonian emphasizes the gross differences in climatic gradient and biogeography that may be incorporated within a single geologic period.

Early Devonian. Our pangaeic reconstruction for the later Early Devonian (Fig. 1) is consistent with the biogeographic data, with the surface current circulation pattern necessary to explain the highly provincial faunas, and with the high climatic gradient of the Early Devonian.

The Early Devonian, and in particular the late Early Devonian, is an interval of high climatic gradient. This is indicated by the occurrence of the high latitude cool-climate Malvinokaffric biogeographic realm contemporary with the warm-climate Eastern Americas realm and the tropical to subtropical Old World realm (*23*). The climatic implications are based on both physical and biotic criteria, with the Eastern Americas realm thought to represent a watermass less warm than that represented by the Old World realm (*24*). Evaporites are largely absent during Early Devonian time, except in Siberia (*25*). Calcretes are present in Svalbard, Nova Scotia, Britain, and southeast China. Their occurrence together with the Siberian evaporites, is consistent with a warm, seasonally dry region at middle to low latitudes. This warm, dry belt was relatively narrow when compared with that present in the Late Devonian.

The bauxites and kaolins in central Eurasia are of Middle Devonian (Eifelian) age (*3*). Together with the southerly perturbation of the Late Devonian arid-humid belt boundary in low to middle latitudes, these Middle Devonian indicators of lateritic conditions suggest a major departure from pure association with latitude that began at least as early as the beginning of the Middle Devonian. The cause or causes of this major climatic perturbation are unknown, although a Uralian-Kazakhstanian orographic feature associated with possible Middle Devonian orogeny and sedimentary facies patterns is a possibility.

The South Pole has been positioned, as for the other Paleozoic periods, by simple inspection of the latitudinally correlated data shown on Fig. 1 (*3*). The South Pole positions show a single trend—moving from northwestern Africa during the Cambrian to southern Africa during the Late Carboniferous and Early Permian. These pole positions accord fairly well with some of those determined purely from paleomagnetic evidence, but this agreement is almost entirely with regard to the Gondwana regions, not with North America and Eurasia.

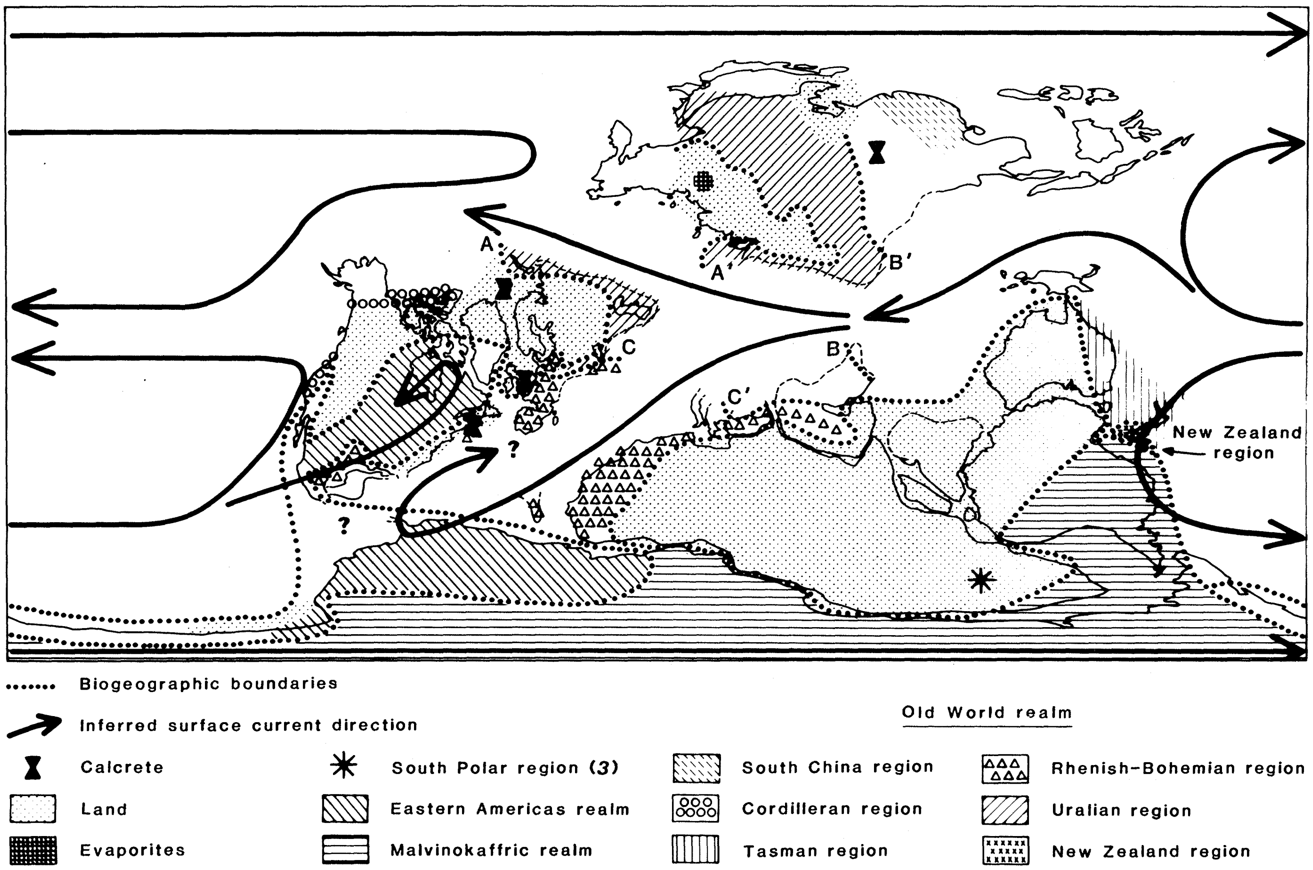
Late Devonian. The Late Devonian (Fig. 2) is an interval of low climatic gradient (*11*) in comparison with the late Early Devonian. In the Early Devonian, Antarctica was a part of the cool-climate Malvinokaffric realm; in the Late Devonian, at least part of Antarctica was occupied by an arid belt, indicated by the presence of a calcrete, one of the class of soil types that form in seasonally dry climates. In comparison with the Early Devonian there is a significant change in the width of the arid belt, although control is poor except through North America and Eurasia. The arid belt (Fig. 2) lies south of a low-latitude humid belt and is characterized by widespread marine evaporites (*25*), calcretes in some places (*3*), and in Scotland, by lake beds with authigenic aegirine (*3*), a mineral precipitated out in seasonally arid, shallow-water lacustrine environments. The Late Devonian calcrete occurrences are in a belt distinctly poleward of the widespread marine evaporites.

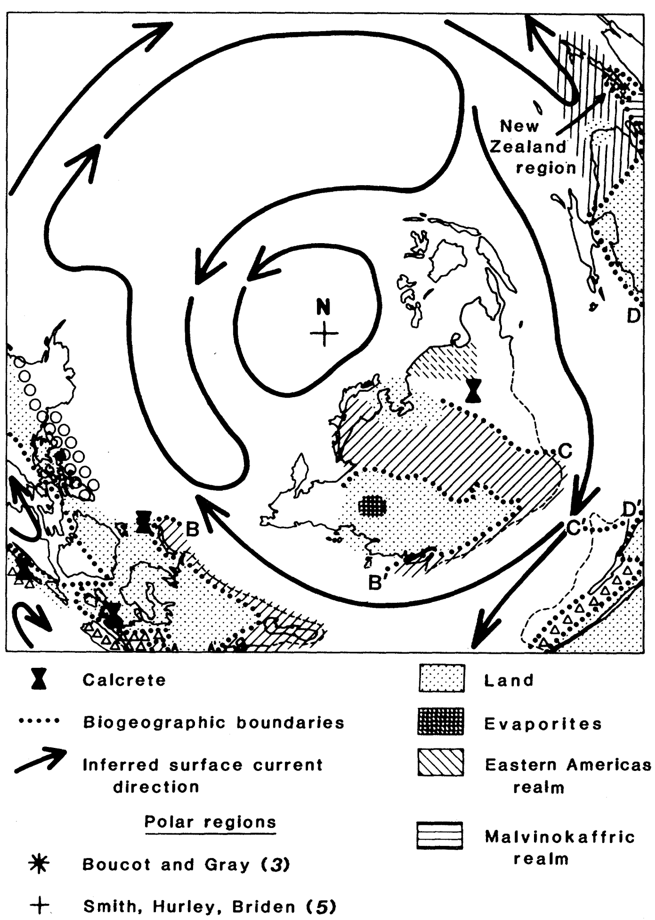
A coal belt, which lies at lower latitudes than the occurrences of marine evaporites, and other indicators of highly seasonal dry climate is consistent with a low-latitude humid region. This coal belt extends from northeastern Alaska across the northern Canadian archipelago to Bear Island between northern Norway and Svalbard and to northernmost Russia (the Timan-Pechora) region.

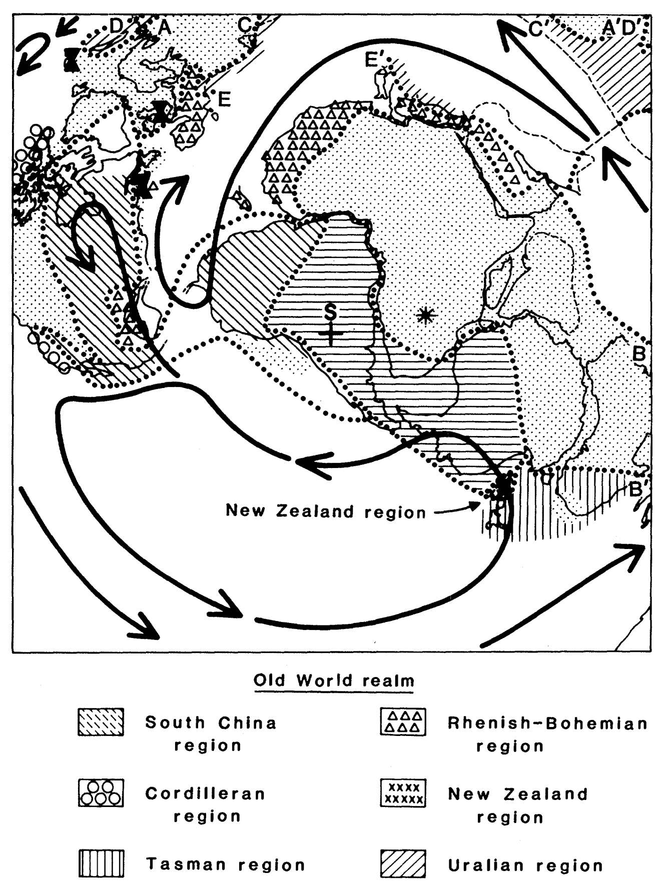
The presence at high latitudes (Fig. 2) in Bolivia, Argentina, and South Africa, formerly portions of the Malvinokaffric realm, of warm climate marine taxa (*26*) is further evidence of a low climatic gradient in the early Late Devonian and of a contraction of the cool to cold climate belt. Low climatic differentiation in the Late Devonian is also indicated by the highly cosmopolitan marine fauna. No biogeographic realms or regions can be distinguished. Because the evidence favors a major change in climatic gradient and level of provincialism within the Devonian, the data of the Early Devonian should not be mingled with those of the Late Devonian. Extreme transgression in the Late Devonian appears to correlate with the cosmopolitan fauna and the lower climatic gradient, but this may be coincidence. Transgression in parts of the Ordovician and in the Late Cretaceous correlate with provincialism, and in the Ordovician with a high rather than a low climatic gradient. Only by examining all Phanerozoic time intervals is it possible to see whether there is a statistical basis for such conclusions rather than coincidence (*27*).

Comparisons. Figures 3 through 8 show reconstructions based principally on the evidence of remanent magnetism. Figures 3 through 5 are the base maps of Smith, Hurley, and Briden (*5*, maps 69 to 72). Figures 6 and 7 are base maps of Morel and Irving (*10*, figures 10 and 12), and Fig. 8 is the base map of Bambach *et al.* (*18*, figure 10). On these maps, which show only the paleogeography proposed by the authors, we have superimposed other data including the major Early Devonian biogeographic units and certain lithologic features. We have also included the position of our own pangaeic South Polar region and an oceanic surface current circulation pattern that is consistent in each case with the paleogeography. In addition to the inconsistencies in the paleogeographic reconstructions that appear with the additional data, these three paleogeographies are incompatible with each other in the position of the poles, in the proximity of North and South America, and in the degree of fragmentation or integration of Asia.

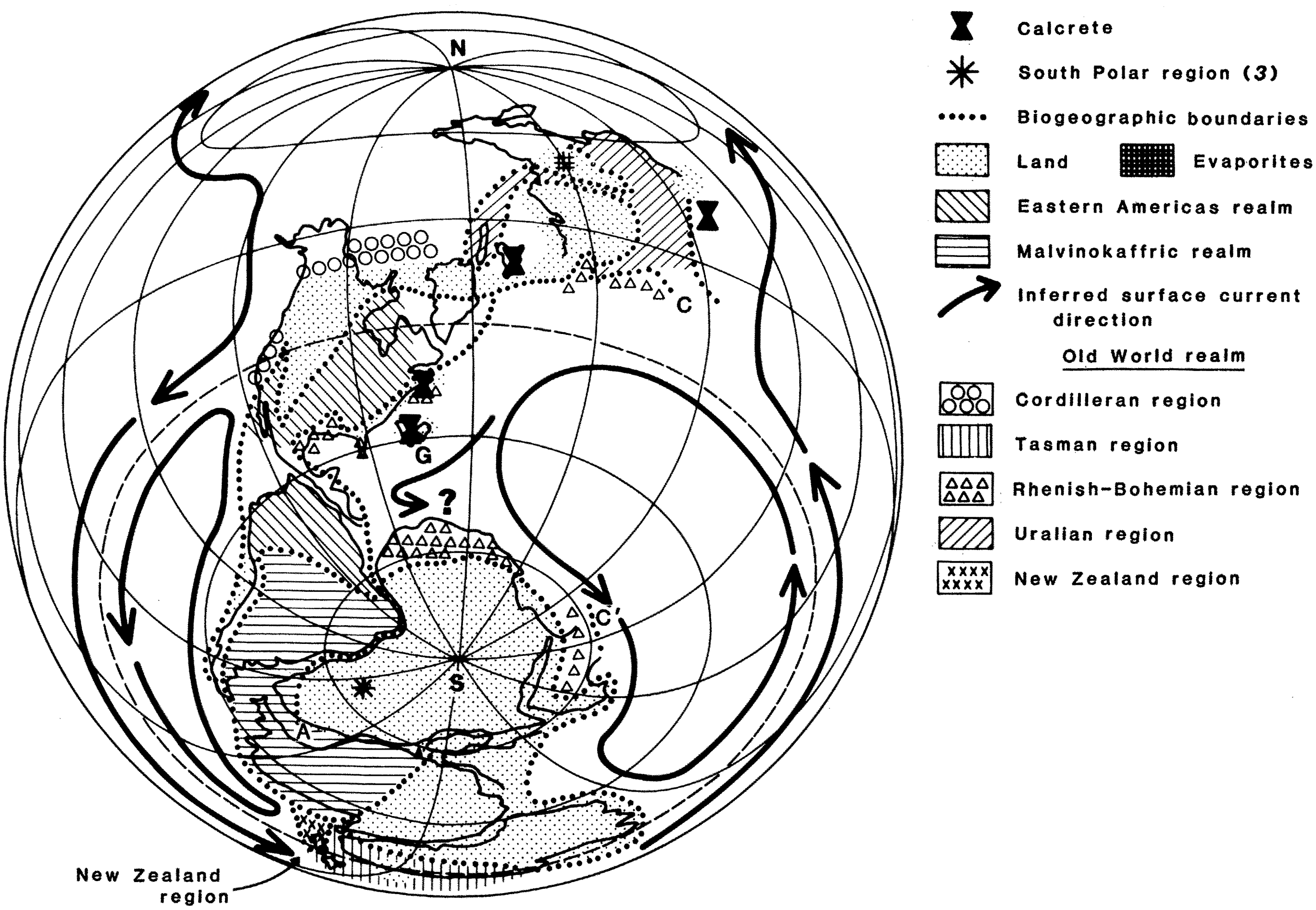
In their reconstruction, Smith, Hurley, and Briden place a South Pole in northeastern Argentina (Fig. 5). They have a Gondwana-type continental assembly that includes much of southeastern Europe, southeastern Iran, Turkey,

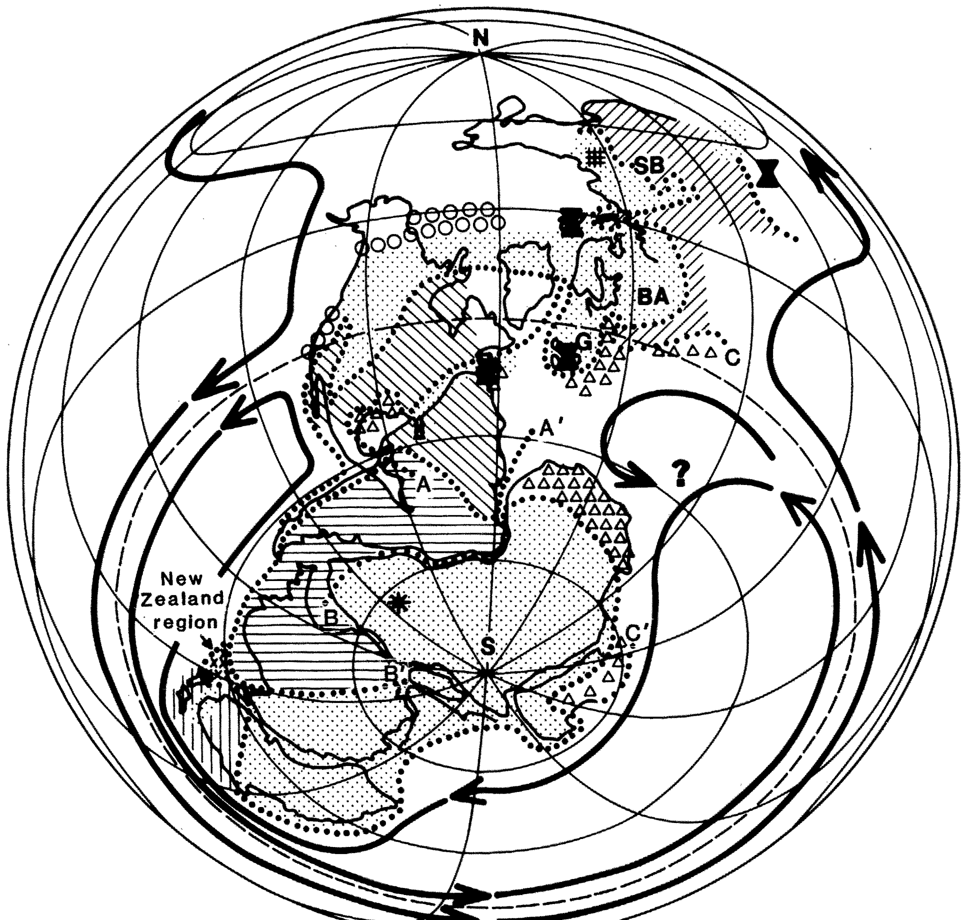






Figs. 3 to 5. Mid-Late Silurian (Ludlovian) reconstructions from Smith, Hurley, and Briden (*5*, maps 69 to 72) with late Early Devonian (Emsian) age biogeography added, as well as a shallow-water circulation pattern consistent with the geography. The age discrepancy is not significant. Occurrences of calcrete and evaporites have also been added. The letter symbols (A, A′, B, B′, and so on) refer to points that would be in contact on a pangaeic reconstruction consistent with the biogeographic evidence. Figures 4 (bottom left) and 5 (bottom right) are North and South Polar projections, respectively.





Figs. 6 and 7. Devonian base maps from Morel and Irving (*12*, figures 10 and 12). Fig. 6 (top) represents the Late Silurian–Middle Devonian interval, and Fig. 7 (bottom) is an alternative reconstruction for the Early to Middle Devonian. S and N, the South and North poles, respectively; G, Great Britain; BA, Baltica; SB, Siberia; and the letter symbols A and A', B and B' refer to points that would be conjunct on a pangaeic reconstruction.

South America, Africa plus Arabia, Antarctica, and greater Australia (Figs. 3 and 5). A second landmass made up of North America (including most of central America) plus Greenland and northern Europe lies north of their Gondwana-type assembly, and a third unit incorporates Asia (including Indonesia and the Philippines). The position of these last two units requires an equatorial, oceanic seaway in the Northern Hemisphere.

Their reconstruction has a number of problems in terms of biogeographic units and climatic indicators. It is impossible, for example, to provide their map with a shallow-water circulation pattern that maintains reproductive isolation between many of the known Early Devonian biogeographic units. At the same time, reproductive communication between the North and South American portions of the Eastern Americas realm is not possible in this reconstruction, nor their isolation from the European, North American, and North African–Arabian portions of the Rhenish-Bohemian region of the Old World realm. This reconstruction also cannot account for the biogeographic distinctiveness of the Tasman and New Zealand regions of the Old World realm. In addition there is difficulty in transporting certain Eastern Americas realm and Tasman region genera into central Asia from Kazakhstan on the west to Heilongjiang on the east.

The similar lithostratigraphy and biostratigraphy of Europe, North Africa, and the Near East, during this time interval does not support their separation and fragmentation and is in biogeographic-geologic error when it places the eastern Uralian region on the western rim of Asia, far removed from the western Uralian region of easternmost Europe. The presence of high northern latitude marine evaporites in Siberia and of Northern Hemisphere calcretes at unusually varied latitudes is meteorologically unlikely.

Figures 6 and 7 employ two alternative base maps provided by Morel and Irving for the Devonian (*10*, figures 10 and 12). Figure 6 shows a South Pole in central Africa near the southeastern side of the Sahara and Fig. 7 shows a South Pole in Ethiopia. Neither reconstruction has a low-latitude intracontinental ocean because of the presence of a junction between North and South America on the one hand (Fig. 6) and of western South America abutting North America on the other (Fig. 7). Morel and Irving do not indicate the positions of China or of most of Asia, except for Siberia. Siberia is shown in high northern latitudes to the north rather than to the east of a truncated northern Europe. The position of southern Europe is not shown.

Their Gondwana assembly maintains South America, Africa, Antarctica, peninsular India, Australia, and New Zealand in contact, and the biogeographic integrity of the Malvinokaffric realm. However, it is impossible with their reconstructions to (i) maintain the biogeographic separateness of the Eastern Americas realm and the Rhenish-Bohemian region of the Old World realm without mixing their taxa; (ii) account for the large-scale disruption of the Rhenish-Bohemian region; and (iii) transport certain genera from the Eastern Americas realm and Tasman region into central Asia where they are found locally from Kazakhstan to northern China. In one reconstruction (Fig. 7) the Rhenish-Bohemian realm fauna in Oklahoma and northeastern Mexico would have been totally cut off from reproductive communication with congeners.

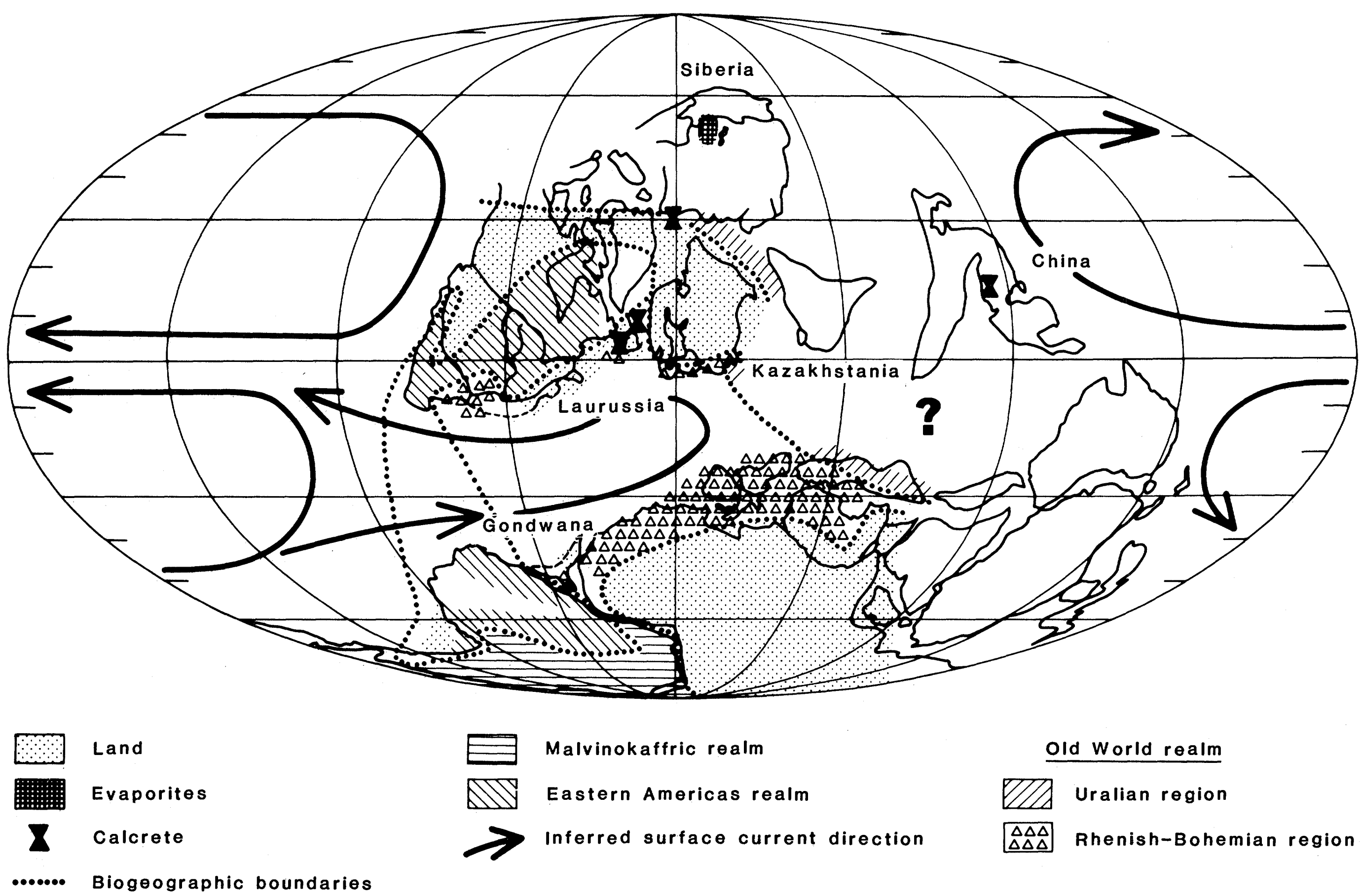


Fig. 8. Later Early Devonian (Emsian) paleogeography from Bambach *et al.* (*20*, figure 10) modified by the addition of a shallow-water circulation pattern consistent with the geography, later Early Devonian biogeographic units pertinent to testing the pattern, and some lithologic entities useful for considering its reliability. We have omitted data from the original reconstruction that is not pertinent to the questions examined here.

In addition, the high northern latitude position of the Siberian evaporites is unlikely meteorologically; the distribution of the Northern Hemisphere calcretes makes little climatic sense; the separation of North Africa from Europe is inconsistent with their very similar lithostratigraphy and biostratigraphy.

Figure 8 employs a base map from Bambach *et al.* (*20*, figure 10) for the later Early Devonian, with a South Polar region in southern Africa. Their Gondwana assembly includes Spain, Turkey, and most of the other Mediterranean areas, in addition to the customary landmasses. Their Laurussia incorporates most of North America, except for parts of Alaska and Central America, with northern Europe, north of a line from central France through southern Poland. They position a Siberia far north of Laurussia. Kazakhstania is a chunk of central Asia, and China is an irregular area that includes southern China, Korea, Thailand, and so on. Most of the extra-Gondwana pieces are situated in low northern latitudes, except for Siberia, which is placed at moderate to high latitudes. The positioning of some major biogeographic units and biogeographic boundaries and the addition of a logical, low-latitude current system shows that this solution (*20*, figure 8), like those of Smith, Hurley, and Briden (*5*) and Morel and Irving (*12*), fragments the biogeography. The required, major, shallow-water current flow at low latitudes clearly cannot account for the pattern of marine benthic endemism of the Early Devonian fossils. Note as well the impossibility of maintaining reproductive communication between the Eastern Americas realm of North and South America and between the Rhenish-Bohemian region when these are split up among eastern North America, northern Europe, North Africa–Arabia, and southern Europe. Either the reconstruction is erroneous or biogeographic data accumulated for more than a century have limited significance.

Geologically, the separation of a portion of central Asia (their Kazakhstania) from the southern end of the Ural Mountain system and from adjacent Mongolia–Inner Mongolia is inconsistent with the well-known lithofacies evidence discussed earlier (*21*). The separation of North Africa, southern Europe, and the Near East from northern Europe is most unlikely in view of their similar lithostratigraphy and biostratigraphy during this time interval.

The presence of evaporites in Siberia is anomalous unless the climatic gradient was much lower in the Northern Hemisphere than that in the Southern Hemisphere, where the cool to cold Malvinokaffric realm existed at equivalent latitudes, and unless one accepts an arid region at high northern latitudes surrounded by ocean on three sides—a meteorologically unlikely possibility.

Conclusion

Early Devonian paleogeographies based largely on interpretations of paleomagnetic data fail to satisfy both biogeographic and climatic indicators. In particular, the placement of certain land bodies, such as Siberia, in high northern latitudes is questionable. Also questionable is the validity of splitting central Asia from the Urals, China and Mongolia from central Asia and Siberia, and Europe from Africa. None of these splits is supported by lithofacies or biofacies evidence.

Paleozoic reconstructions that rely largely or wholly on the data of remanent magnetism also fail to come to terms with the following (*3*): (i) the presence in the Andean region throughout the Paleozoic of a single, essentially stable, north-south boundary that separates warm water from cold water faunas; (ii) the steady southerly movement of the east-west, warm-cold water boundaries in the Americas and in the Old World (southern North America in the Cambrian to south of the Amazon by the Permian; northern Europe in the Cambrian to North Africa by the Permian); and (iii) the extensive mixing of faunal elements from different biogeographic realms from the Cambrian through the Devonian in southeastern Kazakhstan and the presence of a similar mixed Devonian fauna in northern China (Inner Mongolia and Heilongjiang). The first two of these facts are readily explained by a steady northward movement of a pangaeic supercontinent. The last is consistent with an oceanic circulation pattern implied by the presence of a Pangaea.

This comparison of the remanent magnetism paleogeographies with a pangaeic paleogeography that considers principally biogeographic, lithologic, and climatic data has been restricted to the Devonian, although similar, biogeographic, climatic, and lithofacies inconsistencies in pre-Devonian and Carboniferous paleogeographies have also been proposed (*5, 12, 20*). Paleogeographers relying largely on paleomagnetic data need to rethink their pre-Permian sampling and the conclusions drawn from that sampling. Mingling of data from Paleozoic periods and portions of Paleozoic periods has been common rather than exceptional in many biogeographic reconstructions. This practice should be avoided because it confuses the value of the varied indicators of paleoclimates in the geographic reconstructions. Habicht (*28*), for example, has mingled arid region evaporites in the Early Carboniferous of Nova Scotia with humid region coals from the Late Carboniferous.

The pangaeic reconstruction suggested herein relies chiefly on paleobiogeographic data and on varied climatic indicators. It is also consistent with paleomagnetic data for the Gondwana region. Although it reconciles varied classes of presently available data, it need not be the best possible reconstruction. Until more lithofacies are incorporated into reconstructions (*30*), it would be premature to suggest that our Pangaea is other than a preliminary step toward a resolution of this problem.

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13. There are major changes in climatic gradient within the following Paleozoic periods: Cambrian (low in Early Cambrian; high in Middle and Late Cambrian); Ordovician (high in Early and Middle Ordovician; very high in Late Ordovician); Silurian (very high in earliest Silurian; high in remainder of Silurian); Devonian (high in Early and Middle Devonian; very low in Late Devonian); Carboniferous (very low in Early Carboniferous; very high in Late Carboniferous); and Permian (very high in Early Permian; moderately low in Late Permian). Climatic gra-

dients can be estimated, regardless of the paleogeography employed, by taking note of the presence or absence of widespread, sea level, continental glaciation (such as that of the later Ordovician and earliest Silurian, and the Late Carboniferous and Lower Permian), and the size of the areas occupied by cool- to cold-climate type sediments and fossils (Atlantic, Malvinokaffric, and Gondwana) as contrasted with warm to hot types (Pacific, Paleotethyan, North Silurian realm, and Old World realm) during the Paleozoic (*3*).
14. Isotopic paleothermometry is available for Cenozoic and younger Mesozoic deposits, but suitable material is sparse prior to the Jurassic. The cost in time and money has prevented paleothermometry from becoming widely used for routine purposes in the pre-Triassic.
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16. There are major changes in level of biogeographic provincialism within the following Paleozoic periods (*3*): Ordovician (Early Ordovician, highly provincial; Middle and Late Ordovician, moderately provincial); Devonian (Early and early Middle Devonian, highly provincial; remainder of Middle Devonian, moderately provincial; and Late Devonian, highly cosmopolitan); Carboniferous (Early Carboniferous, highly cosmopolitan; Late Carboniferous, moderately provincial).
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21. The lithofacies data consist of: (i) a belt of volcanic and associated geosynclinal rocks present in the eastern Urals and beneath the southwestern corner of the west Siberian lowland that extends southeast through southeastern Kazakhstan, east through northern Xinjiang and southern Mongolia and adjacent Inner Mongolia, and into western Heilongjiang; (ii) a carbonate belt bordering the volcanic belt on the west and south in Novaya Zemlya, Pay-Khoy and Vaygach, the western Urals and adjacent Russian platform, the Tien Shan (both Soviet and Chinese), and the North China platform; and (iii) a carbonate belt bordering the volcanic belt on the east and north in the Nyurol'ka Basin, the Siberian platform (including the Kolyma platform in the earlier Paleozoic), the Altay-Sayan (including Soviet, Mongolian, and Chinese portions), together with nonvolcanic platform rocks situated between the carbonates and the volcanic belt in northern and central Mongolia. The geologic evidence also strongly favors the integrity of north and south China as a single unit during the Phanerozoic. Chinese geology may be characterized as deceptively complex—that is, a fairly simple, largely platform type late Precambrian to Triassic marine sequence, followed in large part (except for Tibet) by nonmarine sedimentation from the Jurassic to the present—with the complex map pattern of the present due to Cenozoic faulting and folding for the most part.
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26. These warm climate taxa include the goniatite cephalopod *Tornoceras* and the brachiopod *Tropidoleptus* in Bolivia, *Tornoceras* in west-central Argentina, and *Tropidoleptus* in South Africa.
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RESEARCH ARTICLE

Homeostasis of the Antibody Response: Immunoregulation by NK Cells

Lynne V. Abruzzo and Donald A. Rowley

The primary antibody response to most bacterial, viral, and other antigens is characterized by an exponential increase in the number of B lymphocytes secreting specific immunoglobulin M (IgM) antibody (direct plaque-forming cells or PFC). The increase in PFC begins about 1 day and terminates 4 to 6 days after immunization (*1*). The mechanism of termination has been variously attributed to: (i) exhaustion of antigen, (ii) terminal differentiation of essential cells, (iii) antibody feedback suppression, (iv) anti-idiotypic feedback suppression, or (v) suppressor T cells. However, the first two mechanisms are not supported by experimental evidence, and antibody, anti-idiotypic antibody, and suppressor T cells are only potent and specific suppressors when given to animals or added to cultures just before or at the time of immunization, not when given two or more days after immunization (*2*). Thus the mechanism of termination is an enigma.

Abstract. *When injected into mice, the synthetic double-stranded polynucleotide poly(inosinic) · poly(cytidylic) acid induces high natural killer (NK) cell activity within 4 to 12 hours. Induction of NK activity in mice immunized 2 or 3 days previously, or the addition of NK cells to cultures immunized in vitro 2 or 3 days previously, promotes early termination of the ongoing primary immunoglobulin M antibody response. A target for NK cells is a population of accessory cells that has interacted with antigen and is necessary for sustaining the antibody response. The inference is strong that NK cells induced normally by immunization also terminate the usual antibody response in vivo by elimination of antigen-exposed accessory cells.*

We decided to explore an unconventional mechanism of regulation when we observed the kinetics of the response of purified B cells to a T-cell independent antigen on adoptive transfer to lethally irradiated (600 R) mice. Both the rate and duration of increase and decrease in PFC paralleled that observed in intact mice. In a large series of experiments we could not account for termination of the response of the adoptively transferred cells by any of the usual mechanisms and were led, therefore, to consider the possibility that regulation might be mediated by an x-ray–resistant, non-B–non-T-cell population present in x-irradiated recipients. Cells that are relatively resistant to x-irradiation include the heterogeneous population of cells that have the gross morphology of lymphocytes but are nonspecifically cytotoxic for diverse, virally infected, or tumor cells. Such cytotoxic cells, present in normal and nude or athymic mice that have had no known exposure to the target antigen, are referred to as natural killer (NK) cells (*3*). Natural killer cells are themselves a heterogeneous population, but for our purposes NK cells are: x-ray resistant, nonadherent to plastic culture dishes or to carbonyl iron particles, cytotoxic for YAC-1 tumor target cells, inducible by poly(inosinic) · poly(cytidylic) acid [poly(I) · poly(C)], and are cells whose cytotoxic activity is eliminated by an-

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